Randall W. Myster *Editor*

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Dedicated to my great-great grandparents Hans and Kari Myster, who came over on the boat from Norway in 1862 and settled near Oslo, Minnesota.

Oscar Wilde on writing (paraphrased):
“While working on a poem today I spent all morning taking a comma out, and all afternoon putting it back in”.

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Chapter 1
Introduction

Randall W. Myster

1.1 The Neotropics

The Neotropics is defined as the part of the American landmass and associated islands between the Tropic of Cancer (~23.5° N latitude) and the Tropic of Capricorn (~23.5° S latitude: Fig. 1.1). And so, it has hard, real, and distinct physical, chemical, and biological boundaries—to the North (the Tropic of Cancer), to the South (the Tropic of Capricorn), to the East (the Atlantic Ocean), and to the West (the Pacific Ocean)—which give it ecological meaning. The Neotropics is not defined by arbitrary, convenient, or political borders.

The Tropics of Cancer and Capricorn are those major delineations of the earth that mark the most northerly and southerly positions at which the Sun may appear directly overhead at its zenith. This positioning of the sun greatly reduces sunlight and temperature seasonally allowing year-round plant growth, which may contribute to making the Neotropics the most diverse and speciose place on earth. The northerly delineation is called the Tropic of Cancer because when it was named ~2000 years ago, the Sun was positioned in the constellation Cancer (Fig. 1.2) during the June solstice. The southerly delineation is called the Tropic of Capricorn because when it was named ~2000 years ago, the Sun was positioned in the constellation Capricornus (Fig. 1.2) during the December solstice. Today, however, the Sun is positioned in the constellation Taurus during the June solstice and in the constellation Sagittarius during the December solstice.

While temperatures within the Neotropics can attain 38 °C, the usual range is between 17 and 27 °C, and its annual precipitation can reach 6 m with seasonal wet and dry cycles influenced by El Niño southern oscillations that occur every 3–7 years (Mabberley 1992). Many Neotropical soils are old, highly weathered, and leached oxisols and ultisols that are well drained with a thin litter layer and low organic

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Fig. 1.1 Satellite image of the Neotropics with names and boundaries of countries added (https://earth.google.com)

matter content (Mabberley 1992). Also common among soils in the Neotropics are andisols derived from volcanic activity, and so very fertile and supportive of intensive agriculture. In general, Neotropical soils have a higher clay content than do soils in the Neotemperate zone and are relatively low in phosphorus (which may limit plant growth: Vitousek 1984).

The Neotropics includes more tropical rainforest than anywhere else on earth and as a result is critical to the entire earth's climate and biogeochemical cycling (e.g., the water cycle, the oxygen cycle, the carbon cycle). Before humans arrived, the Neotropics was dominated by broadleaf evergreen forests (moist and dry, flooded and unflooded: Walter 1979) with savannas, shrublands, grasslands (see chapters on the Andean grasslands páramo, puna, and steppe in Myster 2012a), deserts, and mangroves also common (Schultz 2005). With human colonization came cultivation which was difficult in savannas, shrub-lands, and grasslands due to periodic droughts and also obviously difficult in deserts and mangroves (Mabberley 1992). Cultivation, however, has always been very productive in cleared broadleaf evergreen forests (Myster 2008) largely due to the abundance of mycorrhizae in the soil which could facilitate the uptake of phosphorus and other plant nutrients.

Within the stark boundaries of the Neotropics (Fig. 1.1) are laid out three large series of spatial coordinates (1) across/along *latitudes* between the Tropic of Cancer and the Tropic of Capricorn (Fig. 1.3), (2) across/along *longitudes* between the Atlantic Ocean and the Pacific Ocean (Fig. 1.3), and (3) across/along several

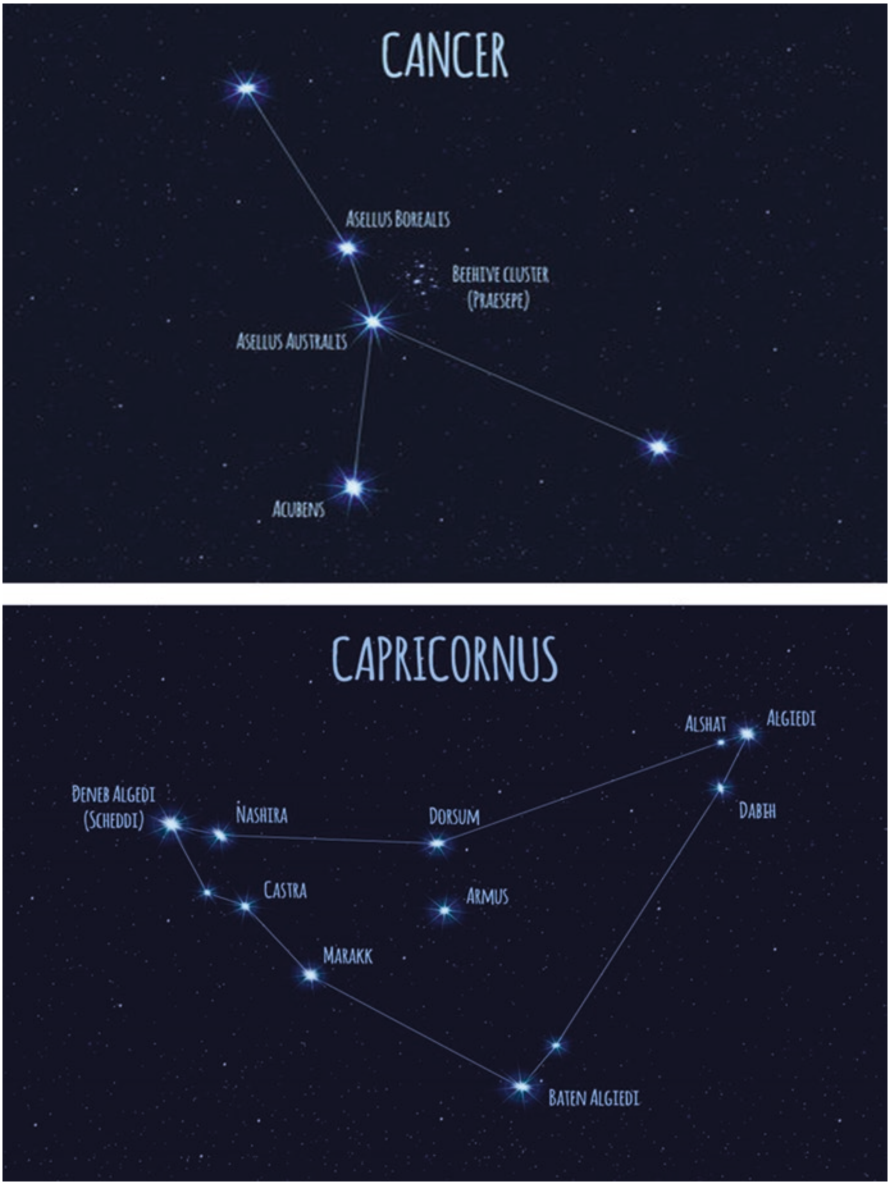

Fig. 1.2 The constellation Cancer (latin:crab) in the Northern hemisphere located near the constellations Leo and Gemini. The constellation Capricornus (latin:goat + horn) in the Southern hemisphere located near the constellations Aquarius and Sagittarius. Major stars in each constellation are labeled

Fig. 1.3 The latitudinal gradient (°North and °South of the equator) and longitudinal gradient (°West of the prime meridian) of the Neotropics

altitudes (elevations). Among those elevational coordinate series, the Andean mountains are the largest, ranging from sea level to Mount Aconcagua at 6959 m above sea level (a.s.l: Fig. 1.4). Indeed, these "Andes" are the longest continuous mountain range in the world and also have the most volcanoes. The Andes are not just a single mountain range however, but rather a succession of parallel and transverse mountain ranges called "cordilleras" along with their intervening plateaus and depressions (Oncken et al. 2006). The Andes are delineated to the east by Eastern flank cordilleras that most often descend to Western Amazonia (Fisher et al. 2013; Cardenas et al. 2014; Myster 2016a) and to the west by Western flank cordilleras that descent to the coastal ecosystems of the Pacific (Rehak et al. 2010). The Andes and their cordilleras are at least 7000 km long starting in the country of Venezuela,

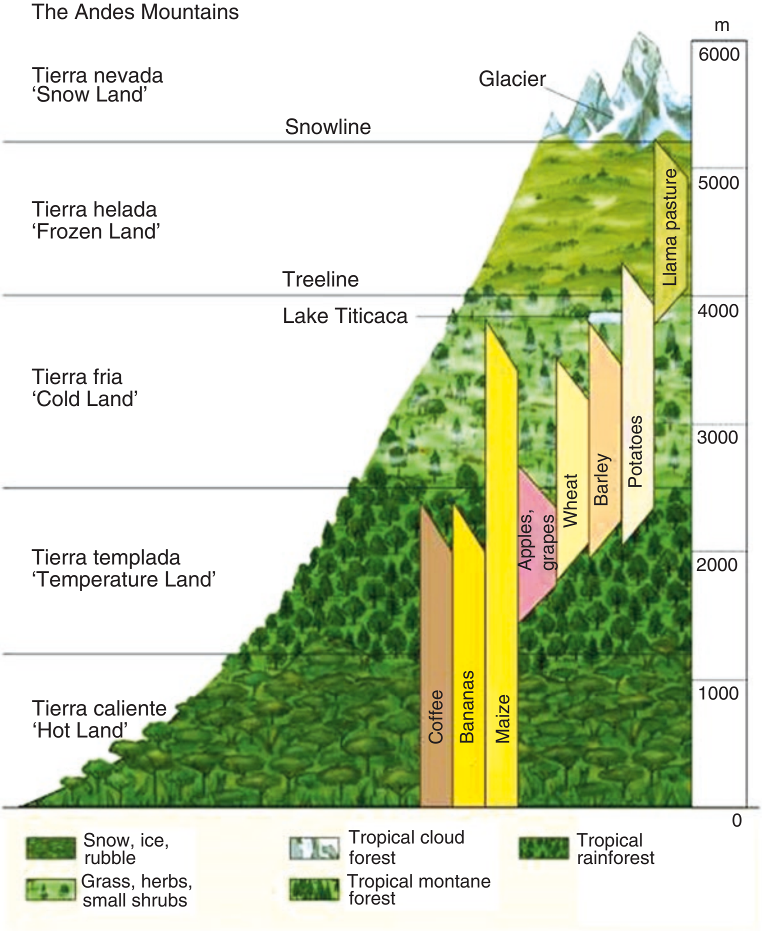

Fig. 1.4 The elevational (altitudinal) gradient of the Andes, showing common ecosystems and where common crops can be grown

continuing through Colombia, Ecuador, Peru, Bolivia, and Argentina, and ending in Chile (Knapp 1991).

Abiotic and biotic quantities measured across any of the three large series of spatial coordinates can be spatial gradients. For example, in the Andes as altitude increases, (1) spatial gradients of irradiance, wind frequently and intensity, evaporation, precipitation, and snow cover duration increase, while (2) spatial gradients of temperature—which has a linear decrease of 0.6 K for every increase of 100 m in altitude—and humidity decrease (Beck et al. 2008; Larcher 2001). Moreover, all of these altitudinal gradients (and all the other altitudinal gradients in the Neotropics) also exist as latitudinal gradients (and conversely, latitudinal gradients have a correspondence on altitudinal gradients) because moving away from the equator toward either of the Tropics by 1000 km in latitude is ecologically equivalent to moving up

1 km in altitude (Holdridge 1967; Jump et al. 2009). This means that any place on a latitudinal gradient can have similar plant and animal taxa, associations, and adaptations somewhere on an altitudinal gradient and vice versa (within the ranges of the gradients themselves: Holdridge 1967; Myster 2012b). Neotropical longitudinal gradients do not have this correspondence. Their ecosystem structure, function and dynamics, however, seems to depend more on proximity to major mountain chains like the Andes (e.g., both tree richness [ter Steege et al. 2006] and tree fisher alpha diversity [Wittmann et al. 2006] decrease with increasing distance east from the Andes) and/or to major bodies of water like the Atlantic or Pacific oceans.

These examples and others in the chapters that follow will show again and again that the biota of the Neotropics has evolved with, is adapted to, and continues to respond on spatial gradients laid out on these three fundamental spatial coordinate series: latitude, longitude, and altitude. The Neotropical biota is also influenced by other spatial gradients in (for example) temperature, precipitation (Holdridge 1967), soil characteristics (Schweitzer et al. 2014), and flooding (which creates a spatial gradient of decreasing maximum flooding depth and duration with increasing distance from a river: Myster 2007a, 2010a, 2015a, 2018c). In fact because the Neotropics is largely defined by its abundance of sunlight (see discussion of the Tropics of Cancer and Capricorn above), its biota is very greatly affected by that (perhaps) most fundamental ecological gradient. Sunlight creates a spatial gradient when it leaves the sun and decreases in intensity (dissipates as entropy increases) as it travels through space to earth. When it hits the earth's outer atmosphere, sunlight forms a latitudinal spatial gradient (because of the tilting of the earth and other revolutional and rotational abnormalities) which may then form other spatial gradients as it filters down (dissipates as entropy increases) through the atmosphere, vegetation, bodies of water, and the soil and rocks.

The Neotropical biota has also evolved with, is adapted to, and continues to respond on temporal gradients consisting of measured quantities laid out on temporal coordinate series, many of which are initiated by disturbances (Pickett 1976; Myster 2002). The disturbances common to the Neotropics include the natural disturbances of tree-fall (Myster 2014, 2015b, 2017a, 2018b) and landslide (Myster and Sarimento 1998), and the human-caused disturbances of slash-and-burn forest clearing with subsequent agriculture and pasture and the building of roads and urban areas (Myster 2004a, b, 2007b, 2009, 2012b, 2013). All these disturbances can potentially initiate temporal gradients along which ecosystems are then "put back together" with inputs of energy and time, that include the creation of spatial gradients (Müller 1998). Moreover, because disturbances in general open up space (Myster 2018a) sunlight, for example, can enter initially and then decrease over time as that space closes, creating a temporal gradient of light. Indeed, often in ecosystems disturbances occur at places on spatial gradients (Myster 2002)—as I showed in Peru when trees fell across a flooding gradient (Myster 2007a, 2012a), in Ecuador across an elevational gradient after banana (*Musa* sp.) and sugarcane (*Saccharum officinarum* L.) cultivation (Myster 2017a, 2018b), and in Puerto Rico after a landslide (Myster et al. 1997)—which creates temporal gradients as the ecosystem regenerates.

1.2 Gradients

A gradient is precisely defined as "changes in the value of a quantity with change in a given variable, e.g., per unit distance in a specified direction" (https://www.merriam-webster.com/dictionary/gradient). That gradient is either (1) a spatial gradient made up of quantities measured on a series of spatial coordinates [($x_{1,}$ $y_{1,}$ z_1), (x_2, $y_{2,}$ z_2), (x_3, y_3, z_3)…] at a fixed point in time or (2) a temporal gradient made up of quantities measured on a series of temporal coordinates [(t_1), (t_2), (t_3)…] at a fixed point in space where—according to the definition—those measured quantities must vary "with" those series coordinates. This could mean, for example, having a significant correlation or covariance (SAS 1985) or fitting a mathematical model like those used in Sects. 1.6.1 and 1.6.2, with the series coordinates. Whatever the method used, however, gradients must have "systematic" variation with the series coordinates, which makes them a kind of variation over space and time.

Thus, altitude becomes a gradient when you measure it with an altimeter across spatial coordinates going up a mountain and it varies with those coordinates. Likewise, both latitude and longitude become gradients when you measure them with a sextant as you travel across coordinates on land or sea and they vary with those coordinates. But measured quantities across a coordinate series are not always gradients; for example, quantities measured across a forest floor transect that do not vary with those spatial coordinates are not part of a gradient (Myster 2012c). These definitions make it clear that quantities are never measured across a gradient, but instead are measured across a spatial or temporal coordinate series where a gradient may have also been measured (e.g., temperature and elevation gradients measured across the same spatial coordinate series going up a mountain). If you do have a spatial gradient though (e.g., a temperature gradient that decreases as you go up a mountain: Myster 2020a), there will be a "sister" spatial gradient consisting of those same measurements across that same series of spatial coordinates but read in the opposite direction (e.g., a temperature gradient that increases as you go down the same mountain). Because time can only increase however, any series of temporal coordinates can only increase (i.e., be directional or a vector: Pickett 1976, 1982; Myster and Pickett 1988) and therefore there are no sister temporal gradients.

Spatial and temporal gradients often operate together to structure the same ecosystem, even with the same measured quantities. For example, in abandoned agricultural fields there is a spatial gradient of increasing tree seedling abundance from the surrounding forest into the old field, and temporal gradients of the same increase in tree seedling abundance over time at various places within the old field (Myster 2008). Multiple gradients can also be seen structuring ecosystems when several temporal gradients occur along a single spatial gradient (e.g., different landslides at different times during recovery going up a mountain: also see Fig. 1.5a, Myster et al. 1997) and several spatial gradients occur along a single temporal gradient (e.g., those tree seedling densities increasing over time from different places in the forest going into an old field: also see Fig. 1.5b, Myster 2008). Further, spatial or temporal gradients can also be fractals if they reoccur at larger and larger spatial or

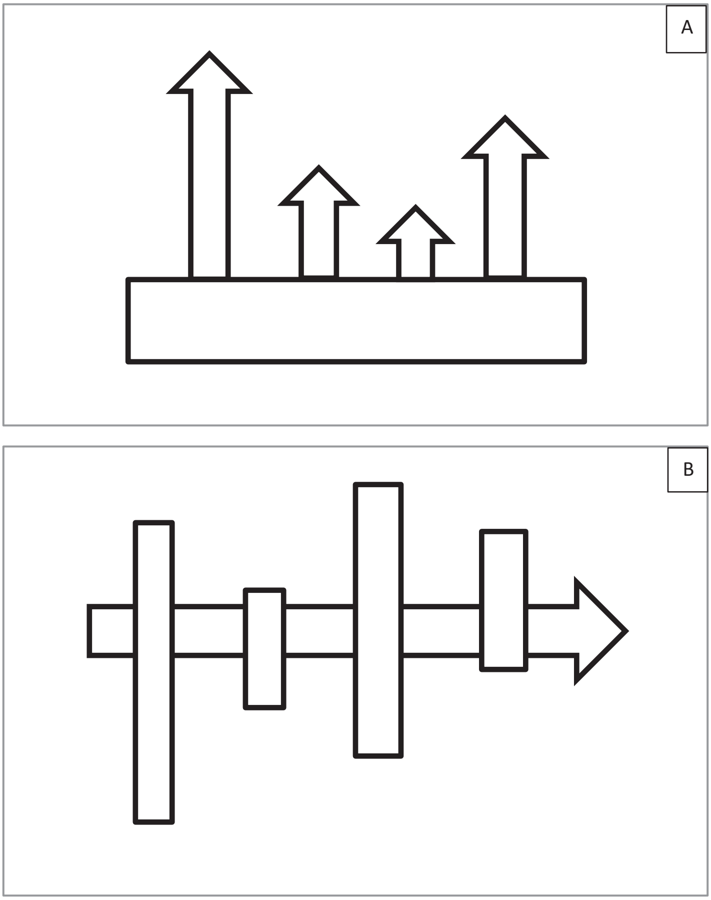

Fig. 1.5 (**a**) Representation of several temporal gradients occurring along a single spatial gradient. (**b**) Representation of several spatial gradients occurring along a single temporal gradient

temporal scales (Mandelbrot 1983). Mechanistically speaking (1) different places on the same gradient may influence each other (e.g., metacommunites), (2) different gradients on the same coordinate series may influence each other, (3) different gradients on different coordinate series that share some of their coordinates may influence each other, or (4) different gradients on different coordinate series that do not share some of their coordinates but have places on those gradients that are "close" in time and space may influence each other.

Combining the spatial and temporal coordinate series together creates a series of spatiotemporal or "space-time" coordinates [(x_1, y_1, z_1, t_1), (x_2, y_2, z_2, t_2), (x_3, y_3, z_3, t_3)…] across which a third type of gradient—a space-time gradient—which consists of quantities measured across those space-time coordinates that (again) must vary with them. An example of this space-time gradient is when quantities are measured in several plots (each plot having different spatial coordinates) at different start times and for different lengths of time (each plot thus also having different temporal coordinates) and then arranged along a common timescale (a space-for-time substitution: Pickett 1989; Myster and Malahy 2008).

Gradients are very common objects of study in the Neotropics. For example, the LTER (Long-Term Ecological Research) program at the University of Puerto Rico and the US Forest Service in Puerto Rico (http://luq.lter.network), funded by the US National Science Foundation, has measured many physical, chemical, and biological quantities in their ecosystems—up and down the Luquillo Mountains and over time after hurricane disturbance—which were spatial, temporal, or space-time gradients (see chapters in Gonzalez et al. 2013). In Sect. 1.9, I describe my own gradient research in Puerto Rico as a CO-Principal Investigator of that LTER. In that section and in all chapters of this book, it is ecological gradients that are investigated where biological quantities, and/or the physical and chemical quantities that living things interact with, are the quantities that are measured across those gradients. Those biological quantities are alive and thus may be much more variable in their responses (e.g., plants exhibiting plasticity) than any physical or chemical quantities. Ecological gradients are commonly used to investigate species distributions and tolerances (Austin 1976) including ecotones (Myster 2012a).

1.3 The Analysis of Gradients

It was Whittaker (1967) who first made the distinction between *direct gradient analysis* where a gradient has been well-established through past sampling on a spatial, temporal, or space–time coordinate series, and one may then analyze that gradient (Ter Braak and Prentice 1988; Fiedler and Beck 2008), and *indirect gradient analysis* where the gradient has not been established or sampled but may "emerge" from multivariate analysis performed on a matrix of plots across spatial, temporal, or space–time coordinate series *x* quantities measured in those plots (Okland et al. 2001). That multivariate analysis then generates synthetic axes (that are interpreted as complex gradients) and new coordinates for those plots along the new axes (now gradients: SAS 1985).

I propose a rephrasing of this traditional dichotomy into four general approaches to the analysis of gradients, presented in decreasing order of their ability to meaningful interpret gradients and add to our knowledge of them.

1. A direct gradient analysis where the spatial, temporal, or space–time gradient has been well-established (e.g., using landsat remote-sensing at large spatial scales: Walker et al. 2014), and one may continue to measure qualities across those coordinates in a regular, uniform, and systematic fashion (e.g., using remote-sensing ground-truthing). For example, sampling every 100 m in elevation going up a mountain and forming a spatial gradient (Myster 2020a, b) or sampling every year over time after abandonment in an old-field and forming a temporal gradient (Myster and Pickett 1994). Such data can then be plotted to

create response curves over space (Myster 2020a, b) or time (Pickett 1982; Myster and Pickett 1988). And those curves may then be "fitted" to different mathematical models (Guest 2013) including a symmetric unimodal model, a skewed unimodal model, a linear model, and a plateau model (Oksanen and Minchin 2002; Rydgren et al. 2003). This curve-fitting analysis often uses least-squares regression (after the appropriate transformation: Sokal and Rohlf 1981; McCain 2005; Marini et al. 2010) which, to be significant, requires at least 10 sampled quantities along the gradient and a p-value no larger than 0.05, and works best when it uses data measured along the gradient quantitatively—that is with an independent continuous number that could be measured anywhere within the spatial, temporal, or space–time coordinate series (e.g., along a transect)—rather than qualitatively (e.g., measuring in distinct forest, shrub, and grassland areas only). Researchers have also used correlation analysis, classification techniques, and simulations to explore relationships among the quantities measured along gradients (Muenchow et al. 2018).

2. A direct gradient analysis where the spatial, temporal, or space-time gradient has been well-established but you measure quantities across those coordinates in an irregular, non-uniform, and unsystematic fashion. For example, at 50 m, 200 m, and 600 m going up a mountain or at year 1, year 5, and year 12 after abandonment in an old field. The problem with this kind of direct gradient analysis is that sample points may aggregate along the spatial, temporal, or space–time coordinate series and so any analysis may reflect information about the gradient at those clusters of coordinate points only, and not be indicative of the entire spatial, temporal, or space–time gradient. In other words, results may be an artifact of where/when/where-when you sampled with some of the quantities even outliners (Sokal and Rohlf 1981). In both of these kinds of direct gradient analysis, one may explore discontinuities of sampled quantities along a gradient (e.g., ecotones: Ludwig and Cornelius 1987; Myster 2012c) and, if different quantities are measured in the same space/at the same time/in and at the same space–time, they can be compared using ordination and clustering (Myster and Pickett 1990).
3. An indirect gradient analysis where the gradient is not known but may "emerge" after multivariate ordination performed on a matrix of plots located on a series of spatial, temporal, or space–time coordinates x quantities measured in those plots (which are most meaningful if all the measured quantities are of the same kind: Pielou 1984). The ordination creates axes—each one defined by correlations with several of the measured quantities and capturing a percentage of the variation in the original matrix—which are then taken as complex, synthetic gradients. Ordinations also generate scores which can be used to graph the original plots along those axes/gradients (Death 1999). As with any ordination, cluster analysis can then be used to explore how close plots are to each other on that graph (e.g., using minimum spanning trees on old field plots after ordination: Myster and Pickett 1990). More than one kind of ordination is often used—for example principal components analysis (PCA: Pielou 1984) and non-metric multidimensional scaling ordination (NMDS: Rydgren et al. 2003)—because comparison of the placement of the plots by multiple ordination procedures

allows an examination of possible distortion by one method (Myster and Malahy 2008). The problem with indirect gradient analysis is that ordination axes never capture 100% of the original variation in the matrix. Information is lost and so axes are at best partial gradients, which are also subjective, complex, and hard to interpret (Pielou 1984). Finally, while both direct and indirect gradient analysis may help identify key ecologically important factors determining (for example) species distribution, experimental manipulations are still needed to more precisely suggest causality and the relative importance of various environmental factors.

4. A simple descriptive analysis of graphing measured quantities using their series of coordinates (1) in multivariate (x, y, z, t) space using all known coordinates, (2) by holding all but one of the variables constant each time, that is graphing points under consideration along the x-axis (x_1, x_2, x_3…) only, then along the y-axis (y_1, y_2, $y_{3\ldots}$) only, then along the z-axis (z_1, z_2, z_3…) only, and then along the t-axis (t_1, t_2, t_3…: Pickett 1982) only, and (3) in two- or three-dimensional space using different combinations of the variables used in the series of coordinates (e.g., x and y, y, z, and t).

Finally, how experiments can use points on gradients as treatments, and then use different kinds of analysis of variance (ANOVA) to explore effects of those treatments, needs to be included in the methodological discussions here. These methods include (1) field experiments that use different areas and/or times in naturally occurring gradients as treatments (e.g., top/down and side to side spatial gradients in a landslide [Myster and Schaefer 2003], seeds and seedlings laid out on a spatial gradient from forest into old field [Myster 2004b]), (2) field experiments that use areas and/or times that could be arranged into a gradient (e.g., forest stands that differ in soil fertility [Myster 2017b], flooded forests that differ in flooding frequency [Myster 2015a]), (3) field experiments in one area and/or time where treatments are applied that are the same as points on a naturally occurring gradient (e.g., litter [Myster and Pickett 1993], light [Everham et al. 1996]), (4) greenhouse experiments that apply treatments that are based on field sampling on a naturally occurring gradient (e.g., light, phosphorus, nitrogen [Myster 2006]), and (5) field/greenhouse combination experiments that both use naturally occurring gradients (e.g., seedlings collected from points on naturally occurring field gradients are taken into the greenhouse where those points are treatments, as well as greenhouse treatments based on field sampling of naturally occurring gradients [Myster and Fetcher 2005]).

1.4 Gradients and Ecosystems

All ecosystems exist on series of spatial, temporal, or space–time coordinates and often have gradients of structure, function, and dynamics across those coordinates (Müller 1998). Among those three fundamental characteristics of ecosystems, I have argued for dynamics to be an investigative priority (Myster 2012b, 2018a) because an ecosystem's structure and function occur at single points of time during its dynamics and thus are a consequence of that dynamics. I have also argued (Myster 2012b, 2018a, 2020b) that the plant–plant replacement process is a fundamental temporal gradient in terrestrial ecosystems, determining much of their dynamics. Plants replace plants three ways (1) by growing into available space (within physiological limits: Myster 2013) for example when the branch of a tree grows into a bordering old-field, (2) by growing into available space with asexual clones which may later separate and grow independently (Myster 2013) for example when the roots of a tree grow into a bordering old field and have sprouts/suckers, or (3) by dispersing seeds/spores into available space which may then germinate and grow (Myster 2013) for example when a tree disperses its seeds into a bordering old field. Much of the space that becomes available in ecosystems for the plant–plant replacement process does so through the loss of plant biomass (Myster 2018a) either partially (e.g., a tree loses a branch) or totally (the plant dies). These are not necessarily independent events, however, because one plant's loss of biomass can affect another plant's for example when a tree loses a branch (or dies) and brings down another tree's branch or kills it in the process of falling.

Plant replacement through seed/spore dispersal is most common, and because seeds are usually not in limited supply (Myster 2017d), plant regeneration mechanisms (PRM) operating on seeds after dispersal and on seedlings arising from those seeds are most important in determining plant-plant replacements (Grubb 1977). Thus, plants are less important to the dynamics—and to the structure and function—of terrestrial ecosystems as they age. These PRM work hierarchically first on dispersed seeds and then secondly on the seedlings that germinated as seeds (creating the *first* hierarchy of plant regeneration: Myster 2004a, 2012c). For seeds the PRM are first the action of predators and pathogens that determine seed survivorship and secondly the workings of factors that control the availability of resources such as light, water, and temperature (potentially including both living and non-living agents [see below for seedling examples]) which act as "cues" for the germination of those seeds that survived predators and pathogens (Myster 2004b, 2015b, 2017b, 2018b; Myster and Pickett 1993). Thus, PRM for seeds creates a *second* hierarchy of plant regeneration, which is imbedded within the first hierarchy.

For seedlings (and asexual clones that grow independently of the "mother" plant), the PRM are first the action of herbivores and pathogens that determine seedling survivorship and secondly the workings of factors that control the availability of resources such as light, water, and soil nutrients. Those factors include the action of (1) a living agent(s) such as a single plant (competition) or more than one plant acting together (diffuse competition), and (2) a non-living agent(s) such as when the shading of a seedling is caused by a rock or when a drought is caused by global warming (Myster 2006, 2012c; Myster and McCarthy 1989; Myster and Schaefer 2003). If the principle of parsimony (Sober 1981) is at work, the action of these non-living agent(s) for both seeds and seedlings may be more common than the action of living agent(s). Thus, PRM for seedlings create another *second* hierarchy of plant regeneration, also imbedded within the first hierarchy. There is also a *third* hierarchy made up of the seedling responses to all of the PRM: first seedling survivorship, second the growth of those seedlings that survived, third the allocation of biomass to plant organs—leaf, stem, root, reproductive—during the growth of those seedlings, and fourth the architecture/chemistry of those seedling organs (e.g., the shape and thickness of leaves, the branching patterns of stems and roots, grams of nitrogen per kilogram of dry organic matter). This third hierarchy (of seedling responses)—(1) survivorship, (2) growth, (3) allocation, (4) architecture/chemistry—also applies to asexual clones that grow independently and to all of the later stages of a plant's life cycle such as sapling, mature plant, and mature plant that is reproducing.

1.5 Toward a Theory of Gradients

The development of a theory of ecology (Scheiner and Willig 2011) is a necessary part of its maturity as a science and thus needs to be founded on the rigor of mathematical constructs, formalisms, and logic (Curry 2010). I suggest that a theory of gradients (GT: Fox et al. 2011) be a significant part of any theory of ecology and that it may be facilitated by the gradient definitions, results, and insights from this chapter and those that follow. For example, GT should include the idea that gradients are either spatial, temporal, or spatiotemporal, that ecological gradients are either physical or chemical or biological, and that ecosystems are under the influence of, and respond to, multiple interacting gradients. In addition, formulas could be developed in GT to express relationships among gradients, among data points on different gradients that are measured on the same or shared coordinates, or to express relationships among data points measured at other nearby coordinates. I also suggest that for those gradients that are directional and therefore also vectors ($\vec{v}$), vector algebra (Joag 2016) may be useful in representing and calculating some of these and other interactions.

1.6 Case Study: Reserva Biologica San Francisco, Ecuador

The Reserva Biologica San Francisco (RBSF: 3° 58′ 30″ S, 79° 4′ 25″ W, Bussmann 2001; Beck et al. 2008) covers 1000 ha of the northern slopes of Cordillera de Consuelo in Zamora-Chinchipe Province, Ecuador, adjacent to Podocarpus National Park. RBSF extends between 1800 m and 3150 m a.s.l and is covered by cloud forest. Soils are Dystrudepts and Haplosaprists at lower elevations and Petraquepts and Epiaquents at higher elevations (Bussmann 2003). Temperatures range from 15–17 °C at lower elevations to 9–11 °C at upper elevations and annual precipitation from 2200 mm per year at lower elevations to 5000 mm per year at upper elevations (Bussmann 2003).

1.6.1 Physical Gradient (Spatial: Elevation): Curve-Fitting Tree Species and Family Patterns Along that Gradient

In January 2019, my field assistants and I first set up and then sampled all trees at least 10 cm diameter at breast height (dbh) in ¼ ha plots at 10 different elevations (1900 m, 2000 m, 2100 m, 2200 m, 2300 m, 2400 m, 2500 m, 2600 m, 2700 m, 2800 m) across from the Rio San Francisco, next to the RBSF field station. The dbh measurement was taken at the lowest point where the stem was cylindrical, and for buttressed trees above the buttresses. Trees were identified to family, genus, and species using Martinez (2005) and the Missouri Botanical Garden website http://www.mobot.org as taxonomic sources.

I first used this data set to compile the number of stems in each species and each family at each sampling point on the elevational gradient. The species and familial data were then subjected to curve-fitting analysis (Wilson 1991; Guest 2013) for these four mathematical models (1) a symmetric unimodal model, (2) a skewed unimodal model, (3) a linear model, or (4) a plateau model (Austin et al. 1994; Oksanen and Minchin 2002; Rydgren et al. 2003) using least-squares regression analysis after the appropriate transformation (Hill 1977; SAS 1985; Bongers et al. 1999; McCain 2005; Marini et al. 2010), as was done to generate dominance-diversity curves (Myster 2010b). Elevation was the independent variable (and the gradient) and number of stems was the dependent variable in all cases.

There were 12 most common species—two in the family Clusiaceae, three in the family Lauraceae, three in the family Lauraceae, two in the family Rubiaceae—all of which showed individual distribution patterns with *Tapirira* cf *guianensis* peaking at 2000 m in elevation, *Clusia alata* at 2200 m, *Clusia ducuoides* at 2300 m, *Alchornea lojaensis* at 2300 m, *Nectandra membranacea* at 2200 m, *Ocotea* sp. at 2500 m, *Persea weberbaueri* at 2600 m, *Graffenried emarginata* at 1900 m, *Miconia punctata* at 2700 m, *Tibouchina lepidota* at 2400 m, *Myrcia sp. nov* at 2500 m, *Palicouria latifolia* at 2000 m, and *Elaeagia obovata* at 1900 m. Four of those species fit curves significantly: a symmetric unimodal model for *Clusia alata* and skewed unimodal models for *Nectandra membranacea*, *Graffearieda enarginata,* and *Miconia punctata*.

There were 29 total families sampled over the 10 sampling locations along the elevational gradient again showing an individualistic distribution pattern. The most abundant families were Melastomataceae (with 461 stems), Lauraceae (430), Clusiaceae (182), and Rubiaceae (180). The rarest families were Solanaceae (with 1 stem), Malvaceae (3), Annonaceae (4), Cyatheaceae (4), and Hypericaceae (4). Clusiaceae, Lauraceae, and Melastomataceae were the only families to have stems at all 10 sampling locations. Annouiaceae, Hypericaceae, Malvaceae, Monimiaceae, Solanaceae, and Sapindaceae were the only families to have stems at only one location. 2400 m was the only sampling location with more than one (2) of those families. There were 10 families with significant curve-fitting results (1) a symmetric unimodal model for Aquifoliaceae, Clusiaceae, Euphorbiaceae, Primulaceae, and Podocarpaceae, (2) a skewed unimodal model for Lauraceae and Melastomataceae, (3) a linear model for Myrtaceae, and (4) a plateau model for Primulaceae and Rubiaceae.

1.6.2 Physical Gradient (Spatial: Elevation): Curve-Fitting Physical Structure Patterns Along that Gradient

I then used the same data set to compute these structural parameters for each plot at each elevation: (1) the total number of tree stems, the total number of tree stems divided into four size classes: 10 ≤ 19 cm dbh, 20 ≤ 29 cm dbh, 30 ≤ 39 cm dbh and ≥ 40 cm dbh, and mean dbh, (2) tree family, genus, and species richness, (3) fishers α diversity using the formula in Fisher (1943) as realized by the Javascript program in http://groundvegetationdb-web.com/ground_veg/home/diversity_index, (4) the sum of the basal areas of all individual tree stems ($\sum \pi r^2$; where r = the dbh of the individual stem/2), (5) above-ground biomass using the formula in Nascimento and Laurance (2002) suggested for tropical trees of these stem sizes, and (6) canopy closure using the formula in Buchholz et al. (2004) for tropical trees. These parameters were subjected to curve-fitting analysis (Wilson 1991; Guest 2013) for these four mathematical models (1) a symmetric unimodal model, (2) a skewed unimodal model, (3) a linear model, or (4) a plateau model (Austin et al. 1994; Oksanen and Minchin 2002; Rydgren et al. 2003) using least-squares regression analysis after the appropriate transformation (Hill 1977; SAS 1985; Bongers et al. 1999; McCain 2005; Marini et al. 2010). Elevation was the independent variable (and the gradient) and number of stems was the dependent variable in all cases. Curves with zero slope were not considered ecologically meaningful and not reported, even if significant.

Total tree stems increased with elevation from 269/ha (1900 m) to 423/ha (2800 m), but not monotonically decreasing from 2100 m to 2200 m. The smallest stem size was always the most common, becoming all the stems at 2800 m. And the next smallest size had almost all of the remaining stems, with very few stems over 29 cm dbh. Four elevations had no tree stems over 29 cm dbh and there were no tree stems larger than 39 cm dbh in any elevation higher than 2100 m. This was a strong exponential decline in stem size with elevation, with the smallest mean stem size at 2800 m elevation. No elevation showed a large number of families, genera, or species, and fisher's α diversity was always low. All canopies were in the 60–70% closure range. Total stems had a significant linear model, % stems 20 < 29 cm dbh had a significant linear model, and % stems >40 cm dbh had a significant plateau model.

Total stems in this cloud forest were comparable to other Neotropic Cloud forests but basal area was less than other Cloud forests in the Neotropics. Richness could not be compared among forests because of different plot sizes. The study gradient had more stems than at 1400 m in another part of Ecuador but was comparable to sampling in Venezuela at the same elevations. Stems were larger at 1400 m at another site in Ecuador and in Costa Rica at the same elevations. Species richness and basal area, however, compared better to the other Ecuador site than to Costa Rica or Puerto Rico. There were many more stems in this Cloud forest than in Amazon forests both flooded (várzea, igapó) and unflooded (*terra firme,* palm, white sand). This Cloud forest stems were also smaller, closest in size to stems in palm forest. Basal area is similar among the forests but ABG is much higher in the Amazon forests except again in igapó forests. The study Cloud forest has a more closed canopy than Amazon forests, most similar to the unflooded and species-rich *terra firme* forest. Forests in the Amazon had less stems per ha than the study Cloud forest but larger stems. Basal area was comparable, but above-ground biomass was less in the study Cloud forest and Amazon forests were more open except for *terra firme* forest (Myster, unpub. data).

1.7 Case Study: Maquipucuna Reserve, Ecuador

Maquipucuna Reserve (MR: 0° 05′ N, 78° 37′ W; http://www.maqui.org; Myster and Sarmiento 1998) was established in 1987 and is located in northwestern Ecuador near the town of Nanegal. MR occupies the Andean piedmont at the southern limit of the Choco biotic province and is a hotspot for biodiversity. The reserve lies between 1150 m above sea level (a.s.l.) at the Umachaca River bridge to 1970 m a.s.l. at the summit of Mount Montecristi. MR is classified as tropical lower montane wet/cloud forest (Edmisten 1970) and has deeply dissected drainages with steep slopes. It has an annual precipitation of 3198 mm (measured from Nanegal) and the temperature ranges yearly between 14 and 25 °C, with an average temperature of 18 °C. The reserve's fertile andisol soil is developed from recent volcanic ash deposits. Within MR is primary cloud forest and various secondary cloud forests many of them recovering sugarcane plantations, banana plantations, and pastures seeded with the grass *Setaria sphacelata* before cows were allowed to establish (Myster 2014).

1.7.1 Biological Gradient (Temporal): 1 ha Primary Cloud Forest

In May 2012, my field assistants and I set up and sampled a one ha permanent plot in a primary cloud forest at MR at an elevation of 1200 m a.s.l. We tagged and measured the diameter at breast height (dbh) of all trees at least 10 cm dbh in the 1 ha plot. The dbh measurement was taken at the nearest lower point where the stem was cylindrical, and for buttressed trees, it was taken above the buttresses. The tagged trees were identified to species, or to genus in a few cases, using Romoleroux et al. (1997) and Gentry (1993) as taxonomic sources. We also consulted the website of the Missouri Botanical Garden (http://www.missouribotanicalgarden.org).

From this data set floristic tables of family, genus and species were first complied. There were a total of 18 families—Actinidiaceae (24 stems), Asteraceae (1), Bromeliaceae (1), Cecropiacea (7), Fabaceae (49), Lauraceae (118), Melastomataceae (10), Mimosaceae (7), Monimiaceae (1), Moraceae (2), Myristicaceae (9), Myrtaceae (4), Piperaceae (5), Rubiaceae (11), Solanaceae (5), Tiliaceae (2), Urticaceae (12), Verbenaceae (24)—in the plot. Lauraceae was by far the most common family and all families were dominated by a small number of genera and species. The families Actinidiaceae, Fabaceae, and Verbenaceae were also common, but three families (Asteraceae, Bromeliaceae, Monimiaceae) had only one stem. The families Asteraceae, Bromeliaceae, Fabaceae, Melastomataceae, Moraceae, Myrtaceae, Piperaceae, Rubiaceae, Solanaceae, Tiliaceae, Urticaceae, and Verbenaceae had a monotonic decline in stem number as stems get thicker. This was not true, however, of the families Actinidiaceae, Cecropiacea, Lauraceae, Mimosaceae, Monimiaceae, and Myristicaceae. The most common species were *Erythrina megistophylla* and *Nectandra acutifolia*.

These structural parameters were also generated for the plot (1) the total number of stems in the 1 ha plot, the mean and maximum among those stems, and the total number of stems divided into four size classes: $10 \leq 19$ dbh, $20 \leq 29$ dbh, $30 \leq 39$ dbh, and ≥ 40 dbh, (2) the stem dispersion pattern (random, uniform, clumped) computed by comparing plot data to Poisson and negative binomial distributions using chi-square analysis and, if clumped, greens index was also computed to access degree of clumping (Ludwig and Reynolds 1988), (3) canopy closure using the formula in Buchholz et al. (2004) for tropical trees with the resulting percentage of the 1 ha plot area closed, (4) total basal area as the sum of the basal areas of all individual stems (Πr^2; where r = the dbh of the individual stem/2) and (5) above-ground biomass (AGB) using the formula in Nascimento and Laurance (2002) suggested for tropical trees of these stem sizes.

There were 294 total tree stems in the plot, with 153 stems between 10 and 19 cm dbh, 82 stems between 20 and 29 cm dbh, 46 stems between 30 and 39 cm dbh, and 13 stems 40 cm dbh or greater. The mean stem size was 23.2 cm dbh. Family richness was 18, genus richness 24, and species richness 25. Basal area was 11.2 m^2, above-ground biomass (AGB) 198.4 Mg and canopy closure was 46.3%.

The one ha plot was resampled in 2014 and in 2016, using the same protocol and setting up a temporal gradient. The data were examined for plant-plant (here tree-tree) replacements happening over time, which define plant community dynamics (Myster 2012d, 2018a). Each living tree had a location within the plot, a species, a dbh, and a neighborhood space defined as a circular area with the tree at the center and the radius = 25 × dbh/2 (Canham et al. 2004), making the minimum neighborhood space for each sampling a circle of diameter 1.25 m. This definition of neighborhood space captured the effect of shading/canopy cover of each tree. The neighborhood space is graphed for each living tree in the 2012 sampling, in the 2014 sampling, and in the 2016.

Comparing the 2014 sampling to the 2012 sampling, (1) 12 trees died of which 10 were in the first size class and 2 were in the second size class, (2) there were 14 new trees all in the first size class, and (3) for the rest of the trees 20 went from size class 1 to size class 2, 5 went from size class 2 to size class 3, and 2 went from size class 3 to size class 4. There were no trends due to species identity or spatial location. Changes in the neighborhood spaces suggest that there were 3 none = > one replacements, 4 one = > none replacements, 3 one = > one replacements, 1 one = > many replacement, and 1 many = > one replacement. Theory suggests that there were probably many none = > none replacements (Myster 2018a).

Comparing the 2016 sampling to the 2014 sampling, (1) 13 trees died of which 9 were in the first size class, 3 were in the second size class and 1 was in the third size class, (2) there were 13 new trees all in the first size class, and (3) for the rest of the trees 22 went from size class 1 to size class 2, 7 went from size class 2 to size class 3, and 2 went from size class 3 to size class 4. There were no trends due to species identity or spatial location. Changes in the neighborhood spaces suggest that there were 4 none = > one replacements, 1 none = > many replacement, 4 one = > none replacements, 2 one = > one replacements, and 2 many = > one replacements. Theory suggests that there were probably many none = > none replacements (Myster 2018a).

In the replacements found in the temporal gradient, size of stem seemed to be a more important factor than species. Species replacement patterns followed the ranking of species due to abundance—that is, the more common a species is, the more likely it would be in replacements. This is supportive of the neutral theory (Hubbell 2001) of plant community dynamics that would preserve species ranking of abundance, and thus species richness over time. Such rankings may be, however, the result of niche-specific recruitment mechanisms (Myster 2018a). More sampling is needed to explore these patterns and so I have replicated this plot and sampling protocol in igapó forest (Myster 2018c).

1.7.2 Biological Gradient (Temporal): 1 ha Secondary Cloud Forest Recovering After Sugarcane Cultivation, After Banana Cultivation, and After Use as Pasture

In June of 1996, I started a long-term study by selecting (as suggested by local field assistants) six just abandoned agricultural fields: two recent sugarcane (*Saccharum officinarum*) plantations, two recent banana (*Musa* sp.) plantations, and two recent pastures seeded in *Setaria sphacelata* all at an elevation of 1300 m a.s.l. In each field, twenty-five 5 m × 2 m contiguous plots were laid out making all six fields 250-m^2 rectangles. They were located within a few hundred meters of each other and had the 25 m plot border next to primary cloud forest. The plots did not have any remnant trees or sprouting tree roots at the beginning of the study, and their tree seed bank was very small. Starting in 1997 each of the 5 m × 2 m subplots of each of the six plots were sampled annually (setting up a temporal gradient) to identify each plant species and sample its percent cover—an indication of a species' ability to capture light and, therefore, to dominate these areas in the process of becoming forested communities—estimated visually in relation to each plot's area. We also sampled the diameter at breast height (dbh) of each tree stem at least 1 cm. Maquipucuna plant taxonomists, trained at the University of Georgia, USA, where voucher specimens are kept on file, assisted in the identification of species by using specimens located on site. They also used Romoleroux et al. (1997) and Gentry

(1993) as taxonomic sources, as well as Missouri Botanical Garden (http://www.missouribotanicalgarden.org).

These plots are part of the longest and largest old-field study in the Neotropics (Myster 2004a, b, 2007b, 2009, 2010b, 2012b, 2014, 2015b, 2017c, 2018a) funded by the US National Science Foundation as part of the long-term ecological research (LTER) program at the University of Puerto Rico (see Myster 2013 for details). All the data are archived as LTERDATB #97, LTERDATB #100, LTERDATB#101 and LTERDBAS#109 at the LTER website (http://luq.lternet.edu). The LTER program has been a continuous part of the University of Puerto Rico and the U.S. Forest Service in Puerto Rico since 1988.

I used this data in four analyses. First I found that permanent plots in sugarcane fields showed grass dominating early in the temporal gradient (mostly sugarcane itself, *Saccharum officinarum*) and then declining to 50% cover levels, with *Panicum* spp. and *Brachiaria subquadripara* also present, ferns (e.g., *Nephrolepsis* sp., *Thelypteris deltoidea*) and forbs (e.g., *Desmodium* sp., *Bidens pilosa*, *Lantana camara*) as a small part of the flora that begins to decline immediately with cover of woody species increasing steadily, trees showing this gradual increase with members of the family Melastomataceae most common, and *Piper aduncum* more common here than in other fields (Myster 2007b). In sugarcane fields, *Acalypha platyphylla, Piper aduncum,* and *Vernonia pallens* were common. Further, *P. aduncum* was more common in sugarcane fields than in other fields, and there were 18 tree species in sugarcane fields and 21 in banana fields. For the sugarcane fields, total cover, an indicator of stratification and developing structure, was greater compared with the other fields, and banana greater than pasture, starting at 200% cover and gradually declining with time. Species richness was also greater in the sugarcane fields compared with the other fields, and banana had more species than did pasture.

In the plots located in recovering banana fields, grass and *Musa* sp. dominate early and then decline, but to greater cover levels than in the sugarcane. Ferns attain greater cover levels in banana than in sugarcane but forbs are a small part of the flora. Also, woody species increase, but at smaller cover levels than in sugarcane. There were many of the same tree species in banana fields as in sugarcane fields, but with additional species (e.g., *Cecropia monostachya*) present. *Piper aduncum* was frequent in the permanent plots. Total stems were slightly more in the banana fields compared with the sugarcane fields, and pastures had few stems. Compared with banana, mean stem height was also greater in the sugarcane and increased through time, while pasture stems remained small. Basal area stabilized at 500 cm^2 for sugarcane and banana fields.

Finally, in the seeded pastures, grass dominated almost completely (mainly the planted grass *Setaria sphacelata*), with a few woody plants showing in year five. Fern and forb cover was small, and pastures had few trees, but the species they did have were common to the sugarcane and banana fields. There were life-form changes such as a domination by grass (e.g., *Panicum* sp., *Axonopus compressus*) that peaks in cover in year three and then declines, fem (*Nephrolepsis* sp., *Thelypteris* *deltoidea*) and herbaceous (e.g., *Commelina* sp., *Desmodium adscendens*, *Clidemia hirta*) cover that also peaks in year three but at lower cover levels than grass, woody vines (e.g., *Ipomea* sp.) that continue to increase in cover over the first 5 years, and trees and shrubs that enter, peak, and decline in an individualistic pattern.

Total cover, an indicator of stratification and developing structure, was greater in the pastures than in the other fields. The cover started at 200% in pastures and gradually declined. Species richness was greater in sugarcane fields than in the other fields, with more species in pastures than in banana fields. The total number of stems was greatest in sugarcane fields and pastures whereas mean stem height was greatest in the pastures. Basal area increased to 500 cm^2 in sugarcane and banana fields but remained low in pastures.

I next pooled the data in each of the 25 subplots and tabulated a total percent cover for each species for the entire plantation or pasture per sampling year. Those total percent cover data were first sorted in decreasing order, then log10-transformed, and finally plotted for the first 20, most common, species to create dominance-diversity curves for the sugarcane and banana plantations and pastures, for each sampling year in the temporal gradient. Sampling data were then fitted to Preston's log-normal model, MacArthur's broken stick model, and both the geometric and the harmonic series using least-squares regression after the appropriate transformation. I found that the sugarcane and banana plantations had a significant log-normal pattern for the first 5 years and then flattened out. The plots in pasture, however, showed a significant geometric pattern over the first 7 years of succession. Pastures lag behind plantations and do not resemble them within this sampling time frame (Myster 2010b).

Then, I used the plot data to investigate relationships between productivity and both richness and turnover in these fields. I found that species richness had a significant positive relationship with productivity, where the slopes of the regression lines decreased over time for all fields taken together suggested the early upswing, leveling off, and later downswing of a unimodal curve. This unimodal pattern held true both in the recovering sugarcane (*Saccharum officinarum* L.) and in the recovering Banana (*Musa* sp.) plantations. There was a delay (later in the temporal gradient), however, in the development of the unimodal pattern in the seeded pasture, perhaps due to root competition between the residual tussock grass (*Setaria sphacelata*) and Neotropical tree seedlings (Myster 2009).

Finally, I used the plot data to investigate significant positive associations between pairs of old field species were first computed and then clustered together into larger and larger species groups. I found that no pasture or plantation had more than 5% of the possible significant positive associations, clustering metrics showed groups of species participating in similar clusters among the five pasture/plantations over a gradient of decreasing association strength, and there was evidence for repeatable communities—especially after Banana cultivation—suggesting that past crops not only persist after abandonment but also form significant associations with invading plants (Myster 2012b, 2013).

1.7.3 Biological Gradient (Spatial): Recruitment Experiments in a 1 ha Secondary Cloud Forest Recovering After Sugarcane Cultivation, After Banana Cultivation, and After Use as Pasture

Tree seeds were placed in a spatial gradient from forest into oldfields. I found there was more predation in the forest compared to the old field/forest border and more seed disease away from the forest compared to in it. Tree seeds put out in sugarcane fields, banana fields, and pastures showed that seed predation took more seeds that seed pathogens or that germinated in all fields and pastures, but this was less that in primary closed-canopy forest and tree-fall gaps. Pathogens took most of the remaining seeds and most seeds that survived, germinated. *Solanum ovalifolia* seeds (only species that had seeds germinate without any losses to pathogens) in banana fields and *Piper aduncum* in all fields and pastures were the most significantly different among all treatments. Insect predation was lower in the forest border microsite for *P. aduncum*, seed disease greater at 10 m from border. All planted seedlings died in the pasture, 25% survived in banana, and 15% survived in sugarcane, and there was less growth away from the forest border. Results taken together with primary forest suggest that forests may recover faster after human disturbance (here agriculture) than after natural disturbance (here tree-fall: Myster 2004b, 2015b).

1.7.4 Biological Gradient (Spatial): Landslide

To understand landslide regeneration and provide information necessary for restoration, I sampled seed rain, seed pool, and plant cover along a spatial gradient from forest into two Ecuadorian landslides. We trapped 1304 seeds and found that, while most seeds were in the family Asteraceae, there was substantial variation in seed rain among plant families. Four hundred and seventy-five seedlings emerged from soil samples, including nonvascular and vascular families; again, species in Asteraceae dominated, with species in Piperaceae also very common. Plant cover, consisting of members of four fern families and 20 vascular plant families—with species in Asteraceae, Melastomataceae, and Poaceae most common—was scored as a percentage of the total plot area. Principal components analysis (PCA) showed that, for all three of these plant life stages (seed rain, seed-propagule pool, plant cover), spatial variation was dominated by differences between the two landslides rather than within-landslide plot differences. PCA also showed that plots separated best on axes defined by the families Cecropiaceae, Urticaceae, Melastomataceae, Papilionaceae, Asteraceae, and Araceae with clumping of families in PCA space suggesting common successional strategies. Another multivariate technique, canonical correspondence analysis (CCA), showed that the combined seed rain and seed pool data could predict the percent cover of the family Verbenaceae and that the current plant cover families could predict Asteraceae seeds and seedlings. Finally, we use our past and present landslide data, along with multivariate modeling results, to suggest strategies for successful landslide restoration (Myster and Sarimento 1998).

1.8 Case Study: Area de Conservacion Regional Comunal de Tamshiyacu-Tahuayo, Peru

The Area de Conservacion Regional Comunal de Tamshiyacu-Tahuayo (ACRCTT: www.perujungle.com, Myster 2007a, 2010a, 2015a) is located in Loreto Province, 80 miles southeast of Iquitos (~2° S, 75° W) with an elevation of 106 m. The reserve is part of one of the largest (420,080 ha) protected areas in the Amazon (https://natureandculture.org/tag/procrel/) containing wet lowland tropical rainforest of high diversity. ACRCTT is comprised of low, seasonally inundated river basins of the upper Amazon and named for two of the major rivers (the Tahuayo and the Tamshiyacu) which form boundaries to the north and west and create large fringing floodplains. The substrate of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. Annual precipitation ranges from 2.4 to 3.0 m per year and the rainy season is between November and April. The average temperature is relatively steady at 26 °C.

Within the ACRCTT are areas of regular, seasonal black-water runoff containing tannins leached from litter, making the water acidic and low in nutrients. This creates primary igapó forests of differing flooding frequency, duration, and maximum water column height. Common tree species in those igapó forests include *Calycophyllum spruceanum*, *Ceiba samauma*, *Inga* spp., *Cedrela odorata*, *Copaifera reticulata,* and *Phytelephas macrocarpa* with understory palms *Guazuma rosea*, and *Piptadenia pteroclada* also common.

1.8.1 Physical/Chemical Gradient (Spatial): Primary Igapó Forest Flooding × Tree-Fall Gap Plots: Soils, Floristics, and Physical Structure

I set up plots in primary igapó forests at ACRCTT: underwater 1–2 months every year, underwater 3–5 months every year, and underwater at least 6 months every year, setting up a spatial flooding gradient of black-water igapó forests. All plots were in primary unlogged forests with fresh average-sized (100–300 m^2: Brokaw 1982) tree fall gaps within them. Specifically, I set up five replicate, randomly placed 100 m^2 (10 m × 10 m) plots within each of the three primary forest types and also in the center of each of their tree fall gaps, for a total of 30 plots (5 × 3 plus 5 × 3). These data are housed in the archives of the Long-Term Ecological Research (LTER) site in Puerto Rico (LTERDBAS #150: luq.lternet.edu).

Within those plots, I first took five soil samples without litter in May 2009 at five different random locations in each of the three 1° forest plots. I found soil pH increased monotonically slightly from 3.65 to 3.82 in forests as months under water increased as did organic matter (32.20–40.64%), phosphorus (25.50–39.00 ppm), and potassium (107–137 ppm), but nitrogen decreased monotonically from 148 to 101 ppm across the same flooding gradient. I next sampled the plots for tree stems using the same protocol as in the 1 ha plot (see Myster 2007a, 2010a, 2015a) and found for floristics (1) common species between all three forest types and their gaps as well as among all three forest types, (2) tree stem density and richness decreased in forests as number of months under water increased, and (3) dominance–diversity curves have more dominance by single species in the least-flooded forest compared to other forests.

For physical structure, there was a significant effect of tree fall gap formation on canopy average height, canopy maximum height, basal area, density, AGB, turnover, and alpha diversity, and a significant effect of forest type on species richness, genera richness, density, turnover, and alpha diversity. In general, there were fewer trees, but they were larger, and more productive in the forest plots compared with the gap plots; and the most flooded plots had fewer trees, species, and genera compared with both the less flooded forest and non-flooded forest. In addition, the greatest amount of turnover was in the most flooded forests, and the intermediately flooded forest had the greatest richness and alpha diversity. Canopy structure was determined by traditional gap dynamics, but much of canopy diversity depended on the type of forest, tree density decreased as flooding increased, especially among the smallest stems, and there was evidence to suggest that the high biodiversity of the Amazon may be maintained in part by the existence of moderately flooded forest and gaps.

I found (1) increased flooding (along the gradient) decreased family richness in the closed-canopy forests but increased it in their gaps, with no trends for number of unique species, (2) flooding decreased stem size everywhere as did the number of stems as size increased especially for larger stems, (3) Green's index showed clumping only for least-flooded forests with the closed-canopy forest showing more than its tree fall gap, and (4) both flooding and tree fall gap creation decreased canopy coverage perhaps as an additive effect. Further, among the stem size classes, only the smallest stems were significantly affected by openness and by type of forest, with a significant interaction term where flooding significantly decreased the number of these smaller stems in all forests and their gaps, except those with the highest level of flooding. Also, tree fall gaps had significantly more, smaller stems than their forests in the two most flooded forests, but not in the least-flooded forest. I conclude that flooding is a greater stressor and influence on the structure of these forests than tree fall, and so, in these forests, gradients and disturbances overlap in their traditional roles (Myster 2007a, 2010a, 2015a).

1.8.2 Physical/Chemical Gradient (Spatial): Primary Igapó Forest Flooding × Tree-Fall Gap Plots: Seed Predation, Seed Pathogens, Germination

I set out seeds on transects for a week in these same three plots (the same spatial flooding gradient as above) and found (1) seed predation took more seeds than either seed pathogenic disease or germination for most seed species, but there were a few species that lost more seeds to pathogens than predators. Germination was lower than predation and pathogens for most species, but there were a few species where germination was higher than pathogens, and (2) predation decreased monotonically (and pathogens increased monotonically) as months under water increased in black-water forests. I conclude that seed predation is the major post-dispersal filter for regeneration in these forests but pathogenic disease can play a major role, especially in forests that have water in them for long periods each year so that flooding may change those forests dramatically by altering the actions of seed mechanisms and tolerances (Myster 2017c).

1.9 Case Study: The Luquillo Experimental Forest in Puerto Rico, USA, the Tropical Long-Term Ecological Research (LTER) Site of the U. S. National Science Foundation

The Luquillo Experimental Forest (LEF) lies within the Caribbean National Forest, Puerto Rico, USA (18° 20′ N, 65° 45′ W). LEF receives 3.8 m rainfall per year, has an average temperature of 18 °C, and is found between 325 m and 1080 m in elevation. LEF has rough, deeply dissected drainages with steep slopes and its soils are fertile and derived from volcanoclastic primary substrate that has weathered into clay ultisols. The climate of LEF is dominated by trade winds that produce moisture-bearing clouds year round with a rainfall of between 2 m and 5 m per year. The wettest months are between July and October, and the driest months are between January and April. The average temperature is approximately 18 °C.

The LEF's plant communities are dominated by tropical lower montane wet forest containing tabonuco (*Dacryodes excelsa*), ausubo (*Manilkara bidentata*) and motillo (*Sloanea berteriana*) below 600 m, palo colorado (*Cyrilla racemiflora*) and palm (*Prestoea montana*) between 600 m and 850 m, and cloud forest above 850 m. The dynamics of the LEF includes the natural disturbances of treefall (Everham et al. 1996) and hurricanes but is also recovering from landslides (Myster and Walker 1997) and past agriculture (Myster 2012b). Common landslide vegetation includes the ferns *Cyathea arborea* and *Gleichenia bifida* in the bare soil areas and *Cecropia schreberiana, Miconia racemosa,* and *Nepsera acuatica* in the lower debris areas (Myster and Fernandez 1995). Landslides in the LEF are predominantly rainfall-induced shallow soil slips, debris flows, and slumps.

1.9.1 Physical Gradient (Spatial: Elevation): Forest Tree Ecotypes

A greenhouse experiment was performed to investigate ecotypic differentiation among tropical trees along an elevation gradient in Puerto Rico, USA, using *Clibadium erosum* cuttings and *Prestoea acuminata* var. *montana* seedlings. *Clibadium erosum* cuttings (1) grew more after nitrogen (N) addition and after phosphorus (P) addition but there was no N + P effect, (2) were larger from El Verde (elevation 350 m) compared with Pico del Este (1000 m), (3) showed increased photosynthesis after N addition, and (4) from Pico del Este were higher in photosynthesis during one sample period but lower in the other. We also found that *P. acuminata* var. *monatona* seedlings (1) had greater growth after N addition, (2) had different leaf parameters after N addition, and (3) showed an increase in photosynthesis after N addition. We conclude that because only three out of ten plant traits showed differentiation, ecotypes for these two tree species on this neotropic mountain range may not exist (Myster and Fetcher 2005).

1.9.2 Biological Gradient (Spatial Gradient/Temporal Gradient Interactions): Pastures and Coffee Plantation Plots After Abandonment

A long-term permanent plot study was set up in a natural, unseeded pasture in Puerto Rico that had been grazed for decades before it was abandoned. This study pasture has been the site of many of my other LEF LTER studies (e.g., Myster 2004b, 2007b; Myster and Malahy 2008; Myster 2009, 2010b, 2012b). It borders the LEF close to the town of Sabana at low elevation. In 1996, twenty-five 5 m × 2 m contiguous plots (the total plot was 25 m × 10 m) were laid out on the border with the LEF in 1996 with the long side parallel to the forest in order to maximize any forest edge effects. There were not any remnant trees or sprouting tree roots in the plots at the beginning of the study. Starting in May of 1997 and continuing annually for 10 years, the plots were sampled for percent cover of each plant species creating a temporal gradient. Percent cover— an indication of a species' ability to capture light and, therefore, to dominate these areas in the process of becoming forested communities—was estimated visually in relation to each plot's area. Every tree stem and all stems for every shrub at least 1 m tall were measured for height, and for basal diameter at ground level in each subplot. Each stem was also identified to species. These data are archived as LTERDBAS#97 and may be visited on the LUQ web site (http://luq.lternet.edu).

The first analysis of this data set used only the first 5 years of pasture sampling and showed that (1) grass dominated peaking at year three but still constituting 75% of the total plant cover after 5 years, (2) forbs also peaked at year three and then declined to 40% after 5 years, and (3) both ferns and woody species increased steadily to 45% and 15% total cover respectively after 5 years. During these first 5 years of succession, total percent cover ranged between 160% and 300% due to strata formation, percent species turnover declined to 25% in year four, species richness plateaued at 20 and species evenness stayed around 0.75. Focusing only on the trees and shrubs, the woody plants were present in the first sampling with greatest density close to the forest edge (the spatial gradient). The dominant species were the trees *Syzygium jambos* (an exotic species), *Calophyllum calaba*, and *Tabebuia heterophylla* and the dominant shrubs *Clidemia hirta* and *Miconia* spp., all peaking in abundant individualistically (Pickett 1982) in different years. Together these woody species showed (1) a maximum productivity of 400 g/m^2/year and a maximum total number of stems of 300, both in year two, (2) an increasing mean height of 240 cm in year five, and (3) a plateauing of total basal area of 950 cm^2 after year two. The community parameters that peaked within the first 5 years after abandonment were productivity (at 400 g/m^2/year), total basal area (at 1000 cm^2), and richness (at 19 species). The spatial locations of each tree by basal diameter and species in year five were mapped and showed that trees invaded and grew from the forest edge (the spatial gradient), again in an individualistic manner (Myster 2004a).

The next use of the data set was to generate species associations and found a total of 307 significant pair-wise positive associations between species and 55 significant pair-wise negative associations. And so facilitation may be more common than competition in these stressful, early successional environments. Care must be taken, however, not to fall into the Nietzsche's "Cornaro" misinterpretation of causality because species that associate together may not be reacting to each other but to some other species or environment factor. Species that formed the most positive associations with other plants were the trees *Syzygium jambos, Guarea guidonia*, *Ocotea leucoxylon*, and *Prestoea montana*. Species that formed the most negative associations with other plants were the grass *Panicum* spp., the fern *Gleichenia bifida*, and the tree *T. heterophylla* (Myster 2012b). The positive associations were also used to construct a clustering hierarchy of increasing species inclusiveness, in order to define post-agricultural communities (Myster 2012b). These Spearman coefficients of rank associations can implicate plant interactions because controlled field experiments performed elsewhere have confirmed that species that interact significantly also form significant associations with each other.

Finally, the data set was used to generate allometric above-ground biomass equations for each of the ten most abundant tree and shrub species, which account for over 90% of the total stems and over 90% of the total basal area. Using those equations, I found that the most productive species were *Syzygium jambos*, *Miconia impetiolaris*, *Miconia prasina*, *Calophyllum calaba*, and *Clibadium umbrella*. These productivity data were then plotted against turnover. The first 2 years of succession showed a slightly positive slope between productivity and turnover, but starting in year 3 there was a significant negative slope which became more negative with time. Turnover was also plotted against richness. There was a slightly negative slope between richness and turnover in the first year which became more negative with time. I found tree species turnover was greatest at year 2 and then declined monotonically until year 10. Production was highest in the first 2 years after abandonment at 0.5 kg m^{-2} $year^{-1}$, then declined to about half its maximum level in year three, and stayed there for the remaining years. Richness increased in year two and stayed at that level (~7 species in each subplot) for the remaining years (Myster 2016b).

The same plot design and sampling protocol was employed in a sun coffee plantation located on private land in 1996. The plots were sampled in 1997 and in 1998 (creating a temporal gradient), but could not be continued because the farmer wanted the land back for other purposes. Plots showed that the Coffee trees themselves persisted, having 30% cover in year one and 23% cover in year two. Like the pasture plot, grass dominated (94% in year one, 90% in year two) and *Ichnanthus pallens* most common, with forbs (45%, 50%: *Phytolacca icosandra* and *Musa* spp. most common) and woody vines (64%, 67%: same species as in the pasture plots) also common. Ferns were at low cover (5% in year one, 6% in year two: same species as in the pasture plots) but at greater levels than in the pasture plots (Myster 2004a). Trees were much less common after Coffee cultivation than in the pasture plots and the three most dominant trees and shrubs found in pasture were absent in Coffee. However, *Tabebuia heterophylla*, *Miconia* spp., and fruit trees were just as common. *Andira inermis* and *Guarea guidonia* attained greater cover in Coffee than in pasture but *Inga* spp. was not found. There were several species unique to the Coffee plots (Myster 2004a) and *Cecropia schreberiana* was again absent.

The same plot design and sampling protocol were also employed in four pastures of different starting ages located close to the LEF: CoRd (5 years old), Los Davilas (13 years old), CoRd 9948 (18 years old), and Puente Roto (23 years old). These four pastures were first sampled in 2000 and then sampled annually creating a temporal gradient. The three permanent plot data sets (Sabana pasture, Coffee plantation, these four pastures that started in different years) were then used for an analysis of dominance-diversity curves. There was a significant log-normal pattern regardless if the plots were in a coffee plantation or in the Sabana pasture. The Sabana, CoRd990, CoRd9948, and Puente Roto pastures showed this pattern flattening over time with only the Los Davilas pasture maintaining a significant log-normal pattern (Myster 2010b). Also, there was no lag time seen for any pasture compared to Coffee plantation. The first 10 years of sampling in the permanent plots of the Sabana pasture was combined with the first 5 years of sampling in these other four pastures, started at different times (combining the temporal gradients). This hybrid study, combining permanent plot data with chronosequences (space-for-time substitution), was also used to provide enough overlapping of sampling years and pastures to predict succession in these pastures better than using chronosequences by themselves. Total plant richness and total plant cover did form long continuous patterns among the samplings, but species composition was too unique to each pasture to be able to combine into a single timeline. Consequently, this approach may work best for broad structural parameters, but not for predicting individual species abundances (Myster and Malahy 2008). All those data are archived as LTERDATB #100 at the LEF web site http://www.luq.lternet.edu.

1.9.3 Physical, Chemical, and Biological Gradients (Spatial Gradient/Temporal Gradient Interactions): Landslide

I sampled a LEF landslide and found that total daily photosynthetic photon flux density was 50 times greater in the landslide compared to the surrounding forest (a spatial gradient), but similar between landslides. The red: far red ratio was homogenous in the open areas of the landslides, but in areas covered by vegetation it was similar to those ratios found in the forest border. The soil had average extractable phosphorus of 0.108 g/m^2 to 9 cm depth. Nitrogen was 0.10% of average soil mass, carbon was 1.83% of average soil mass, and there was a 69% average moisture content. Seed rain averaged 31 seeds per trap with the seed pool showing an average of two seedlings per sample. Vesicular-arbuscular mycorrhizal fungi covered 7% of the average length of roots sampled, and the vegetation (dominated by species *Cyathea arborea, Cecropia schreberiana, Miconia* spp., and *Nepsera acuatica*) had two structural levels on average. For these factors, the strongest spatial gradient was from the forest into the landslides from the side rather than from the top of the landslide to the bottom or between landslides. Evidence of distinct patches was found where patch structure was defined by levels of light, seed pool, fungi, vegetation, soil N, and soil C. In addition, light, the key abiotic factor, showed very significant negative correlations with the key biotic factors of mycorrhizal fungi and vegetation, implying causal relationships (Myster and Fernandez 1995).

I next explored the predictive value of common landscape characteristics for several landslide vegetative stages in the Luquillo Experimental Forest of Puerto Rico using four different analyses. Maximum-likelihood logistic regression showed that aspect, age, and substrate type could be used to predict vegetative structural stage. In addition, it showed that the structural complexity of the vegetation was greater in landslides (1) facing the southeast (away from the dominant wind direction of recent hurricanes), (2) that were older (a temporal gradient), and (3) that had volcaniclastic rather than diorite substrate. Multiple regression indicated that both elevation (a spatial gradient) and age (a temporal gradient) could be used to predict the current vegetation, and that vegetation complexity was greater both at lower elevation and in older landslides. Pearson product–moment correlation coefficients showed that (1) the presence of volcaniclastic substrate in landslides was negatively correlated with aspect, age, and elevation, (2) that road association and age were positively correlated, and (3) that slope was negatively correlated with area. Finally, principal components ordination analysis showed that landslides were differentiated on axes defined primarily by age, aspect class, and elevation in the positive direction, and by volcaniclastic substrate in the negative direction. Because several statistical techniques indicated that age, aspect, elevation, and substrate were important in determining vegetation complexity on landslides, we conclude that landslide succession is influenced by variation in these landscape traits. In particular, we would expect to find more successional development on landslides which are older (further down the temporal gradient), face away from hurricane winds, are at lower elevation (further up the spatial gradient), and are on volcaniclastic substrate. Finally, our results lead into a hierarchical conceptual model of succession on landscapes where the biota respond first to either gradients or disturbance depending on their relative severity, and then to more local biotic mechanisms such as dispersal, predation, and competition (Myster et al. 1997).

Finally, I laid out litterbags with leaves of three different tree species in three landslide microsites. Bags were collected after 1, 2, 4, 8, and 16 weeks and chemical results were dominated by tree species rather than microsite (the spatial gradient). Organic matter showed exponential decay and there was immobilization for nitrogen, phosphorus, and calcium (for two of the species: Myster and Schaefer 2003).

1.10 Monteverde Cloud Forest, Costa Rica

Monteverde Cloud Forest (MCF) Reserve of Costa Rica (10″ 12′ N, 84″ 42′ W) is dominated in the overstory by *Lauraceae, Moraceae,* and *Araliaceae* and in the understory by *Rubiaceae, Solanaceae, Acanthaceae, Gesneriaceae, Piperaceae,* and *Arecaceae (Palmae)* (Lawton and Dryer 1980). Landslide vegetation is dominated by *Gunnera insignis* in the bare soil areas and *Chusquea pohlii, Cecropia polphlebia,* and *Palicourea standleyana* in the lower debris areas (Myster 1993). MCF has well-weathered soils of volcanic origin. The climates of both LEF and MCF are dominated by trade winds that produce moisture-bearing clouds year-round. Total water input is similar between the two sites, although MCF receives more moisture deposition from mist-bearing winds (MCF averages 3.3 m/year with 2.5 m/year as rain and 0.8 m/year as deposition; LEF averages 3–5 m/year, almost all in rainfall with small amounts in deposition. In addition, LEF has a dry season between late spring and summer and MCF has a dry season during the first few months of the year (Holdridge 1967). Normal wind speeds above the canopy also have overlapping ranges (MCF 5–15 km/h; LEF 2–10 km/h). The two landslides studied at MCF were in the Rio Penas Blancos watershed at 1300 m, approximately 2000 m′ in size and were 5–15 year old.

1.10.1 Biological Gradient (Spatial): Landslide

This study was undertaken on two 15- to 20-year-old landslide sites and compared the number of seedlings emerging from the soil samples (the seed pool) with the number of seeds per fruits collected in sampling traps over a 2-week period. The former was much greater than the latter (even after adjustment for the differing time scale) and also varied among families (mainly represented by the Asteraceae and the Melastomataceae). There were also significant differences between landslides, and some microhabitat differences (the spatial gradient) within landslides. Eighteen families were represented in the vegetation sampling, and principal components ordination analysis suggested the importance of the Arecaceae and Euphorbiaceae in defining the plots. The revegetation process seemed to consist first of patch dynamics (when the soil was unstable and undeveloped, and plant invasion largely stochastic) and later followed the resource ratio hypothesis (where plants compete and trade-off for resources: Myster 1993).

1.11 Comparing Landslides at LEF and MCF (Large Spatial Gradients): Regeneration

Seed mortality (caused by predators and pathogens) and germination were compared between Puerto Rico (LEF) and Costa Rica (MCF) on landslides in lower montane wet forest. Seeds of six common species on five Puerto Rican landslides and four common species on two Costa Rican landslides were used with a *Cecropia* sp. and a *Gonzalagunia* sp. included at both sites. In the Puerto Rican experiments, *Cecropia schreberiana* was the only species to show significant seed predation (which was due to insects), pathogens grew from all species, and fewer seeds were lost to predators than pathogens. Also, in Puerto Rico mean germination across all species was 57% before dispersal (filled seeds collected while still on the tree) and 71% after, with *Phytolacca rivinoides* seeds germinating most abundantly, followed in descending order by *Ocotea leaucoxylon, Cecropia* sp., *Miconia racemosa, Palicourea riparia,* and *Gonzalagunia spicata.* In the Costa Rican experiments, three species had significant predation: *Cecropia polphlebia* and *Urera caracasana* (due to insects) and *Witheringa coccoloboides* (due to mammals): pathogenic disease caused more seed loss than predation, and germination was high (61% pre-dispersal, 69% post-dispersal). Similarities between these island and mainland sites (which different in both latitude and longitude, LEF is north and east of MCF) included (1) percentage of seeds lost to predation and percentage lost to pathogens (all in the 5–15% range), (2) generalist pathogens which claimed more seeds than predators, and (3) majority germination with a general increase after dispersal. Finally, sites were dissimilar only in the number of species with significant predation loss and whether it was b) insects or mammals, casting doubt on the traditional island/mainland dichotomy (Myster 1997). Possible LEF insect predators included 6 orders and 18 families where spatial gradients within landslides were not different than between landslides. MCF insects were from 7 orders and 30 families. Beetles in Coleoptera and ants were most abundant at both sites, with a few other families dominating (Myster 1994).

1.12 About This Book

The Neotropics is a large part of the earth's biosphere, and so understanding it is critical in helping us prepare for our shared human future. I have argued in this introductory chapter that understanding Neotropical ecosystems must include the study of their gradients. This book is motivated by that research objective, which includes helping researchers everywhere analyze their ecological gradients better, more completely and in more detail (Muenchow et al. 2018). Chapters and references that follow will facilitate such additional, more rigorous research. Chapter authors will explore all types of gradients and interactions between spatial gradients, temporal gradients including those initiated by common Neotropical disturbances such as treefall, landslides, agriculture and urban development, and space-time gradients. They will also investigate the regularity of gradient patterns, and whether or not any casualty can be inferred. And while all authors will compare and contrast their specific gradients, relating their results to the three major Neotropical gradients of latitude, longitude, and elevation will be an important focus.

Here, I take advantage of my 30+ years publishing on Neotropical gradients in Ecuador, Peru, Puerto Rico (USA), and Costa Rica to edit this book. This research was facilitated by 12 years as a CO-PI for the LTER site in Puerto Rico (http://luq.lter.network), three research/teaching awards from the Fulbright Foundation (http://www.iie.org/fulbright) and grant no. 6168-98 from the National Geographic society (https://www.nationalgeographic.org/funding-opportunities/grants). You may check my personal website (*www.researchgate.net/profile/Randall_Myster*) for a complete listing of my Neotropical gradient publications and chapters in my previous books. For many of those publications, I worked with professors, researchers, students, and technicians in various Neotropical countries.

This is the first research book focused exclusively on Neotropical gradients—and thus its chapter scope and detail is unique—but there have been a few books written about gradients at one specific site in the Neotropics (e.g., the Reserva Biologica San Francisco in Ecuador [Beck et al. 2008], the Luquillo Experimental Forest in Puerto Rico [Gonzalez et al. 2013]) or have contained chapters about Neotropical gradients (e.g., Nadkarni and Wheelwright 2000; Bruijnzeel et al. 2010). These past books provide background and context for this book which, like my five previous books, is an international effort with authors from many countries throughout the Neotropics. Editing these books has been a rewarding and effective way for me over the years to collaborate with my fellow Neotropical scientists, and also to give them—many of whom were of limited means—an important vehicle for publishing their research.

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References

Austin MP (1976) On non-linear species response models in ordination. Vegetatio 33:33–41

Austin MP, Nicholls AO, Doherty MD, Meyers JA (1994) Determining species response functions to an environmental gradient by means of a β-function. J Veg Sci 5:215–228

Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (2008) Gradients in a tropical mountain ecosystem of ecuador. Springer, Berlin

Bongers F, Poorter L, Van Rompaey RSAR, Parren MPE (1999) Distribution of twelve moist forest canopy tree species in Liberia and Cote d'Ivoire: response curves to a climatic gradient. J Veg Sci 10:371–382

Brokaw NVL (1982) The definition of treefall gap and its effect on measures of forest dynamics. Biotropica 11:158–160

Bruijnzeel LA, Scatena FN, Hamilton LS (2010) Tropical montane cloud forests: science for conservation and management. Cambridge University Press, Cambridge, UK

Buchholz T, Tennigkeit T, Weinreich A (2004) Maesopsis eminii – a challenging timber tree species in Uganda – a production model for commercial forestry and smallholders. Proceedings of the international union of forestry research organizations (IUFRO) conference on the economics and management of high productivity plantations, Lugo, Spain

Bussmann RW (2001) The montane forests of Reserve Biologica San Francisco. Erde 132:9–25

Bussmann RW (2003) The vegetation of Reserva Biológica San Francisco, Zamora-Chinchipe, Southern Ecuador – a phytosociological synthesis. Lyonia 12:71–177

Canham CD, LePage PT, Coates KD (2004) A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can J For Res 34:778–787

Cardenas ML, Gosling WD, Pennington RT, Poole I, Sherlock SC, Mothes P (2014) Forests of the tropical eastern Andean flank during the middle Pleistocene. Palaeogeogr Palaeoclimatol Palaeoecol 393:76–89

Curry H (2010) Foundations of mathematical logic. Dover, New York

Death G (1999) Principal curves: a new technique for indirect and direct gradient analysis. Ecology 80:2237–2253

Edmisten J (1970) Some autoecological studies of Ormosia krugii. In: Odum HT, Pigeon RF (eds) A tropical rain forest. National Technical Information Service, Springfield. Chapter D-8

Everham EMIII, Myster RW, VanDeGenachte E (1996) Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. Am J Bot 83:1063–1068

Fiedler K, Beck E (2008) Investigating gradients in ecosystem analysis. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 49–55

Fisher RA, Corbet AS, Williams CB (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. J Anim Ecol 12:42–58

Fisher JB, Malhi Y, Torres IC, Metcalfe DB, van de Weg M, Meir P, Silva-Espejo JE, Huasco WH (2013) Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes. Oecologia 172:889–902

Fox GA, Scheiner SM, Willig MR (2011) Ecological gradient theory: a framework for aligning data and models. In: Scheiner SM, Willig MR (eds) The theory of ecology. The University of Chicago Press, Chicago, pp 283–307

Gentry A (1993) A field guide to woody plants of Northwest South America (Colombia, Ecuador, Peru). Conservation International, Washington, DC

Gonzalez G, Willig MR, Waide RB (2013) Ecological gradient analyses in tropical ecosystems. Ecological bulletins 54, US Forest Service

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Guest RG (2013) Numerical methods of curve fitting. Cambridge University Press, Cambridge, UK

Hill MO (1977) Use of simple discriminant functions to classify quantitative phytosociological data. In: Diday E, Lebart L, Pages JP, Tomassone R (eds) First Inern. Symposium on data analysis and informatics, Versailles, 7-9 Sept. 1977. Vol. 1. Institute de Recherche d'informatique et d'automatique, Domaine de Voluceau, Rocqnencourt B. P. 105, 78150 le Chesney

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Joag PS (2016) An introduction to vectors, vector operators and vector analysis. Cambridge University Press, Cambridge, UK

Jump AS, Matyas C, Penuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol Evol 24:694–701

Knapp G (1991) Andean ecology: adaptive dynamics in Ecuador. Westview Press, Boulder

Larcher W (2001) Physiological plant ecology: ecophysiology and stress physiology of functional groups. Springer, Berlin

Ludwig JA, Cornelius JM (1987) Locating discontinuities along ecological gradients. Ecology 68:448–450

Ludwig JA, Reynolds JF (1988) Statistical ecology. Wiley, New York

Mabberley DJ (1992) Tropical rain forest ecology. Chapman and Hall, New York

Mandelbrot BB (1983) The fractal geometry of nature. Macmillan

Marini L, Bona E, Kunin WE, Gaston KJ (2010) Exploring anthropogenic and natural processes shaping fern species richness along elevational gradients. J Biogeogr 37:1–7

Martinez CEC (2005) Manual de Botanica: Sistematica, Etnobotanica y Metodos de Estudio en el Ecuador. Ditorial Universitatia, Quito, Ecuador

McCain CM (2005) Elevational gradients in diversity of small mammals. Ecology 86:366–372

Muenchow J, Dieker P, Kluge J, Kessler M, von Wehrden H (2018) A review of ecological gradient research in the tropics: identifying research gaps, future directions, and conservation priorities. Biodivers Conserv 27:273–285

Müller F (1998) Gradients in ecological systems. Ecol Model 108:3–21

Myster RW (1993) Spatial heterogeneity of seed rain, seed pool and vegetative cover on two Monteverde landslides, Costa Rica. Brenesia 39-40:137–145

Myster RW (1994) Landslide insects show small differences between an island (Puerto Rico) and the mainland (Costa Rica). Acta Cientifica 8:105–113

Myster RW (1997) Seed predation, disease and germination on landslides in Neotropical lower montane wet forest. J Veg Sci 8:55–64

Myster RW (2002) Mechanisms of plant response to gradients and after disturbances. Bot Rev 67:441–452

Myster RW (2004a) Post-agricultural invasion, establishment and growth of neotropical trees. Bot Rev 70:381–402

Myster RW (2004b) Regeneration filters in post-agricultural fields of Puerto Rico and Ecuador. Plant Ecol 172:199–209

Myster RW (2006) Light and nutrient effects on growth and allocation of *Inga vera* (Leguminosae), a successional tree of Puerto Rico. Can J For Res 36:1–8

Myster RW (2007a) Interactive effects of flooding and forest gaps on tree composition and abundance in the Peruvian Amazon. Folia Geobot 42:1–9

Myster RW (2007b) Early successional pattern and process after sugarcane, banana and pasture cultivation in Ecuador. New Zealand J Bot 46:101–110

Myster RW (2008) Post-agricultural succession in the neotropics. Springer, Berlin

Myster RW (2009) Are productivity and richness consistently related after different crops in the neotropics? Botany 87:357–362

Myster RW (2010a) Flooding duration and treefall interactive effects on plant community richness, structure and alpha diversity in the Peruvian Amazon. Ecotropica 16:43–49

Myster RW (2010b) A comparison of tree replacement models in oldfields at Hutchenson Memorial Forest. J Torrey Bot Soc 137:113–119

Myster RW (2012a) Ecotones between forest and grasslands. Springer, Berlin

Myster RW (2012b) A refined methodology for defining plant communities using data after sugarcane, banana and pasture cultivation in the neotropics. Sci World J 2012:365409, 9 pages. https://doi.org/10.1100/2012/365409

Myster RW (2012c) Spatial and temporal heterogeneity of light and soil water along a terra firme transect in Amazonian Ecuador: effects on tree seedling survivorship, growth and allocation. Can J For Res 42:P1–P4

Myster RW (2012d) Plants replacing plants: the future of community modeling and research. Bot Rev 78:2–9

Myster RW (2013) Long-term data from fields recovering after sugarcane, banana and pasture cultivation in Ecuador. Dataset Papers Ecol 2013:468973.10 pages. https://doi.org/10.7167/2013/46873

Myster RW (2014) Primary vs. secondary forests in the neotropics: two case studies after agriculture. In: Forest ecosystems: biodiversity, management and conservation. Nova Publishers, New York, pp 1–42

Myster RW (2015a) Flooding x tree fall gap interactive effects on black-water forest floristics and physical structure in the Peruvian Amazon. J Plant Interact 10:126–131

Myster RW (2015b) Seed predation, pathogens and germination in primary vs. secondary Cloud forest at Maquipucuna Reserve. Ecuador J Trop Ecol 31:375–378

Myster RW (2016a) Forest structure, function and dynamics in Western Amazonia. Wiley-Blackwell, Oxford, UK

Myster RW (2016b) Turnover-productivity and turnover-richness relationships in a Puerto Rican pasture. Trop Ecol 57:701–707

Myster RW (2017a) Gradient (elevation) vs. disturbance (agriculture) effects on primary cloud forest in Ecuador: floristics and physical structure. N Z J For Sci 47:1–7

Myster RW (2017b) Comparing and contrasting flooded and unflooded forests in Western Amazonia: seed predation, seed pathogens, germination. Community Ecol 18:169–174

Myster RW (2017c) Forest structure, function and dynamics in Western Amazonia. Wiley-Blackwell, Oxford, UK

Myster RW (2017d) Does the seed rain limit recruitment, regeneration, and plant community dynamics? Ideas Ecol Evol 10:12–16

Myster RW (2018a) The nine classes of plant-plant replacement. Ideas Ecol Evol 11:29–34

Myster RW (2018b) Gradient (elevation) vs. disturbance (agriculture) effects on primary cloud forest in Ecuador: seed predation, seed pathogens and germination. N Z J For Sci 48:4

Myster RW (2018c) Igapó (black-water) forests of the Amazon Basin. Springer, Berlin

Myster RW (2020a) Introduction. In: Myster RW (ed) The Andean Cloud forest. Springer, Berlin, pp 1–23

Myster RW (2020b) Disturbance and response in the Andean cloud forest: a conceptual review. Bot Rev 86:119–135

Myster RW, Fernandez DS (1995) Spatial gradients and patch structure on two Puerto Rican landslides. Biotropica 27:149–159

Myster RW, Fetcher N (2005) Ecotypic differentiation and plant growth in the Luquillo Mountains of Puerto Rico. J Trop For Sci 17:163–169

Myster RW, Malahy MP (2008) Is there a middle-way between permanent plots and chronosequences? Can J For Res 38:3133–3138

Myster RW, McCarthy BC (1989) Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. Oikos 56:145–148

Myster RW, Pickett STA (1988) Individualistic patterns of annuals and biennials in early successional old fields. Vegetatio 78:53–60

Myster RW, Pickett STA (1990) Initial conditions, history and successional pathways in ten contrasting old fields. Am Midl Nat 124:101–109

Myster RW, Pickett STA (1993) Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. Oikos 66:381–388

Myster RW, Pickett STA (1994) A comparison of rate of succession over 18 yr in 10 contrasting old fields. Ecology 75:387–392

Myster RW, Sarmiento FO (1998) Seed inputs to microsite patch recovery on Tropandean landslides in Ecuador. Restor Ecol 6:35–43

Myster RW, Schaefer DA (2003) Species and microsite effects on litter decomposition in a Puerto Rican landslide. Community Ecol 4:157–162

Myster RW, Walker LR (1997) Plant successional pathways on Puerto Rican landslides. J Trop Ecol 13:165–173

Myster RW, Thomlinson JR, Larsen MC (1997) Predicting landslide vegetation in patches on landscape gradients in Puerto Rico. Landsc Ecol 12:299–307

Nadkarni NM, Wheelwright NT (2000) Monteverde: ecology and conservation of a tropical cloud forest. Oxford University Press, New York

Nascimento HEM, Lawrance WF (2002) Total aboveground biomass in central Amazonian rainforest: a landscape-scale study. For Ecol Manag 68:311–321

Økland RH, Økland T, Rydgren K (2001) Vegetation environment relationships of boreal spruce swamp forests in Østmarka Nature Reserve, SE Norway. Sommerfeltia 29:1–190

Oksanen J, Minchin PR (2002) Continuum theory revisited: what shape are species responses along ecological gradients? Ecol Model 157:119–129

Oncken O, Chong G, Franz G, Giese P, Götze H, Ramos VA, Strecker MR, Wigger P (2006) The Andes: active subduction orogeny. Frontiers in earth sciences. Springer, Berlin

Pickett STA (1976) Succession: an evolutionary interpretation. Am Nat 110:107–119

Pickett STA (1982) Population patterns through twenty years of oldfield succession. Vegetatio 49:45–59

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens GE (ed) Long-term studies in ecology: approaches and alternatives. Springer, Berlin

Pielou EC (1984) The interpretation of ecological data: a primer on classification and ordination. Wiley, New York

Rehak K, Bookhagen B, Strecker MR, Echtler HP (2010) The topographic imprint of a transient climate episode: the western Andean flank between 15.5° and 41.5°S. Earth Surf Process Landf 35:1516–1534

Romoleroux K, Foster R, Valencia R, Condit R, Balslev H, Losos E (1997) Especies Lenosas (dap => 1 cm) encontradas en dos hectareas de un bosque de la Amazonia ecuatoriana. In: Valencia R, Balslev HR (eds) Estudios Sobre Diversidad y Ecologia de Plantas. Pontificia Universidad Catolica del Ecuador, Quito, pp 189–215

Rydgren K, Okland RH, Okland T (2003) Species response curves along environmental gradients. A case study from SE Norwegian swamp forests. J Veg Sci 14:869–880

SAS (1985) SAS user's guide: statistics. SAS Institute, Cary

Scheiner SM, Willig MR (2011) The theory of ecology. The University of Chicago Press, Chicago

Schultz J (2005) The ecozones of the world. Springer, Berlin/Heidelberg/New York

Schweitzer JA, Juric I, van de Voorde TFJ, Clay K, van der Putten WH, Bailey JK (2014) Are there evolutionary consequences of plant–soil feedbacks along soil gradients? Funct Ecol 28:55–64

Sober E (1981) The principle of parsimony. Br J Philos Sci 32:145–156

Sokal R, Rohlf FJ (1981) Biometry: the principles and practice of statistics in biological research. Freeman, New York

Ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Adv Ecol Res 18:271–317

Ter Steege H, Pitman NCA, Phillips OL, Chave J, Sabatier D, Duque A, Molino JF, Prevost MF, Spichiger R, Castellanos H, von Hildebrand P, Vasquez R (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443:444–446

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285–298

Walker JJ, deBeurs KM, Wynne RH (2014) Dryland vegetation phenology across an elevation gradient in Arizona, USA, investigated with fused MODIS and Landsat data. Remote Sens Environ 144:85–97

Walter H (1979) Vegetation of the earth and the ecological systems of the geo-biosphere. Springer, Berlin

Whittaker RH (1967) Gradient analysis of vegetation. Biol Rev Camb Philos Soc 42:207–264

Wittmann F, Schongart J, Montero JC, Motzer T, Junk WJ, Piedade MTF, Queiroz HL, Worbes M (2006) Tree species composition and diversity gradients in white-water forests across the Amazon basin. J Biograp 33:1334–1347

Chapter 2
Mountain Gradients in the Neotropics: A Bracken Fern Perspective

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2.1 Introduction

Theoretically, a gradient is a measure of change of a set of independent variables with physical distance. As such, gradients acquire the properties of a vector. When this basic mathematical concept is applied to the geographical dominion, a set of physical variables showing distance-dependent values must be taken into account, e.g., soil and air temperature, water precipitation (rain/snow/fog) amount and time-dependent regime, relative humidity, effective sun radiation and wavelength distribution, elevation, physical, chemical, and microbiological characteristics of soils, topography, prevailing wind direction and force, and others. Although some of these variables are interdependent, such as elevation, sun radiation, and temperature at a fixed latitude, others are more difficult to interpret as truly independent. After adding inevitable confounding factors, the study of geographic clines, the interpretation of combined data, and its implications on ecosystems become a most challenging endeavor.

Organisms manage to colonize and thrive along these gradients through tolerance, avoidance, or acclimation strategies to physical—abiotic—constraints, in addition to competition for resources against other species and predation avoidance/deterrence. As these biological entities, plants and soil microorganisms in particular, progress to mature forms through succession cycles, other types of gradients appear as a result of modifications of the physical environment created by the changing plant cover, the accompanying microcosmos, and the animal community. These changes can be substantial at the micro- and macroscales. Water retention in the leaf canopy of forests, roots and soil, surface wind flow and local temperature,

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sun radiation reaching the ground, cloud cover, rainfall, soil mineralization, and nutrient recycling are obvious examples of these modifications. Animal populations, seasonal behavior, and niche establishment become closely associated with the changing biome created by the plant community, leading to very complex ecological relationships one observes along gradients defined by a combination of abiotic and biotic inputs.

Few places on earth offer more intricate and varied gradients than the Neotropical Andean range (Josse et al. 2011). Within this large area covering about one and a half million km^2 from 11° N to 23° S, gradients possibilities related to elevation from the low hills to summits beyond the 6500 m asl (above sea level from here on) mark are practically infinite, as one moves from the megathermic lowlands on the cordillera's fringe slopes to the snow fields of the cryozone.

In the Northern Andes, elevation contrasts are most prominent in the Eastern Cordillera of Ecuador, Colombia, and the central sections of the Eastern branch of the Venezuelan Andean range. These mountains rise abruptly above the eastern lowlands up to the tropical cryozone (>4500 m) and reach 5300 m asl overseeing the *llanos* of the Casanare, Apure, Putumayo, and Napo river basins (180–250 m asl) only a short distance away (40 km in some cases).

This chapter describes over 20 years of research aimed at understanding strategies of colonization, encroachment, and expansion of the two Neotropical bracken fern species, *Pteridium caudatum* and *Pteridium esculentum* subsp. *arachnoideum* of the Northern Andes with special emphasis in studies of populations of the Sierra Nevada de Merida, in western Venezuela, and in Ecuador. These plants thrive in a wide spectrum of habitats at elevations ranging from near the sea level to the fringes of the night freeze line in the Andean *paramo*. Sections of this research have been published in the past, while others appear in print for the first time in this chapter.

Embarking on the study of these ubiquitous and powerfully invading ferns growing in these complex set of habitats demands as a first step to be familiar with the large picture, these mountains represent at the continental scale as well as a detailed knowledge of the sites selected along a given gradient of study. In this manner, one can put together the results from various research groups currently working in bracken ecology in other Andean countries.

2.2 The Andean Barrier as an Atmospheric Water Trap and Impact on Vegetation

Mountain ranges of high elevation are geologic protrusions of earth crust into the troposphere that strongly interfere with low-altitude wind currents. In reference to the Ecuadorian, Colombian, and Venezuelan Andes, this continental backbone runs from south to north, and northeast for the most part. Having this topographical configuration, they form a nearly perpendicular barrier blocking the predominant low-level eastern jet of the Intertropical Convergence Zone (ITCZ: Insel et al. 2010). Moisture is transported to the west by ITCZ winds in large quantity from the distant equatorial Atlantic Ocean and water recirculation through the rain-evapotranspiration cycle across the Amazon River rainforest basin (Swan and Koven 2017). This interaction feeds abundant rainfall to the eastern face of these mountains during most of the year. Upon encountering the high ground and colder temperatures under the dew point, cloud condensation occurs as rain or snow, depending on altitude and humidity contained in the air masses. There is also the so-called occult precipitation (fog and drizzle) which contributes significantly (7–28%) to the overall atmospheric water load, according to recent measurements in the Colombian *paramos* (Cardenas et al. 2017) and the cloud forests of the central Peruvian Andes (Gomez-Peralta et al. 2008). High-altitude plants capture water particles by leaf pubescence, a convergent trait among many humid *paramo* plant forms, which highlights the giant rosettes of the Espeletiinae subtribe (Asteraceae) and characterize plant communities of high elevations north of the equator in South America. The thickness of the cuticular pubescence increases with altitude, as observed in *Espeletia schultzii* along a gradient from 2600 to 4200 m in the Venezuelan Andes (Meinzer et al. 1985). The hairy cuticular cover was interpreted as an adaptive response to decreasing rainfall along the observation transect and enhanced protection against solar UV-B radiation. Leaf morphological convergence as regards to pubescence, in addition to other markers, occurs in plant species adapted to high elevation from geographically distant mountains such as New Zealand, New Guinea, eastern Africa, and South America (Halloy and Mark 1996), rendering an evolutionary convergent characteristic.

Changing water transport in the lower troposphere during the interaction of air masses with the complex orography of the Northern Andes also gives rise to a variety of rainfall regimes and temperature patterns in inner valleys and adjacent slopes. A mosaic of local bioclimatic zones results, spanning from densely forested areas to xerophytic scrubs and deserts. Many of these habitats harbor acclimatized plant/animal communities of great species richness known also as biodiversity hotspots (e.g., Guzman et al. 2014). The environmental differentiation along these clines appears to be sufficiently explicit, as revealed by extensive studies of Southern Ecuador (Beck et al. 2008) and elsewhere in the Northern Andes (Posner et al. 1982). A profuse variety of vegetation forms are organized in clearly discernible altitudinal belts in accordance with their adaptative capacities, separated by ecotones (e.g., Llambi 2015). As many as 133 ecosystems have been recognized in the tropical Andes (Josse et al. 2009).

2.3 The Complex Andean Topography as a Gene Flow Barrier

The combination of abiotic and biotic gradients associated with elevation and the physical barriers of the rough terrain constitute effective filters against gene flow. These forces induce physiological stress of newly arriving individuals for the expansion of the ecological range of plant species and animals using them as food sources and refuge. The ensuing selection and the formation of microecological islands create conditions for endemism. Although still poorly understood, areas of extremely high endemism of plant and animal species have been recorded from the Bolivian and Peruvian Eastern Andean slopes (Kessler et al. 2001; Swenson et al. 2012) to Venezuela (e.g., Stefano et al. 2009). As much as 31% endemic species have been recorded in the northern Andes only in the mosses group (Churchill 2009). Moving in the opposite direction, within-species genetic diversity and plasticity expressed in ecophysiological flexibility contribute to ecological adaptation to diverging environments, thus widening the colonization window and impact on existing ecosystems, as observed in some Neotropical mountain plant and animal species (e.g., Hendrickson 2013; Hereford 2009; Gratani 2014; Ibanez et al. 2021).

2.4 The Question of Invasive Plant Species in the Andes

Global warming and anthropogenic disturbance constitute key drivers for the successful entry of invasive plant species and insect pests, be these foreign or native, in the Tropical Andes. Large portions of road-accessible areas have been extensively impacted by agriculture, logging, and pasture exploitations in both sides of the Andes in Ecuador (Mosandl et al. 2008), parts of Colombia (Rodriguez-Eraso et al. 2013), and to a lesser extent in Venezuela (Pacheco et al. 2014; Portillo-Quintero et al. 2012).

Having a more benign climate, mountain valleys of tropical America have been inhabited by a number of cultures centuries before the arrival of Europeans and thereafter. Many other mountain regions of the world are equally affected (e.g., Jepson and Millington 2008; Akomolafe and Rahmad 2018). As the native vegetation is removed for agriculture and cattle husbandry or urban development, the land turns into a very simplified species-poor ecosystem, in which water dynamics is profoundly altered (Ataroff and Rada 2000; Buytaert et al. 2006). Fast-growing weeds and first succession seedlings mixed previously with the soil, seeds transported by wind from nearby seed banks in surrounding vegetation or frugivores/graminivorous droppings, a phenomenon known as natural seed or propagule rain and recorded in mountain forests of Colombia and Venezuela, compete for the cleared land, giving rise to a first-stage succession (Cardenas et al. 2021; Velasquez et al. 2015).

A case in point is the colonization by invading weeds, either natural or alien species by propagule rain (including fern spores) over fallow cropland, a subject of major importance for agriculture worldwide and especially relevant in small plots and open soil caused by landslides (Myster 1993), both common in the tropical Andes. Among the few reports in this area, there is a recent study about the course of a potato fallow field in the Venezuelan Andes of the Merida cordillera (Villa et al. 2017). The parcel of land was located in a mosaic of naturally forested and cattle pasture and was monitored for the natural appearance of seedlings after harvest in twenty 2 × 2 m subplots. The annual rain regime (2000 mm), moderate average temperatures (13–19 °C), and elevation (1920 m asl) were adequate for a species-rich ecosystem composed of grasses, broadleaf shrubs, and woody relics from the lower edge of the vicinal montane cloud forest. Samplings were carried out in five periods of 60 days each after harvest, up to 240 days. The abundance of individual species was recorded in terms of number, density, relative frequency, and absolute importance index. A total of 35 species of weeds belonging to 32 genera and 17 families were observed, hence playing witness to the high species richness of the surrounding area. *Bidens pilosa* L. (Asteraceae), originally from South America and currently widely distributed across temperate zones of the world, was by far, the most abundant in the first 60 days survey, followed by *Paspalum decumbens* Sw. grass (Poaceae), also from tropical America, in addition to 24 other weed species. Moreover, *Pennisetum clandestinum* Hochst. (Poaceae), known as “kikuyu grass,” an exotic species introduced originally from Kenya as cattle pasture across the Northern Andes and successfully naturalized there, became the most abundant and persistent growth alongside *Paspalum decumbens* in the second survey (120 d) and up to the end of the sampling period (240 d). Their dominant colonization of the fallow plot could be explained by adjacent cattle grazing plots planted with these grasses. Notably, no bracken fern (*Pteridium* spp.) sprouts, a highly invasive weed and a central subject of this chapter, was found in the fallow plot in spite of the occurrence of fern thickets in the vicinity. As will be reviewed in the next section, this could only occur if there were no rhizomes with viable buds under the potato field or were very deep in the soil due to frequent mechanical soil management. Such intervention is known to break and remove near-surface rhizomes (20–30 cm). On the other hand, bracken spores could not compete successfully against fast-growing forbs seedlings under the management conditions of the potato field in question, but experiments in this connection were not conducted.

At much higher elevation, unfarmed land and roadsides in the Andean *paramo* also undergo a relatively fast regeneration of plant coverage, mostly by native species, following anthropogenic disturbances, chiefly agriculture, cattle and horse trampling, and fire (Sarmiento et al. 2003; Lippok et al. 2013; Fernandez-Murillo et al. 2015), as it occurs in the lowlands (Myster 2008). However, prevailing low temperature, declining moisture, higher UV-B sun radiation, and other abiotic constraints intervene as selection filters. Pursuant of assessing the effect of altitudinal filters to the establishment of new plant species in land patches of varying disturbance, a systematic survey of native (N) and alien (A) plant species was undertaken, spanning a long transect from 1150 to 4000 m asl along a road in the Eastern face of the Ecuadorian Andes (Sandoya et al. 2017). Elevation and relative disturbance were observed to influence the species patterns of both species groups spanning a total of 771 species (97.2% N, 5.5% A, and 6.8% endemic). The number of N species decreased linearly with elevation, whereas A plants showed a hump distribution with maximum diversity in the 2000–3000 m asl belt. Alien species of temperate origin were better adapted to this climatic region than the N group and cosmopolitan species from lower ecosystems. Importantly, as many as 39 A species were found at 3500 m asl, the largest number of alien species so far recorded in the Northern Andes. What is more, disturbed habitats favored the establishment of nonnative plants. These findings suggest that anthropogenic disturbances at intermediate and high elevations in the Andes open the road to an increased invasion capacity of A plants causing a concomitant decline of N species. Propagules of invasive pioneer species are carried long distances by wind, mammals, birds, growing vehicle traffic and tourism, impinging on habitat disturbance and eventually forming different vegetation assemblages from the original plant community (Barros et al. 2015; Alexander et al. 2016).

It is also of note that *Pteridium esculentum* subsp. *arachnoideum*, the most common bracken fern found as dense invasive thickets in many mesophile phytocommunities of Ecuador and other parts of the Northern Andes, was not reported in the species inventory of Sandoya and coworkers research (2017). It can be argued that the relative isolation of the road following the altitudinal transect, the >4000 m asl elevation of the summits to the west, and the absence of bracken thickets upwind from the east owing to dense, old-succession, and little perturbed forest may be compounding barriers to bracken spore penetration.

A growing number of studies on the adaptation and acclimation strategies of plants to high-altitude habitats away from their original source have appeared in the last two decades (e.g., Lütz 2013; Magana-Ugarte et al. 2019). For example, the phenotypic plasticity of the Alpine perennial grass *Festuca eskia* Ramond (Poaceae), clones planted along a 1500–2500 m altitudinal transect in the Pyrenees was put to test (Gonzalo-Turpin and Hazard 2009). Authors observed a reduction of plant stature and increased specific leaf area with increasing elevation, a likely phenotypic response to constraints limiting resource acquisition. Other plant morphological functional trait (PFT) responses to abiotic stresses related to elevation, which include plant height, specific leaf area, leaf dry matter content, as well as carbon and nitrogen concentration, have been observed frequently in plant adaptation strategies in European and North American mountains, although less so in the Neotropical sierras.

2.5 Bracken (*Pteridium* spp.), an Invasive Fern Taxa of Neotropical Mountains

A particularly successful genus of invading species of mesophile regions in the Neotropics, the *Pteridium* clade (Dennstaedtiaceae), constitutes one of the five most damaging weeds known at the world scale. These ferns are notorious for their success as pioneer species and thriving invaders of cropland, pastures, and fire-affected land in five continents. Bracken ferns of the New World's *Pteridium* genus are among the limited number of pteridophytes capable of thriving in the forest understory—as most ferns do—and tolerate habitats under full sun as well, due in part to a well-developed vascular system. The stark differences expected in photosynthetic rates and evapotranspiration in these two contrasting ecosystems is an indication of the remarkable adaptive plasticity of this plant.

Bracken ferns are commonly found in fallow fields, burned land, and pastures in the Northern Andes, forming dense swards that exclude other vegetation forms. The latitudinal ecological range of these ferns in the New World spans from North America and the Caribbean islands to Northern Argentina, including vast regions of Brazil. As forests are removed for logging and other land exploitation purposes the moderate population of bracken fronds turns into a fast-growing low stature and dense canopy. Data from Ontario, Canada, rate bracken as one of three dominant early-succession plant species after logging (Quinby 2000).

Two species have been fully characterized in Central and South America *Pteridium esculentum* (G. Forst.) Cockayne subsp. *arachnoideum* (Kaulf.) (*PEA* henceforth) and *P. caudatum* (L.) Maxon (PC hereafter) (Thomson and Alonso-Amelot 2002; Thomson 2012). Additionally, six morphotypes of *PEA* have been identified recently in the east–west axis from Eastern Brazil to the Galapagos islands of Ecuador (Schwartzburd et al. 2018), enriching the Pteridium clade collection of 15 taxa recognized thus far in the world (Der et al. 2009).

Mountain brackens in northern South America are invasive weeds with potential to outcompete other native or foreign weeds and agricultural pests such as *Rumex* species (Fig. 2.1). Brackens and *Rumex* are both rhizomatous plants resistant to slash and burn field clearing since buds in underground parts remain active to yield new aerial growth before propagules of the seed rain have a chance to germinate. In addition, both plant species possess a wide altitudinal range, the high mountain

Fig. 2.1 Image of bracken blades (*Pteridium caudatum*)(Dennstaedtiaceae) in an early-succession field near Merida, Venezuelan Andes, (2200 m asl) interspersed among *Rumex acetosella* (Polygonaceae, red inflorescences). Both plants are highly competitive weeds and severe agricultural pests, due in part to their drought- and fire-resistant rhizomes. The ecotone at the background is formed by a first wall of partially withered fronds from an earlier bracken growth alongside live and taller fern blades, backed by a mass of native vegetation of the lower montane forest. (Photo by M. Alonso)

tropical bracken (*PEA*) reaching 3200 m, and *Rumex acetosella* L. up to 4200 m well within the periglacial band (Arellano 2003).

2.6 Herbivory on Andean Brackens

It is well established that, among the constraints to growth and expansion, herbivory accounts for an important fraction of plant damage (Hendrix 1988; Crawley 1997; Maron and Crone 2006). Although it was thought that ferns in general sustained a much lower load of herbivory than angiosperms (e.g., Cooper-Driver et al. 1977; Balick et al. 1978), other authors supported the opposite point of view attributing this difference to the fact that arthropods on ferns had been undersampled (e.g., Hendrix 1980; Mehltreter et al. 2010). Indeed, *Pteridium aquilinum* (L.) Kuhn in the Old World supports a herbivorous insect collection comparable to that of angiosperms in the same habitat (Lawton 1976). In the insect, species-rich ecosystems of the Neotropics invertebrate herbivores-bracken fern interactions would be expected to be substantial (Lawton et al. 1987). Because temperatures are known to be a limiting factor for species diversity, population numbers, and activity of non-adapted insects to increasingly demanding abiotic conditions of high mountain gradients, the question of the herbivore–fern interaction and its impact on fern growth and development needs to be addressed. Early studies about insects feeding on *Pteridium* spp. in this region suggest that populations seem to be insufficient to cause significant damage to the blades at the thicket scale (Salinas and Ortega 1990; Martins et al. 1995). In recent years, however, new insights have shed light on this concern in the northern Andes.

2.6.1 Arthropod Herbivory on Andean Bracken

Before discussing the current knowledge about the impact of mountain gradients on insect species richness and populations, it is constructive to review what is known as regards to invertebrate visitors and exploiters of bracken ferns, as this plant is loaded with a number of xenobiotic deterrents and toxins. Natural herbivorous predators and fungal diseases are not decidedly threatening biotic forces against mountain bracken ferns. Little biological control over bracken aerial growth can be expected, despite promising discoveries awaiting application in reference to endophytic fungi (Petrini et al. 1992). Although some phytophagous insect species have been reported in bracken fronds from the British isles, New Guinea, the United States, and Venezuela, few of these, except for the Japanese beetle (*Popillia japonica* Newman; Scarabaeidae), a major agricultural pest, and some of the 30 insect species found on New Guinean bracken, appear to be a threat to the growth bracken fronds worth considering for effective biological control (Lawton 1976; Gilman and Cooper-Driver 1998; Kirk 1982, 2007; Avila-Nuñez et al. 2008).

As regards to brackens in the northern Andean range, the list of insect exploiters has been considerably expanded by a recent detailed survey (Avila-Nuñez and Otero 2019). Samples were massively collected from sympatric patches of *PC* and *PEA* in a secondary succession plot at 1980 m asl near Merida, in the central Venezuelan Andes, during a one-year period. Although brackens formed the dominant canopy, the plant community also included grasses, forbs, and a mosaic of relic trees of the neighboring deciduous, cloud, and riparian forests, which could be sources of polyphagous insect visitors. Out of 1650 individual insects collected in the two 100-m^2 plots, both bracken species harbored about the same number of insect species/morphotypes: 83 and 79, respectively, distributed in nine orders, 26 families and 41 genera. The species list included the first sawfly species described for the Venezuelan Andes: *Aneugmenus merida* Smith (Hymenoptera: Tenthredinidae) (Smith 2005; Avila-Nuñez et al. 2007) (Fig. 2.2a). The larvae of the sawfly *A. merida*, like others species of this genus, are closely associated with *Pteridium*, and feed on *PC* and *PEA* in Venezuelan Andes (Fig. 2.2a). Also, the leaf miner *Phytoliriomyza* sp. (Diptera: Agromyzidae) and *Tricimba* sp. (Diptera: Chloropidae), a gall inducer attacking the blade rachis, and a voracious beetle, the *Bolax palliata* Burmeister (Coleoptera: Scarabaeidae) were collected from Andean bracken in this survey

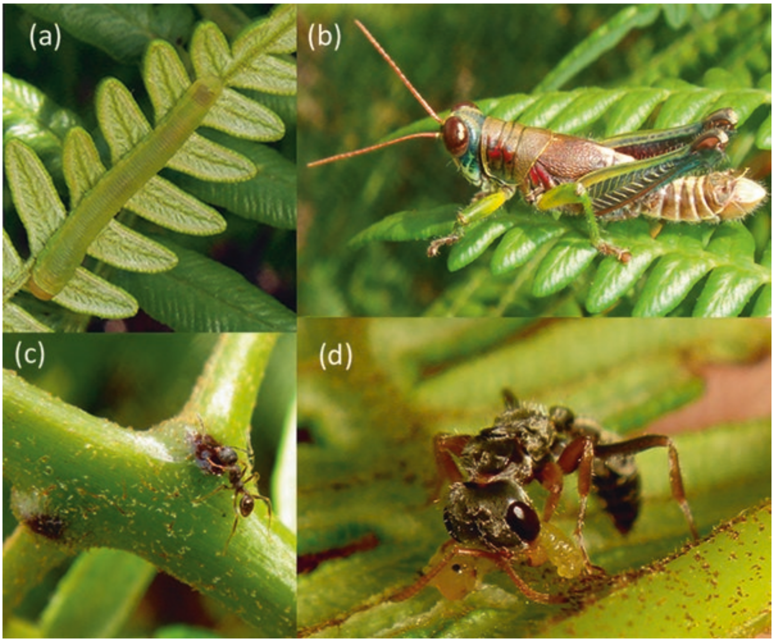

Fig. 2.2 Examples of insect- *Pteridium* interactions in Venezuelan Andes. (**a**) Larva of the sawfly *Aneugmenus merida* on *Pteridium caudatum*; (**b**) male of the grasshopper *Timotes malleatus* on *P. caudatum*; (**c**) a worker of the ant *Pheidole* sp. visiting a extrafloral nectary of *P. caudatum*; (**d**) a worker of the ant *Pseudomyrmex gracilis* predating a first-instar larva of *A. merida* on *P. esculentum* subsp. *arachnoideum*. (Photographs by JL Avila-Nuñez)

(Avila-Nuñez and Otero 2019). The latter is a polyphagous agricultural pest of fruit trees and timber species in the Neotropics, reportedly destructive of *Pteridium* fronds as well in the Venezuelan Andes (Avila-Núñez et al. 2008).

2.6.2 Bracken Arthropods and Altitude

While there has been an increasing interest in the distribution of insects along altitudinal clines, a controversial issue in itself (e.g., McCoy 1990; Garcia-Robledo et al. 2016; Moreira et al. 2018; Sanders 2002; Supriya et al. 2019; Corcos et al. 2018; Hodkinson 2005; Lemoine et al. 2017) and source of illuminating ecological hypotheses (e.g., Rasmann et al. 2014a, b), there is a shortage of such reports in the Northern Andes. One of the few is the case of the sawfly *Aneugmenus merida* we observed on *PC* and *PEA* between 1800 and 2200 m asl in Venezuelan Andes and reported as well in Colombia between 1500 and 2600 m asl (Malagon-Aldana et al. 2019). Because the pupa development occurs in the soil and the activity of the adult fly depends on air temperature (Avila-Nuñez et al. 2007), lower temperatures are a likely direct abiotic constraint limiting its habitat at higher altitudes and thus the fly is unable to exploit PEA at higher elevations. Surveys beyond the 2600 m asl mark will have to be carried out alongside the corresponding thermometrics to determine the limits of *A. merida* ecological range in the northern Andes.

By contrast, the polyphagous grasshopper *Timotes malleatus* Ronderos & Cerda (Acrididae: Melanoplinae) (Fig. 2.2b) invades a wider altitudinal spectrum, as we have observed it on *PC* and *PEA* from middle elevations (1800 m asl) up to 3200 m asl (*PEA* only), and further up to the *paramo* and the periglacial band (3900–4600 m asl.) Through laboratory tests (Alonso-Amelot and Calcagno-Pisarelli, unpub. data), we reproduced the consumption of *PEA* segments by *T. malleatus* and *Chibchacris meridensis* Ronderos (Acrididae: Melanoplinae), which can be found in large numbers in the high *paramo,* without deleterious consequences for the survival of the grasshoppers.

Body thermoregulation is one of the most important challenges of high-altitude insects. Tolerance to low temperatures and desiccation have been observed in grasshoppers from the Venezuelan Andean *paramos* (3600 and 4200 m asl), although the physiological mechanisms remain obscure. In laboratory experiments, adults of the grasshopper *Meridacris subaptera* Roberts (Acrididae: Melanoplinae) high resistance to desiccation and survival at −6 °C during several hours, as is the case under natural conditions in the periglacial zone, was observed (Søme 1986). The continuation of these research efforts would be an important addition to our knowledge of the high *paramo* biota.

2.6.3 The Case of Bracken Ants in the Northern Andes

Opportunistic predatory and nectarivorous ants patrol bracken fronds frequently and some aggressive species provide protection against herbivorous insects (Avila-Nuñez and Otero 2013). Ants are attracted to the secretion of extrafloral axillary nectaries located at the junction of the blade rachis and the axis of the first pair of pinnae (P1: Fig. 2.2c, see Fig. 2.3 for fern blade nomenclature). Secreted nectar contains sugars and amino acids, a nutritious offer to insects. Nectaries are more active in young fronds, whereas secretion ceases as blades mature. This is a common trait found throughout the bracken clade (Page 1982a; Rumpf et al. 1994). At least five species of ants have been observed to be frequent visitors of bracken croziers at mid-altitude in the Merida Andes of Venezuela, in addition to aphids and one species of long-horned grasshoppers (Orthoptera: Tettigoniidae) (Avila-Nuñez and Otero 2013, 2019). Interestingly, bracken nectaries are sufficiently valuable for ants to spark hostilities between belligerent ant species such as *Solenopsis geminata* Fabricius, the notorious fire ant, and *Pheidole radoszkowskii* Mayr (Formicidae: Myrmicinae) (Avila-Nuñez and Otero 2020). *S. geminata* goes as far as building protective structures in the bracken's fiddlehead proper, near and around the axillary nectaries, using bits of plant debris and soil particles. These agglomerates serve as shelter and protective barriers to exclude competing ants. This strategy has been observed elsewhere in other species of foraging ants to cover food sources and protect them from competitors and desiccation (e.g., Anderson and McShea 2001; Blüthgen and Feldhaar 2010). Shelter-building activity of ants does not appear to jeopardize the crozier development.

The potential of an ant-fern mutualistic relationship model emerged inevitably in early ecological studies (Douglas 1983; Lawton and Heads 1984) although this thesis has been debated, upon contending that ferns did not benefit from ant protection against insect herbivory (Tempel 1983 and ensuing works by this author). At any rate, the ant-fern mutualism proposal was later tested successfully in field studies of bracken in southern California (Eatough Jones and Paine 2012). When allowed free access to bracken fronds, ants (mostly *Tapinoma sessile* (Say) —75%) reduced significantly the bracken-feeding larvae population of the sawfly *Strongylogaster distans* Norton (Tenthredinidae) relative to fronds protected from ant visits using plastic cones at the frond base.

Analogous exclusion experiments have not been conducted yet in South America, but the sole number of predatory ants observed in Andean bracken might in principle suggest a similar ant-fern mutualistic relationship. In the *PC* and *PEA* study in Venezuelan Andes (Avila-Nuñez and Otero 2019), nine species of the Formicidae taxon were identified, two of which were predators, in addition to three parasitoid wasps and seven predatory species of other insect orders. As a group, ants are generally involved in about 80% of predation events in tropical Andes, in consonance with higher predation rates of insects and their parasitoids at lower elevations (Camacho and Aviles 2019). Ants constitute, therefore, a commanding predatory pressure as opportunistic commensals. Even so, for a true mutualistic insect–plant association a concomitant development schedule of each organism partaking in this relationship is of the essence. In the interaction of the sawfly *A. merida* with the Andean bracken species, we observed that oviposition and larval feeding activity of the sawfly on bracken segments began once fronds became fully unfurled. By then, all the secretory activity of axillary nectaries had ceased and ants showed no further interest in the blades; hence, the ant–larvae contact never occurred.

There are other ant-bracken associations leading to true mutual benefit. We discovered ants of the *Pseudomyrmex* genus (Formicidae: Pseudomyrmecinae), as they patrolled the fronds and attacked mature bracken exploiters such as lepidopteran and *A. merida* larvae (Fig. 2.2d) without the lure of nectaries. Furthermore, we have records of *Pseudomyrmex gracilis* Fabricius on *PC* at 1800 m and on *PEA* at 2100 m and 2400 m asl. At the latter elevation, we spotted one frond harboring an ant colony in the hollow rachis of bracken fronds. A conspicuous feature of the genus *Pseudomyrmex* is that most species have generalized twig-nesting habits, occupying dead stems and branches of plants, usually in cavities previously excavated by other insects. In other cases, ants colonize hollow cavities in live plant tissues and in most instances appear to provide protection to the plant (Ward and Downie 2005) as in the iconic ant-acacia mutualism, a true lesson in coevolution (Janzen 1966).

Of additional interest is the potential use of bracken substances by some insects after ingestion to deter attackers, which provides an expanded dimension to the ecological influence of bracken ferns as a result of its altitudinally dependent phytochemistry. The predator–prey encounters between tropical insects *Abracris flavolineata* De Geer grasshoppers (Acrididae: Ommatolampidinae) and *S. geminata* ants was tested as a model (Calcagno-Pissarelli et al. 2004). Both species occur concomitantly in bracken territory in the Andes of Merida. Grasshoppers and Lepidoptera larvae use food regurgitates as a primitive form of antipredator deterrents (Eisner 1970; Lymbery and Bailey 1980; Ortego et al. 1997; Sword 2001). Substances contained in this enteric fluid originate in their food plant in addition to their own digestive juices.

A. flavolineata, a polyphagous grasshopper, accepts bracken pinnae as food in captivity and presumably in the wild as well. As other Acrididae, they tolerate foods with a high content of phenolics and condensed tannins typically produced by bracken ferns, and some may even be assimilated as carbon nutrients (Bernays et al. 1981, 1983). Phenolics-rich lettuce (*Lactuca sativa* L.) (e.g., Liu et al. 2007) and *PC* pinnae were given ad libitum to separate groups of fasting *A. flavolineata* adults in a laboratory chamber, while the predatory *S. geminata* ants were maintained on chicken meat. After 2 days to allow for digestion, regurgitation was induced by gentle pressing of live grasshoppers and the enteric liquid was collected, used for chemical analysis, solids content, and bioassays with the ants. Properly concentrated water extracts of both food plants containing the phenolics fraction were then dosed to a sucrose solution, in parallel with *A. flavolineata* regurgitates at various dilutions with sucrose water. Droplets of control (C) and treated (T) solutions in serial concentrations were presented to the ant cage in glass slides and the number of visits by the ants was recorded at time intervals. A deterrence index was calculated using the difference of the fraction of ants feeding on T and C droplets relative to C and time spent on them. The phenolics/tannins content of the plant extracts was also determined by standard spectral means.

Authors observed that:

1. The fluid egested by *A. flavolineata* from *PC* or lettuce contained statistically similar amounts of solids (305 and 274 mg/mL), which implies a substantial cost of wasted food in the defense response.
2. The fluid from *PC* at various dilutions led to a significantly greater deterrence index than that from lettuce. The bracken versus lettuce difference was greatest at 50 mg/mL of regurgitate, which 64.5 ± 8.9% versus 16.7 ± 2.9% of the ants, respectively, rejected the T droplets.
3. Importantly, aqueous extracts of lettuce at the same concentration found in the egested liquor elicited a similar partial rejection but those from *PC* evoked complete rejection, even at the lowest concentration of the tested dilutions series.
4. Also worth noting was that 53% of bracken low molecular weight phenolics and 93% of condensed tannins, a notorious group of digestion inhibitors, had anyway been assimilated by the grasshoppers after 48 h of ingestion, whereas similar compounds in lettuce remained in larger quantity in their digestive track. Authors also proved that no less than 30% of the feeding deterrent activity of the regurgitate was due to substances not pertaining to lettuce but to the insect's gut liquor.

In a nutshell, *A. flavolineata* and other bracken-feeding insects may have developed means of coping with bracken's bioactive allelochemicals through digestive processes, while at the same time, they take advantage, at least temporarily, of its deterrence effect against predatory insects and possibly bird species. Because the chemical composition of Andean brackens is influenced by altitude, sun exposure, water stress, etc. (see Sect. 2.5), the nutritional and defensive potential of *A. flavolineata* and other herbivores feeding on bracken may also be impacted accordingly, thus showing that exploitation of plant food resources by herbivores in mountain habitats is subjected to highly complex and intertwined environmental and biological determinants (Jones 1983).

2.6.4 The Impact of Temperature on Ants in the Northern Andes

The declining temperatures linked to elevation impacts substantially the population of ants and many insect species. Recently, a study of activity rates and density of predation of insects along a 4000 m elevation gradient was tested at several sites located on both sides of the Andean range of Ecuador, one facing the Amazon basin and the other, the Pacific Ocean (Camacho and Aviles 2019). Researchers used baits of live adult laboratory-bred flies (*Lucilia sericata* Meigen [Diptera: Calliphoridae]) and allowed natural predators to approach and perform. Both, the rate of predator attack and their density declined rapidly with elevation, down to negligible values at altitudes higher than 2000 m asl. Authors propose a model where lower air temperature (*T*) is the dominant abiotic factor underlying the declining predation by way of two parallel effects. Lower *T* first decreases the metabolic rate of the predator, limiting its activity, hence the predation rate, and also affects primary productivity, restraining predator density and predation. These observations suggest that Neotropical brackens growing above 2000 m asl do not profit from ant protection assuming that herbivory is negligible.

Supporting evidence comes from the decreasing ant diversity along an elevational transect in the Venezuelan Andes reported by Janzen et al. (1976). They collected 13 species of ants at 1600 m asl and none at 3600 m asl. A similar tendency was found by van der Hammen and Ward (2005) in the Colombian Andes, reporting a maximum of species richness between 900 and 1700 m asl, and very few between 2300 and 2750 m asl, whereas no ants were found beyond that elevation. As will be shown in the section devoted to bracken growth with altitude, the optimal growth tier of *PC* in the Northern Andes falls between 900 and 1700 m asl while higher altitudes are more adequate for *PEA* encroachment. Therefore, one would expect a greater diversity in the associations of bracken with ants at mid-elevations, whereas these interactions become weaker and eventually disappear above 2000 m asl. Consequently, it appears that the axillary extrafloral nectaries are relic traits unnecessarily preserved in the evolutionary context. The question will not be solved though, until it is ascertained whether the bracken nectaries remain active at high elevations, leading to non-profit physiological cost, or ceases altogether soon after the emergence of the crozier, as it does in the mature fronds at lower elevation (Rumpf et al. 1994).

2.7 Vertebrate Herbivory on Andean Bracken

There is a paucity of field records as regards to damage to bracken caused by small wild mammals. In the surrounding area of Merida, we have spotted sporadically the traces left by other herbivores capable of chopping off cleanly the head of the crozier as if armed with precision scissors and carrying it away or consume it entirely in the place, but the culprit has escaped detection. Because the morsel includes the only meristem of the blade, the bud is killed. As will be underlined in the section about phytochemistry and altitude, the bud's head contains the highest concentration of bracken's deterrent xenobiotics and so this mysterious animal must be unusually tolerant or resistant to bracken's chemical protection. Clues of its identity emanate from the British Isles where small rodents (*Clethrionomys glareolus* (Schr.) and *Apodemus sylvaticus* (L.)) of the Cricetidae family reportedly use *P aquilinum* thickets for food and shelter (Watts 1968; Pakeman and Marrs 1992), although very little is known about this behavior. As it happens, two mice species of this precise family (*Microryzomys minutus* Tomes and *Oligoryzomysfulvescens* Saussure) have been described in our bracken sampling area by the Albarregas river in Merida

(Piñango 1996), as well as other countries to the south of the Continent but very little else is known about these diminutive rodents.

Field qualitative observations of large stock animals—sheep, goats, and cattle—show them to be occasional consumers of bracken during periods of scarcity caused by overgrazing/drought and massive invasion of bracken swards which reduce substantially the pasture offer. Free hogs and wild boars unearth, consume, and destroy rhizomes near the soil surface. Most large farm mammals, however, are deterred from eating bracken fronds by two notoriously effective strategies of these plants. The first of these is based on the accumulation of bitter prunasin in young croziers in addition to tannins as blades mature while prunasin concentration wanes (see Sect. 2.5.1). Livestock may tolerate these deterrents urged by scarcity of other edibles. This is when a second front of chemical defense intervenes. Xenobiotics of the illudane group of sesquiterpenes, (see Sect. 2.5.2) known to occur in all species of bracken in various concentrations depending on species and phenology of frond growth, lead to acute diseases in sheep and cattle, spanning from sudden death and bright blindness to bovine enzootic hematuria (e.g., Fenwick 1988; Gil da Costa et al. 2012a). Plant-destructive wild and domesticated ruminants become acutely sick soon after consuming bracken fronds in sufficient quantity and die, impacted by unspecific hemorrhages and other intoxication symptoms, whereas equines develop a nerve crippling thiamine avitaminosis due to the thiaminase enzyme produced by these ferns. Both animal groups are therefore overwhelmed rapidly by bracken substances. As a result, small- and medium-sized low-tech cattle farms are economically devastated in many parts of the Northern Andes and abandoned. Bracken growth takes over the unoccupied land for many years.

Susceptible breeds develop intestinal hemorrhages, severe thrombocytopenia, bone marrow degeneration, declining immune response accompanied by profuse bleeding, inability to cope with infectious diseases, and eventually bovine hematuria stemming from urinary bladder cancer—a frequent disease in bracken-infested areas of the Andes and other parts. Therefore, these large herbivores become unable to cause further damage to bracken fronds. Importantly, some of these deadly ailments are passed on to calves through milking (Evans et al. 1971), an occurrence reported in cattle husbandries of Ecuador and Venezuela (pers. communication from breeders) and presumably observed elsewhere. It was in our laboratory at Merida, Venezuela, where the actual detection of the toxicogenic principle of bracken—ptaquiloside (PTQ)—was discovered in milk from cows maintained in pens. Animals were systematically offered a single morning dose of fresh *P. caudatum* fronds of known illudane content (Alonso-Amelot et al. 1993, 1996) along the usual fodder. Although these observations have been confirmed in dairy farms of the province of Bolivar in the Ecuadorian Andes (Calderon et al. 2013) and southern Italy (Virgilio et al. 2015), similar analyses of pooled milk from cattle in open bracken infested fields in Tolima, central Colombia, failed to detect PTQ (Rincon et al. 2016). This result might be due to (1) a dilution effect in pooled milk and/or (2) the relatively fast decomposition of PTQ in warm (38 °C) raw milk if not cooled promptly after milking (Alonso-Amelot et al. 1993).

The frequency of these pathologies impacts as much as 17% of herds (Sanchez-Villalobos et al. 1999) in bracken-affected regions and causes severe economic losses in mid-elevation Andean farms. Human carcinogenesis may possibly result from the passage of carcinogenic illudanes across three trophic levels: bracken-livestock (cow, sheep, goat)-milk-human, or direct consumption of illudane-laden bracken croziers by people after brief processing (Shahin et al. 1999; Alonso-Amelot and Avendaño 2002; Gil da Costa et al. 2012a; Virgilio et al. 2015). The toxicogenic effects of Neotropical brackens in bovines continue to be documented in all Tropical Andean countries, with relevant extensions to northwestern Argentina, Uruguay, and Brazil (e.g., Sanchez-Villalobos et al. 1999; Marrero et al. 2001; Herencia et al. 2013; Lozano and Diaz 2013). The problem is compounded by the occurrence of toxicogenic illudanes in other members of the Pteridaceae accessible to cattle in the field (e.g., Micheloud et al. 2017; Schneider de Oliveira et al. 2020). One of the authors (Alonso-Amelot) has collected personal reports of farmers using goats to reduce bracken growth in their pastures before cattle is herded in. Apparently, goats are not susceptible to bracken poisoning for as yet unknown reasons. Authors have no evidence of Andean farmers taking advantage of this strategy, otherwise observed personally in some farms in Scotland.

In the Neotropical mountains, there is a worrisome altitudinal overlap between bracken fern and cattle pastures. As will be reviewed in Sect. 2.5, altitude influences bracken xenobiotic production, but there is a paucity of data on the putative relationship between elevation and the incidence of bracken toxicosis on farm animals. Currently, emphasis revolves around bracken control measures but systematic studies are scarce in the Northern Andes. The task is far from simple as bracken ferns have evolved a variety of potent strategies for reproduction, encroachment, and growth (Alonso-Amelot et al. 2001; Alonso-Amelot 2002a) that resist weeding and application of the majority of herbicides (Marrs et al. 2000).

2.8 Intraplant Competition in Neotropical Mountain Brackens

In a nutshell, bracken outcompete effectively other plant growth in early successions through resistance to fire of its underground rhizome network, fast growth of aerial parts, inhibition of competing seeds by allelopathy, resource sequestration, and suffocation by a dense blade canopy. Andean brackens display all these strategies, although systematic studies in this regard are currently in their infancy.

One particularly successful proliferation mechanism is the vegetative expansion of the rhizome network. In encroached stands, peripheral rhizomes creep underneath the existing vegetation at depths of 80–100 cm forming a long-lived underground matrix (Oinonen 1967; Page 1982b; Alonso-Amelot and Rodulfo-Baechler 1996). Numerous fast-developing croziers emerge from shoots in rhizomes near the surface soon after the plant cover is removed by slashing and/or fire and sufficient moisture remains in the soil. Bracken's rhizome bud sprouting is induced by fire as a result of the high temperatures of the soil (2–4 cm deep) during a passing fire front (Roos et al. 2010). The physical break of dormancy in hard-coated seeds of some wild legume and other hardy species by bushfires is also on record in Australia, South Africa, and Florida, which contribute to the recovery of plant cover (e.g., Auld and Bradstock 1996; Santana et al. 2010). The expansion of the bracken coverage is also enormous in northern Europe and the British Isles (Page 1982b), although fire is not a modeling ecological force of major significance as it is in the intertropical band of the planet.

To the best of our knowledge, comparable studies have not been conducted in Andean seeds despite the inordinate impact of land fires in this region, save for the bracken study of Roos et al. (2010). However, research performed in the remote Gran Sabana of the Guayana Shield in southeastern Venezuela (Dezzeo et al. 2008) reports that, in fire disturbed parcels, *Pteridium* ferns constituted 9% of the early succession plant community whereas it was absent in adjacent undisturbed plots. This proportion was maintained after 6 years. While authors did not establish whether extant unexpressed rhizomes supported this growth, the lack of bracken fronds in the immediate vicinity suggests once more that colonization of land without preexisting rhizomes through germination of fern spores carried long distances by wind and water runoff is a naturally viable process of bracken expansion. Although all spores of bracken and other ferns on the soil surface are charred by fire, 77% of those buried just 1–2 cm under the soil surface do germinate, a figure close to 86% reported for unburned controls (Ramirez-Trejo et al. 2010).

Bracken growth in second- or even third-stage succession plant communities may be an indication of earlier agricultural activity or logging exploitation and abandoned fields as a result of migration of farmers, an expanding form of human exploitation of virgin land in the northern Andes at various elevations (Gonzalez-Diaz et al. 2019). Active land use with inadequate technology facilitates bracken invasion (Curatola-Fernandez et al. 2013). In one of the few systematic studies in this area, it was revealed that the surface expansion of bracken cover reaches nearly 100% in a 21-year period, (southern Yucatan), Mexico (Schneider and Nelun-Fernando 2010).

The end result is that bracken ferns have become one of the most persistent weeds in the world with the aid of anthropogenic activity, and particularly so in Neotropical montane areas undergoing man's disturbance (e.g., Hartig and Beck 2003). We felt from the start that these ferns were an ideal, unique, and ecologically impacting model for studies of plant acclimation and adaptation in the superb altitudinal gradients offered by the Northern Andes.

The purpose of this chapter is to demonstrate the various adaptive responses in Neotropical mountain clines, as regards to growth rates of aerial and underground parts, exclusion mechanisms of competing seedlings and phytochemical responses to elevation that we and others have studied in the past two decades. A preliminary report of some of these aspects has been published (e.g., Alonso-Amelot et al. 2000), as well as other related findings (see references in the following text), whereas more recent discoveries appear published here for the first time.

2.9 Differences Between *P. caudatum* (*PC*) and *P. esculentum* subsp. *arachnoideum* (*PEA*)

These bracken species are easily recognized in the field by traits expressed in the pinnulae and leaflets also known as segments in fern terminology (Fig. 2.3). In some restricted areas though, there are intermediate forms (H?) which have not been fully characterized yet. Specimens like this were systematically disregarded as a confounding and infrequent component in the studies being described here.

In the Northern Andes, these brackens are segregated by elevation: *PC* generally occupies the 600–2100 m asl band with occasional swards at lower and higher elevations with sufficient moisture, whereas *PEA* is found more frequently above 1800 m, up to 3200 m asl in the transitional ecotone between the upper cloud forest and the lower humid *paramo* (Alonso-Amelot 2002b). *PEA* grows also at much lower elevations in Central America and Andean countries south of Colombia (except Chile). Reasons for this altitudinal discrimination are poorly understood and we pursued to find the most relevant, based on the hypothesis that, relative to *PC, PEA* evolved increased resistance to abiotic constraints found at high elevation, including lower air and soil temperatures, reduced water availability, and an increasingly damaging UV-A/B sun radiation. In any case, bracken preferential growth overlaps precisely the elevations at which the anthropogenic intervention is more frequent in these mountains, leading to accelerated degradation of the intervened ecosystems.

2.9.1 Macroscopical Differences

While fronds of *PC* and *PEA* have apparently similar frond architectures (but clearly defined taxonomic keys), a quantitative assessment of fundamental features reveals that *PEA* is distinctively larger and more robust than *PC*, according to data obtained in a 1700-m^2 plot at 2150 m asl in the Albarregas river basin near Merida, Venezuela (Alonso-Amelot and Rodulfo-Baechler 1996). At the study site in which a previous wildfire had destroyed existing shrubs, grasses, and earlier bracken frond masses, round-shaped *PEA* and *PC* swards rapidly developed without intertwining of the aerial expression. Major macroscopical features were monitored in several 3 × 3 m blocks during an 8-month period (September to April). Results (Table 2.1) clearly show substantial differences in robustness of the two bracken species growing sympatrically under similar conditions.

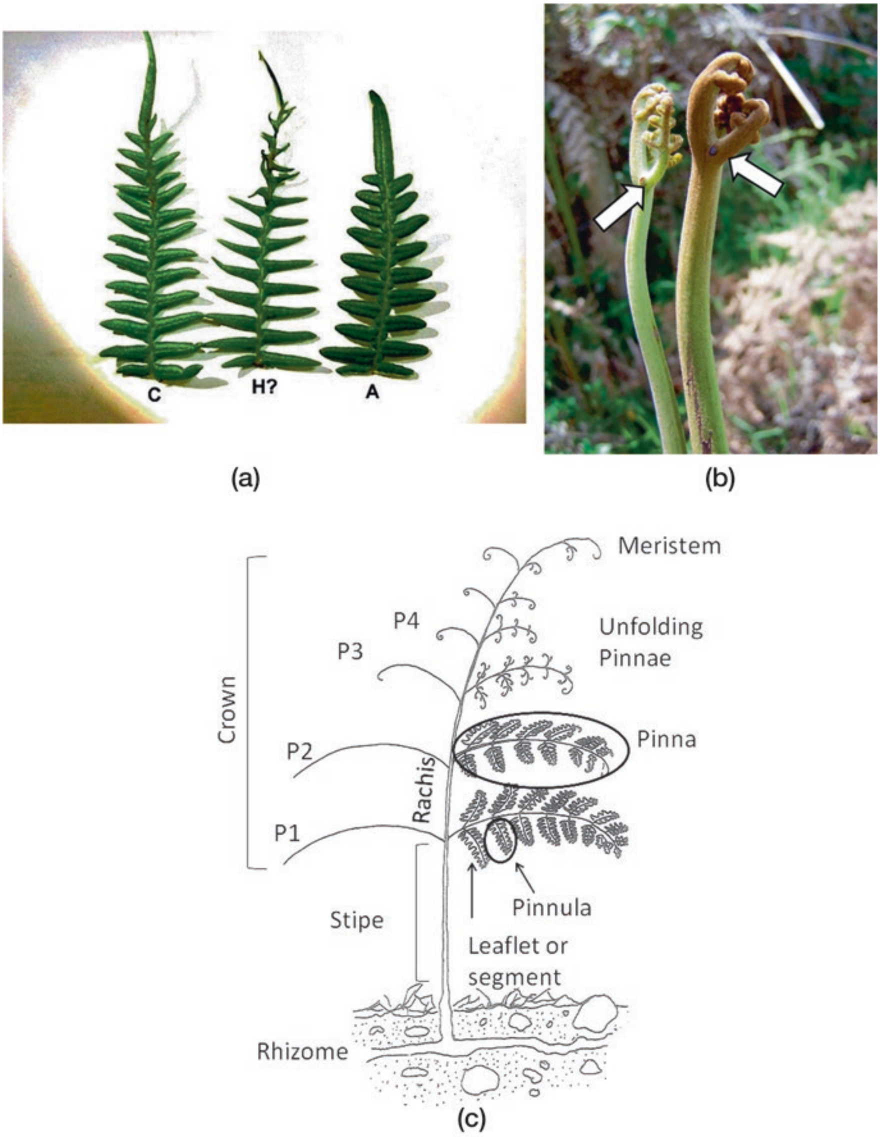

Fig. 2.3 (**a**) Pinnulae ends of *Pteridium caudatum* (C), *P. esculentum* subsp. *arachnoideum* (A), and a third uncharacterized bracken phenotype (H?). (A) shows a characteristic lobe under the leaflets (segments) growing perpendicularly from the pinnula axis. The lobe is absent in (C). (**b**) Early growth (croziers) of *P. caudatum* and *P. esculentum* subsp. *arachnoideum* (right) underlining anatomical differences at this stage: smooth tan pubescence and robustness of the latter. Mark the appearance of axillary nectaries (arrows) in both fiddleheads at the base of the still unfolded first pair of pinnae and the meristem at center. (**c**) Schematic drawing of a bracken frond and nomenclature used in this chapter. Rachis length: *L*r, Stipe length: *L*s. (Photographs and drawing by M. Alonso)

Table 2.1 Summary of the most relevant features of *Pteridium caudatum* and *P. esculentum* subsp. *arachnoideum* measured in two sympatric bracken stands in a 1700 m^2 parcel at 2150 m above sea level in the central Andes of Venezuela

	Bracken spp	
Trait	*P. caudatum*	*P. esculentum ssp arachnoideum*
Mean frond height (cm)	45.0 ± 5.5 ($N = 60$)^a	89 ± 6.1 ($N = 60$)^b
Mean rachis length (cm)	76.6 ± 0.9 ($N = 375$)^a	124.00 ± 1.6 ($N = 594$)^b
Maximum frond density (N°/m^2) Mean frond density(N°/hectare)	7.3 16,000 ± 111 ($N = 54$)^a	41.6 51,000 ± 195 ($N = 54$)^b
Frond biomass (kg/hectare)	532 ± 47^a	2874 ± 224^b
Rhizome biomass (kg/hectare)	1432 ± 84^a	5648 ± 390^b
Blade maturation period (days)	44 ± 4 days^a	72 ± 3 days^b

The plot was divided into 3 × 3 m cells and maps of the area were drawn from visual recordings of each cell. Frond biomass was calculated from excellent linear regressions of rachis length and biomass of nearby stands of the two bracken species, ($r^2 > 0.8$; $P < 0.05$) to avoid disturbance of the surveyed plots that would be caused by excising a large number of pinnae ad brought to the laboratory. Rhizome biomass was determined by unearthing rhizome and root fractions from holes dug along a line crossing each stand from the edges to the cells of greatest blade density, once all other measurements had been recorded. Different letters (a, b) (column items) denote statistical differences at $p < 0.05$. (Data from Alonso-Amelot and Rodulfo-Baechler (1996))

2.9.2 Microscopical Differences

It was also of interest to determine whether these brackens reflected the differences of gross growth parameters in the internal structure of pinnules representing the photosynthetically functional surfaces of the blades. The pinnules grow almost perpendicularly along the secondary axes of the fronds which branch out from the main axis (rachis) that supports the entire blade from the ground up. Together, they constitute the functional crown of the blade. To this end, we selected four populations of ferns in well-drained parcels at three elevations in the northwestern face of the Venezuelan Andean range in Merida State: site I: 60 m asl, a megathermic humid zone at the foothills over the Maracaibo Lake basin, with yearly average temperature $t_{\text{y-avg}} = 27$ °C; a mesothermic site II, 2150 m asl, $t_{\text{y-avg}} = 16$ °C; and a cold site III 3100 m asl; $t_{\text{y-avg}} = 8$ °C (Arellano 2003). Sites I and II typified the extremes of the altitudinal range of *PC*, although both bracken species were dominant components at site II, thus allowing vis-à-vis comparisons; *PEA* was the only *Pteridium* representative at site III, reaching the humid *paramo*. This is the highest elevation so far reported for any bracken species anywhere.

A consistent increase in the overall thickness of pinnulae of *PC* was the most outstanding feature in the *PC* population of site II relative to site I (Table 2.2). A two-cell layer of the upper (adaxial) epidermis instead of the more usual single-cell layer and a thicker cuticle were observed, in addition to an increase in the width of the mesophyll. This change is a likely adaptive response of *PC* to increased UV-A/B solar radiation associated with elevation which is a likely limiting factor against *PC* colonization of higher ground. Additionally, by exposure of histological

Table 2.2 Measurements of anatomical traits of *Pteridium caudatum* (PC) and *P. esculentum* subsp. *arachnoideum* (PEA) pinnulae obtained from histological cuts of the middle third of the leaflets observed optically (400×)

Part	Site I (PC)	Site II(PC)	P^a	Site II(PEA)	Site III(PEA)	P^a
Vascular bundle diam.	449 ± 31	601 ± 31	<0.001	685 ± 30	639 ± 36	0.001
Lamina thickness	256 ± 32	336 ± 55	0.001	408 ± 30	375 ± 29	0.004
Adaxial epidermis+cuticle	39 ± 4	56 ± 8	<0.001	49 ± 5	51 ± 7	0.650
Abaxial epidermis	14 ± 1	14 ± 2	0.780	13 ± 1	13 ± 1	0.719
Palisade parenchyma	61 ± 10	86 ± 9	<0.001	113 ± 8	104 ± 8	0.014
Spongy parenchyma	52 ± 5	53 ± 10	0.650	48 ± 6	54 ± 14	0.046
Indusium	641 ± 175	1333 ± 287	<0.001	1704 ± 0.4	1398 ± 167	0.002
Stomatal density (N mm^{-2})	147 ± 20	143 ± 29	0.850	308 ± 37	229 ± 25	<0.001

Specimens were collected from three sites I-III at 60, 2150, and 3100 m asl in the Cordillera de Merida, Venezuela. Values in micrometers ± SD (*N* = 15). (Data from Arellano (2003))

[a] Paired *t*-test for comparisons between data of PC at sites I and II, and PEA data at sites II and III

preparations of pinnulae to aqueous ferric chloride, which oxidizes phenylpropanoids to dark quinone derivatives, the accumulation of these compounds in cell vacuoles became apparent as a dominant trait in epidermal and mesophyll cells of *PC* samples from site II relative to site I. Such staining was optically denser in cuticle and vacuoles of epidermal and palisade cells in all PEA samples from sites II and III.

Stomatal density is known to decline with increases of air temperature (e.g., Beerling and Chaloner 1992, 1993) and atmospheric CO_2 partial pressure (PP_{CO2}) found at lower elevations (e.g., Woodward and Bazzaz 1988; Qiang et al. 2003). However, similar trends have not been confirmed in over 200 species from low and high elevation ecosystems as a response to historical increases of natural atmospheric CO_2 (Körner 1988). *PC* stomatal density did not respond accordingly (Table 2.2) and *PEA* showed an opposite trend from that reported by Woodward and Bazzaz (1988) for still unknown reasons. Conceivably, gas exchange, carbon uptake, and evapotranspiration dynamics, the most important stomatal functions, achieve distinct tradeoffs in the two contrasting ecosystem characteristics of sites II and III, which include obscuring environmental factors related to temperature, light and water regime, CO_2 diffusion, and lower partial pressure. A recent report about *Pteridium esculentum* grown under greenhouse conditions in shaded and sun-exposed placements revealed the expected trend towards higher stomatal density in the sun-exposed fern group (102.8 ± 3.9 (shade) and 179.2 ± 11.6 (sun) stomata mm^{-2}), following the trend of other tested ferns and angiosperms (Carins-Murphy et al. 2017). These observations confirm the high stomatal density recorded by us in Andean *PEA* at mid-elevations (Table 2.2, last entry).

2.10 Growth of *PC* Along a Systematic Elevational Gradient

In view that the ecological range of Tropical Andean brackens as regards to elevation is very wide, we became interested in exploring the strategies of acclimation and adaptation that allowed the very successful encroachment of tropical brackens in such a variety of abiotic conditions. Our geographical area, Merida State of western Venezuela, which encompasses the Sierra Nevada, a variety of high-elevation *paramos*, and the central section of the Venezuelan Andean range—see Fig. 2.4—appeared ideally suited for studying this question.

2.10.1 Establishing an Observational Altitudinal Gradient. Site Description

Having at hand the preliminary results of the previous section, we embarked on measuring a series of macroscopical growth parameters of *PC* at three locations along an altitudinal transect 2.5 km long and 800 m elevational range in a hill

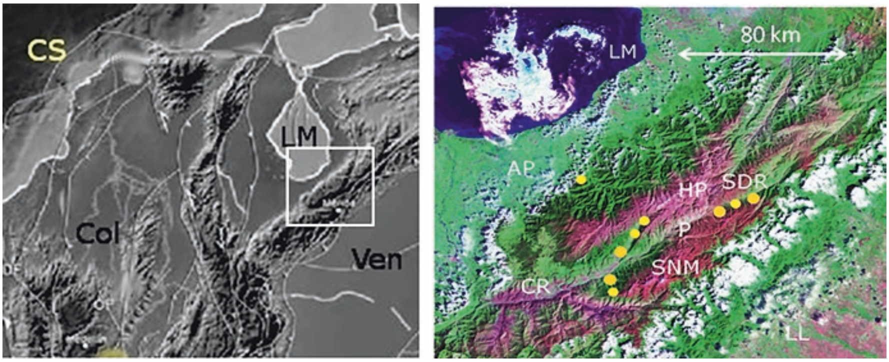

Fig. 2.4 Maps of the northern end of the Andes range approaching the Caribbean sea (CS). Left: The Perija and eastern branches stemming from the Cocuy knot of Colombia (Col) into Venezuela (Ve) showing Lake Maracaibo (LM) and the alluvial plain to the north east. Right: false color satellite picture of the framed region at left showing the central Andes of Venezuela. Densely vegetated areas are shown in green, reddish-brown areas mark ground above 3000 m asl, and purple shows xerophytic and semi-arid zones to the southwest. This photograph comprises the Sierra Nevada de Merida (SNM), one of the various *paramo* (P) and *hyperparamo* (HP) zones, the Santo Domingo Range and (SDR) and the homonymous river to the northeast, and the Chama river (CR) to the southwest. The river turns sharply to the north cutting across a gorge and discharges into LM. The Venezuelan Andean branch intrudes between the flatlands of the eastern Llanos (LL) of the Orinoco basin to the south east and the lowlands of Lake Maracaibo to the northwest. Easterly winds across the Llanos and Caribbean trade winds from the north bring moisture to both sides of the Cordillera. White shapes are cloud masses carried by easterly winds, typically shouldering the southeast Andean barrier. Yellow dots indicate areas of altitudinal gradient studies described in this chapter

overlooking the middle course of the Chama river (map, Fig. 2.4), which cuts a deep gorge along the center of the Andean range. The selected sites were: M-I, 1180 m asl, foothill rising abruptly 150 m away from the Chama river bank; relics of the riparian forest and dominance of earlier *PC* growth; M-II, 1450 m asl on an exposed hillside 1 linear km from M-I, shrubland and mountain savannah tall grasses mixed with bracken thickets; and M-III, 1970 m asl, 1.4 linear km from M-II, patches of dense montane forest near the lower limit of the cloud forest, affected by anthropogenic activity and cattle husbandry. All three sites had undergone wild fires during the previous dry season. Abundant bracken croziers emerged soon after with the start of the rainy season; hence, fern fronds became early succession growth in competition with other seed-based vegetation components. The sharp upper ecotone with densely forested zones suggested frequent bushfires in the vicinal hills as the main recent modeling agent, chiefly induced by farmers to clear land for cattle husbandry and small plot cultivation of staples. All sampling sites were accessible by road at a distance of no less than 20 m from the curb. At this distance, there was no distinguishable road effect as regards to frond stature and abundance, or temperature modified by the road pavement. Only *PC* was found at all sites.

2.10.2 Climate: Temperatures

The distribution and survival of high elevation plant species are often related to climate and climate-dependent biotic-ecological factors (Körner 2002; Pauli et al. 2007). The hydrological, sun radiation, and temperature regimes at each habitat are generally considered dominant climatic contributors. In the Venezuelan Andes of Merida, there is a three-month long dry season in the inner valleys of the range, (December to early March). Abundant rain for the rest of the year provides robust vegetation growth except during years of dry spells and in well-defined xerophytic zones where bracken ferns are absent. Therefore, no soil moisture scarcity extremes were noticed by typical plant water stress responses during the study period in the observation sites (March to July). This period encompasses the first wave of the bimodal rain regime in this region, the second starting in late September after a short moderately dry season in August (Chacon-Moreno and Suarez del Moral 2020). Incoming air currents from three directions, northeast from the llanos after surmounting the cold *paramos* in the high Chama river basin in eastern Merida state, the southern air mass passing across the high peaks of the Sierra Nevada, and the northern air mass fueled by the daily expansion of the humid and torrid Maracaibo lake basin at low altitude, create a complex pattern of local climatic conditions, depending on season and hour of the day (Aranguren et al. 2012). The resulting combination of temperature, moisture and topography forms a mosaic of ecosystems and as many as 12 ecologic units in the relatively small area of the Chama river basin (Ataroff and Sarmiento 2002). Dry premontane deciduous forest, montane savannah, cloud forest and *paramo* in addition to cultivated and fallow fields and pastures, with a variety of ecotones in the fragmented vegetation types are found there. Many of these ecological units are colonized successfully by *Pteridium* ferns.

Temperature differences associated with elevation were expected to be a dominant factor impinging on bracken growth. In the Tropical Andes, a decrease of 0.6 °C annual average per 100 m elevation is relatively constant throughout the year but this general pattern varies with air currents flowing from lower zones upwards and also in the opposite direction, from cold summits to valleys, causing substantial thermal variations during the circadian cycle and on a daily basis, as we indeed recorded in our gradient studies described herein. The utilization of field loggers was therefore a must.

A first approximation reveals that average temperatures per month tend to be conservative (Table 2.3), with a moderate decline from March to July. The latitude of the Sierra Nevada de Merida in particular is 7° 40′ N, and therefore, large-scale weather patterns respond to the long-distance seasonal changes of the boreal hemisphere with intervening perturbations of the Intertropical Convergence Zone and incoming dry winds from the south. If so, in principle July should be the warmest month in the northern Andes. But it is just the opposite in the upper and middle Chama river basin. The drop in the average temperature is more likely the result of the increased cloudiness associated with the rainy season and changes in the local wind patterns (legend of Fig. 2.4).

To better appreciate the impact of air temperature since plants respond to short-term changes, the course of daily average values in addition to maximum and minimum temperatures ($T_{\max}$ and $T_{\min}$) were put together for the bracken frond growth period (Fig. 2.5). The following features stood out:

I. T records covering the growth period reflected a similar pattern whereby the daily $T_{\max}$ was attained in the early to mid-afternoon.
II. The $T_{\text{(average)}}$ and $T_{\max}$ traces at sites M-I and M-II are similar, as if the nearly 270 m difference in altitude did not suppose any thermal influence. Temperatures showed a moderate course during day and night (not shown) in site M-III only.
III. T increased steadily during the first half of the day as a result of frequent clear skies. Clouds are formed at mid-day causing an expected irregular thermal course.

Table 2.3 Monthly mean air temperatures (°C) (1 m above the ground) of three sites selected along an altitudinal gradient in the Sierra Nevada de Merida, Venezuela, from the start of the rainy season in the area. Data points recorded every 12 min with field loggers

	Mean (°C ± SD)				
	March	April	May	June	July
SITE M-I (1180 m)	23.9 (1.25)	23.6 (0.60)	23.8 (1.2)	22.8 (0.8)	22.4 (1.38)
SITE M-II (1450 m)	23.3 (0.91)	23.1 (1.17)	21.9 (1.3)	21.1 (0.9)	20.8 (1.14)
SITE M-III (1970 m)	18.2 (1.24)	17.8 (0.70)	17.8 (0.6)	16.8 (0.6)	14.6 (0.65)

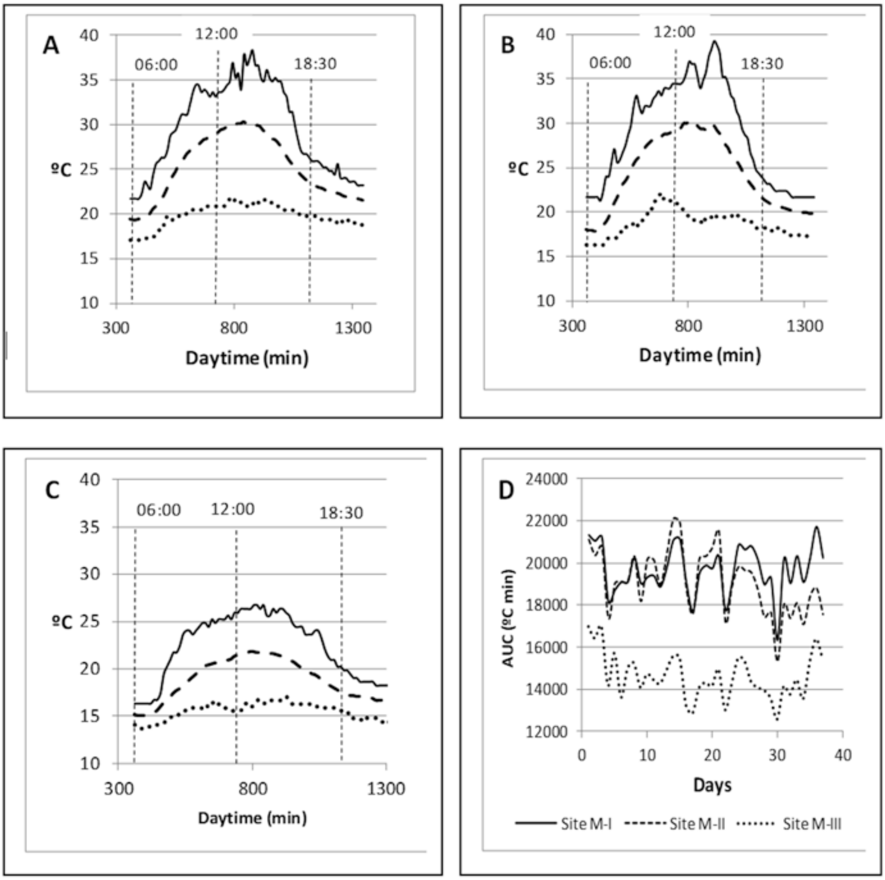

Fig. 2.5 Average daily air temperature (*T*) courses, during the day from sunrise to dawn, of three sites along a 800 m altitudinal gradient in the Sierra Nevada de Merida, Venezuela, for the monitoring of *Pteridium caudatum* frond growth during the rainy season (March–June). Dashed line: average *T*; Solid line: maximum *T* (T_{max}); Dotted line: minimum *T* (T_{min}). (**a**) Site M-I, 1180 m asl; (**b**) Site M-II, 1450 m asl; (**c**) Site M-III, 1970 m asl. Dashed vertical lines indicate the daytime at the indicated hours. (**d**) Daily results of the area under the curve (AUC) of air temperatures recorded from 6:00 am to 18:30 pm at the three sites during 38 days between mid- April to the end of May, during the peak of bracken frond growth. All registries were recorded every 12 min using field loggers at 1 m from the ground

IV. The range of T_{min} and T_{max} at the two lower sites respond to the contribution of cloudy days associated with rain.

V. Only M-III showed distinct $T_{(average)}$, T_{min} and T_{max} traces, and were expected to impinge on the growth of bracken fronds.

VI. Unexpectedly high temperatures approaching 40 °C were recorded at sites M-I and M-II but never at M-III, suggesting a stratification of warmer air masses below 1900 m. Such high temperatures are very unusual for the Merida valley and are likely the result of winds flowing from the torrid Maracaibo basin through the Chama river gorge.

In this concern, the atmospheric model proposed Aranguren et al. (2012) for the Central Andes of Venezuela in general, and the Chama river basin (CR, Fig. 2.4) in particular gives a reasonable explanation. By observing the map of Fig. 2.4, one can see that this basin begins at the high *paramo* (HP) to the east, which characterizes the lowest temperatures in the country. During the night and early morning, this air mass spreads downwards along the CR valley to the west. Fueled by heat from the sun during the morning hours, the lower atmosphere over the Lake Maracaibo (LM) basin and the adiabatic expansion in addition to northern winds from the Caribbean Sea push the hot low altitude air against the Andean front towering above the LM lowlands. This air mass finds its way through the CR gorge (see Fig. 2.4 legend), in the opposite direction of the cold air flow from the *paramo*. A series of weather stations dotted across the Merida region allowed Aranguren et al. (2012) to measure this irruption of warmer air into the Chama and Merida valley, rising the local temperature accordingly. We also recorded this heat wave that waned later in the day. Although this clash of air masses is characteristic of many valleys of the Tropical Andes, it is particularly notorious in the CR basin.

Although vascular plants respond rapidly to changes in sunlight intensity and temperature by opening and closing stomata, the period of time a given temperature in the air around the foliage is of the essence for the photosynthesis apparatus. This is better assessed by the calculated integration of temperatures and time between measurements (area under the curve—AUC—at 12-min intervals), rather than time point data. Figure 2.5d depicts the AUCs from which one can infer that:

I. Daily AUCs are highly variable at all sites. Weather patterns vary on a daily basis.
II. Sites M-I and M-II undergo nearly undistinguishable AUC traces except of the last week of the measuring period corresponding to the end of May. Consistent with this, average temperatures declined more sharply in M-II relative to M-I in the May–July period.
III. The AUC of site M-III followed a parallel course but several degrees-hour lower (around 25%) all across the board.

Based on temperature profiles alone, we anticipated a comparable bracken frond growth at M-I and M-II with a distinctively restrained growth at M-III, which would be in line with the elevation limit of *PC* ecological range.

2.10.3 Frond Growth: Parameters and Frond Stages

We recorded physical measurements of frond key parameters at the three sites every 3 days for 3 months: the development of stipe (*L*s), and rachis (*L*r) (see Fig. 2.3 for frond nomenclature). Croziers were tagged as soon as we spotted them emerging from the ground and followed their growth thereafter. About 70% of the fronds had to be rejected because of imperfections, lack of symmetry of the lateral pinnae, fungal disease or breakage by wind or heavy rain or interruption of crozier development for undetermined reasons. In addition, a number of fronds in various growth stages were excised in each site and carried to the laboratory to determine biomass, moisture content, and the sum of the pinnae axes (Sum of *Li* from P1 to P10—the tenth pinnae) which constitute the crown. This section of the blade contains thousands of leaflets or segments, where photosynthesis takes place, hence blade development involves the rapid unfolding of these structures. At the end of the growth period, mature frond density was measured in several 0.5 × 0.5 m squares at each site. Adequate correlations between *L*r, ΣLi, and biomass were established in order to determine growth parameters with a minimal perturbation of the living fronds being monitored in the field.

The growth of bracken blades was divided into five stages according to the following anatomical criteria: Stage 1: crozier from emergence of the ground until the ramification of the axis of the first lateral pinnae (P1) once the length of the midrib of this pinna (Li; $i = 1$) was >2 cm; stage 2: P1 was completely unfurled while the second pinna (P2) continued to expand towards its final length (*L*2); 2 or 3 days after the beginning of this stage the lengthening of the stipe ceased; stage 3: complete expansion of P1 and P2 while the rest of the frond (rachis and P3, P4…) was still expanding; stage 4: the frond reached the final rachis elongation *L*r(max), all pinnae were unfurled with the full opening of the leaflets, but still keeping a soft apex. This meristem hardens within a few days and shortens slightly (~1 cm). Partial water loss, segment roughness, and darker appearance typified stage 5 that would last several months until the spore production stage that may start soon after and until the end of the rainy season. Only a fraction of fronds produced sporangia in the indusium of segments. We have used this standard in all our previous studies and other authors have done so as well.

It is important to note that *L*s is usually much shorter in early succession brackens when the growth of competing vegetation has not started yet, nor self competition. This triggers the early expansion of P1 and P2 and photosynthesizing segments appearing on the lateral pinnae. The pinnulae accumulate starch for energy in the spongy parenchyma and for relocation to replenish starch reserves in rhizomes used during further crozier growth later in the season. A model for starch translocation from blade to rhizome (Pakeman et al. 1994) in *P. aquilinum* in Britain proposes a net carbohydrate translocation in the said direction late during the blade growth period (stages 3 and 4). A number of environmental factors are included in the theoretical model and therefore might be applied to different abiotic conditions found, for example, in the Tropical Andes.

On a first processing round of data collected in the field along the 3 months of the growing season (mid-March–mid-June in our geographical area), *L*r, *L*s, biomass (BM), time required to complete stage 4, and frond density were surveyed as diagnostic indicators of acclimation or stress related to altitude. Based on an excellent linear correlation between *L*r and *L*s (used to estimate the size of the blade crown by subtracting the contribution of the stipe) and the sum of *Li* (ΣLi) representing the crown lateral expansion measured in the laboratory (Fig. 2.6), the frond architecture at the three sites, could be compared.

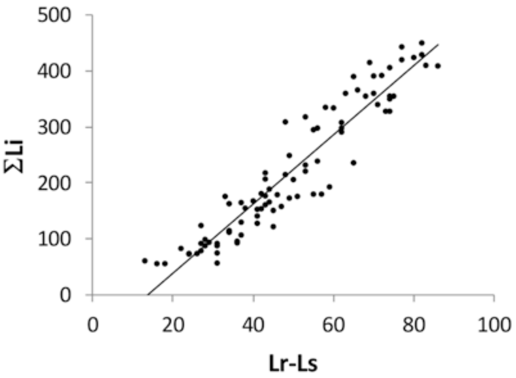

Fig. 2.6 Linear regression between the rachis length measured from the first pair of pinnae to the meristem after subtracting the stipe length (*Lr*–*Ls*, cm) and the sum of all secondary axes length (Σ*Li*, cm) of second to fourth growth stages of *Pteridium caudatum* fronds ($N = 86$, r^2: 0.8904)

2.10.4 Variation of Dimensional Parameters of PC Fronds

2.10.4.1 Maximum Rachis Length of Mature Fronds: *L*r(max)

Comparable *L*r(max) were recorded on average for the three sites (Fig. 2.7- plot A), showing only a marginally shorter rachis in site II ($p = 0.023$) relative to site III, possibly because a measure of water stress in the more sun and wind exposed hillside of this site (Table 2.4, row 1). Whereas the moisture content of stage 4 blades (site I: 56.38% ($CL_{95\%}$ 54.84–57.94%); site II: 55.12% ($CL_{95\%}$ 53.57–56.68); site III: 57.94 ($CL_{95\%}$ 56.43–59.45)) was conservative on average, a significant differentiation was noted only between samples from the warmest and coldest parcels [*p(I–II)* = 0.244, *p(I–III)* = 0.149, *p(II–III)* = 0.0103)]. As opposed to slightly shorter Lr(max), site II displayed marginally wider fronds by about 7% relative to sites I and III as shown by Σ*Li* ($p = 0.038$ and 0.017, respectively) (see Table 2.5 for complete statistical differentiations).

In reference to *L*r(max) frequency distribution (Fig. 2.8), a major proportion of fronds had comparable rachis length in all three sites around their median values in the 80–110 cm interval (dark gray bars). By contrast, the fraction of larger *L*r(max) blades (110–150 cm) was significantly smaller in site II and was compounded by a much greater fraction of smaller fronds (black bars). The frequency distribution of *L*r(max), however, did not constitute an altitudinal trend.

2.10.4.2 Time-Dependent Elongation of Stipe and Rachis

There were reasonably good linear correlations between the various anatomical parameters of mature fronds in the three study plots. In particular, *L*r and *L*s were associated by linear regressions with comparable slopes (Site M-I: 1.369 ± 0.212;

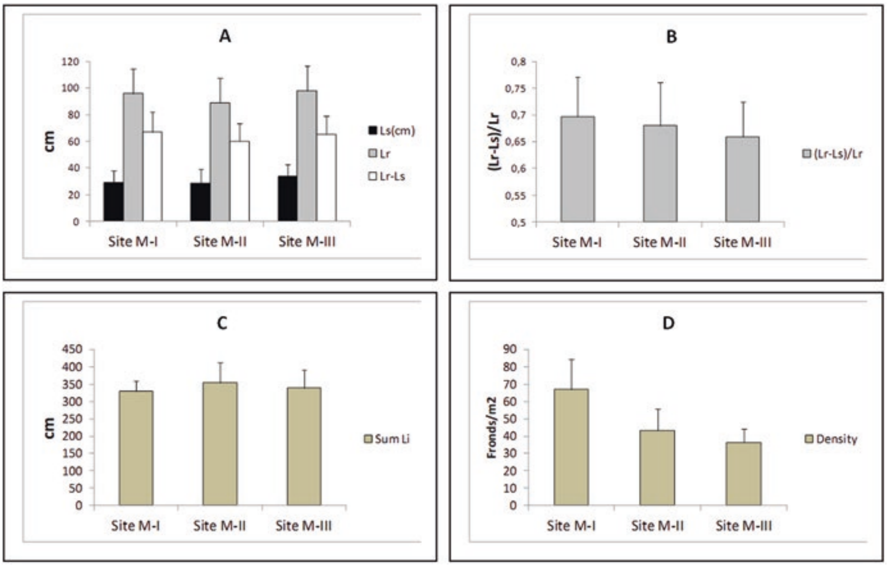

Fig. 2.7 Comparison of selected anatomical parameters of mature fronds of *Pteridium caudatum* along an altitudinal gradient in the northern Andes of Mérida, Venezuela. (**a**) stipe length (*L*s, cm); total rachis length (*L*r, cm); length of the central axis of the blade from the first pinna to the frond's meristem (*L*r–*L*s, cm) ($N = 50$ per site). (**b**) fraction of the blade crown size relative to total rachis length. (**c**) Sum (cm) of the secondary axis from the first to the tenth pinna of the fern blade (Sum *Li*) ($N = 50$). (**d**) Number of fronds per square meter (density), data collected from 36 randomly selected 0.5 × 0.5 m squares at each site. Elevations (m above sea level): M-I, 1180 m; M-II, 1450 m; M-III, 1970 m. Averages ± SD. For statistical significance, see Table 2.5

site M-II: 1.215 ± 0.208; site III: 1.396 ± 0.212, $p < 0.05$ in all cases). Therefore, the length attained by the rachis in the mature fronds was equally proportional to the distance from the ground to the first pinna (P1) (stipe length). This result suggests at first that competition for sun radiation between neighboring blades growing at large densities would not respond to abiotic factors related to elevation, were it not for the fact that (a) *L*s was distinctively longer at site III relative to the other sites at lower altitude (Fig. 2.7, plot A, black bars); and (b) given that the stipe generally grows vertically and then the rest of the crown expands diagonally in order to better expose unfurling pinnae to sunlight, a longer *L*s would ensure better capture of sun radiation than competing early emerging plants, while the frond expanded towards growth stages 3 and 4. Self-competition against new bracken croziers appearing later in the season may also modulate bracken's own growth at a later stage, and avoid exhaustion of resources in the rhizome and soil. This plasticity feature is probably under sunlight control but requires formal testing.

On the other hand, the blade crown size relative to the stipe length expressed by the ratio (*L*r–*L*s)/*L*r appears to be sensitive to elevation (Fig. 2.7, plot B) but this is not reflected in the lateral expansion of the blade surface expressed in terms of Σ*Li* (Fig. 2.7, plot C); nor does it correlate well with the significant reduction we

Table 2.4 Average of maximum rachis elongation *L*r(max) (cm) of *P. caudatum* fronds, time *T*[*L*r(max)] (days) required to achieve *L*r(max), average rate Δ*L*r(max)/Δ*T*[*L*r(max)] (cm/day) [95% confidence limits], and frequency distribution (FD) of *T*[*L*r(max)] of fronds within a time interval of 30–42 days, in sites M-I, M-II and M-III (see text for details) along an altitudinal gradient in the Central Andes of Merida, Venezuela. $N = 48$ fronds per site

Parameter	Site M-I	Site M-II	Site M-III
*L*r(max) [$\text{CL}_{95\%}$] (cm)	95.77 [90.32–101.21]	89.00 [83.20–94.80]	97.98 [92.85–103.11]
T[*L*r(max)] [$\text{CL}_{95\%}$] (days)	37.13 [35.44–38.81]	37.66 [36.41–38.90]	36.92 [35.51–38.34]
Δ*L*r(max)/Δ*T*[*L*r(max)] [$\text{CL}_{95\%}$] (cm/day)	2.62 [2.45–2.79]	2.38 [2.22–2.54]	2.68 [2.54–2.81]
FD of *T*[*L*r(max)] (%) in the 30–42 days int.	72.3%	75.6%	80.8%

observed in bracken blade density with elevation (Fig. 2.7, plot D). Frond density early in the growing season responds to the number of rhizome buds and their sprouting rate. In turn, this is a function of the carbohydrate energy stored in the rhizomes and temperature of the rhizosphere, other factors being equal. Although the effect of high temperatures caused on the ground by wildfires have an enhancing effect on bracken rhizome budding and germination of gametophytes (Roos et al. 2010), the influence of low temperatures as a limiting factor on bud sprouting in Neotropical bracken has not been studied yet in controlled greenhouse experiments. Within the experimental limits of this study, noon soil temperatures of the B horizon at 20 cm depth where budding rhizomes are found more frequently, measured during the growing season, were highest at mid-elevations (site II, 22.8 ± 0.3 °C) and comparable to that of site I (22.5 ± 0.1 °C), whereas it dropped to an average of 18.8 ± 0.4 °C in site III, and further down at 2100 m asl (16.4 ± 0.3 °C) near the upper limit of *PC* elevational range. Soil temperature is probably a key factor in the timing of crozier sprouting. Delays should bear consequences in the future fitness of the bracken ramet in the face of other plant growth in the early succession that may be better adapted to lower temperatures for seedling and root/shoot growth.

2.10.4.3 Frond Biomass (BM)

This parameter was assessed according to two experimental designs: (a) direct measurements in the laboratory of BM, *L*r, and Σ*Li* of excised fronds from the three sites, and (b) estimation of BM of living fronds in the field by simulations of correlations between *L*r, *L*r–*L*s or Σ*Li* and BM.

We found that the BM of fronds from site M-II was distinctively larger than from site III despite the shorter *L*r and blade crown length at the former site (Fig. 2.9, plot A), whereas brackens in sites I and III were statistically undifferentiated (Table 2.5). Fern blades at intermediate elevation displayed a greater lateral expansion as indicated by Σ*Li* (Fig. 2.7, plot C). Given that the difference in Σ*Li* is relatively minor, the greater BM recorded for site M-II may be a response to more exposed habitat to

Table 2.5 One-way ANOVA statistical differentiation of anatomical parameters of *Pteridium caudatum* aerial parts and frond density, shown in Fig. 2.7, collected at three different elevations along a gradient in the Merida Andes of Venezuela

	Statistical significance: $P(F)$ between sites		
Parameter	M-I/M-II	M-I/M-III	M-II/M-III
*L*r(max)	0.09 (2.94)	0.553 (0.35)	0.023 (5.46)
*L*s	0.969 (0.00)	0.01 (6.85)	0.018 (5.77)
*L*r–*L*s	0.028 (4.98)	0.548 (0.36)	0.080 (3.13)
(*L*r–*L*s)/*L*r	0.314 (1.03)	0.008 (7.38)	0.163 (1.98)
Σ*Li*	0.038 (4.47)	0.453 (0.57)	0.017 (6.05)
Density	<0.001 (44.93)	<0.001 (96.42)	0.007 (7.73)
BM per frond	<0.001 (17.54)	0.157 (2.06)	<0.001 (27.24)
% Moisture	0.244 (1.38)	0.149 (2.14)	0.0103 (7.00)

$N = 42$ per site; level of significance: $p < 0.05$

wind and sun radiation at mid-altitudes of the barren hillside leading to thicker segments and a sturdier rachis. Evidence for this could be gathered from the thicker cell walls of the collenchyma and sclerenchyma we observed (400×) in segments and petioles of site M-II relative to the other sites. Both structures provide support and resistance to mechanical forces in plants such as wind, rain, and self-abrasion against neighboring fronds in the dense thickets.

The indirect assessment of frond biomass could be obtained by carefully measuring *L*r of tagged blades in the field to avoid disturbing the growing thickets. Satisfactory correlations between *L*r(cm) and BM(*g*) after log(*e*) transformation emerged (Fig. 2.9, plot B) (r^2 = 0.8535 for site M-III; 0.8301 for site M-II; and 0.7972 for site M-III). Curve simulation took the general expression of Eq. 2.1:

$$BM\left(g\right) = e^{\left(A+BX\right)} \tag{2.1}$$

where $X = Lr$

Compatible results were obtained from the crown size assessed by *L*r–*L*s and Σ*Li* measurements in laboratory specimens. This expression was applicable to growth stages 2, 3, and 4. As expected, point dispersion was greater in intermediate growth stages 2 and 3 because of their wider range of expansion. The increasing contribution to frond BM of lateral growth of pinnae branching off from the rachis was responsible for the exponential accretion of biomass across growth stages 2–4 (Fig. 2.9, plot C) once the stipe meristem branched out at the beginning of stage 2. Larger BM accretion started to become discernible at stage 3. For all three sites, curve fitting furnished the general expression:

$$BM\left(g\right) = Ae^{BX} \tag{2.2}$$

where X was the *growth stage* categorical variable, and $r^2 > 0.997$ for all three sites. Statistical differentiation between sites was observed only among stage 4 fronds (Table 2.5).

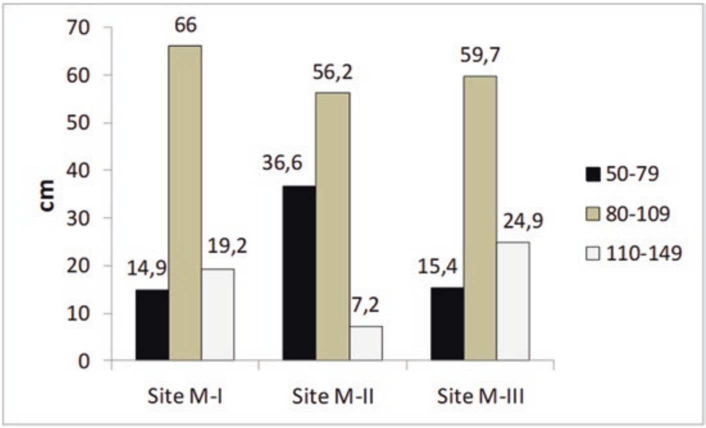

Fig. 2.8 Fraction (%) of *Pteridium caudatum* stage 4 (mature) frond size according to the frequency distribution of maximum rachis length *L*r(max), recorded at three sites M-I to M-III along an altitudinal gradient (see text) in the Sierra Nevada de Merida, Venezuela

2.10.5 Growth Rate

The consistency of the blade's anatomical measurements and their linear regressions led us to determine whether time-dependent relationships of these parameters would provide valid information about their comparative growth rates and determine whether the altitude would have any influence on them. The following parameters were surveyed:

A. Total number of days for blades to achieve the maximum rachis length, [*L*r(max)] in growth stage 4, put here as *T*[*L*r(max)]. We found an extremely conservative value of *T*[*L*r(max)] in all three sites (Table 2.4, entry 2) averaging 37 days, despite differences in *L*r(max) (entry 1). By day 47, all tagged fronds were fully expanded although new croziers continued to emerge until the end of the rainy season in late December. The frequency distribution analysis of the normally distributed frond population showed a trend in the increasingly larger fraction of fronds reaching maturity around the median *T* (Table 2.4, entry 4). This was compounded by a greater percentage of larger fronds [as per *L*r(max)] in site M-III (Fig. 2.8, light gray bars).
B. Rate of rachis elongation Δ*L*r(max)/Δ*T*[*L*r(max)]: This ratio provided the overall rate of *L*r elongation from crozier to stage 4 fronds. Ferns at sites M-I and M-III expanded at similar rates (Table 2.4, entry 3, $p = 0.312$) whereas a distinctly lower figure was recorded for site M-II ($p = 0.006$). It is generally accepted that water uptake is the main driving force for cell expansion in vascular plants and is likely to be the case in bracken ferns as well. Therefore, the

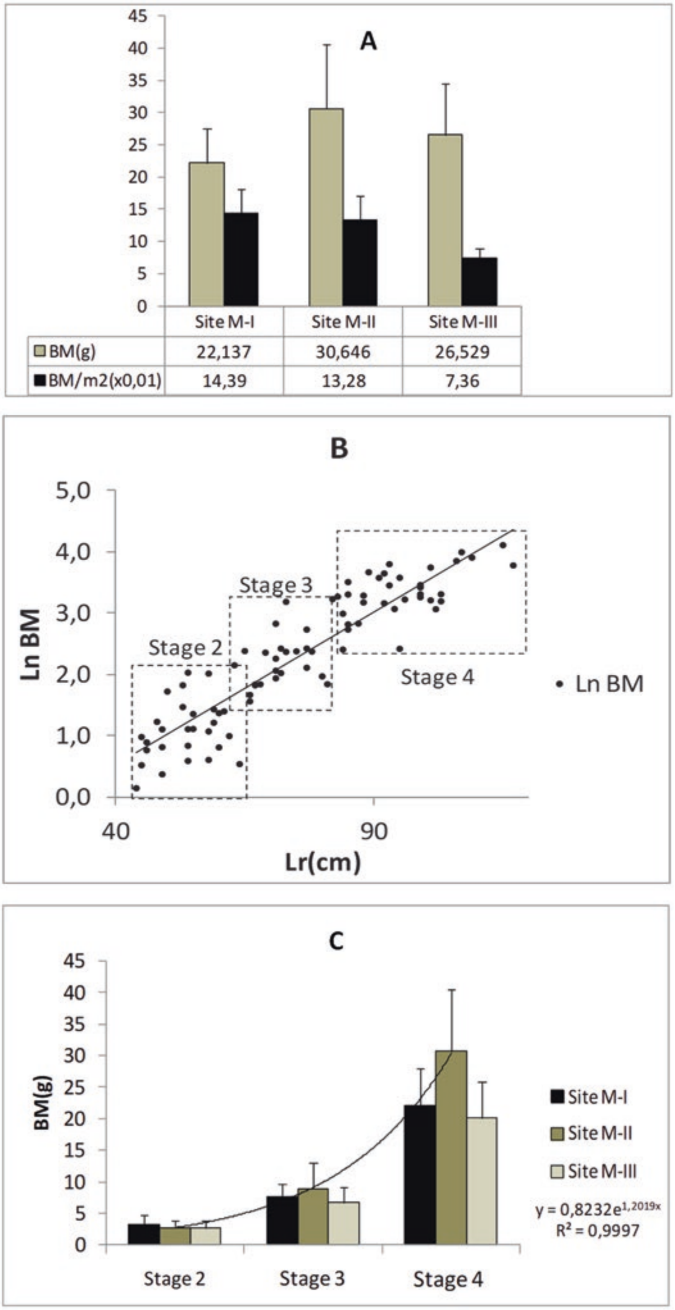

Fig. 2.9 Biomass (BM) assessment of bracken (*Pteridium caudatum*) blades from three sites along an altitudinal gradient in the Venezuelan Andes. (**a**) laboratory measurements of excised mature (stage 4 growth) fronds; BM (×0.01) (g/m^2) of fully grown thickets calculated from frond density recordings in the field (Fig. 2.7d). (**b**) Linear correlation between frond BM and *L*r, after log (*e*) transformation obtained from laboratory measurements of excised fronds of growth stages 2, 3, and 4. (**c**) BM accretion across the said growth stages showing the best fit governing equation for Site II

observed disparity may result from temporary reductions of water availability in the steeper hillside of this site and enhanced rainwater drainage. Lower temperatures at the highest site M-III may have contributed to water retention in the soil and increased $\Delta L\mathrm{r}(\max)/\Delta T[L\mathrm{r}(\max)]$ relative to site M-II.

C. The daily rate of *L*r expansion $\Delta L\mathrm{r}/\Delta T$ was estimated by the expression:

$$\Delta L\mathrm{r} / \Delta T = L\mathrm{r}\left(Ti\right) - L\mathrm{r}\left[T\left(i-1\right)\right] / \left[Ti - T\left(i-1\right)\right] \tag{2.3}$$

where T_i is the time in days of the i^{th} record elapsed since the first emergence of the crozier above the ground level, and $T(_{i-1})$ is the time in days since the previous i^{th} measurement, three days on average. We anticipated that the set of $\Delta L\mathrm{r}_i$ for each site across the survey period would respond to effects related to altitude. The daily formation of frond biomass was estimated similarly after application of Eq. 2.1.

Maximum rates of *L*r elongation along the growing period occurred very early in all three sites, on growth day 7th since the first appearance of the crozier (Fig. 2.10, solid markers, left axis). In the three elevations, the growth investment of bracken fronds supported entirely by resources stored in the rhizomes was focused on elongating the stipe to place the apical meristem at the highest possible distance from the ground before pinnae began to unfurl. In the absence of competing vegetation after the wildfire destruction, fern growth proceeds further with expansion of the crown surface to rapidly develop photosynthetic pinnulae to support growth.

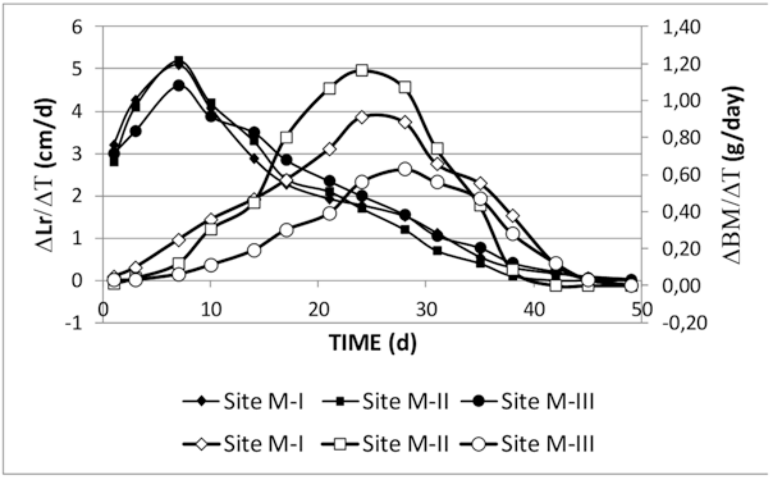

Fig. 2.10 Rate of *Pteridium caudatum* growth at three sites, M-I to M-III (see text) along an altitudinal gradient in the northwestern flank of the Sierra Nevada de Merida, Venezuela, expressed as time-dependent rachis elongation: $\Delta L\mathrm{r}/\Delta T$ (cm/day) on the left axis (solid markers), and biomass development $\Delta \mathrm{BM}/\Delta T$ (g/day) (open markers), based on field measurements of frond crown characteristics described in the text

Although $\Delta Lr/\Delta T$ was only marginally slower in the highest elevation site M-III as well as during the rest of the growing period, this difference was not statistically relevant.

The biomass growth $\Delta BM/\Delta T$ followed a different profile (Fig. 2.10, open markers, right axis). Maximum values were attained on day 24 for low and mid-altitude sites, and day 28 for the highest site. The disparity of crown rachis elongation maxima (7 days) and BM profiles can be explained by the increasing contribution of the unfurling side pinnae in late growth stage 3 and early 4 when blade crown expansion ceases.

Elevation had a clear impact not only on delaying and reducing the maximum value of $\Delta BM/\Delta T$, but also on the total frond BM build-out. This was illustrated by the area under the curve (AUC) of the $\Delta BM/\Delta T$ plots of Fig. 2.10 [Site M-I, 20.697; Site M-II, 21.825; Site M-III, 12.980] which matches the BM of stage 4 fronds shown in Fig. 2.9 plot A. Among the limiting factors for BM build-out in fronds derived from elevation, air and soil temperatures in the rhizosphere are of special importance, influencing the physiology of underground parts of plants and edaphic microorganisms (Onwuka and Mang 2018). Lower temperatures may decrease the nutrient transport dynamics through limited vascular capacity of ferns relative to angiosperms. Additionally, stomatal conductance that influences photosynthesis and BM formation is also a function of temperature. At both, high mid-day or low average ambient temperatures stomatal conductance is reduced, leading to a chain of consequences in CO_2 uptake, evapotranspiration and metabolism that influences biomass development (Urban et al. 2017). The much larger stomatal density we observed in *PEA* in the Merida Andes (Table 2.2, last entry) may be part of the acclimation strategy of the latter to colonize higher elevations than *PC*.

2.11 *PEA* Fronds in Mid- to High Elevations in the Northern Andes

2.11.1 General Frond Features and Selected Descriptive Parameters

As said above, *PEA* persists at higher altitudes than *PC* in the northern Andes. We focused our interest on the semi-quantitative study of the frond architecture of *PEA* at higher elevation in our geographical area that could supplement the data collected previously (Alonso-Amelot and Rodulfo-Baechler 1996) and find contrasts with *PC*. performance. We selected a parcel of land with two sympatric stands of *PC* and *PEA* at 2090 m asl and determined the most relevant characteristics already discussed here (Tables 2.1 and 2.2). Two other sites were marked in the humid *paramo* (P in Fig. 2.4). The great majority of fronds were green but a lower and dense withered stratum was also present. This network of sturdy sessile fronds offered support to the standing blades exposed to winds at high elevations. When we clipped off carefully about 50% of these dead blades, the entire set of living fronds collapsed within a few days.

The symmetric arrangement of frond architecture could be assessed, as in other bracken populations, from the adequate linear regressions between crown length—after discounting the stipe (*L*r–*L*s)—and the development of lateral pinnae (Σ*Li*) ($r^2 = 0.8095$, $p < 0.001$, $F = 46.7$). As regards to biomass (BM), no estimates based on hypothetical Σ*Li* versus BM correlations were advanced owing to the variance in the thickness of segments (Table 2.2) that would contribute to BM as a likely response to increasingly strenuous environmental conditions found at higher elevations, commented earlier in this chapter.

2.11.2 Study Sites

Plots with abundance of bracken fronds were selected at 2090, 2850, and 3100 m asl and identified as A-I, A-II, and A-III, respectively. Site A-I was located on a hillside of the Albarregas river near the city of Merida whereas A-II and A-III were in the upper Santo Domingo river basin. All plots were on well-drained, humid soils, and sun-exposed away from taller plants. Both, *PC* and *PEA* thickets, either mixed or as individual stands, were found in A-I, whereas *PC* was absent the latter two and surrounding areas. A-II was at the transitional cloud forest upper edge and the sub *paramo* bush/forbs belts. The *PEA* thicket of A-III was found 8 km away in the humid *paramo* above the natural tree line with the exception of *Polylepis sericea* Wedd. (Rosaceae) trees (Goldstein et al. 1994). This typical ecosystem of Neotropical high mountains is characterized by an open grassland matrix, adapted low stature forbs, lichens, cushion plants, and conspicuous caulescent rosette species of the *Espeletia* group (*frailejones*) communities. If *PEA* was a dominant species in the A-I plant community, it only formed limited islands in the selected A-II and A-III plots that restricted the selection of sufficiently healthy blades for valid measurements. Due to the remoteness of these sites and considering also that the area was a state protected zone, fronds could not be removed and taken to the laboratory for a deeper insight. Therefore, the accessible data were limited to field measurement of rachis, stipe, and lengths lateral pinnae (*L*r, *L*s, and Σ*Li*, respectively), from which one could estimate the relative frond crown size and robustness. Climate parameters were nonetheless accessible with field stations.

2.11.3 Climate

The water regime was chiefly rainfall in A-I, whereas there was a substantial but as yet non-quantified contribution of occult precipitation in A-II and A-III due to frequent fog interception by plant surfaces, especially pubescent species. A fair amount of data is available about fog and mist water fluxes in cloud forests of Neotropical mountains but similar studies in Andean *paramos* are scarce (e.g., Cardenas et al. 2017). The rainfall regime in the central Venezuelan Andes follows a bimodal pattern of two dry seasons (December to March and mid-August to September), and two rainy seasons peaking in June and October. This pattern, however, varies from year to year and influences the population of local plants and animals (Santiago-Paredes and La Marca 2006). Dry spells also occur irregularly and are caused by large-scale changes in weather patterns across northern South America and the eastern Pacific Ocean. Water stress and higher temperatures during these inordinate events have produced undue plant withering including brackens in past years (e.g., Curatola Fernandez et al. 2013).

As well as, air temperature and solar radiation strongly influence plant performance at high elevations in the Neotropics (e.g., Bader et al. 2007), although other modeling forces including wildfires are at play. Therefore, we examined these abiotic components in the study plots in search of conditions that would limit the further encroachment of *PEA* at higher altitudes.

2.11.3.1 Air Temperature Along the Altitudinal Gradient A-I to A-III

Daily profiles adopted the well-known bell-shaped pattern with abrupt fluctuations due to the interplay of solar radiation, hour of the day and cloud cover (Fig. 2.11 plot A). As expected, daily extremes were more pronounced at high elevation, but it was surprising to observe two differing features in sites A-II and A-III, separated by 250 m of altitude: on one given day (plot A), maximum temperatures could reach

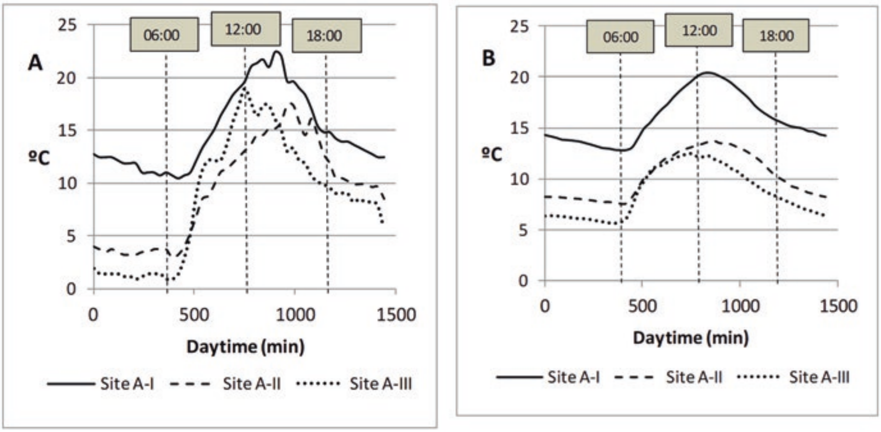

Fig. 2.11 Temperature patterns of sites A-I, 2090 m asl, Site A-II, 2850 m asl, site A-III, 3100 m in the Sierra de Santo Domingo of the northern Andes, Merida, Venezuela. (**a**) 24 h Temperature profile (30 min resolution) of a single, typical day during the rainy season (June) in the three sites. (**b**) Average air temperature profile of the June–August season

higher marks in A-III than A-II and occurred 2–3 h *earlier*. This frequent occurrence was observed also on the monthly average traces (Fig. 2.11 plot B).

It is worth noting that minimum air temperatures recorded at site A-III reached down to a few tenths of degrees above freezing during most of the night in a cold day (Fig. 2.11 plot A, dotted line). Neotropical *PEA* is probably unable to resist freezing temperatures for several hours found at elevations above 3100–3200 m asl. Northern brackens in temperate regions are known to senesce immediately after the first autumn frosts. Emerging fiddleheads are sensitive to freezing conditions the following spring, retarding sprouting (Pakeman et al. 1994). As regards to the daily temperature gradient in site A-III, plants had to cope also with sharp 16 °C contrasts (2–18 °C) in a matter of a few hours (dawn to mid-morning). We monitored air temperatures during the February–July period when bracken crozier sprouting was more intense after the first rains in March.

In addition, temperature and solar radiation were recorded during February (dry) and October (second rain peak), when cloud cover showed opposite extremes. The basic average air temperature values (Table 2.6) displayed a parsimonious behavior with no substantial differences in the said time span, as one could anticipate in the equatorial band of the northern Andes. Average T_{max} around noon hours (11:30 to 15:00 h) (Table 2.6 second row) reflect the increased cloud cover in lower and upper sites A-II and A-III at the middle of the rainy season (June). This is consistent with T_{max} results (row 4) at A-II versus A-III sites.

On the other hand, it is well established that plants are sensitive to CO_2 partial pressures (CPP) in combination with environmental temperature. Although the relative concentration of CO_2 does not vary in the first half of the troposphere, CPP is substantially lower at 3000 m than at sea level, which may be anticipated to hold back photosynthetic carbon fixation. This question has been debated over the years. Systematic studies of selected *paramo* plant species have revealed a consistent decrease of CO_2 assimilation rates (CAR) with elevation. Cabrera and coworkers (1998) selected *Acaena cylindristachya* Ruiz & Pav., a small rosette plant (Rosaceae), as an example of the plant community growing flat just above

Table 2.6 Comparative air temperature regimes (1 m above the ground) of three bracken fern study plots along an altitudinal gradient in Sierra Santo Domingo, Merida, Venezuela: Site A-I, 2090 m asl, Site A-II, 2850 m asl, site III, 3100 m asl

Parameter	Site A-I Feb/July	Site A-II Feb/July	Site A-III Feb/July
Avg Temp (°C) (±SD)	17.0(3.4)/16.0(2.9)	10.0(1.1)/10.3(0.7)	8.6(1.6)/8.6(2.4)
Avg T_{max} (°C) (±SD)[a]	23.5 (2.7)/20.1(2.3)	13.0(1.5)/14.5(1.2)	14.1(2.6)/12.1(2.1)
Avg T_{min} (°C) (±SD)[b]	13.9 (0.5)/13.1(0.9)	7.3(0.5)/6.8(1.5)	5.0(0.5)/5.9(1.5)
T_{max}(°C) of the period	28.7/25.1	15.8/17.7	19.3/19.0
T_{min} (°C) of the period	12.7/10.4	3.5/3.0	1.7/0.6

Data were recorded with calibrated field data loggers, point records every 6 min for 28 days per indicated month

[a] Measured between 11:30 and 15:00 h

[b] Measured between 03:00 and 07:30 h

the ground level, and therefore more dependent on microclimatic conditions protected from wind drafts while profiting from the soil-accumulated heat of sun radiation. They also chose *Senecio formosus* H. B. K., (Asteraceae) as an example of a plant with a taller canopy 20–50 cm above the ground and therefore, more exposed to air temperature and sudden changes due to air drifts. CAR decreased with increasing elevation in both plants (*A. cylindristachya*: 9.0, 5.2, and 3.9 micromol CO_2 m^{-2} s^{-1} at 2900, 3550, and 4200 m asl, well within the cryozone, respectively; *S. formosus*: 7.5, 5.8, and 3.6 micromol CO_2 m^{-2} s^{-1} at the said elevations). In addition, net photosynthesis–temperature relations showed differences in the temperature for optimum photosynthesis (T_{opt}) with elevation. In air drafts-exposed *S. formosus,* T_{opt} decreased following the sequence 21.7 °C (2900 m), 19.7 °C (3550 m), and 15.5 °C (4200 m) in parallel with a lowering trend of air *T*. These observations suggest an adaptive acclimatization to the prevailing abiotic conditions and that CAR and therefore metabolism and growth would be constrained by air and soil temperatures at the root sphere.

A different picture nevertheless emerges from Körner and Diemer (1987) who studied the CO_2 net assimilation of 12 herbaceous species examined in pairs at 600 and 2600 m asl in the Alps of western Austria, near Innsbruck. These plants developed naturally from seeds and were also transplanted a few years before the experiments. CPP at the two sites were 317 and 251 microbars. Authors found that, as a group, low- and high-altitude plants do not differ in their rate of carbon uptake, despite the 21% lower CPP at the high-elevation site. Representative species of high-altitude show significantly higher rates, while species with a wider altitudinal range maintain their net carbon assimilation. Authors contend that the overcompensation of lower CPP is the result of more efficient CO_2 diffusion in the leaf mesophyll rather than enhancement of the stomatal path. It would be of interest to carry out similar studies in *PEA* given its wide altitudinal range in the tropics.

Photosynthesis and CO_2 assimilation on which plant growth depends is also strongly regulated by leaf temperature (T_i), in addition to air/soil moisture and sun radiation, and several other factors of plant anatomy. A highly detailed theoretical model of plant growth, matching experimental observations, has been developed for *PEA* in a deforested site (2100 m asl) near the city of Loja, in the Andes of southern Ecuador (Silva et al. 2012). T_i at which net photosynthesis reaches a maximum value of 18 micromol m^{-2} s^{-1} of CO_2 was 25 °C, although it was highly sensitive to periods of direct and cloud shaded sunlight sequences. Peaks and valleys between 4 and 13 micromol m^{-2} s^{-1} of CO_2 with a few minutes difference were recorded, in consonance with a C4 grass species (*Setaria sphacelata*) that was tested at the same sites. Leaf temperatures varied within the 15–24 °C range with ample daily fluctuations, in consonance with our observations, and followed closely the seasonal soil (and air) temperature profile. Net canopy photosynthesis and average air temperature were linearly correlated within extreme values around 200 mmol m^{-2} day^{-1} of CO_2 at 13 °C and 600 mmol m^{-2} day^{-1} of CO_2 at 19 °C. Authors conclude that although bracken is less sensitive to environmental changes of sunlight and air temperature than *Setaria*, the production of dry mass per day is reduced by 20% in the cloudy and cold rainy season (July–August) relative to the warmer, less cloudy days of the short semi-dry season (March–May). Actual productivity figures of aboveground biomass of *PEA* by these and other authors yield contrasting figures: 3 kg m^{-2} $annum^{-1}$ in New Zealand (Bray 1991) and southeast Brazil (Portela et al. 2009), 5.55 kg kg m^{-2} $annum^{-1}$ in Ecuador (Silva et al. 2012), and 8.5 kg m^{-2} $annum^{-1}$ in the Sierra Nevada de Merida, Venezuela, that we obtained earlier at site A-I of the study here described (Alonso-Amelot and Rodulfo-Baechler 1996). Substantial abiotic contrasts in these geographically distant places may influence productivity differences. The varieties of studied clades (*P. esculentum* in New Zealand; *PEA* in South America), in addition to blade anatomical disparities in the latter subspecies we and others have been able to observe in Venezuela, Ecuador, and Southeastern Brazil, must be also contributing factors to the recorded variances.

Additionally, when Silva et al. (2012) photosynthesis models were applied to three *PEA* populations and compared with the *Setaria* grass performance along an elevational gradient at 1835, 2110 and 2825 m asl in Southern Ecuador (Knuesting et al. 2018), the net carbon gains decreased markedly with altitude, from 573 (±22) to 395 (±3) mmol CO_2 m^{-2} day^{-1} in *Setaria* whereas *PEA* appeared much less sensitive: 512 ± 22, 452 ± 3, and 499 ± 2, from the lowest to the highest site, respectively. There was a clear advantage of *PEA* over this particular grass in its resistance to the environmental changes associated with elevation within this range, in which temperature drop and increased UV-B solar radiation play fundamental roles.

In view that resistance of bracken underground growth to high temperatures caused by bushfires with the concomitant destruction of the aboveground mass has been explored (Roos et al. 2010) but not to low temperatures associated with winter or high tropical mountains, we opted for combining Silva et al. and Cabrera et al. concepts to trace an arbitrary bottom line of 10 °C across the sunlight daily period and the monthly average temperatures of our three *PEA* observation sites (Fig. 2.11 plot B). In principle, this line would define a limit below which CAR and net photosynthesis would fall below 200 mmol CO_2 m^{-2} day^{-2}, down from maximum values of 700–750 mmol CO_2 m^{-2} day^{-2}, at 20 °C according to Silva et al. (2012, Fig. 2.10 in that paper). As a result, conditions would not be as favorable for carbon fixation in *PEA* below 10 °C. Plant growth, and synthesis of adaptive compounds including chemical defenses such as polyphenolics, resins and terpenoids, would therefore be curtailed. The area under the curve (AUC) of the time–temperature curves of Fig. 2.11 within a given set of limits would provide a semiquantitative assessment of bracken potential stress caused by these abiotic constraints. These limits were a daytime photoperiod comprised between 06:00 and 18:00 h and the average monthly temperatures >10 °C within this time period. Data from the 30 days of June were selected as the middle section of the rainy season in the area and are collected in Table 2.7. AUCs showed that under the said assumptions *PEA* should encounter increasing impediment to growth with elevation alongside a much shortened daily period for net effective photosynthesis, as far as the temperature–daylight cycle goes.

Table 2.7 Area under the curve (AUC) of the monthly average (June) air temperature profiles above 10 °C recorded at sites A-I, A-II, and A-III described in the text and Fig. 2.11

Site (elevation – m asl)	AUC (°C min)	Init – final hour	Min/day	Day Time fraction
A-I (2150)	1147	09:40–16:40	420	0.58
A-II (2850)	7513	08:30–18:00	570	0.79
A-III (3100)	12,646	06:00–18:00	720	1.00

Number of minutes per day and fraction of the daily period for effective net carbon assimilation

2.11.3.2 Solar Radiation

Radiation intensity and wavelength reaching chloroplasts are highly variable depending on abiotic factors associated with atmosphere filtering (clouds, aerosols, dust) all of which vary with elevation. Frequently unpredictable and rapidly changing weather patterns within the same day alter substantially the photon flux. Biotic interference includes inter- and intraplant shading, as well as plant anatomy characteristics (leaf reflectance/transmittance, incidence angle, adaxial pubescence, concentration of radiation filtering compounds stored in epidermis and palisade cell vacuoles) and others. For the high-altitude *PEA* study in the Venezuelan Andes, we measured sunlight radiation (400–700 nm) using field loggers during the dry and rainy months at sites A-I/II/III.

At a randomly selected non-rainy day of April, 1 month into the rainy season (Fig. 2.12 plot A) differences in morning and afternoon periods were clearly discernible at all three sites. At A-I (solid line), sun radiance appeared only partially obscured by atmospheric filtering during the morning hours, whereas heavy clouds appeared in the second half of the day. Afternoon storms are invigorated by local, morning sun-driven evaporation in tropical and subtropical zones forming convective rain clouds, whereas morning precipitation, when it occurs, responds more likely to extensive weather patterns and stratiform clouds (Houze 1993). Both cloud types differ in their formation, form and rain characteristics. The manner in which the complex topography of high tropical mountains like the Andes perturb these patterns is a subject of current interest (e.g., Kumar et al. 2020b; Seidel et al. 2019) and leads to the notion that a sharp classification of both raincloud types is not generally applicable in these cordilleras as it is in lowlands and over the sea.

By comparing sun radiation profiles in high sites A-II and A-III, two quite different patterns emerged (Fig. 2.12 plot A, dashed and dot lines, respectively). Obscuring clouds appeared earlier in the day over A-II and dissipated only in the early afternoon. By contrast, the early and up to mid-morning hours in A-III were free of significant cloud obstruction but spread over the area briefly and either passed on or dissipated. Afternoon clouds then appeared following the usual pattern in the area. What these profiles show is the penetration of the moist easterly winds from the Venezuelan lowlands carrying low altitude clouds into the Santo Domingo East-oriented basin, a frequent occurrence throughout the year in this place that locals are quite familiar with (white masses in the map of Fig. 2.4). Air

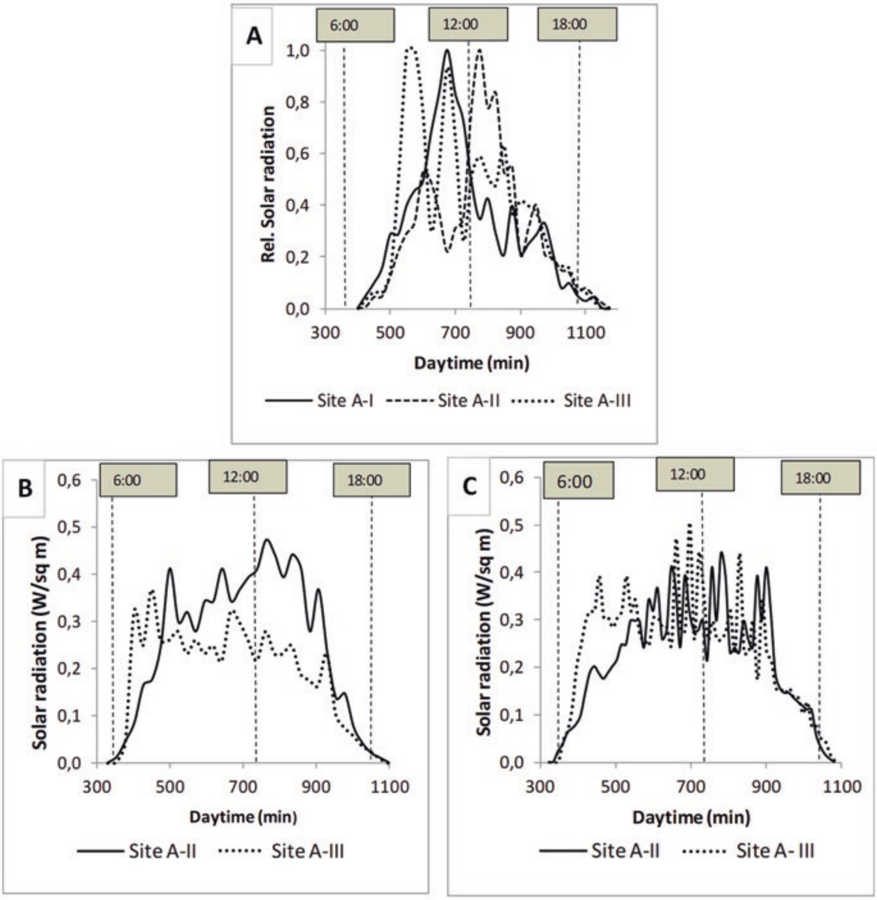

Fig. 2.12 Solar radiation patterns (400–700 nm, equivalent values at 550 nm) at sites A-I, A-II, and A-III described in the text (Sect. 2.4.2). (**a**) Radiation fraction relative to the maximum value recorded on a randomly selected day (April 20th) one month into the rainy season in the area. Site A-I (solid line); Site A-II (dashed line); Site A-III (dotted line). (**b**) One month (June) daily average radiation (W m^{-2}) course with hour of the day for sites A-II (solid line) and A-III (dotted line). (**c**) Same as B recorded in October. Data points every 6 min for 30 days

moisture raises sharply in A-II at 2850 m asl with the entrance of these clouds in the form of dense fog a few hours before it reaches the drier A-III site at 3100 m asl, 8 km up the valley.

Thirty days average sun radiation recorded every 6 min in A-II and A-III were also compared during the rainy months (which include the peaks of the rainfall bimodal yearly regime) of June and October (Fig. 2.12 plots B and C, respectively). In June, while the higher A-III site was clear in the early hours, dense cloud cover persisted for the rest of the day, and more intense radiation reached the lower A-II site. As opposed to this, the stormy October period (Fig. 2.12 plot

C) affected both elevations almost equally. Sharp peaks, which were unexpected for 30 days average values, likely result from frequent turbulence and rapid passage of cloud masses close to the ground level during the October season, at similar times of each day.

2.12 *PEA* Growth Response to Elevation

2.12.1 Maximum Rachis and Stipe Lengths of Mature Fronds: L*r(max),* L*s(max)*

These parameters were measured in fully grown stage 4–5 vegetative active fronds. Results are compiled in Fig. 2.13 plot A. The higher elevation *PEA* fronds were slightly larger [*L*r(max)] but were statistically undifferentiated (Table 2.8,

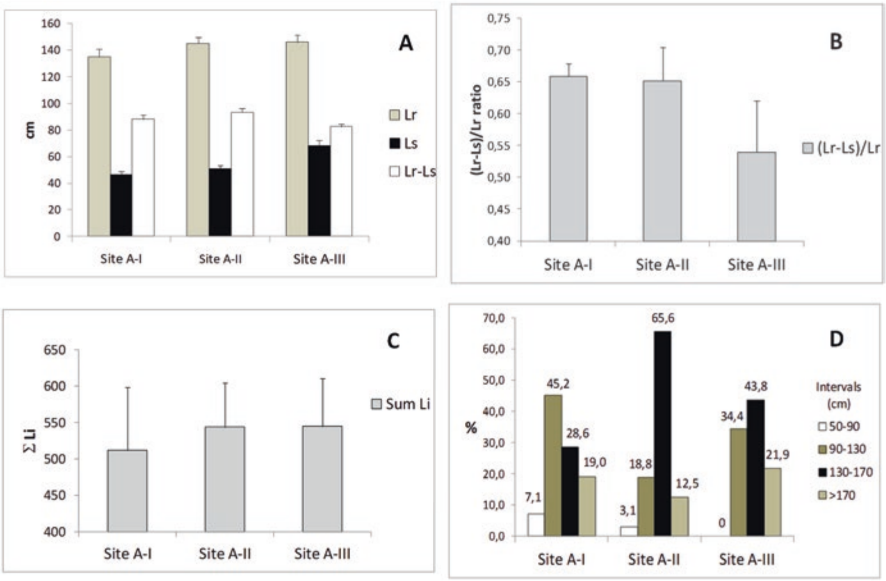

Fig. 2.13 Comparison of basic frond architecture parameters *P. esculentum* subsp. *arachnoideum* (PEA) from three sites along a altitudinal gradient recorded at sites A-I to A-III along a 1010 m altitudinal gradient, up to the highest known site for bracken (3100 m asl) in the Sierra de Santo Domingo, northern Andes, Merida, Venezuela. (**a**) Rachis and stipe lengths *L*r and *L*s, respectively (cm), and the difference (*L*r–*L*s) related to the frond's crown size. Error bars are SE of the means ($N = 53$). (**b**) Ratio of crown size and total rachis length (*L*r–*L*s)/*L*r (± SD). (**c**) Sum of the axis length of the lateral pinnae (± SD). (**d**) Fraction (%) (numbers at the bar tops) of PEA frond size according to the frequency distribution of maximum rachis length *L*r(max). For statistical comparisons, see Table 2.8

Table 2.8 One-way ANOVA statistical differentiation of anatomical parameters of *Pteridium esculentum* subsp. *arachnoideum* aerial parts, shown in Fig. 2.7, collected at three different elevations along a gradient in the Merida Andes of Venezuela

	Statistical significance: *P*(*F*) between sites:		
Parameter	M-I/M-II	M-I/M-III	M-II/M-III
*L*r(max)	0.1824 (1.81)	0.160 (2.02)	0.9076 (0.01)
*L*s	0.2117 (1.59)	<0.0001 (23.98)	0.0004 (13.78)
*L*r–*L*s	0.1918 (1.74)	0.0203(1.74)	0.0001 (17.86)
(*L*r–*L*s)/*L*r	0.6604 (0.19)	<0.0001 (88.12)	<0.0001 (61.38)
Σ*Li*	0.0868 (3.01)	0.0837 (3.08)	0.9452 (0.00)

$N = 53$ per site; level of significance: $p < 0.05$

first row). Stipe length (*L*s) was distinctively longer in A-III than in the other two lower sites (Fig. 2.13 plot A, black bars, Table 2.8, second row). Both bracken species respond to the high canopy of surrounding plants including its own older or dead blades by extending the stipe near the canopy's upper edge and then unfolding the first pair of lateral pinnae and the photosynthetic segments above this canopy for sun radiation capture. Meanwhile, the meristem continues to grow and produce additional pairs of pinnae numbering 10 and more to form the blade crown. At site A-III, there was a community of competing low humid *paramo* forbs of greater density than in A-I and II, to which bracken responded by spreading the blade crown above these plants.

2.12.2 Blade Crown Size

The difference of stipe and rachis dimensions (*L*r–*L*s), and the fraction of this difference relative to *L*r (Fig. 2.13 plots B and C) as well as the sum of the secondary axis of the unfolded pinnae Σ*Li*, is a measure of the size of the triangular blade crown. Taking into account that the number of segments per length unit of pinnae axis remains constant in *PEA* samples collected from several sites (data not shown), one can safely assume that the total photosynthetic surface of the pinnulae segments is proportional to crown size. Although there was an apparent reduction trend in crown size with elevation owing to a longer stipe (Fig. 2.13 plot B), Σ*Li* was statistically similar at all sites (Table 2.8, fifth row). More relevant, however, was the distribution of *L*r in the population at each site considering that one frond is equivalent to a single leaf, as complex as it may be, of one or a few bracken clones extending their rhizomes underground. Figure 2.13 plot D depicts the size distribution of *L*r which is proportional to Σ*Li*. At the lower site A-I, 45.2% of blades developed *L*r in the 90–130 cm range, whereas the major part of A-II and A-III populations were distinctively larger in the 130 – >170 cm breath, reaching up to 250 cm. No indication of elevational stress expressed in reduced size of mature fronds was thus found.

2.12.3 Additional Phenotypic Responses of PEA to High Elevation

PEA appears well adapted to the intense solar radiation and temporary dryness of tropical high elevations. On the one hand, segments display an abundance of non-glandular trichomes or cuticular hairs on the abaxial epidermis, especially in A-II and A-III sites, whereas adaxial surfaces appeared nude (Arellano 2003). Pubescence is a common trait in stems and leaves of many *paramo* angiosperms. Pubescence contributes to increase leaf temperature, screen excess solar UV radiation in clear days, avoiding damage of mesophyll cells, and reduce transpiration (Lange et al. 1981; Meinzer et al. 1985). Cuticular hairs also condense fog droplets that may regulate leaf temperature and water intake (Konrad et al. 2015). This latter function appeared to be the case in *PEA* since cuticular hairs formed bundles around secondary veins and were longer in samples from high elevations. Non-glandular curly trichomes are on record in other bracken species and have been used as a taxonomic marker of this plant group (Thomson and Martin 1996). A measure of leaflet up-curling in the *PEA* thickets at 3100 m was the most noticeable phenotypic response to high elevation. This characteristic has been observed in Alpine plants and also related to resistance to water loss (Codignola et al. 1987). Leaf curling has been attributed also to UV-B radiation affecting high-altitude habitats (Zuk-Golaszewska et al. 2003).

Additionally, we observed that *PEA* at high elevation develops segments of cartaceous texture. Transversal sections at 400 X magnification show a double-layered epidermis with thicker cell walls in contrast to the single-layered epidermis of *PEA* segment specimens from 2000-m zones.

2.13 Overall Impact of Altitude on *PEA*

Taken together, one may conclude that:

A. *PEA* is a more robust bracken than *PC*.
B. Neotropical *PEA* is better adapted to acclimation in higher elevations, maintaining sustained growth at altitudes within the lower humid Andean *paramo*
C. The basic architecture of *PEA* fronds expressed as *L*r(max) does not change sensibly with elevation. Two components do show differences following the altitudinal trend. The frond size distribution indicates an increasing fraction of larger blades with elevation, passing from 50% of the blade population >130 cm at 2090 m to 78% at 2850 m and 65% at 3100 m.
D. *L*s of mature fronds is distinctly longer at high elevation, but this is probably a response to competition from lower *paramo* forbs assemblages forming a canopy of 50–100 cm from the ground surface, and the persistence of withered fronds of bracken from earlier seasons. Therefore, the effects related to succession stage rather than elevation induce this phenotypical response.

E. The upper limit of *PEA* ecological range in the geographical area of the central Andes of Merida (and potentially elsewhere in the Neotropical Andes) appears to be the night frost line sustained for several hours. *PEA* probably resists brief freezing. The current planetary warming trend tends to raise this line to higher altitude, and create conditions for the further expansion of the aggressive *PEA* weed.

F. The absence of predatory ants above 2800 m leaves *PEA* young fronds unprotected from insect herbivory despite the presumably still inactive nectaries. Plants count only on their own resources to fend off exploiters. The actual case is, nevertheless, that at such elevation no indication of activity by phytophagous insects on *PEA* fronds could be confirmed in laboratory controls. In any case, the risk of non-specialist herbivores exists in the lower *paramo*, represented by abundant grasshopper populations such as *T. malleatus* (Ronderos & Cerda 1982) found also among the bracken insect survey of Avila-Nuñez and Otero (2019) in Merida state, Venezuela. Tests of feeding preferences, insect behavioral and reproductive performance upon feeding brackens, and absolute damage caused to *PEA* and *PC* from various elevations with captured and laboratory-acclimatized *T. malleatus* and other herbivores need to be conducted before advancing adaptive exploitation hypotheses.

G. *PEA* acclimation includes modifications of adaptive secondary metabolites, to be reviewed in the following section.

2.14 Phytochemical Responses of Neotropical Brackens to Elevational Gradients

A gamut of research examples substantiate the fact that plants synthesize adaptive substances by primary and secondary metabolism to contend with the challenges of survival at different elevations and that metabolomic profiles are the result of abiotic and biotic forces changing with altitude (e.g., Alonso-Amelot 2002b; Rodriguez-Hernandez 2019). Exhaustive phytochemical analyses of bracken species around the world have revealed well over 120 secondary metabolites (Tempel 1981; Fenwick 1988; Cooper-Driver 1990; Alonso-Amelot 2002a; Gil da Costa et al. 2012a; Agarwal et al. 2018; O’Connor et al. 2019). A combination of a limited number of ecologically relevant xenobiotics in brackens may confer protection against insect herbivory (Jones and Firn 1979; Oldenkamp and Douglas 2011) whose populations vary greatly with habitat characteristics and generally decrease along altitudinal gradients. On the plant competition front which strongly depends on elevation, although in a nonlinear manner, brackens possess allelopathic potential early found in the California’s *P aquilinum* (Gliessman and Muller 1972; Gliessman 1976) and confirmed several times elsewhere (e.g., Jatoba et al. 2016). In this front Andean *PC* yields easily isolable quantities of coumarin and o-coumaric acid (Alonso-Amelot et al. 1995; Naya et al. 2016), both of them potent phytotoxins causing inhibition of germination, root elongation and root cell death, plant growth and specific gene silencing (e.g., Zheng et al. 2012). *PC* is the only *Pteridium* species known to produce these phenylpropanoids, which confer added encroaching capacity in the highly competitive environment of the tropics.

Additionally, bracken pluripotent allelochemicals include a plethora of bioactive and UV absorbing aromatic derivatives: protein-binding condensed tannins, small molecular weight phenolics, benzoic and cinnamic acid derivatives, a cyanogenic glycoside, sesquiterpenoid pterosins, as well as UV-B inactive illudanes, thiaminase (an enzyme that destroys vitamin B1—thiamine), a steroidal insect molting hormone, and other materials. The production and accumulation of these compounds involve metabolic costs with a potentially concomitant limitations for frond growth, although a tradeoff exists between rate of expansion and the advantages of better chemical protection against natural enemies of bracken and abiotic stresses. The evolution of these opposing forces results in enhanced fitness. Needless to say, chemo-ecological interactions may be exceedingly complex as the dynamics (plant part and concentration) of bioactive plant metabolites varies with plant age as illustrated by many of the compounds just mentioned. Moreover, some of them may move across one or more trophic levels, such as ptaquiloside and its congeners. Besides, none of the bracken compounds is known to be sequestered by herbivores for their own protection against predators and parasitoids (e.g., Naya et al. 2016). Thus, devising a unique ecological model of bracken performance in such a large ecological range is a fruitless task. A more productive approach is to place the focus on a few of these substances, which might offer clues on the phytochemical contribution to fitness of these plants to biotic and abiotic forces. We selected feeding deterrent prunasin, toxic ptaquiloside, and UV-B filtering organic compounds specifically low and high molecular weight phenolics and tannins.

2.15 Prunasin

Prunasin is a widely distributed cyanogenic glycoside in vascular plants that modulates palatability (Cooper-Driver et al. 1977) on account of its acute bitterness, although this particular taste response depends on the receptor species. Bitter taste receptor genes have been identified in vertebrates, leading to the notion that it is a widespread evolutionary trait to avoid toxic foods (Dong et al. 2009). When combined with prunasinase, a gene expressed glycosidase produced in a separate cell compartment, prunasin is hydrolyzed to release equimolar amounts of toxic hydrogen cyanide, benzaldehyde, and glucose when tissues are crushed during chewing by non-specialized polyphagous invertebrate and vertebrate herbivores (Cooper-Driver and Swain 1976; Alonso-Amelot and Oliveros-Bastidas 2005; Oliveros-Bastidas and Alonso-Amelot 2010). HCN and benzaldehyde production requires that the producer organism, bracken in this case, expresses prunasin- (p) and prunasinase (e) producing genes (p_1e_1 genotype). As a result, the frequency of the p_1e_1 genotype in comparison with the $p_{-1}e_{-1}$ genotype is ecologically relevant in as much as cyanogenesis is an effective herbivore deterrent and pathogen protective process (Zagrobelny et al. 2004). Further ecological relevance is gained if cyanogenic plants relocate these allomones in soft tissues and valuable plant parts such as meristems and reproductive organs. Because the population of plant predators vary with elevation and cyanogenic capacity is an effective defense against non-specialist herbivores, the relative frequency distribution of $p_{+1}e_{+1}/p_{-1}e_{-1}$ alleles in brackens would be expected to respond to biotic pressure in altitudinal gradients.

To address this question, we examined the quantitative cyanogenesis response of *PC* during the rainy season, which were collected at 7 sites between 1100 and 2100 m asl in the geographical gradient of the M-series of locations used in the growth studies. Because [Pru]t content varied very rapidly with crozier elongation, measurements were performed in the more stable second-stage fronds in this species. *PEA* accessions were also submitted to scrutiny in the more stable crozier tips from 8 locations, 1800 to 2950 m asl in the mid-Chama basin and upper Mucujun river valley, a tributary of the Chama river, in the northern Andes of Merida State, Venezuela (Oliveros-Bastidas and Alonso-Amelot 2010). Analyses were performed by a modified picrate trap method of evolved HCN (Alonso-Amelot and Oliveros-Bastidas 2000). We found that:

1. The overall $p_{+1}e_{+1}$ genotype frequency of *PC* and *PEA* amounted to 84.3% and 98.6%; respectively, hence both species are [Pru]-HCN polymorphic with prevalence of the $p_{+1}e_{+1}$ form. However, PC fronds from the lower sites at 1100 and 1180 m and half of frond samples at 1450 m were $p_{-1}e_{-1}$ genets, since fiddleheads not only were unreactive upon crushing but also aqueous extracts were impervious to added prunasinase.
2. The concentration of total prunasin [Pru]t in $p_{+1}e_{+1}$ genets was highly dynamic and strongly dependent on frond age. The highest [Pru]t was recorded in young croziers of *PC* and *PEA* followed by a sharp drop to 1–10% by stage 2 and nearly zero by stage 3. Comparisons of bracken populations among and between sites were thus performed using fiddleheads only.
3. [Pru]t in *PC* croziers and stage 2 fronds was only a fraction of *PEA* figures in all sites (*PC*: 1.095 ± 1.295 mg/g dw; *PEA* 18.600 ± 12.840 mg/g dw). In consonance, the first-order rate constants of HCN evolution from croziers immediately after crushing were markedly different (*PC*: 0.28 ± 0.09 microg min^{-1} g^{-1} dw; *PEA*: 10.54 ± 1.57 microg min^{-1} g^{-1} dw). In both cases, the rates were first rate in prunasin (Alonso-Amelot and Oliveros-Bastidas 2005; Oliveros-Bastidas and Alonso-Amelot 2010).
4. [Pru]t in 2nd growth stage PC, which was selected because more stable values were obtained, was linearly associated with elevation in the range 1100–2100 m asl (Fig. 2.14 – plot A) ($r^2 = 0.9837$). [Pru]t was also tightly tied to elevation in *PEA* at altitudes comprised within its ecological range (Fig. 2.14 – plot B) but in the opposite direction. Croziers could be grouped at each site according to their [Pru]t. In some cases, they were distinct enough to be associable with a different overlapping clone. Soil analyses performed in all sites showed that nitrogen and

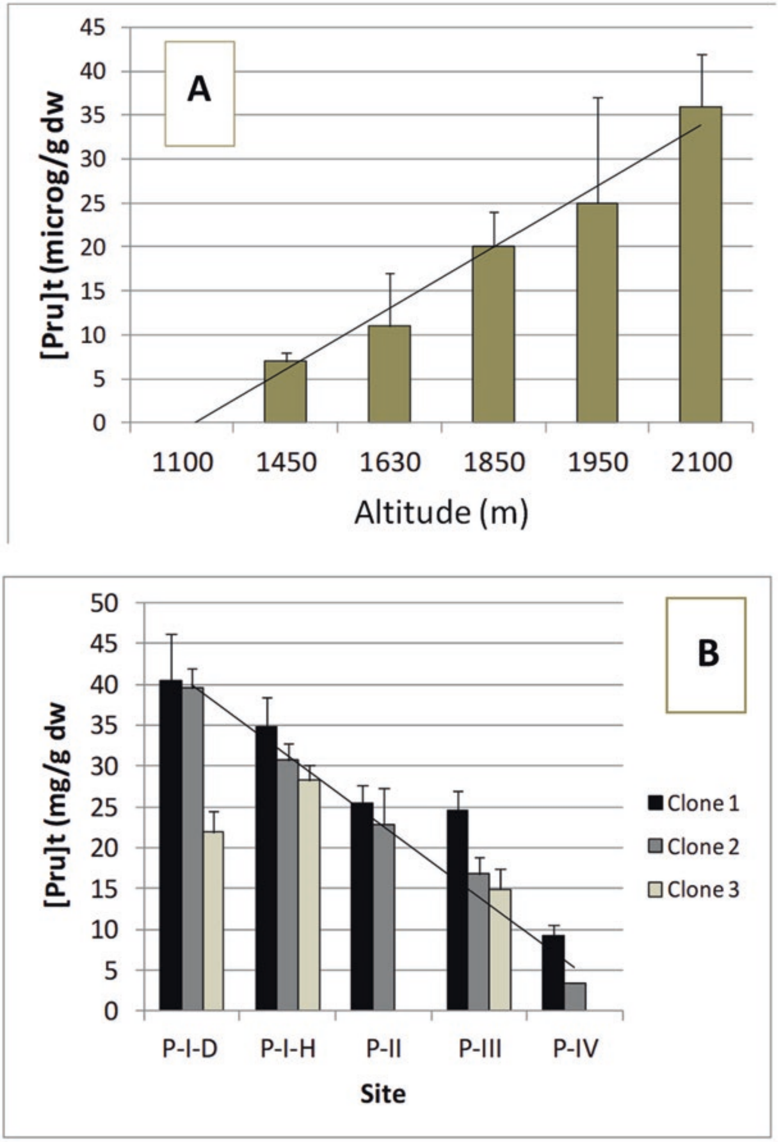

Fig. 2.14 Variation of total prunasin content [Pru]t of (**a**): *Pteridium caudatum* in an altitudinal gradient between 1100 and 2100 m along the M sequence and intermediate sites described in Sect. 2.2. (**b**): *P. esculentum* subsp. *arachnoideum* fiddleheads at various sites along an altitudinal gradient in the Mucujun river valley in the northern Andes, Merida, Venezuela. Elevations (m asl) were as follows: P-I: 2250; P-II: 2450; P-III: 2650, and P-IV: 2930. P-I-D = Site I during a dry spell in June, P-I-H = Site I after 1 month of frequent rain in July. Clones are independent per site ($N = 12$ per clone and site). All other sites were sampled that same month. The linear correlation ($r^2 = 0.9703$) corresponds to dark gray bars from P-I-H down to P-IV in the lower humid *paramo*

Table 2.9 Content of total prunasin [Pru]t in a crozier of *Pteridium esculentum* subsp. *arachnoideum* divided into three sections shown below

Crozier part	[Pru]t (mg g^{-1} dw)	Initial Pru HCN rate (μg HCN g^{-1} min^{-1})
Head	97.57	103.77 ± 7.00
Upper half of stipe	13.72	5.89 ± 0.58
Lower half of stipe	2.42	0.33 ± 0.01

The sample was collected at a $p_{+1}e_{+1}$ thicket and a high cyanogenic response from a site at 2150 m asl. The first rate kinetics was followed during the first 180 min after crushing the frozen crozier tissue in 0 °C sand, and warming to room temperature immediately after; sampling at 20-min intervals using the gas diffusion method into picrate. (Data from Oliveros-Bastidas and Alonso-Amelot (2010))

water content were not limiting factors; hence, abiotic constraints related to elevation are probably responsible for the dwindling trend of [Pru]t in *PEA*.

5. On the occasion of a dry spell during the growing season (June), [Pru]t on a dry weight basis was found to be statistically higher in two of the three *PEA* clones tested relative to croziers appearing after 1 month of frequent rain the following month at the same sampling areas of the previously spotted clones in site P-I at 2150 m asl. Moisture content of croziers during the dry weeks did not vary relative to rainy periods (84.4 ± 1.0% and 82.5 ± 1.3%, respectively) so water stress caused by soil dryness elicits the synthesis of prunasin in *PEA* for reasons still to be established.
6. [Pru]t varied noticeably with crozier part. A freshly collected and nearly frozen crozier of a highly cyanogenic *PEA* clone at 2150 m asl was cut into three sections, fiddle at the top, and the remaining stipe in two sections of equal length and then crushed thoroughly in frozen sand. Preparations were placed in flow chambers warmed to room temperature in a water bath and evolved HCN captured in a picrate trap. [Pru]t and the initial rate of the prunasin to HCN hydrolysis were determined (Table 2.9). Both parameters decreased sharply along the crozier gradient. Likewise, second-stage fronds were divided in upper rachis (section A) and the lower axis from which the first pair of pinnae was fully unfurled (section B) and submitted to the same procedure. Section A contained an average of three times more prunasin than section B.

These findings led us to conclude that:

(a) In principle, *PC* and *PEA* contain enough prunasin and are sufficiently cyanogenic to deter predators following the established ecological hypothesis (Vetter 2000), although cyanide tolerant herbivores and cyanogenic glycoside sequestration by specialists weaken the protection of the producer organism, brackens in this case (Gleadow and Woodrow 2002). Moreover, the higher frequency of $p_{-1}e_{-1}$ *PC* genets at lower elevation and the fact that [Pru]t was tightly related to altitude in this bracken clade [Pru]t in $p_{+1}e_{+1}$ genotypes was incompatible with the expected decrease in plant predator species diversity and population with elevation. By contrast, *PEA*, whose ecological range encompasses elevations where insect and small mammal predation declines sharply with altitude, but contains a much larger proportion of prunasin, even though elevation imposes constraints to prunasin synthesis-accrual in soft, valuable frond parts: crozier head, frond meristem (Fig. 2.14). The initial rates of HCN evolution after crushing of croziers were also in line with a more potent HCN-based defense line of *PEA*, despite the expected decline in herbivore population.

Alternatively, prunasin and plant cyanogenic glycosides have also been envisioned as nitrogen carriers for primary metabolic use in the synthesis of a variety of amino acids, including asparagine, as well as amines and proteins downstream, as shown for example in the seedling development of flax (Zuk et al. 2020) among other plants.

(b) It is conceivable, therefore, that the greater [Pru]t reserve allocated to the meristem section of croziers and developing fronds may play a role of organic nitrogen transport in metabolic demand enabling the faster tissue generation of *PEA* relative to *PC* during frond growth. Information about this particular concern in bracken is still pending.

(c) Prunasin is synthesized from phenylalanine stored in the rhizome and then translocated to the crozier. This amino acid is also a key precursor of a large number of phenylpropanoid secondary metabolites serving as protective filters against sun UV-B radiation for *Pteridium* ferns growing at high elevation (see Sect. 2.5.3). Because there is competition for the phenylalanine pool by diverging metabolic pathways leading to prunasin as nitrogen carrier under declining herbivory pressure, on the one hand, and phenylpropanoid synthesis for abiotic protection on the other, regulatory mechanisms of biosynthesis must be involved to achieve a trade-off balance for better fitness (e.g., Ganjewala 2010). Moreover, the gene expression of phenylalanine ammonia lyase (PAL), a gate enzyme that diverts phenylalanine from the primary carbon metabolism to the synthesis of phenylpropanoids in plants, is induced by UV radiation (Takeda et al. 1997; Maeda et al. 2005), among other multifaceted elicitors (Zhang and Liu 2015). Increasing UV light would divert the resources to phenylpropanoids synthesis. Among these is lignin a polyphenolic polymer, which *PEA* contains in large amount relative to other plants. The PAL and tyrosine ammonia lyase pathways required for lignin synthesis contribute to the abiotic and biotic stress response through lignin accumulation not only in bracken but many other plants (Moura et al. 2010). The aromatic amino acid demand may thus drive the phenylalanine pool to the lignin-related response to the altitudinal abiotic stresses reducing [Pru]t. By contrast, *PC* tolerates the level of solar UV-B radiation at the high tear of its ecological range with its baseline load of phenolic substances and does not respond to elevation in terms of prunasin content. It would be of interest to perform a systematic survey of herbivores species and populations along the altitudinal transect in which *PC* proclaims such a fine-tuned cyanogenic response and determine whether the $p_{-1}e_{-1}$ clones show the unmistakable marks of herbivory.

2.16 Ptaquiloside (PTQ)

PTQ and a few homolog xenobiotics (O'Connor et al. 2019) are sesquiterpenoid glycosides produced by *Pteridium* ferns apparently fulfilling the concept of protective secondary metabolites, considering their acute toxicity to livestock and the damage these large herbivores inflict on bracken stands by feeding on the soft immature fronds. Croziers, however, are avoided by most animals. Although this is an oversimplified view, it was nevertheless of special relevance to explore the elevational gradient effects on the accumulation of this notorious toxin (O'Connor et al. 2019).

Before the gradient study was carried out, three questions had to be addressed:

1. Is the concentration of ptaquiloside ([PTQ]) comparable in *PC* and *PEA*?
2. Does [PTQ] vary with frond ontogeny?
3. Since PTQ is a water-soluble glycoside, does rain leach it from the plant?
4. Because the illudalane pterosin B (PTB) is an end product of PTQ, are the dynamics of these two compounds tied to frond ontogeny?

Our early studies in the Andes answered all four questions (Alonso-Amelot et al. 1995, 1996) by means of the quantitative analysis of specific metabolites in bracken ramets of all four growth stages. Average sized healthy blades were selected randomly from three 20 × 20 m plots at 1850 m asl by the Albarregas river near the city of Merida, Venezuela, and pooled in groups of three samples. There were three groups per development stage per bracken species per plot. Results collected in Table 2.10 demonstrated quantitatively for the first time that:

(a) [PTQ] acquired maximum values at the crozier stage. Because croziers hardly produce any photosynthase, PTQ is translocated from rhizome reserves, also rich in PTQ, [data not shown but substantiated by others (e.g., Rasmussen et al. 2003)]. [PTQ] declined rapidly with frond ontogeny in both bracken species, as observed in other Pteridium species. Senescent fronds retained from zero to very small quantities of PTQ.

(b) *PC* accrued more PTQ than *PEA* on a per frond dry weight basis but the ontogenic PTQ/PTB dynamics in fronds was similar. This feature has been reported in non-Andean *PEA* (e.g., Ribeiro et al. 2020). While *PEA* generated a much larger frond biomass per unit area than *PC*, on a per hectare basis, the load of PTQ was still greater in *PC* (30.88–167.58 g/ha) than of *PEA* (1.62–2.08 g/ha) under the conditions of the study plots, assuming a 100% population of fully grown fronds and average [PTQ]. *PEA* from other South American sites furnishes a much larger [PTQ] (Table 2.10, 4th section). Moreover, studies of bracken samples excised from various points in the central Ecuadorian Andes found conservative [PTQ] values independent of altitude (Tobar et al. 2014).

(c) [PTB] follows the same declining trend with frond development and was loosely correlated with [PTQ] in both *PC* and *PEA*. This is consistent with the ease of conversion of PTQ to PTB under laboratory conditions in acidic and especially in alkaline medium, followed by brief treatment in slightly acidic aqueous

Table 2.10 Variation of basic anatomic parameters and concentration of ptaquiloside [PTQ], a potent bracken xenobiotic, and pterosin B [PTB], an end product of PTQ metabolism, in fronds of sympatric populations of *Pteridium caudatum* (*PC*) and *P. esculentum* subsp. *arachnoideum* (*PEA*) from a parcel at 1850 m asl near the Albarregas river in the Sierra Nevada de Merida, Venezuela

Characteristic			*PC*		*PEA*	
Frond density			16,000 ± 1300/ha		51,000 ± 4200/ha	
Frond biomass			249 ± 18 kg/ha		2274 ± 180 kg/ha	
Rhizome biomass			555 ± 33 kg/ha		5156 ± 360 kg/ha	
Ptaquiloside dynamics						
Blade stage		*PC*			*PEA*	
		[PTQ] (mg g^{-1} dw)			**[PTQ]** (mg g^{-1} dw)	
	Plot A	**Plot B**	**Plot C**	**Plot A**	**Plot B**	**Plot C**
1	1.975	3.901	3.140	0.032	0.655	0.449
2	0.371	0.642	0.696	0.14×10^{-4}	1.66×10^{-4}	1.37×10^{-5}
3	0.751	0.007[a]	0.679	7.29×10^{-5}	BDL	BDL
4	0.124	0.673	0.205	7.11×10^{-4}	BDL	9.14×10^{-4}
Pterosin B dynamics						
Blade stage		*PC*			*PEA*	
		[PTB] (mg g^{-1} dw)			**[PTB]** (mg g^{-1} dw)	
	Plot A	**Plot B**	**Plot C**	**Plot A**	**Plot B**	**Plot C**
1	0.147	0.517	0.453	2×10^{-3}	0.031	0.099
2	0.015	0.019	0.241	1×10^{-3}	3.9×10^{-4}	5.9×10^{-4}
3	0.015	0.006[a]	0.038	1.3×10^{-4}	3.5×10^{-4}	3.0×10^{-4}
4	0.011	0.014	0.024	4.8×10^{-4}	2.8×10^{-4}	2.7×10^{-4}
[PTQ] and [PTA] in *PEA*, from other locations						
Country		Frond stage	**[PTQ]** (mg g^{-1} dw)	**[PTA]** (mg g^{-1} dw)	Ref.	
Central & SE Brazil		1	12.5–18.8	4.03–10.4	Ribeiro et al. (2020)	
Central & SE Brazil		4	2.49–2.75	0.68–0.88	"	
Ecuador (Bolivar prov)		1	0.59	–	Tobar et al. (2014)	
Ecuador (Bolivar prov)		4	0.56	–	"	

BDL below detection limit set at 1×10^{-6} mg/g dw. (Alonso-Amelot et al. 1995, 1996)

[a] Heavy rain during the previous night

medium. These reactions have been amply substantiated and used almost universally for the quantification of PTQ as its more stable PTB derivative. All other illudanes have their pterosin equivalent in the plant.

(d) These facts suggest that PTQ and similar illudanes are intermediate metabolites en route to illudalanes (pterosins) and other still unknown end products downstream. The toxicity of PTQ might as well be a transitory consequence rather than a xenobiotic response to evolutionary pressure or adaptive trait. Supporting evidence is found in the fact that there is a substantial population fraction of other species of the *Pteridium* clade elsewhere that do not yield measurable amounts of PTQ (e.g., New Zealand, see Rasmussen et al. 2008); hence, brackens (at least *P. esculentum*) are genetically PTQ-polymorphic although all seem to produce pterosins. At any rate, no cases of PTQ-free brackens have been reported in the Neotropics to the best of our knowledge, although other South American registries indicate an ample range of PTQ content in fronds, again an indication of its transitory character.

(e) The unexpected drop of [PTQ] in third-stage blades of *PEA* and *PC* in plot B (Table 2.10) was observed in samples collected after heavy rain. This led us to propose (Alonso-Amelot et al. 1996) that water-soluble PTQ had been leached from the plant by rain throughfall. This early finding was later pursued in depth by a Danish bracken group who developed the alarming notion that PTQ passes on to the environment by rain runoff under bracken stands and migrates to water catchments in sufficient quantity to become a potential risk to human and animal consumers (Rasmussen et al. 2003, 2005, 2008). Quantities in the nano- to low-microgram range of PTQ per liter of soil solutions (up to 2.5 micrograms/L) were detected (Rasmussen et al. 2003; Clauson-Kaas et al. 2014). A model proposing pulses of PTQ released by bracken stands eventually reaching nearby streams have been realized in northern England (Clauson-Kaas et al. 2016) with peak concentrations up to 2.2 microg/L in the stream. One hour after the storm event finished [PTQ] returned to a baseline of 61 ng/L or less.

The complex combined dynamics of frond growth, PTQ contents, leaching from bracken and soil/water characteristics have been compiled in a single model that can be applied to other water-soluble toxins in the soil and water runoffs (Garcia-Jorgensen et al. 2020). Models like this one will be useful in understanding the impact of plant xenobiotics leached into soils in the steep gradients of species-rich Andean slopes. PTQ degrades under alkaline and acidic conditions, though, and kinetic studies show that decomposition occurs rapidly (Ayala-Luis et al. 2006) through molecular mechanisms examined by quantum mechanical methods (Density Functional Theory DFT) (Rios-Gutierrez et al. 2017). Of note is that Neotropical *Pteridium* ferns grow primarily in highly acidic soil (pH 3.96–5.23) (Alonso-Amelot, unpublished) from 10 different bracken sites at various elevations in the Mucujun river valley, Merida central Andes, conditions under which PTQ would not last but for a few hours. Recent studies rate PTQ half-life from 6.5 to 47 days in groundwater in Denmark at “natural pH (6 to 7.1)” and 8.0 °C (Wu et al. 2021). Additionally, PTB is also degraded rapidly (initial half-life: 0.7–3.5 h) in soils owing to microbial activity, since no dissipation was recorded in sterilized soil, but it becomes irreversible adsorbed in soil particles (Skourti Stathaki et al. 2016); hence, the ecological impact is probably negligible unless PTQ is somehow accumulated along an as yet unknown trophic sequence. Degradation products have not been identified as of now.

The well-known toxicity of PTQ to small and large mammals, as opposed to PTB, brings support to the notion that illudanes in brackens may have evolved as a result of biotic pressure, despite its passing presence in the developing plant. This perception is buttressed by two issues:

(i). The PTQ molecule includes two strategically situated electron-deficient carbons. Their reactivity increases sharply as the sugar moiety is removed leading to highly reactive electrophilic intermediates. These transient species are capable of forming adducts irreversibly with numerous cell nucleophiles essential to cell functioning, including amines, amino acids, proteins, nucleosides, RNA, and DNA (Yamada et al. 2007). These reactions create multiple genotoxic consequences including disruption, breakage and deletion of chromosome sections, gene mutations, immune cell disruption, cancer, and a variety of catastrophic biomolecular failures (e.g., Gil da Costa et al. 2012b). Only a well-tuned molecular design can achieve this array of activities in such a small molecular bullet, which strongly suggests the participation of modeling forces of natural selection.

(ii). The *Pteridium* genus is not alone in the production of PTQ. The occurrence of toxic illudanes closely similar to PTQ has been verified in a variety of ferns unrelated to the *Pteridium* clade (Pathania et al. 2012; Saito et al. 1989; Somvanshi et al. 2006). Chiefly, it is well documented that mammals consuming sizable quantities of bracken fronds rapidly develop crippling symptoms and die, thus diminishing herbivory stress on bracken stands. Chronic ingestion for several months leads to irreversible degenerative conditions and death to feeding animals. Herds can be decimated after several months while bracken withstands frond destruction, and rapidly recovers as the large mammals die off or learn to reject it.

(iii). This picture has its drawbacks, however. If it is true that chronic and acute toxicity caused by PTQ impacts livestock in many bracken infested areas around the world, cases of bracken poisoning among wild animals under natural conditions or in zoo captivity have been reported only rarely (e.g., Scala et al. 2014). Wild mammal herbivores avoid feeding on *Pteridium* ferns on account of poor nutrition value, high tannin content and other feeding deterrents, unless forced by food scarcity. PTQ is not reported to act as deterrent against invertebrates or possess known antibacterial/antifungal or allelopathic properties. Additionally, PTQ concentration is toxicogenically significant only in croziers and 2nd growth stage fronds, varying from zero up to 13 mg/g dw (Smith et al. 1994), but declines sharply in 3rd and 4th frond growth phases (Alonso-Amelot et al. 1992, 1995). This line of evidence speaks against PTQ acquiring the status of an evolutionary adaptive response to direct biotic threat, in spite that the many poisons in wild extant plants substantiate the thesis of coevolution between plants and animals. The multitrophic passage of this compound in livestock which damages and kills their suckling offspring, a property shared by other plant toxins (Panter and James 1990), occurs in such an extended time lapse that the feedback effect on the producing plant is lost. One might nevertheless argue that mechanical damage such as herbivory and equivalent forms of abiotic stress have an eliciting effect of PTQ accumulation. For example, it has been shown that cutting bracken croziers and blades or damaging rhizomes repeatedly as well as inducing root zone stress increases the PTQ content of subsequent fronds (Rasmussen et al. 2015).

These conflicting views led us to test the effects of a 1000 m altitudinal gradient (1100–2100 m asl) on [PTQ] in *PC* swards distributed within its natural ecological range in the Northern Andes. We selected five sites along the same M-gradient used in our frond growth studies described in Sect. 2.3 of this chapter (Figs. 2.7, 2.8, 2.9 and 2.10), adding two sites of compatible habitat characteristics at 1610 m in the exposed mountain savanna and an open parchment within the limits of a neighboring cloud forest at 2090 m along the same roughly linear cline. Because of the active changes in [PTQ] of younger fronds, only fourth-stage ramets (second pinnae P2) were analyzed. P2 provided healthy, undisturbed, sun-exposed representatives of the blades and enough tissue to analyze the expected small amounts of PTQ. In addition, while fronds were studied during the rainy season (May–August), care was taken to avoid sampling after rain events because of the previously annotated leaching. Also, fronds collected in the dry period of February–March were studied for reference, although the growth period, generally less profuse than the wet season, continued in undisturbed fields.

[PTQ]s were generally lower than anticipated from our previous assessment at a different location at 1850 m asl described above (Alonso-Amelot and Rodulfo-Baechler 1996). This result suggested that the environmental influence on bracken chemical performance is subjected to not only altitude but other independent factors to which plant metabolism is also responsive.

As Fig. 2.15 shows, there was a clear-cut descending trend in [PTQ] with elevation that could be represented tightly by a second-degree polynomial ($r^2 = 0.9952$). As regards to the PTQ response to dry and wet seasons, there was a minor contrast rated at 8.24 ± 0.8 and 3.6 ± 0.7 micrograms/g dw, respectively, at the 2090 m site. Attempts to pursue the quantification of PTQ in *PEA* at higher elevations met with

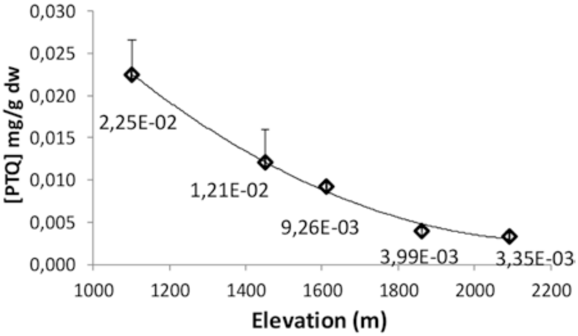

Fig. 2.15 Variation of ptaquiloside concentration ([PTQ)] (mg/g dw ± SD, $N = 9$ per site) in fully developed fourth-stage fronds of *Pteridium caudatum* along a 990 m elevational gradient between 1100 and 2090 m, in a hill of the Sierra Nevada de Merida, Venezuela. Sampling was performed during the rainy season (but avoiding rain during the previous 24 h to prevent PTQ leaching) at the same sites of the growth study described in Sect. 2.3 of this chapter, with two additional sites at 1610 and 2090 m asl put forward in the text. (Data from Alonso-Amelot et al. (2000) and additional records, 2003–2006)

failure owing to minute and highly variable quantities found in fourth-stage fronds that approached the analytical detection limit.

One may conclude that elevation reduces the capacity of mature fronds to produce and accumulate PTQ, probably as a result of metabolic constraints posed by lower temperatures found at the upper edge of *PC* ecological range.

This feature was also observed in a reduction of growth rates and biomass production of *PC* fronds in the same mountain gradient (Figs. 2.9 and 2.10). At the mature stage, there is a net translocation of photosynthase and minerals from the blade to the rhizome in preparation for future sprouting. If PTQ performs any xenobiotic protection against major herbivory as discussed earlier, it disappears at the mature stage for all practical purposes in the *PC* genets of the northern Andes and is of little value to *PEA* in this region and elevation owing to its very low [PTQ]. A more likely ecological model would be that mammal herbivores are sickened by *PC* and *PEA* after consuming younger and softer bracken fronds with a higher load of PTQ, once bitter compounds there like prunasin have waned and tissues become more palatable. Mature ramets resort to other protection alternatives such as reducing nutrient amount and quality by translocation, accumulation of tissue-hardening lignin, and an assortment of deterrent phenolics (Sect. 2.5.3) so herbivores chose other resources after a few testing morsels While there is a clear correlation between the prevalence of no-PTQ bracken genets and absence of bracken poisoning in overlapping mammals and/or health degradation, as reported for *P. esculentum* in New Zealand (Rasmussen et al. 2008), there is no biological evidence of increases of herbivory damage in fronds with lower PTQ content. Other physiological effects in potential natural enemies of bracken ought to be found before further ecological conjectures about [PTQ] dynamics with frond ontology, elevational gradient stresses, and impingement on plant fitness can be advanced.

2.17 Polyphenolics in Neotropical Brackens and Elevation

Monomeric and polymeric phenolics, belonging to an ubiquitous family of secondary metabolites in the plant kingdom, are synthesized and accumulated in various plant organs, not only as a result of physiological, structural or biotic defense needs (Bryant et al. 1991) but also under the influence of extrinsic forces (Waterman and Mole 1989; Naikoo et al. 2019). Among these, accidental injury, water stress, extremes of cold, and solar electromagnetic radiation appear as the most powerful inducers (Lovelock et al. 1992; Sharma et al. 2019). The added injury of UV-prompted oxidative damage further enhances the production of specific, well-known antioxidant phenylpropanoids (Martinez et al. 2016) including flavonols, p-hydroxycinnamic, coumaric, ferulic, caffeic and protocatechuic acids, as well as proanthocyanidins, also reported in Pteridium ferns (Glass and Bohm 1969) and known to be seasonally variable (Vysochina et al. 2012).

One of the main abiotic sources of stress to plants associated to elevation is UV-B sun radiation (280–320 nm). Typically, vascular plants are known to develop a series of convergent strategies for protection against this environmental aggression (Tevini and Teramura 1989). Many plants create protective shields in exposed tissues to reduce the penetration of destructive UV radiation to susceptible cell organs including photosystem II proteins and DNA (Britt 1996; Stapleton et al. 1997).

2.17.1 Altitudinal Stress Related to Increasing UV-B Solar Radiation Energy

It is well known that altitudinal, as well as latitudinal gradients cause steep UV radiation increases (e.g., Caldwell et al. 1980). For example, Blumthaler et al. (1992) observed an increase of 11% per 1000 m elevation of UV-B solar radiation annual flux when comparing measurements at 577 and 3576 m asl in western Austria. Increases of 20%/1000 m UV-B direct solar radiation have been reported in an altitudinal gradient up to 5500 m asl under the clear skies of the deserts of northern Chile at the Tropic of Capricorn at summer peak months of January and February (Piazena 1996). Predictably, solar ultraviolet radiation is strongly modulated by cloud scattering. We tested this effect at noon in 2 days of contrasting cloud cover (August), at the *paramo* bracken site of 3100 m asl, using a data logging UV photometer (320–380 nm) fitted with a semispherical optical diffuser and recorded 3.02 mW cm^{-2} in a cloudless day in contrast to only 0.52 mW cm^{-2} under heavy clouds, an 82% reduction. From this perspective, the cloud cover changes registered in the plots of Figs. 2.11a and 2.12 acquire special relevance, assuming that the recorded visible spectrum (400–700 nm) is proportional to the UV-B radiation reaching the plants at the same site.

2.17.2 Exploring the Intervening Factors of Phenolic Production in Neotropical Bracken

The task of establishing associations between elevation and phenolic accumulation in Pteridium fronds was not a simple one considering the number of potential modulating factors: leaflet transmittance in the UV-B, frond ontogeny as a whole, differential contribution of pinnae, self-shading versus sun-exposed tissues, water stress and bracken species, *PC* and *PEA* in our case, in reference to their ecological distribution governed by elevation, as discussed previously. Because it was not feasible to study all these variables in bracken wild populations in distant sites along our Andean gradients, we examined these intervening factors one at a time.

2.17.2.1 UV-B Absorbance of Leaflet Epidermis

Our first indication that brackens from the northern Andes growing at high altitude developed chemically based UV-B filters was the comparatively strong light absorbance we recorded in isolated epidermises of *PC* and *PEA* segments from blades at mid-elevation (1850 m) and *PEA* at high altitude (3100 m). The obstruction to epidermal transmittance has been studied in other plants as a response to enhanced UV-B radiation (e.g., Robberecht and Caldwell 1978). Using their technique, we prepared tissues that included epidermis and cuticle ($N = 10$ per site and species) by mechanically removing the parenchyma from the middle section of the segment and placing the wet sample on the inner wall of a quartz cell under the collimated light beam of a UV spectrometer set at 300 nm (Arellano 2003). Then, each epidermis was washed with water-methanol-hydrochloric acid to remove phenolic materials and the light absorbance was read again. The compiled results of Table 2.11 show that:

(a) The 300 nm radiation was captured more effectively by epidermises of *PEA* than in *PC* at the same elevation (1850 m). It was pointed out earlier in this chapter that the segments of both species at this location form one row of epidermal cells under the cuticle, so the difference in UV-B absorption was likely due to the UV-active chemical components of the large vacuoles of these cells and/or such compounds bonded to the cell walls.

(b) This notion was confirmed by two sources of evidence: (i) Once compounds were removed by methanolic acid treatment, light transmittance increased markedly (Table 2.11, WMA entries), and (ii) transversal slices of segments exposed to aqueous acidic ferric chloride, ferric sulfate, or Prussian blue reagent and observed under 400× magnification showed a densely dark cellular matrix of epidermal and palisade cells, a reaction expected for the oxidation of phenolic material stored in vacuoles, caused by these reagents. This effect was observed in all *PC* and *PEA* samples to a different extent but was particularly noticeable in *PEA* from the *paramo* site at 2950 m asl (Alonso-Amelot et al. 2004a). This finding was in line with the strong UV-B filtrating power of the

Table 2.11 Absorbance (300 nm) of epidermises isolated from the middle section of bracken fern segments excised from fourth-stage fronds

Entry	Bracken sp	Site elevation (m asl)	Treatment	Absorbance (AU, 300 nm)	*p*
1	PC	1850	None	0.31 ± 0.10	1 vs 2: 0.003
2	PC	1850	WMA	0.21 ± 0.09	–
3	PEA	1850	None	0.44 ± 0.15	1 vs 3: 0.013
4	PEA	1850	WMA	0.26 ± 0.11	3 vs 4: 0.003
5	PEA	2950	None	1.13 ± 0.17	3 vs 5: 0.000
6	PEA	2950	WMA	0.89 ± 0.22	5 vs 6: 0.003

Bracken species: *PC Pteridium caudatum*, *PEA Pteridium esculentum* subsp. *arachnoideum*, *WMA* water-methanol-hydrochloric acid
Data from Arellano (2003)

mono- and polyaromatic molecular sections of plant phenolics stored in leaf cuticles (Krauss et al. 1997), and the fact that the biosynthesis of these compounds in plants is activated by UV-B radiation (e.g., Jaakola et al. 2004; Li et al. 2010).

2.17.2.2 Synthesis-Accrual of Phenolics in Bracken, Electronic Spectra, and Frond Stage

Bracken ferns synthesize a series of monomeric flavonoid glycosides, their aglycones, and aromatic acids, in addition to polymeric phenolics (proanthocyanidins) and lignins (e.g., Tanaka et al. 1993; Jatoba et al. 2016; Knuesting et al. 2018). We grouped them into low and high molecular weight phenolics, LMP and HMP, respectively, to facilitate pattern interpretation. Substantial amounts of quercetin, kaempferol, rutin, luteolin, and apigenin (LMPs) found in Andean *PEA* (Knuesting et al. 2018) show spectral maxima in the order of 340–360 nm, well within the UV-A/B boundary, hydroxycinnamic acid derivatives at 330 nm. Condensed tannins (HMPs), with a shoulder shifted to lower wavelengths (270 nm), still display generous absorption in the 300–320 nm range (Jurasekova et al. 2006; Likhanov 2014). The accumulation of these compounds would thus be expected to offer an effective screen against solar UV-B radiation in high altitude.

LMP and HMP could be separated by size exclusion chromatography and studied as individual sets. In order to determine the dynamics of phenolic compounds for selecting the best representative frond of *PC* and *PEA*, the change of LMP and HMP groups' load across the frond growth stages was analyzed in the sympatric swards at the 1850 m asl site near the riparian forest of the Albarregas river in Merida, Venezuela. Except for croziers, each freshly collected frond ($N = 8$ per stage) was split in two equal halves along the middle rib. One side was processed for exhaustive phenolics extraction by aqueous-acetone sonication of an equal number of pinnulae randomly cut from the lateral pinnae, followed by exclusion chromatography of aliquots through Sephadex and application of Folin–Ciocalteu spectral quantitation against pertinent calibration curves based on salicylic acid and quebracho tannic acid standards for LMP and HPM, respectively (Alonso-Amelot et al. 2004b).

The results in Table 2.12 illustrate that LMP content increased about 290% at growth stage 4 relative to the crozier phase in *PC* and 425% in *PEA*, but were statistically distinct only in the mature fronds. There is an average of 28 and 45 days between first– and fourth-stage fronds in both bracken species, which might explain the enhanced phenolic concentration. As for HMP content, there was a steeper increase in *PEA* as compared with *PC*, and a statistical difference from the first-stage onwards. It may be concluded safely that *PEA* is better prepared for resisting the UV-B aggression at altitudes higher than that of the test site.

Table 2.12 Variation of low and high molecular weight phenolics (LMP and HMP) with phenological frond stage in two sympatric swards of *Pteridium caudatum* (PC) and *P. esculentum* subsp. *arachnoideum* (PEA) at 1880 m asl near the Albarregas river course in Merida, Venezuela, in June, 3 months into the rainy season

Stage		LMP			HMP	
	PC	PEA	*p*	PC	PEA	*p*
1	5.54 ± 0.87	5.86 ± 0.49	0.636	1.91 ± 0.37	5.34 ± 1.36	0.0008
2	13.88 ± 2.20	10.88 ± 1.78	0.294	4.70 ± 0.69	16.49 ± 1.40	0.0008
4	15.72 ± 1.17	25.00 ± 2.18	0.003	9.93 ± 1.06	32.39 ± 4.17	0.0008

N = 8 per growth stage and species. LMP is expressed in mg/g dw equivalents of salicylic acid and HMP in mg of quebracho tannin equivalents/g dw. Comparison of the means was performed with the Mann–Whitney test. (Alonso-Amelot et al. 2004b)

2.17.2.3 LMP and HMP and Sun Exposure

We pointed out above that a substantial body of literature supports the induction of phenolic synthesis in plants by sunlight in general and its UV-B component in particular. Bracken fronds have evolved a crown shape for effective exposure of most, if not all of its photosynthesizing segments to ambient light at various sun elevations during the circadian cycle, owing to the dome-like shape that is transversally displayed by all bracken fern species. In spite of this architectural perfection, there are two drawbacks: (i) The second pair of pinnae P2 expands diagonally above the first pair P1 casting a partial shade on the latter, and (ii) the large ramet density in mature swards, frequently exceeding 7 fronds per m^2, creates a self-shading (SS) effect of low and mid-pinnae. The permanence of dead sessile fronds in the thicket accentuates SS of living blades.

In order to perfection the final experimental design of the elevational gradient influence on bracken phenolics synthesis and run a most adequate sampling, we tested the bracken phenolics response to sunlight under three conditions: (1) the effect of shade cast by neighboring high canopy plants; (2) the SS impact of pinnae along the blade rachis, and (3) the SS influence of neighboring bracken blades. We used the *PEA* model owing to the larger amount of phenolics produced by this species (Alonso-Amelot et al. 2007), considering the following points:

1. Shading by other plants: one group of mature PEA fronds was collected from a 2-m-wide ecotone band of the grass/riparian forest line at 1850 m asl, which received direct sunlight during about 30% of the daylight period, according to field loggers. A second set of samples were excised about 10 m away in the fully sun-exposed meadow. In parallel, a *PC* sward was equally tested at its lowest ecological range over a small hill at 100 m asl in the megathermic lowlands of Lake Maracaibo at the base of the Andean range of Venezuela. Both were sufficiently humid habitats so no water stress was apparent. Figure 2.16 shows that these brackens differed in content and response to partial shading by other plants. Phenolics of both types in *PEA* were produced in much lesser amount as a result of shade, reacting more intensely to sunlight, but there was a parsimonious accumulation of phenolics under both sun-exposed and shaded *PC* fronds.

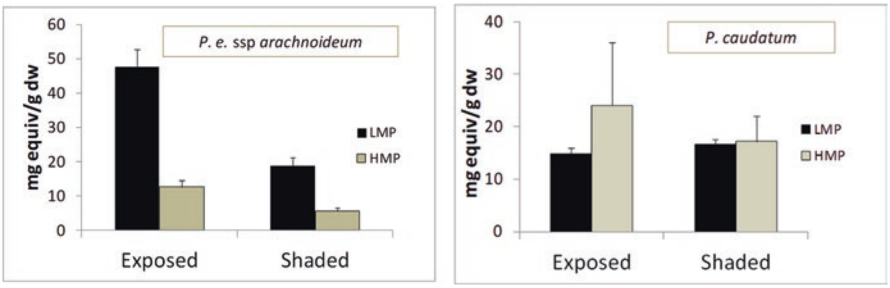

Fig. 2.16 Contents of low and high molecular weight phenolics (LMP and HMP, respectively), in *P. esculentum* subsp. *arachnoideum* (Alonso-Amelot et al. 2007) and *P. caudatum* (Oliveros-Bastidas and Alonso-Amelot, unpublished) in sun exposed and partially shaded stands by nearby vegetation. Both swards were selected at their low elevation ecological range: PEA at 1850 m asl in a humid temperate cul-de-sac close to the riparian forest of the Albarregas river and *PC* at 100 m asl in a hill by the humid megathermic lowlands of Lake Maracaibo, in western Venezuela, both collected in October, during the second peak of the bimodal rainy season

Cloudiness in the rainy season when sampling was performed (October) is particularly dense along the northwestern flank of the Venezuelan Andean range as a result of persistent moisture and heavy rain brought about by trade winds from the Caribbean, blocking the effects of direct sunlight over the plants. This effect was especially noticeable in the lowland site (100 m asl). By contrast, the barrier of the northwestern sierra protecting the inner Andean valley of the Albarregas river furnishes more frequent clear skies and more time of unimpeded sunlight during this period. At any rate, *PC* secondary metabolism yielded lesser quantities of both LMPs and HMPs under the same sun-exposed conditions at 1850 m asl while the concentration of these compounds in mature fronds was comparable to those found at 100 m asl (Table 2.12 and Fig. 2.16).

2. Self-shading by the upper pinnae over the lower blade surfaces was tested by measuring the LMP and HMP synthesis/accumulation. Pinnulae sections were excised from P1 to P4 pinnae assuming increased exposure of the segments towards the upper rachis and analyzed for phenolic content in samples from various elevations. At middle altitudes (<2200 m), there was a modest increase in LMP and HMP content from P1 to P4 in both bracken species, but it became increasingly noticeable as elevations approached the ecological limit of *PEA* bracken species (Fig. 2.17). UV-B radiation is the most likely promoter of this change along the rachis gradient since the upper pinnae (P3 and P4) unfolded a few weeks after the lower pinnae and were supposed to have *less* phenolic material.

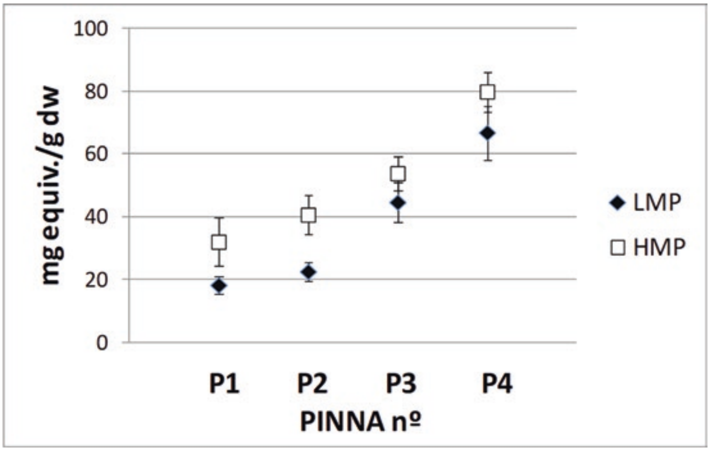

Fig. 2.17 Change in LMP and HMP content of *Pteridium esculentum* subsp. *arachnoideum* pinnae from bottom to top (P1 to P4) of the blade, at a humid *paramo* sward (3190 m asl) during the rainy season. Error bars: standard error of the means, *N* = 12. (Alonso-Amelot et al. 2007)

2.17.2.4 LMP and HMP and Elevation in PC and PEA

Once the best sampling choice of frond growth stage (4th) and frond part (P4 and above) had been determined, two elevational transects were established using the same sites employed for the previous studies of *PC* and *PEA* described earlier in this chapter (Sects. 2.3 and 2.4, respectively). Only mountain sites were surveyed, leaving aside the lower extreme at the Maracaibo Lake basin, because of the unknown effects of the megathermic climate at the base of the Andean range in which *PC* appears only occasionally and is subjected to abiotic and biotic influences that require separate research efforts.

LMP and HMP were analyzed systematically near the end of the rainy season (November) when the great majority of fronds in the bracken thickets reached the mature stage and had been sufficiently exposed to abiotic influences, away from resource constraints imposed by growth.

The results of the phenolic surveys in both species shown in Fig. 2.18 (Alonso-Amelot et al. 2007) led to the following conclusions:

1. Plot A, *PC*: the accumulation of LMP (filled markers) composed by flavonoids, hydroxycinnamic, and hydroxysalicylic acid derivatives was not decidedly associated with altitude across the length of the elevational transect. Some of these compounds are sufficiently soluble in water to be released from the fronds (and rhizomes) by rain and participate in the allelopathic potential of brackens (e.g., Gliessman 1976; Gliessman and Muller 1972; Jatoba et al. 2016). Although frond litter is the major donor of allelopathic compounds in temperate regions, fresh fronds also contribute to the overall allelopathic load of soil beneath the *PC* stands in tropical areas as shown in Costa Rica (Gliessman 1976). By contrast, HMP represented by proanthocyanidins, a group of condensed tannins, was

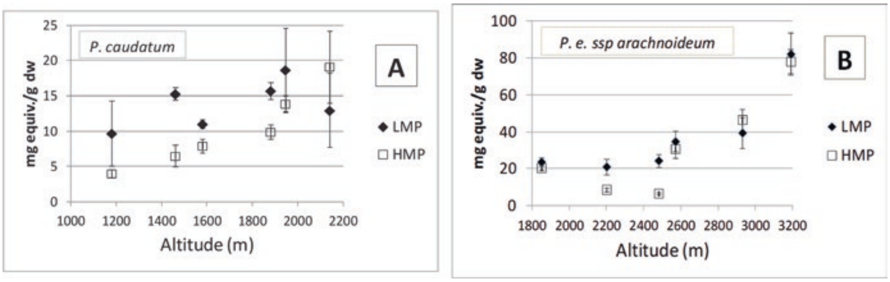

Fig. 2.18 (**a**, **b**) Changes in the concentration of low and high molecular weight phenolics (LMP and HMP, respectively) with altitude of *Pteridium caudatum* and *P. esculentum* subsp. *arachnoideum* in their respective ecological range in two independent elevational transects of the central Andes of the Cordillera de Merida, Venezuela. Error bars are standard errors of the means (*N* = 6 fronds per site. Sampling details are given in the text. (Data from Alonso-Amelot et al. (2004b))

steadily accumulated in increasing amounts with elevation (square markers), despite their moderate water solubility. The acidic ferric sulfate and chloride visualization of these compounds mentioned earlier in this chapter located them in the vacuoles of mesophile cells, out of reach from rainwater. However, incorporation into the soil occurs eventually as withered fronds are slowly degraded.

2. Plot B, *PEA*: the content of both phenolic types remained relatively constant in populations up to 2600 m asl, but increased noticeably from there to the humid *paramo* elevation near the freezing line at 3200 m, where many plant species produce phenolic materials to filter off excess UV-B radiation and quench free radical species from this cause owing to the antioxidant properties of polyphenolics (Martinez et al. 2016).

The limited capacity of *PC* for the synthesis of phenolics-based UV protecting filters is likely to be behind the lack of competence for the colonization of elevations higher than 2200 m unless it is shaded as an understory element in the cloud forest structure. Up to now, there are no reports of such colonies in the Tropical Andes and Mesoamerican mountain ecosystems, to the best of our knowledge.

The large accumulation of proanthocyanidins in high-altitude *PEA* rises to the fore the enhanced antiherbivore protection (Tempel 1981) against abundant *paramo* grasshoppers in addition to the added allelopathic potential of this species to become a dominant newcomer to this delicate environment, already threatened by increasing anthropogenic activity.

2.17.2.5 Influence of Elevation, Solar Radiation, and Water Stress Combined in PEA

Plant phenolics are known to be influenced by water stress (Kumar et al. 2020a), a feature widely employed by the fruit and wine industries to modulate flavor. Plants derive benefits from the enhanced synthesis of phenolics in dry months to gain protection against increased solar radiation and attacks by non-adapted herbivores during the summer months. We became interested in testing the induction of phenolics under the combined effect of water deficit, elevation, and self-shading on the basis of the acquired experience in high-altitude *PEA* described earlier. Thus, we analyzed LMP and HMP phenolics groups at the three sub-*paramo* and *paramo* highest sites in the Cordillera de Merida, with sampling periods in October (rainy season) and February (dry season). The sun angle along the daily course is the same in these two periods around the winter solstice, while air temperatures remained within similar limits. Dense *PEA* thickets frequently expanded their lower pinnae P1 and P2 below the sward canopy. In the surveyed sites, P1 received only an average of 26.9% of the full solar radiation (400–700 nm) relative to the upper pinnae during the circadian cycle in February, which was assumed to be proportional to the reduction in UV-B component. Therefore, live pinnulae excised from P1 and P4 to blade meristem were organized as self-shaded (SS) and sun-exposed (SE) sample groups, and collected during rainy (R) and dry (D) seasons at the three upper locations. Samples were paired to manage comparisons in the same blade.

The results of the influence of the three environmental factors impinging on LMP and HMP of Fig. 2.19 clearly show that:

1. Both LMP and HMP are produced and stored in higher concentrations during the dry season, be it in sun-exposed (E) or self-shaded (SS) pinnulae. The response of the latter was nevertheless more modest.
2. Biosynthesis of both phenolic types in (E) pinnulae improved with elevation, in consonance with the experiment of Fig. 2.18, although this trend was no longer observable in the dry period.
3. There was no LMP response of SS to elevation during the wet season but it became apparent in the dry season when a number of fronds decay into wilting

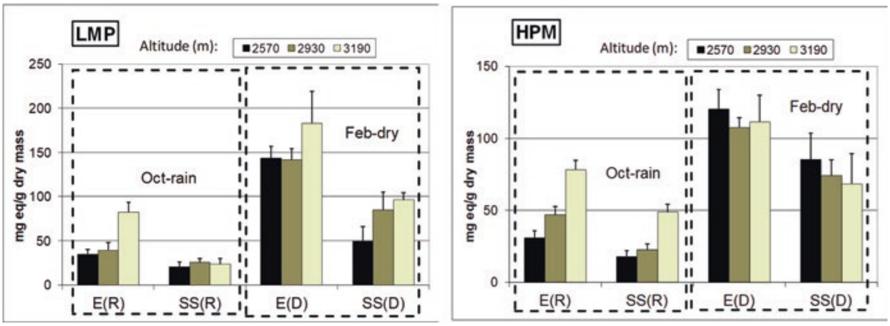

Fig. 2.19 Profile of low and high molecular weight phenolics (LMP and HMP) of fronds of *Pteridium esculentum* subsp. *arachnoideum* from locations around the highest elevational range of this plant in the Neotropics, collected in the second peak of the rainy (R) season (October) and the driest month of the year (D) (February). Details of the sampling area are provided in the text. Frond pinnae were divided into two sections for polyphenolic analyses: sun exposed (E), upper part of the blade crown and self-shaded (SS) lower P1 pinnae. Average ± SE, $N = 12$ per site and season. (Data from Alonso-Amelot et al. (2007))

and the thicket self-shade declines, leading to higher doses of solar UV-B penetrating into the herbage below the fronds' canopy.

4. Plants at lower elevations (data not shown) furnished comparable LMP contents, whereas at higher altitude (>2400 m asl) showed a trend towards increased E/SS differences favoring the exposed pinnulae. This effect was attributed to the increasing UV-B radiation energy reaching the earth surface from this elevation upwards.
5. The combined effects of water stress, UV-B exposure related to elevation, and screening by self-shading furnished a trend towards higher accumulation of LMPs in live pinnulae but HMP levels were independent of elevation in the dry season and their increase obeys chiefly to water stress.

Taken together, the dynamics of phenolic materials in mountain brackens in the Neotropics accommodates well to the established ecological model of biosynthesis by external elicitors and multiple tasks extending from physiological needs of the producer organism to protection against environmental abiotic and biotic aggression.

2.18 Concluding Remarks

High Neotropical mountains are steep geographical gradient generators of major interest to geophysics, climatology, biology, ecology, and chemistry. These masses of earth crust create a unique combination of a wide range of elevations and life zones in a north–south direction cutting across the prevailing low-altitude continental winds, and enabling the growth of a gamut of plant forms and animals of enormous species diversity. Members of these communities have evolved unique adaptation strategies for prospering in the prevailing conditions ranging from the megathermic lowlands to the cryozones of the hyperparamo and the high summits. The term *biodiversity hot spots* in these mountains has been popularized by science reaching the man on the street with an interest in the astounding workings of biological systems of our planet.

While plants become organized in clearly visible vegetation bands under the commands of the many abiotic elements associated with altitude, some species have developed ways to occupy and become encroached successfully in a number of life zones, from foothills to *paramos,* offering conditions generally forbidden for a single species or genus. A handful of plants do manage to achieve this, however, and two species of the Neotropical *Pteridium* clade, *PC* and *PEA* not only grow robust swards along extended altitudinal gradients and plant community types, but attain the notorious echelon of invasive and dominant species wherever they appear some years after their first arrival to new territory.

Bracken ferns are representatives of 15 species of the Dennstaedtiaceae clade spread ubiquitously in five continents with a common architectural frond design. All of them share the status of persistent invaders of shady northern forests understory, sun-bathed grasslands, cold moors, and shrublands as long as the soil resources are not constrained by extremes of temperatures and water.

In temperate zones, bracken fronds die off after the first autumn frosts only to come back in force the following spring. Wilted swards are flattened by winter storms and snowfall. But in the Neotropics where the winter of temperate regions does not exist but a continuum regime of altitudinally ruled temperatures only broken by rain-no rain seasons, bracken fronds grow all year round with a relatively short pause of crozier sprouting during the dry periods. Swards grow to dense thickets mixing live and standing wilted fronds that occupy the land, hence hampering the germination and development of other seedlings.

Studying the domination strategies brackens are endowed with has become an appealing area of research for nearly 80 years since it was realized that cattle browsing these ferns developed a lethal condition known as bracken poisoning. The Andes of Merida in western Venezuela was the first place in South America to explore the ecological chemistry of the two Neotropical brackens in the 90's. Since then, other research institutions in the northern Andes countries, Costa Rica, and Mexico have come into the fray and expanded enormously the current knowledge of these survivor ferns which have been around—since the Cretaceous period—well before the Andean range emerged from the western edge of the South American continent. Therefore, brackens had a great deal of time to evolve survival strategies as mountains were lifting literarily under their rhizomes, while preserving most of its traits and general appearance.

In the meantime, some insects and vertebrates turned to brackens as food sources and developed exploitation strategies. Although paleontology does not give us a fossil record of plants biochemistry, biotic-ecological pressure must have favored genets with the capacity to generate synthetic routes for bioactive xenobiotics in brackens, as well as in many other vascular plants species. Similarly, pressure for the territorial expansion of plant and animals and lower population densities at higher elevation may have driven brackens to occupy higher territory and develop new capacities only limited by genetic expression of functional proteins, secondary metabolism, resource allocation ability in the rhizome-frond photosynthase interplay, and physical robustness, pursuing acclimation and adaptation to the increasingly stringent environmental conditions of higher elevation. These differences must have been instrumental for the success of the said acclimation–adaptation of *PC* and *PEA*. Partition of the territory divided by an altitudinal belt between lower and higher land and its many factors was the end result of separate dominance of these two bracken species. The first of these brackens found ways to enhanced fitness by tolerance to megathermic and temperate climates of tropical hillsides and mountains below 2100 m asl, compensated the limited short-term herbivory of insects by rapid frond growth and maturation to render photosynthase to rhizomes, and long-term protection against major herbivores through a variety of illudanes, resistance to withering during dry spells and a sufficiently large allocation of phenolics to fronds to fend off the high competition of heliophile forbs of exposed hills through suffocation, soil resource sequestration through the extended root–rhizome system, and allelopathy. On its part, the genetic expression of *PEA* conferred an enhanced resistance to altitude up to the night frost line that *PC* was unable to produce, through a highly dynamic resource allocation to larger frond growth, rhizome robustness, and secondary metabolism, particularly exhibited in the LMP/HMP interplay.

In recent decades, brackens have taken advantage of these tremendous biological capabilities to invade and expropriate large tracks of Andean land formerly inhabited by profuse vegetation, now converted into fragmented habitats, primary forest relics among agriculture, pastures, and grassland for cattle husbandry in addition to uncontrolled wildfires stemming from land clearance burning. The current planet warming trend is predicted to rise the night frost line, opening further opportunities for *PEA.* to expand its upper frontier into the receding *paramo*, thus threatening to impoverish the delicate vegetation forms of this unique ecosystem.

In spite of the many advances in the area of bracken acclimation to the challenges of Neotropical Andean gradients, a large number of questions remain unanswered for bracken science to solve in the coming years.

References

Agarwal K, Haldar S, Boland W, Venkatesan R (2018) Chemical ecology of bracken ferns. In: Nowicki L, Kowalska A (eds) Ferns. Nova Science Pub, Hauppauge, Chapter 2, pp 57–96

Akomolafe GF, Rahmad ZB (2018) A review of global fern invasions: mechanisms, management and control. J Res For Wildl Environ 10:42–54

Alexander JM, Lembrechts JJ, Vacieres LA, Daehler C, Haider S et al (2016) Plant invasions into mountains and Alpine ecosystems: current status and future challenges. Alp Bot 126:89–103

Alonso-Amelot ME (2002a) The chemistry and toxicology of bioactive compounds in bracken fern (*Pteridium* spp) with special reference to chemical ecology and carcinogenesis. In: Rahman A-u (ed) Studies in natural products chemistry, vol 26. Elsevier, Amsterdam, pp 685–740

Alonso-Amelot ME (2002b) High-altitude plants, chemistry of acclimation and adaptation. In: Rahman A-u (ed) Bioactive natural products (part N), studies in natural products chemistry, vol 34. Elsevier, Amsterdam, pp 883–892

Alonso-Amelot ME, Avendaño M (2002) Human carcinogenesis and bracken fern: a review of the evidence. Curr Med Chem 9:675–686

Alonso-Amelot ME, Oliveros-Bastidas A (2000) A method for the practical quantification of cyanogenesis in plant material. Phytochem Anal 11:309–316

Alonso-Amelot ME, Oliveros-Bastidas A (2005) Kinetics of the natural evolution of hydrogen cyanide in neotropical *Pteridium arachnoideum* and its ecological significance. J Chem Ecol 31:315–331

Alonso-Amelot ME, Rodulfo-Baechler S (1996) Comparative spatial distribution, biomass, and growth rate of two varieties of bracken fern (*Pteridium aquilinum* L. Kuhn) in a neotropical montane habitat. Vegetatio 125:137–147

Alonso-Amelot ME, Perez-Mena M, Calcagno MP, Jaimes Espinoza R, Castillo U (1992) Ontogenic variation of biologically active metabolites of *Pteridium aquilinum* (L., Kuhn), pterosins A and B, and ptaquiloside in a bracken population of the Tropical Andes. J Chem Ecol 18:1405–1420

Alonso-Amelot ME, Castillo U, De Jongh F (1993) Passage of the fern carcinogen ptaquiloside into bovine milk. Lait 3:323–332

Alonso-Amelot ME, Rodulfo-Baechler S, Jaimes Espinoza R (1995) Comparative dynamics of ptaquiloside and pterosin B in the two varieties (*caudatum* and *arachnoideum*) of neotropical bracken fern (*Pteridium aquilinum* L. Kuhn). Biochem Syst Ecol 23:709–716

Alonso-Amelot ME, Castillo U, Smith BL, Lauren DR (1996) Bracken ptaquiloside in milk. Nature 382:587

Alonso-Amelot ME, Calcagno Pisarelli MP, Perez Inojosa M (2000) Growth and selective defensive potential in relation to altitude in neotropical *Pteridium aquilinum* var *caudatum*. In: Taylor JA, Smith RT (eds) Bracken fern, toxicity, biology, and control. International Bracken Group Special Publication, Manchester, Chapter 6, pp 43–47

Alonso-Amelot ME, Oliveros A, Calcagno-Pissarelli MP, Arellano E (2001) Bracken adaptation mechanisms and xenobiotic chemistry. Pure Appl Chem 73:549–553

Alonso-Amelot ME, Oliveros A, Arellano E, Calcagno MP (2004a) Histochemical studies of bracken fern: localization of phenolic and tannin defenses in bracken accessions along an altitudinal gradient in the neotropics. In: Acamovic T, Stewart CS, Pennycott TW (eds) Poisonous plants and related toxins, chapter 36. CABI Publishing, Glasgow, pp 241–247

Alonso-Amelot ME, Oliveros A, Calcagno-Pissarelli MP (2004b) Phenolics and condensed tannins in relation to altitude in neotropical *Pteridium* spp. a field study in the Venezuelan Andes. Biochem Syst Ecol 32:969–981

Alonso-Amelot ME, Oliveros-Bastidas A, Calcagno-Pissarelli MP (2007) Phenolics and condensed tannins of high-altitude *Pteridium arachnoideum* in relation to sunlight exposure, elevation and rain regime. Biochem Syst Ecol 35:1–10

Anderson C, McShea DW (2001) Intermediate-level parts in insect societies: adaptive structures that ants build away from the nest. Insect Soc 48:291–301

Aranguren A, Andressen R, Henao A (2012) El clima estacional del cinturón montano en el Estado Merida-Venezuela. Revista Geográfica Venezolana 53:187–212

Arellano EJ (2003) Propiedades ecomorfologicas y químicas de adaptación de plantas a condiciones extremas de alta montaña. MSc. Degree Thesis. Group of Chemical Ecology, Faculty of Sciences, University of Los Andes, Merida, Venezuela. pp 205. http://bdigital.ula.ve/documento/25522

Ataroff M, Rada R (2000) Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. Ambio 29:440–444

Ataroff M, Sarmiento L (2002) Unidades ecológicas de los Andes de Venezuela. In: La Marca E, Soriano P (eds) Reptiles de los Andes de Venezuela. Fundacion Polar, CODEPRE-ULA, FUNDACITE, Fundacion Biogeos, Merida, pp 9–25

Auld TD, Bradstock RA (1996) Soil temperatures after the passage of fire: do they influence the germination of buried seeds? Aust J Ecol 21:106–109

Avila-Nuñez JL, Otero LD (2013) Insectos sobre cayados del helecho invasor *Pteridium caudatum* en los Andes venezolanos. Entomotropica 28:99–102

Avila-Nuñez JL, Otero LD (2019) Entomofauna asociada a especies de helechos *Pteridium* (Pteridophyta: Dennstaedtiaceae) en el Cerro de la Bandera de los Andes venezolanos. Ecotropicos 31:e0006

Avila-Nuñez JL, Otero LD (2020) Structures built by *Solenopsis geminata* (Fabricius 1904) near fern nectaries. Entomotropica 35:15–20

Avila-Nuñez JL, Otero LD, Silmi S, Calcagno-Pissarelli MP (2007) Life history of *Aneugmenus merida* Smith (Hymenoptera: Tenthredinidae) in the Venezuelan Andes. Neotrop Entomol 36:22–27

Avila-Nuñez JL, Otero LD, Naya M, Calcagno-Pissarelli MP (2008) Herbivory on bracken (*Pteridium* spp.) by *Bolax palliata* Burmeister (Coleoptera, Scarabaeidae), a polyphagous beetle of the Venezuelan Andes. Neotrop Entomol 37:741–743

Ayala-Luis KB, Hansen PB, Rasmussen LH, Hansen HCB (2006) Kinetics of ptaquiloside hydrolysis in aqueous solution. Environ Toxicol Chem 25:2623–2629

Bader MY, van Geloof I, Rietkerk M (2007) High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. Plant Ecol 191:33–45

Balick MJ, Furth DG, Cooper-Driver G (1978) Biochemical and evolutionary aspects of arthropod predation on ferns. Oecologia 35:55–89

Barros A, Monz C, Pickering C (2015) Is tourism damaging ecosystems in the Andes? Current knowledge and an agenda for future research. Ambio 44:82–98

Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) (2008) Gradients in a tropical mountain ecosystem in Southern Ecuador. Springer-Verlag, Berlin/Heidelberg

Beerling DJ, Chaloner WG (1992) Stomatal density as an indicator of atmospheric CO_2 concentration. The Holocene 2:71–78

Beerling DJ, Chaloner WG (1993) The impact of atmospheric CO_2 and temperature changes on stomatal density: observation from *Quercus robur* lammas leaves. Ann Bot 71:231–235

Bernays EA, Chamberlain DJ, Leather EM (1981) Tolerance of acridids to ingested condensed tannin. J Chem Ecol 7:247–256

Bernays EA, Chamberlain DJ, Woodhead S (1983) Phenols as nutrients for phytophagous insect *Anacridium melanorhodon*. J Insect Physiol 29:535–539

Blumthaler M, Ambach W, Rehwald W (1992) Solar UV-A and UV-B radiation fluxes at two alpine stations at different altitudes. Theor Appl Climatol 46:39–44

Blüthgen N, Feldhaar H (2010) How resources influence ant ecology. In: Lach L, Parr CL, Abbott K (eds) Ant ecology. Oxford University Press, Oxford, pp 155–136

Bray JR (1991) Growth, biomass and productivity of bracken (*Pteridium esculentum*) infested pasture in Malborough Sounds, New Zealand. N Z J Bot 29:169–176

Britt AB (1996) DNA damage and repair in plants. Ann Rev Plant Physiol Plant Mol Biol 47:75–100

Bryant JP, Kuropat PJ, Reichardt PB, Clausen TP (1991) Controls over the allocation of resources to chemical antiherbivore defense. In: Palo RT, Robins CT (eds) Plant defenses against mammalian herbivory. CRC Press, Boca Raton, pp 83–102

Buytaert W, Celleri R, De Bievre B, Cisneros F, Wyseure G, Deckers J, Hofstede J (2006) Human impact on the hydrology of the Andean paramo. Earth Sci Rev 79:53–72

Cabrera HM, Rada F, Cavieres L (1998) Effects of temperature on photosynthesis of two morphologically contrasting plant species along an altitudinal gradient in the tropical high Andes. Oecologia 114:145–152

Calcagno MP, Avila-Núñez JL, Rudman I, Otero LD, Alonso-Amelot ME (2004) Food-dependent regurgitate effectiveness in the defence of grasshoppers against ants: the case of bracken-fed *Abracris flavolineata* (Orthoptera: Acrididae). Physiol Entomol 29:123–128

Calderon A, Mancebo B, Sanchez LM, Chiriboga X, Lucero D et al (2013) Niveles de ptaquilosido en muestras de leche bovina en granjas de San Miguel de Bolivar, provincia de Bolivar, Ecuador. Revista de Salud Animal 35:109–115

Caldwell MM, Robberecht R, Billings WD (1980) A steep latitudinal gradient of solar ultraviolet-B radiation in the Arctic-Alpine life zone. Ecology 61:600–611

Camacho LF, Aviles L (2019) Decreasing predator density and activity explains declining predation of insect pray along elevational gradients. Am Nat 194:334–343

Cardenas MF, Tobon C, Buytaert W (2017) Contribution of occult precipitation to the water balance of paramo ecosystems in the Colombian Andes. Hydrol Process 31:4440–4449

Cardenas S, Echeverry-Galvis MA, Stevenson PR (2021) Seed dispersal effectiveness by oilbirds (*Steatornis caripensis*) in the Southern Andes of Colombia. Biotropica 53:671–680

Carins-Murphy RM, Jordan GJ, Brodribb TJ (2017) Ferns are less dependent on passive dilution by cell expansion to coordinate leaf vein and stomatal spacing than angiosperms. PLoS One 12:e0185648

Chacon-Moreno E, Suarez del Moral P (2020) Mapa bioclimático de la Cordillera de Merida. Ecotropicos 32:e0010

Churchill SP (2009) Moss diversity and endemism in the tropical Andes. Ann Mo Bot Gard 96:434–449

Clauson-Kaas F, Jensen PH, Jacobsen OS, Juhler RK, Hansen HCB (2014) The naturally occurring carcinogen ptaquiloside is present in groundwater below bracken vegetation. Environ Toxicol Chem 33:1030–1034

Clauson-Kaas F, Ramwell C, Hansen HCB, Strobel BW (2016) Ptaquiloside from bracken in stream water at base flow and during storm events. Water Res 106:155–162

Codignola A, Maffei M, Fusconi A, Fieschi M (1987) Leaf anatomy of alpine plants as related to altitudinal stress. Nord J Bot 7:673–685

Cooper-Driver GA (1990) Defense strategies in Bracken, *Pteridium aquilinum* (L.) Kuhn. Ann Mo Bot Gard 77:281–286

Cooper-Driver GA, Swain T (1976) Cyanogenic polymorphism in bracken in relation to herbivore predation. Nature 260:604

Cooper-Driver GA, Finch S, Swain T, Bernays E (1977) Seasonal variation in secondary plant compounds in relation to the palatability of *Pteridium aquilinum*. Biochem Syst Ecol 5:177–183

Corcos D, Cerretti P, Mei M, Taglianti AV, Paniccia D et al (2018) Predator and parasitoid insects along elevational gradients. Oecologia 188:193–202

Crawley MJ (1997) Plant–herbivore dynamics. In: Crawley MJ (ed) Plant ecology. Blackwell Science, Oxford, pp 401–474

Curatola-Fernandez GF, Silva B, Gawlik J, Thies B, Bendix J (2013) Bracken fern frond classification status in the Andes of southern Ecuador: combining multispectral satellite data and field spectroscopy. Int J Remote Sens 34:7020–7037

Der JP, Thomson JA, Stratford JK, Wolf PG (2009) Global chloroplast phylogeny and biogeography of bracken (*Pteridium*: Dennstaedtiaceae). Am J Bot 96:1041–1049

Dezzeo N, Flores S, Chacon N (2008) Seedlings dynamics in undisturbed and adjacent fire disturbed forest in the Gran Sabana, southern Venezuela. Interciencia 33:273–279

Dong D, Jones G, Zhang S (2009) Dynamic evolution of bitter taste receptor in vertebrates. BMC Evol Biol 9:12. https://doi.org/10.1186/1471-2148-9-12

Douglas MM (1983) Defense of bracken fern by arthropods attracted to axillary nectaries. Psyche Am J Entomol 90:086859. 9 pages

Eatough Jones M, Paine TD (2012) Ants impact sawfly oviposition on bracken fern in southern California. Arthropod Plant Interact 6:283–287

Eisner T (1970) In: Sondheimer E, Simeone JB (eds) Chemical defense against predators in arthropods. Academic Press, New York, pp 157–217

Evans IA, Widdop B, Barber GD, Leach H, Jones DL, Mainwaring-Burton R (1971) The possible human hazard of the naturally occurring bracken carcinogen. Biochem J 124:29P–30P

Fenwick GR (1988) Bracken (*Pteridium aquilinum*). Toxic effects and toxic constituents. J Sci Food Agric 46:147–173

Fernandez-Murillo MP, Rico A, Kindlmann P (2015) Exotic plants along roads near La Paz, Bolivia. Weed Res 55:565–573

Ganjewala D (2010) Advances in cyanogenic glycosides biosynthesis and analyses in plants: a review. Acta Biologica Szegediensis 54:1–14

Garcia-Jorgensen DB, Hansen HCB, Abrahamsen P, Diamantopoulos E (2020) A novel model concept for modeling the leaching of natural toxins: results for the case of ptaquiloside. Environ Sci Process Impacts 22:1768–1779

Garcia-Robledo C, Kuprewicz EK, Staines CL, Erwin TL, Kress WJ (2016) Limited tolerance by insects of high temperatures across tropical elevational gradients and the implications of global warming for extinction. Proc Natl Acad Sci U S A 113:680–685

Gil Da Costa RM, Bastos MMSM, Oliveira PA, Lopes C (2012a) Bracken-associated human and animal health hazards: chemical, biological and pathological evidence. J Hazard Mater 203-204:1–12

Gil Da Costa RM, Coelho P, Sousa R, Bastos MMSM, Porto B et al (2012b) Multiple genotoxic activities of ptaquiloside in human lymphocytes: aneugenesis, clastogenesis and induction of sister chromatid exchange. Mutat Res/Genet Toxic Environ Mutag 747:77–81

Gilman A, Cooper-Driver G (1998) Japanese beetle attacks bracken in Vermont. Am Fern J 88:47–48

Glass ADM, Bohm BA (1969) The accumulation of cinnamic and benzoic acid derivatives in *Pteridium aquilinum* and *Athyrium filix-femina*. Phytochemistry 8:371–377

Gleadow RM, Woodrow IE (2002) Constraints on effectiveness of cyanogenic glycosides in herbivore defense. J Chem Ecol 21:1301–1313

Gliessman SR (1976) Allelopathy in a broad spectrum of environments as illustrated by bracken. Bot J Linn Soc 73:95–104

Gliessman SR, Muller CH (1972) The phytotoxic potential of bracken, *Pteridium aquilinum* (L.) Kuhn. Madrono 21:299–304

Goldstein C, Meizer FC, Rada F (1994) Environmental biology of a tropical treeline species, *Polylepis sericea*. In: Rundell PW, Smith AP, Meinzer FC (eds) Tropical alpine environments: plant form and function. Chapter 7. Cambridge University Press, Cambridge, pp 129–149

Gomez-Peralta D, Oberbauer SF, McClain ME, Philippi TE (2008) Rainfall and cloud water interception in tropical montane forests in the eastern Andes of Central Peru. For Ecol Manag 255:1315–1325

Gonzalez-Diaz JA, Celaya R, Fernandez-Garcia F, Osoro K, Rosa-Garcia R (2019) Dynamics of rural landscapes in marginal areas of Northern Spain: past, present and future. Land Degrad Dev 30:141–150

Gonzalo-Turpin H, Hazard L (2009) Local adaptation occurs along an altitudinal gradient despite the existence of gene flow, in the Alpine plant species *Festuca eskia*. J Ecol 97:742–751

Gratani L (2014) Plant phenotypic plasticity in response to environmental factors. Adv Bot 2014:208747

Guzman D, Ruiz JF, Cadena M (2014) Regionalization of Colombia according the average monthly precipitation seasonality, by principal component analysis (PCA) (in Spanish) http://www.ideam.gov.co/documents/21021/21789/Regionalizaci%25C3%25B3n%2Bde%2Bla%2Blluvia%2Ben%2BColombia.pdf/92287f96-840f-4408-8e76-98b668b83664

Halloy SRP, Mark AF (1996) Comparative leaf morphology spectra of plant communities in New Zealand, the Andes and the European Alps. J R Soc N Z 26:41–78

Hartig K, Beck E (2003) The bracken fern (Pteridium arachnoideum Kaulf.) Maxon dilemma in the Andes of Southern Ecuador. Biotropica 9:9–13

Hendrickson SL (2013) A genome wide study of genetic adaptation to high altitude in feral Andean horses of the paramo. BMC Evol Biol 13:273

Hendrix SD (1980) An evolutionary and ecological perspective of the insect fauna of ferns. Am Nat 115:171–179

Hendrix SD (1988) Herbivory and its impact on plant reproduction. In: Lovett Doust J, Lovett Doust L (eds) Plant reproductive ecology. Oxford University Press, Oxford, pp 246–263

Hereford J (2009) A quantitative survey of local adaptation and fitness trade-offs. Am Nat 173:579–588

Herencia BK, Falcon PN, Garcia PM, Chavera CA, Gonzales CC (2013) Prevalencia de hematuria vesical enzootica bovina determinada por urianalisis en Oxapampa. Peru Revista de Investigación Veterinaria Peru 24:50–57, (in Spanish)

Hodkinson ID (2005) Terrestrial insects along elevation gradients species and community responses to altitude. Biol Rev 80:489–513

Houze RA Jr (1993) Cloud dynamics. Academic Press, San Diego

Ibanez VN, Masuelli RW, Marfil CF (2021) Environmentally induced phenotypic plasticity and DNA methylation changes in a wild potato growing in two contrasting Andean experimental gardens. Heredity 126:50–62

Insel N, Poulsen CJ, Ehlers TA (2010) Influence of the Andes mountains on South America moisture transport, convection and precipitation. Clim Dyn 35:1477–1492

Jaakola L, Maatta-Riihinen K, Karelampi S, Hohtola A (2004) Activation of flavonoid biosynthesis by solar radiation in bilberry (*Vaccinium myrtillus* L.) leaves. Planta 218:721–728

Janzen DH (1966) Coevolution of mutualism between ants and acacias of Central America. Evolution 20:249–275

Janzen DH, Ataroff M, Fariñas M, Reyes S, Rincon N et al (1976) Changes in arthropod community along an elevational transect in the Venezuelan Andes. Biotropica 8:193–203

Jatoba LJ, Varela RM, Gonzalez-Molinillo JM, Ud Din Z, Juliano Gualtieri SC et al (2016) Allelopathy of bracken fern (*Pteridium arachnoideum*): new evidence from green fronds, litter and soil. PLoS One 11:e0161670

Jepson W, Millington A (2008) The changing countryside. In: Land change science in the tropics. Springer, Boston, pp 1–10

Jones C (1983) Phytochemical variation, colonization, and insect communities: the case of bracken fern (*Pteridium aquilinum*). In: Denno R, McLure M (eds) Variable plants and herbivores in natural and managed systems. Academic Press, New York, pp 513–558

Jones CG, Firn RD (1979) Some allelochemicals of *Pteridium aquilinum* and their involvement in resistance against *Pieris brassicae*. Biochem Syst Ecol 7:187–192

Josse CF, Cuesta F, Navarro G, Barrena V, Cabrera E et al (2009) Mapa de ecosistemas de los Andes del norte y centro, Bolivia, Colombia, Ecuador, Peru y Venezuela. Lima. Secretaria General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation. CONDESA-Proyecto Paramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA, UNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL

Josse CF, Cuesta F, Navarro G, Barrena V, Becerra MT et al (2011) Physical geography and ecosystems in the tropical Andes. In: Herzog SK, Martinez R, Jørgensen PM, Tiessen H (eds) Climate change and biodiversity in the Tropical Andes. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE). Chapter 10, p 152

Jurasekova Z, Garcia-Ramos JV, Domingo C, Sanchez-Cortes S (2006) Surface-enhanced Raman scattering of flavonoids. J Raman Spectrosc 37:1239–1241

Kessler M, Herzog SK, Fjeldsa J, Bach K (2001) Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. Divers Distrib 7:61–77

Kirk A (1982) Insects associated with bracken fern *Pteridium aquilinum* (Polypodiaceae) in Papua New Guinea and their possible use in biological control. Acta Oecologica et Applicata 3:343–359

Kirk AA (2007) Insect fauna of the weed *Pteridium aquilinum* (L.) Kuhn (Polypodiaceae): a potential source of biocontrol agents. Aust J Entomol 16:403–409

Knuesting J, Brinkmann MC, Silva B, Schorsch M, Bendix J, Beck E et al (2018) Who will win where and why? An ecophysiological dissection of the competition between a tropical pasture grass and the invasive weed bracken over an elevation range of 1000m in the tropical Andes. PLoS One 13(8):e0202255

Konrad W, Burkhardt J, Ebner M, Roth-Nebelsick A (2015) Leaf pubescence as a possibility to increase water use efficiency by promoting condensation. Ecohydrology 8:480–492

Körner C (1988) Does global increase of CO_2 alter stomatal density? Flora 181:253–257

Körner C (2002) Mountain biodiversity, its causes and functions: an overview. In: Körner C, Spehn EM (eds) Mountain biodiversity: a global assessment. Parthenon Publishing, London, p 18

Körner C, Diemer M (1987) In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plant from low and high altitude. Funct Ecol 1:179–194

Krauss P, Markstadter C, Riederer M (1997) Attenuation of UV radiation by plant cuticles from woody species. Plant Cell Environ 20:1079–1085

Kumar S, Nhushan B, Wackchaure GC, Meena KK, Kumar M et al (2020a) Plant phenolics under water-deficit conditions: biosynthesis, accumulation, and physiological roles in water stress alleviation. In: Lone R, Shuab R, Kamili A (eds) Plant phenolics in sustainable agriculture. Springer, Singapore

Kumar S, Del Castillo-Velarde C, Valdivia Prado JM, Flores Rojas JL, Callanaupa Gutierrez SM et al (2020b) Rainfall characteristics of the Mantaro basin over the tropical Andes from a vertically pointed profile rain radar and in-situ field campaign. Atmos (11):248

Lange OM, Nobel PS, Osmond CB, Ziegler H (eds) (1981) Physiological plant ecology I. Responses to the physical environment. Springer, New York

Lawton JH (1976) The structure of the arthropod community on bracken. Bot J Linn Soc 73:187–216

Lawton JH, Heads PA (1984) Bracken, ants and extrafloral nectaries. I. the components of the system. J Anim Ecol 53:995–1014

Lawton J, MacGarvin M, Heads P (1987) Effects of altitude on the abundance and species richness of insect herbivores on bracken. J Anim Ecol 56:147–160

Lemoine NP, Doublet D, Salminen J-P, Burkepile DE, Parker JD (2017) Responses of plant phenology, growth, defense, and reproduction to interactive effects of warming and insect herbivory. Ecology 98:1817–1828

Li FR, Peng SR, Chen BM, Hu YP (2010) A meta-analysis of the responses of herbaceous plants to elevated ultraviolet-B radiation. Acta Oecol 36:1–9

Likhanov AF (2014) Identification of intervarietal affinity of *Rubus idaeus* L. plants on biochemical profiles of phenolic compounds. Scientific Reports of NULES of Ukraine N7(49) 12 p

Lippok D, Beck SG, Renison D, Gallegos SC, Saavedra FV et al (2013) Forest recovery of areas deforested by fire increases with elevation in the tropical Andes. For Ecol Manag 295:69–76

Liu X, Ardo S, Bunning M, Parry J, Zhou K, Stushnoff C et al (2007) Total phenolic content and DPPH radical scavenging activity of lettuce (*Lattuca sativa* L.) grown in Colorado. LWT – Food Sci Technol 40:552–557

Llambi LD (2015) Vegetation structure, diversity and dynamics in the forest-paramo ecotone: a review of the evidence in the cordillera de Merida. Acta Biologica Colombiana 20:5–19

Lovelock CE, Clough BF, Woodrow IE (1992) Distribution and accumulation of ultraviolet-radiation-absorbing compounds in leaves of tropical mangroves. Planta 188:143–154

Lozano MC, Diaz GJ (2013) Poisonous plants for cattle in Colombia: research perspectives. Analecta Veterinaria 33:33–41

Lütz C (ed) (2013) Plants in alpine regions. Cell physiology of adaptation and survival strategies. Springer Verlag, Vienna, p 202

Lymbery A, Bailey W (1980) Regurgitation as a possible anti predator defensive mechanism in the grasshopper Goniaea sp. (Acrididae, Orthoptera). Aust J Entomol 19:129–130

Maeda K, Kimura S, Demura T, Takeda J, Ozeki Y (2005) DcMYB1 acts as a transcriptional activator of the carrot phenylalanine ammonia lyase gene (*DcPAL1*) in response to elicitor treatment, UV-B radiation and dilution effect. Plant Mol Biol 59:739–752

Magana-Ugarte R, Escudero A, Gavilan RG (2019) Metabolic and physiological responses of Mediterranean high mountain and Alpine plants to combined abiotic stresses. Physiol Plant 165:403–412

Malagon-Aldana LA, Smith DR, Vilhelmsen L, Serna F (2019) The sawflies and woodwasps (Hymenoptera: 'Symphyta') of Colombia. Zootaxa 4633(1):001–088

Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. Proc R Soc B Biol Sci 273:2575–2584

Marrero E, Bulnes C, Sanchez L, Palenzuela I, Stuart R et al (2001) Caracterizacion general del cuadro de toxicosis por *Pteridium aquilinum* en bovinos en el departamento de Tarija, Bolivia. Revista de Salud Animal 23:16–22

Marrs RH, Johnson SW, Le Duc MG (2000) Control of bracken and restoration of heathland. VI. The response of bracken fronds to 18 years of continued bracken control and 6 years of control followed by recovery. J Appl Ecol 35:479–490

Martinez V, Mestre TC, Rubio F, Girones-Vilaplana A, Moreno DA et al (2016) Accumulation of flavonols over hydroxycinnamic acids favors oxidative damage protection under abiotic stress. Front Plant Sci 7:838

Martins R, Lewinsohn T, Lawton JH (1995) First survey of insects feeding on *Pteridium aquilinum* in Brazil. Revista Brasileira do Entomologia 39:151–156

McCoy ED (1990) The distribution of insects along elevational gradients. Oikos 58:313–322

Mehltreter K, Walker LR, Sharpe JM (eds) (2010) Fern ecology. Cambridge University Press, Cambridge

Meinzer FC, Goldstein GH, Rundel PW (1985) Morphological changes along an altitudinal gradient and their consequences for an Andean giant rosette plant. Oecologia 65:278–283

Micheloud JF, Coque-Caro LA, Martinez OG, Gimeno EJ, da Silva Freitas Riveiro D et al (2017) Bovine enzootic haematuria from consumption of *Pteris deflexa* and *Pteris plúmula* in northwestern Argentina. Toxicon 134:26–29

Moreira X, Petry WK, Mooney KA, Rasmann S, Abdala-Roberts L (2018) Elevational gradients in plant defences and insect herbivory: recent advances in the field and prospects for future research. Ecography 41:1485–1496

Mosandl R, Günter S, Stimm B, Weber M (2008) Ecuador suffers the highest deforestation rate in South America. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) Gradients in a tropical mountain ecosystem in Southern Ecuador. Springer-Verlag, Berlin/Heidelberg, pp 37–40

Moura JC, Bonine CA, de Oliveira Fernandes Viana J, Dornelas MC, Mazzafera P (2010) Abiotic and biotic stresses and changes in the lignin content and composition in plants. J Integr Plant Biol 52:360–376

Myster RW (1993) Spatial heterogeneity of seed rain, seed pool and vegetative cover on two Monteverde landslides, Costa Rica. Brenesia 39-40:137–145

Myster RW (2008) Post-agricultural succession in the neotropics. Springer-Verlag, Berlin

Naikoo MI, Dar MI, Raghib F, Jaleel H, Ahmad R et al (2019) Role and regulation of plant phenolics in abiotic stress tolerance. An overview. In: MIR K, Reddy PS, Ferrante A, Khan NA (eds) Plant signaling molecules, role and regulation under stressful environments. Chapter 9. Woodhead Publishing, Sawston/Cambridge, pp 157–168

Naya M, Avila-Nuñez JL, Calcagno-Pissarelli MP (2016) Haemolymph defense capacity of the neotropical sawfly *Aneugmenus merida* against ant predation. J Insect Behav 29:459–472

O'Connor PJ, Alonso-Amelot ME, Roberts SA, Povey AC (2019) The role of bracken fern illudanes in bracken-induced toxicities. Mutat Res Rev Mutat Res 782:108276–108239

Oinonen E (1967) The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn) clones and certain periods of site history. Acta Bot Fenn 83:1–51

Oldenkamp RE, Douglas MM (2011) Measuring the effects of "opportunistic defense" of the bracken fern (*Pteridium aquilinum*) by patrolling ants (Hymenoptera: Formicidae) at Pierce Cedar Creek Institute in South Central Michigan. Gt Lakes Entomol 44:34–41

Oliveros-Bastidas A, Alonso-Amelot ME (2010) Cyanogenic polymorphism in brackens, *Pteridium arachnoideum* and *P. caudatum*, from the northern Andes. Quim Nova 33:1520–1524

Onwuka B, Mang B (2018) Effect of soil temperatures on some soil properties and plant growth. Scholar J Agric Sci 6:89–93

Ortego F, Evans PH, Bowers WS (1997) Enteric and plant-derived deterrents in regurgitate of American bird grasshopper, *Schistocerca americana*. J Chem Ecol 23:1941–1950

Pacheco CE, Aguado MI, Mollicone D (2014) Identification and characterization of deforestation hot spots in Venezuela using MODIS satellite images. Acta Amazon 44:185–196

Page CN (1982a) Field observations on the nectaries of bracken, Pteridium aquilinum, in Britain. Fern Gazette 12:233–239

Page CN (1982b) The history and spread of bracken in Britain. Proc Royal Soc Edinburg 81B:3–10

Pakeman RJ, Marrs RH (1992) The conservation value of bracken *Pteridium aquilinum* (L.) Kuhn-dominated communities in the UK, and an assessment of the ecological impact of bracken expansion or its removal. Biol Conserv 62:101–114

Pakeman RJ, Marrs RH, Jacobs PJ (1994) A model of bracken (*Pteridium aquilinum*) growth and effects of control strategies and changing climate. J Appl Ecol 34:145–154

Panter KE, James LF (1990) Natural plant toxins in milk: a review. J Anim Sci 68:892–904

Pathania S, Kumar P, Singh S, Kathoon S, Rawat AKS et al (2012) Detection of ptaquiloside and quercetin in certain Indian ferns. Curr Sci 102:1683–1691

Pauli H, Gottfried M, Reiter K, Klettner C, Grabherr E (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. Glob Chang Biol 12:1–10

Petrini O, Fisher PJ, Petrini LE (1992) Fungal endophytes of bracken (*Pteridium aquilinum*), with some reflections on their use in biological control. Sydowia 44:282–293

Piazena H (1996) The effect of altitude upon the solar UV-B and UV-A irradiance in the tropical Chilean Andes. Sol Energy 57:133–140

Piñango L (1996) Diagnóstico de la fauna epígea de un ambiente de selva nublada intervenida en los Andes venezolanos. Degree thesis, Faculty of Sciences, Universidad de Los Andes, Mérida, Venezuela

Portela RCQ, Matos DMS, Siqueira LP, Braz MIG, Silva L et al (2009) Variation in aboveground biomass and necromass of two invasive species in the Atlantic rainforest, Southeast Brazil. Acta Bot Bras 23:571–577

Portillo-Quintero CA, Sanchez AM, Valbuena CA, Gonzalez YY, Larreal JT (2012) Forest cover and deforestation patterns in the Northern Andes (Lake Maracaibo Basin): a synoptic assessment using MODIS and Landsat imagery. Appl Geogr 35:152–163

Posner JL, Antonini GA, Montanez G, Cecil R, Grigsby M (1982) A classification of steeplands in the Northern Andes. Mt Res Dev 2:273–280

Qiang WY, Wang XL, Chen T, Feng HY, An LZ et al (2003) Variations of stomatal density and carbon isotope values of *Picea crassifolia* at different altitudes in Qilian mountains. Trees 17:258–262

Quinby PA (2000) First-year impacts of shelterwood logging on understory vegetation in an old-growth pine stand in Central Ontario, Canada. Environ Conserv 27:229–241

Ramirez-Trejo MR, Perez-Garcia B, Perez-Salicrup DR, Orozco A (2010) Effect of fire on the germination of spores of *Pteridium caudatum*, an invasive fern. J Trop Ecol 26:457–465

Rasmann S, Alvarez N, Pellissier L (2014a) The altitudinal niche-breadth hypothesis in insect–plant interactions. In: Voelckel C, Jander G (eds) Annual plant reviews, vol. 47, insect–plant interactions. John Wiley & Sons Ltd, Chichester, pp 339–359

Rasmann S, Pellissier L, Defossez E, Jactel H, Kunstler G (2014b) Climate-driven change in plant-insect interactions along elevation gradients. Funct Ecol 28:46–54

Rasmussen LH, Jensen LS, Hansen HCB (2003) Distribution of the carcinogenic terpene ptaquiloside in bracken fronds, rhizomes (Pteridium aquilinum) and litter in Denmark. J Chem Ecol 29:771–778

Rasmussen LH, Hansen HCB, Lauren D (2005) Sorption, degradation and mobility of ptaquiloside, a carcinogenic bracken (Pteridium sp) constituent, in the soil environment. Chemosphere 58:823–835

Rasmussen LH, Lauren DR, Smith BL (2008) Variation in ptaquiloside content in bracken (*Pteridium esculentum* (Forst. f) Cockayne) in New Zealand. N Z Vet J 56:304–309

Rasmussen LH, Donnelly E, Strobel BW, Holm PE, Hansen HC (2015) Land management of bracken needs to account for bracken carcinogens – a case study from Britain. J Environ Manag 151:258–266

Ribeiro DSF, Moura Keller K, Soto-Blanco B (2020) Ptaquiloside and pterosin B levels in mature green fronds and sprouts of *Pteridium arachnoideum*. Toxins 12:288–296

Rincon DF, Diaz GJ, Gardner DR (2016) Detection of ptaquilosides in different phenologic stages of bracken fern (*Pteridium aquilinum*) and analysis of milk samples in farms with haematuria in Tolima, Colombia. Revista CES de Medicina Veterinaria y Zootecnia 11:72–77

Rios-Gutiérrez M, Domingo LR, Alonso-Amelot ME (2017) A DFT study of the conversion of ptaquiloside, a bracken fern carcinogen, into pterosin B in neutral and acidic aqueous medium. ChemistrySelect 2:8178–8186

Robberecht R, Caldwell MM (1978) Leaf epidermal transmittance of ultraviolet radiation and its implication for plant sensitivity to ultraviolet-radiation induced injury. Oecologia (Berlin) 32:277–287

Rodriguez-Eraso N, Armenteras-Pascual D, Retana Alumbreros J (2013) Land use and land cover change in the Colombian Andes: dynamics and future scenarios. J Land Use Sci 8:154–174

Rodriguez-Hernandez D (2019) Secondary metabolites as a survival strategy in plants of high mountain habitats. Boletin Latinoamericano y del Caribe de Plantas Medicinales y Aromaticas 18:444–458

Ronderos RA, Cerda F (1982) El genero *Timotes* Roberts (Orthoptera, Acrididae, Melanoplinae). Revista de la Sociedad Entomologica Argentina 41:1–4

Roos K, Rollenbeck R, Peters T, Bendix J, Beck E (2010) Growth of Tropical bracken (*Pteridium arachnoideum*): response to weather variations and burning. Invas Plant Sci Manag 3:402–411

Rumpf S, Cromey M, Webb CJ (1994) Ultrastructure and function of the nectaries of New Zealand bracken (*Pteridium esculentum* (Forst. F.) Cockayne). N Z J Bot 32:487–496

Saito K, Nagao T, Matoba M, Koyama K, Natori H et al (1989) Chemical assay of ptaquiloside, the carcinogen of *Pteridium aquilinum* and the distribution of related compounds in the *Pteridaceae*. Phytochemistry 28:1605–1161

Salinas PJ, Ortega FJ (1990) Comunidades de artrópodos en la maleza *Pteridium aquilinum* (L.) Kuhn en los Andes venezolanos y primer hallazgo de *Acyrthosiphon cyatheae* Colman (Homoptera, Aphididae) en Sur America. Turrrialba 40:168–171

Sanchez-Villalobos A, Garcia D, De Alvarado C, Villegas M, Vilarroel R et al (1999) Factores de riesgo asociados con hematuria enzootica bovina en el municipio Campo Elias, estado Merida, Venezuela. Revista de Ciencias FCV-LUZ 9:378–387. (in Spanish)

Sanders NJ (2002) Elevational gradients in ant species richness: area, geometry and Rapoport's rule. Ecography 25:25–32

Sandoya V, Pauchard A, Cavieres LA (2017) Native and non-native plants show different responses to elevation and disturbance on the tropical high Andes of Ecuador. Ecol Evol 7:709–719

Santana VM, Bradstock RA, Ooi MKJ, Denham AJ, Auld TD, Baeza MJ (2010) Effects of soil temperature regimes after a fire on seed dormancy and germination in six Australian Fabaceae species. Aust J Bot 58:539–545

Santiago-Paredes S, La Marca E (2006) Comportamiento del clima a finales del Siglo XX en los Altos Andes Venezolanos y el declive de *Atelopus mucubajiensis*. Heterotropicos 3:7–20

Sarmiento L, Llambi LD, Escalona A, Marquez N (2003) Vegetation patterns, regeneration rates and divergence in an old field succession of the high tropical Andes. Plant Ecol 166:63–74

Scala C, Ortiz K, Catinaud J, Lemberger K (2014) Hematuria and urinary bladder lesions compatible with bracken fern (Pteridium aquilinum) intoxication in captive fallow deer. J Zoo Wildl Med 45:380–385

Schneider de Oliveira LG, Boabaid FM, Kisielius V, Rasmussen LH, Buroni F et al (2020) Hemorrhagic diathesis in cattle due to consumption of *Adiantopsis chlorophylla* (Swartz) Fee (Pteridaceae). Toxicon: X 5:100024

Schneider L, Nelun-Fernando D (2010) An untidy cover: invasion of bracken fern in the shifting cultivation systems of Southern Yucatan, Mexico. Biotropica 42:41–48. https://doi.org/10.1111/j.1744.2009.00569.x

Schwartzburd PB, Yanez A, Prado J (2018) Formal recognition of six subordinate taxa within the south American bracken fern, *Pteridium esculentum* (*P. esculentum* subsp. *arachnoideum s.l.* Dennstaedtiaceae), based on morphology and geography. Phytotaxa 333:22–40

Seidel J, Trachte K, Orellana-Alvear J, Figueroa A, Celleri R, Bendix J et al (2019) Precipitation characteristics at two locations in the tropical Andes by means of vertically pointing micro-rain radar observations. Remote Sens 11:2985

Shahin M, Smith BL, Prakash AS (1999) Bracken carcinogens in the human diet. Mut Res/Genet Toxic Environ Mut 443:69–79

Sharma A, Shahzad B, Rehman A, Bhardwaj R, Landi M et al (2019) Response of phenylpropanoids pathway and the role of polyphenols in plants under abiotic stress. Molecules 24:2452

Silva B, Roos K, Voss I, König N, Rollenbeck R et al (2012) Simulating canopy photosynthesis for two competing species of an anthropogenic grassland community in the Andes of southern Ecuador. Ecol Model 239:14–26

Skourti Stathaki E, Clauson-Kaas F, Brandt KK, Rasmussen LH, Hansen HCB (2016) Dissipation of pterosin B in acid soils – tracking the fate of the bracken fern carcinogen ptaquiloside. Chemosphere 165:453–459

Smith DR (2005) Two new fern-feeding sawflies of the genus *Aneugmenus* Hartig (Hymenoptera: Tenthredinidae) from South America. Proc Entomol Soc Wash 107:273–278

Smith BL, Seawright AA, Ng JC, Hertle AT, Thomson JA et al (1994) Concentration of ptaquiloside, a major carcinogen in bracken fern (*Pteridium* spp.) from eastern Australia and from a cultivated worldwide collection held in Sydney. Aus Nat Toxins 2:347–353

Søme L (1986) Tolerance to low temperatures and desiccation in insects from the Andean paramos. Arct Alp Res 18:253–259

Somvanshi R, Lauren DR, Smith BL, Dawra RK, Sharma OP et al (2006) Estimation of the fern toxin ptaquiloside in Indian ferns other than bracken. Curr Sci 91:1547–1552

Stapleton AE, Thornber CS, Walbot V (1997) UV-B component of sunlight causes measurable damage in field-grown maize (*Zea mays* L.): developmental and cellular heterogeneity of damage and repair. Plant Cell Environ 20:279–290

Stefano RD, Stauffer F, Riina R, Huber O, Aymard G, Hokche O, Berry PE, Meier W (2009) Assessment of vascular plant diversity and endemism in Venezuela. Candollea 64:203–212

Supriya K, Moreau CS, Sam K, Price TD (2019) Analysis of tropical and temperate elevational gradients in arthropod abundance. Front Biogeogr 11. https://doi.org/10.21425/F5FBG43104. Retrieved from https://escholarship.org/uc/item/7ts9g1qz

Swan ALS, Koven CD (2017) A direct estimate of the seasonal cycle of evapotranspiration over the Amazon basin. J Hydrometeorol 18:2173–2185

Swenson JJ, Young BE, Beck S, Comer P, Cordova JH et al (2012) Plant and animal endemism in the eastern Andean slope: challenges to conservation. BMC Ecol 12:1. https://doi.org/10.1186/1472-6785-12-1

Sword GA (2001) Testy on the outside but toxic in the middle: grasshopper regurgitation in a host plant-mediated toxicity to a vertebrate predator. Oecologia 128:416–421

Takeda J, Ozeki Y, Yoshida K (1997) Action spectrum for induction of promoter activity of phenylalanine ammonia lyase gene by UV in carrot suspension cells. Photochem Photobiol 66:464–470

Tanaka N, Yuhara H, Wada H, Murakami T, Cambie RC, Bragginfs JE (1993) Phenolic constituents of *Pteridium esculentum*. Phytochemistry 32:1037–1039

Tempel A (1981) Field studies on the relationship between herbivore damage and tannin concentration in bracken (*Pteridium aquilinum* Kuhn). Oecologia(Berlin) 51:97–106

Tempel A (1983) Bracken fern (*Pteridium aquilinum*) and nectar-feeding ants: a non mutualistic interaction. Ecology 64(6):1411–1422

Tevini M, Teramura AH (1989) UV-B effects on terrestrial plants. Photochem Photobiol 50:479–487

Thomson JA (2012) Taxonomic status of diploid southern hemisphere brackens (*Pteridium*: dennstaedtiaceae). Telopea 14:43–48

Thomson JA, Alonso-Amelot ME (2002) Clarification of the taxonomic status and relationships of *Pteridium caudatum* (Dennstaedtiaceae) in Central and South America. Bot J Linn Soc 140:237–248

Thomson JA, Martin AB (1996) Gnarled trichomes: an understudied character of *Pteridium*. Am Fern J 86:36–51

Tobar AC, Jimenez Sanchez A, Sanchez Perera LM, Mancebo Dorvigni B, Marrero Faz E (2014) Risk by human health for invasion of *Pteridium arachnoideum* in Bolivar, Ecuador ptaquiloside content in fronds and in milk. Int J Appl Sci Technol 4:84–94

Urban J, Ingwers M, McGuire MA, Teskey RO (2017) Stomatal conductance increases with rising temperature. Plant Signal Behav 12:e1356534

Van der Hammen T, Ward PS (2005) Ants from the Ecoandes expeditions: diversity and distribution. Stud Trop Andean Ecosyst 6:239–248

Velasquez MT, Naranjo ME, Gamez LE, Murillo J (2015) Seed rain in a cloud forest and a secondary forest in Venezuelan Andes. Ecotropicos 28:1–13

Vetter J (2000) Plant cyanogenic glycosides. Toxicon 38:11–36

Villa PM, Rodrigues AC, Marquez N, Lopes Rodrigues A, Martins SV (2017) Phytosociology of weeds after potato cultivation (*Solanum tuberosum* L.) in the Venezuelan Andes: an agroecological approach. Trop Subtrop Agroecosyst 20:329–339

Virgilio A, Sinisi A, Russo V, Gerardo S, Santoro A et al (2015) Ptaquiloside, the major carcinogen of bracken fern, in the pooled raw milk of healthy sheep and goats; an underestimated global concern of food safety. J Agric Food Chem 63:4886–4892

Vysochina GI, Ershova EA, Kukushkina TA (2012) The seasonal dynamics of biologically active substances content in Pteridium aquilinum (Hypolepidaceae) during the vegetative period in Novosibirsk region. Rastitel'nye Resursy 48:376–383

Ward PS, Downie DA (2005) The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): phylogeny and evolution of big-eyed arboreal ants. Syst Entomol 30:310–335

Waterman PG, Mole S (1989) Extrinsic factors influencing production of secondary metabolites in plants. In: Bernays EA (ed) Insect-plant interactions, vol 1. CRC Press, Boca Raton, pp 107–134

Watts CHS (1968) The foods eaten by woodmice (Apodemus sylvaticus) and Bank voles (Clethrionomys glareolus) in Wytham woods, Berkshire. J Anim Ecol 37:25–41

Woodward FI, Bazzaz FA (1988) The responses of stomatal density to CO_2 partial pressure. J Exp Bot 39:1771–1781

Wu JS, Clauson-Kaas F, Lindqvist DN, Rasmussen LH, Strobel BW et al (2021) Does the natural carcinogen ptaquiloside degrade readily in groundwater? Environ Sci Europe 33:24

Yamada K, Ojika M, Kigoshi H (2007) Ptaquiloside, the major toxin in bracken, and related terpene glycosides: chemistry, biology and ecology. Nat Prod Rep 24:798–813

Zagrobelny M, Bak S, Rasmussen AV, Jørgensen B, Naumann CM et al (2004) Cyanogenic glucosides and plant-insect interactions. Phytochemistry 65:293–306

Zhang X, Liu CJ (2015) Multifaceted regulations of gateway enzyme phenylalanine ammonia lyase in the synthesis of phenyl propanoids. Mol Plant 8:17–27

Zheng G, Jia Y, Zhao X, Zhang F, Luo S et al (2012) O-coumaric acid from invasive *Eupatorium adenophorum*, is a potent phytotoxin. Chemoecology 22:131–138

Zuk M, Pelc K, Szperlik J, Sawula A, Szopa J (2020) Metabolism of cyanogenic glucosides in developing flax: metabolic analysis and expression patterns of genes. Meta 10:288, (13 pages)

Zuk-Golaszewska K, Upadhyaya MK, Golaszewski J (2003) The effect of UV-B radiation on plant growth and development. Plant Soil Environ 49:135–140

Chapter 3
Effects of Agricultural Expansion on Lotic Benthic Macroinvertebrate Communities: A Review and Case Study from Brazil

Elaine C. Corrêa and Ryan M. Utz

3.1 Introduction

Despite high biodiversity and its importance in provisioning ecosystem services (Corbera et al. 2007; Vörösmarty et al. 2010), Neotropical lotic ecosystems rank among the most threatened in the world (Barlow et al. 2018). The conversion of native land cover, typically forest but also grassland, to human-centered land use represents a primary driver of Neotropical biodiversity loss due to a disproportionately large degree of species richness and land conversion (Barlow et al. 2018).

The loss of native land cover especially in riparian zones exerts a strong impact on lotic ecosystem structure and function (Haddad et al. 2015) due to energetic coupling of streams and rivers with terrestrial vegetation (Webster and Benfield 1986; Marcarelli et al. 2011). Resource subsidies from riparian vegetation provides an important organic matter base to aquatic food webs and physical substrate for benthic aquatic macroinvertebrates. Physical and chemical effects result as elevated solar radiation exposure following vegetation loss increases water temperature (Webster and Benfield 1986; Martins et al. 2017) on lotic macroinvertebrates. Sediment and nutrient concentrations also often increase following vegetation conversion and both environmental stressors typically reduce macroinvertebrate biodiversity (Ferreira et al. 2015). Although the effects of agricultural expansion on the physical, chemical, and macroinvertebrate community properties of stream ecosystems are now well-documented, most studies are concentrated in temperate

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climates. Here, we review studies exploring the effects of native terrestrial ecosystem conversion to agriculture in the Neotropics with an emphasis on lotic macroinvertebrates.

3.2 Review: Agricultural Expansion and Benthic Macroinvertebrates in Neotropical Streams

Loss of natural cover to agricultural expansion is particularly acute in tropical and subtropical ecosystems due to an increased demand for agricultural products coupled with population growth and advancing economies (Millennium Ecosystem Assessment 2005; Laurance et al. 2014). In the Neotropics, these transformations in land use for agricultural expansion have been extensive. In Brazil, the Colombia Andes, and the Ecuadorian Andes, for example, vegetation loss to agriculture remains a critical threat to lotic ecosystems and loss of megadiversity (Iniguez-Armijos et al. 2014; Chará-Serna et al. 2015; Strassburg et al. 2017).

In this chapter, we conducted a qualitative review of studies investigating how agricultural expansion impacted benthic macroinvertebrate communities in headwater Neotropical streams between 23.5° N and 23.5° S. Our review included published studies that quantified entire communities, multimetric indices, and/or those with a focus on focal taxa, most commonly aquatic insects such as Ephemeroptera, Plecoptera, Trichoptera, Odonata, and Diptera - EPTOD that were identified to various taxonomic levels (order, family, genera) (see Table 3.1). We analyzed 34 papers that met geographic and scope criteria. The survey revealed that most studies reflect recent efforts, with the most papers published between 2014 and 2019. Furthermore, studies were unevenly distributed geographically, with study sites primarily located in: Brazil ($n = 25$) and Ecuador ($n = 5$) (Figs. 3.1 and Table 3.1). Most Brazilian studies were focused on the southeastern region of the country, where universities and biodiversity researchers are concentrated (Clarivate Analytics, Research in Brazil 2017). Large Neotropical countries, such as Mexico and Peru, apparently lack recent investigations of how agricultural land use conversion impacts lotic macroinvertebrates.

Such geographic disparities also reflect ecological concentrations of effort. Among ecosystems covered, Atlantic tropical moist forest (= 11) and the Brazilian savanna (Cerrado biome) (=10) constituted the study sites for over half of those surveyed. The Atlantic Forest and Cerrado are considered biodiversity hotspots with high endemism (Myers et al. 2000) and rank among the most threatened ecosystems globally (Beuchle et al. 2015; Hunke et al. 2015). Agriculture and pasture cattle grazing converted 88% and 80% of native vegetation in the Atlantic Forest and Cerrado, respectively (Ribeiro et al. 2009; Ferreira et al. 2012; Strassburg et al. 2017). The large number of studies may be related to the need for knowledge about the effects of landscape conversion on streams in these ecosystems (Roque et al. 2021; Albuquerque et al. 2021).

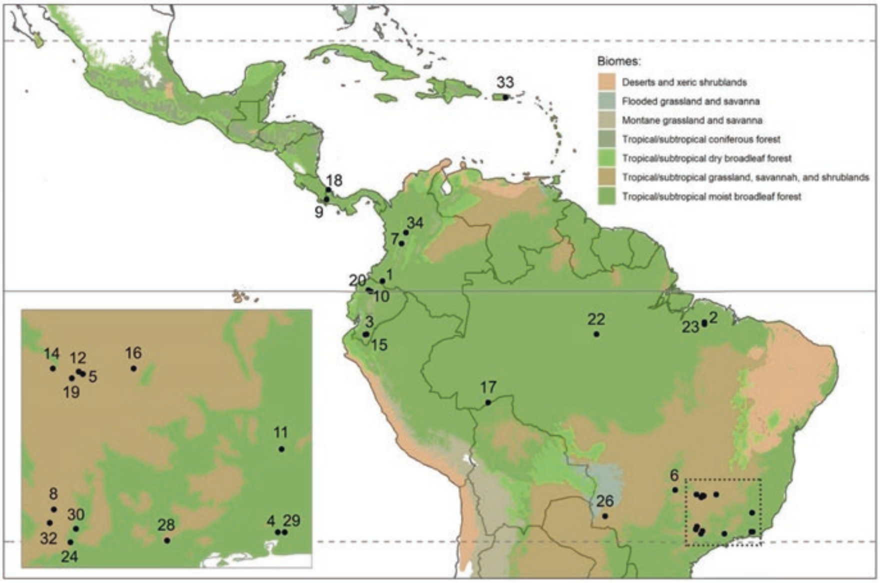

Fig. 3.1 Map showing the distribution of the studies in the Neotropical region

Streams in the Atlantic Forest are under a long and historic degradation due to landscape conversion and many fish and aquatic macroinvertebrates have been largely reduced in this biome (Dala-Corte et al. 2020). Likewise, the Cerrado is the second largest biome in Brazil (after the Amazon) and represents about 23% of the country (Ratter et al. 1997) and has been strongly altered by pasture and crop agriculture (Hunke et al. 2015). It harbors many important large rivers, and its network of headwater streams contain a large diversity of species and ecosystem services (Strassburg et al. 2017).

The impacts of agriculture on Neotropical streams have also been documented in studies in the Brazilian Amazon, montane rainforest, and the tropical moist forest in the Ecuadorian Choco (Chará-Serna et al. 2015; Brito et al. 2019; Morabowen et al. 2019; Lima et al. 2020). In the Brazilian Amazon, for example, agriculture expansion has resulted in the loss of about 18% of the native forest ecosystems (Ferreira et al. 2012) and had considerable impacts on the habitat structure and community composition of many small Amazon streams (Leal et al. 2016).

Similar to related efforts in other regions, a strong majority of studies in Neotropical streams indicated that the loss of native vegetation associated with agricultural practices consistently impacts the structure and composition of aquatic invertebrate communities (Table 3.1). As many studies from temperate zones have demonstrated (e.g., Lammert and Allan 1999; Sponseller et al. 2001; Sweeney et al. 2004), multimetric indices, diversity, and richness tend to decline as agricultural land cover increases in Neotropical watersheds (i.e., Nessimian et al. 2008; Siegloch et al. 2014; Chará-Serna et al. 2015). Community structure also tends to shift toward

Table 3.1 Summary of findings from studies investigating how the loss of native vegetation cover impacts macroinvertebrate communities in Neotropical streams

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
1	Ecuador	Amazon rainforest	Macroinvertebrate densities were > 3 times higher in deforested sites (mean canopy cover 23%) versus forested sites (77%) because opening the canopy increased periphyton biomass. α and β diversity declined with periphyton biomass and increased with canopy cover due to changes in density. Baetidae, Psephenidae, Elmidae, and Tricorythidae increased with canopy loss. Temporal variability of densities was elevated in deforested sites	Family	12	1 to 3	Bojsen and Jacoben (2003)
2	Brazil	Amazon rainforest	Analyses suggested low thresholds of community change at around 9% catchment forest loss and 12% 100 m riparian buffer forest loss but higher values (57% and 75%, respectively) for thresholds where richness declines. Thresholds were much lower than expected, indicating that macroinvertebrates are very sensitive to forest loss	Genus	51	1 to 2	Brito et al. (2019)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
3	Ecuador	Montane cloud forest	Macroinvertebrate densities were higher in deforested (disturbed) sites, possibly due to higher periphyton driven by increased light. Taxonomic richness was comparable among streams, but evenness was lower in deforested streams. Ephemeroptera were more abundant while Odonata were far less abundant in deforested streams	Genus	6	1 to 2	Bücker et al. (2010)
4	Brazil	Atlantic rainforest	Taxonomic richness, but not density, declined by about 20% between reference and disturbed streams. Macroinvertebrates were strongly associated with leaf litter abundance	Genus	7	3 to 4	Buss et al. (2004)
5	Brazil	Savanna (Cerrado)	Taxonomic richness of EPT taxa did not decline from least to most disturbed sites. Functional richness, diversity, and dispersion all decline with loss of native vegetation	Genus	160	1 to 3	de Castro et al. (2018)
6	Brazil	Savannah (Cerrado)	Sites with pasture or sugarcane watersheds supported fewer scrapers, more trophic generalists, and broader niche overlap among taxa. A non-native shrimp (*Macrobrachium amazonicus*) exploits novel niches in disturbed sites	Family	9	2 to 3	de Castro et al. (2016)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
7	Colombia	Montane rainforest	Agricultural land use was associated with significant reductions of a macroinvertebrate multimetric index. A SEM model indicated that the mechanistic pathway was through increases in NH_3-N associated with agriculture	Genus	30	1	Chará-Serna et al. (2015)
8	Brazil	Savanna (Cerrado)	Did not explicitly examine how macroinvertebrate communities change along a gradient but how taxonomic resolution affects assessment indices among watersheds disturbed by agriculture. Identification to family may be sufficient to assess land use impacts	Species	9	1	Corbi and Trivinho-Strixino (2006)
9	Panama	Montane rainforest	Impacts to two macroinvertebrate multimetric indices were largely explained by nutrient enrichment and sedimentation. Pesticide concentrations explained less variation in macroinvertebrate index variability. Macroinvertebrate abundance and richness were not impacted by nutrient enrichment but were reduced by high pesticide concentrations	Family	13	1 to 4	Cornejo et al. (2019)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
10	Ecuador	Montane rainforest	Leaf-shredding macroinvertebrate richness and diversity were comparable between forest and pasture sites, but shredder abundance was much higher in forested sites. Leaf processing by shredders was also lower in pasture reaches. Scrapers were more abundant in pasture reaches	Genus	6	1	Encalada et al. (2010)
11	Brazil	Atlantic rainforest	Odonata assemblages were comparable between agricultural and natural watersheds	Species	10	–	Ferreira-Peruquetti and De Marco Jr (2002)
12	Brazil	Savanna (Cerrado)	Ephemeroptera taxa, the focus of study, responded most negatively to sedimentation. Land use metrics assessed using TITAN included only urban land use, which limits the ability to summarize how natural cover loss affected communities	Genus	183	1 to 3	Firmiano et al. (2017)
13	Brazil	Savanna (Cerrado)	Study explored trait and taxonomic groups associated with multiple gradients, including land use. The group most associated with disturbed watersheds was comprised of obligate aquatic Mollusca and Diptera taxa. Odonata did not appear to be strongly affected by land use gradients	Genus or family	183	1 to 3	Firmiano et al. (2019)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
14	Brazil	Savanna (Cerrado)	Taxonomic richness, community composition, and FFG composition did not differ among pasture, agricultural, and natural landscape streams. Riparian buffers successfully prevented biodiversity loss and changes to communities	Family	13	1 to 3	Guimarães-Souto et al. (2021)
15	Ecuador	Montane rainforest	Detected strong positive linear relationships between multimetric indices and % native vegetation cover at catchment and riparian buffer scales. Dominant taxa linearly negatively increase with natural vegetation loss. Scrapers and shredders both increased with vegetation cover. A threshold of 70% natural cover at the catchment scale was proposed to retain ecological integrity	Genus	23	1 to 3	Iñiguez–Armijos et al. (2014)
16	Brazil	Savanna (Cerrado)	Study aimed to identify land use scale most important in structuring macroinvertebrate communities. Land use disturbances quantified at the catchment scale were far more effective in predicting impacts to macroinvertebrate communities than metrics at the local scale	Genus	80	1 to 3	Ligeiro et al. (2013)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
17	Brazil	Amazon rainforest	Macroinvertebrate community composition and diversity changed as pasture replaced natural cover, with lower collector densities and % EPT in disturbed streams	Family	14	1 to 3	Lima et al. (2020)
18	Costa Rica	Lowland rainforest	Comparisons between forest and pasture reaches suggest that deforestation, even at a very local scale, alters benthic macroinvertebrate communities, reduces diversity, and eliminates sensitive taxa. Riparian forest buffers significantly reduce such effects	Genus or family	12	–	Lorion and Kennedy (2009)
19	Brazil	Savanna (Cerrado)	Benthic macroinvertebrate richness was moderately negatively correlated with wetland and agricultural land use	Family	80	1 to 3	Macedo et al. (2014)
20	Ecuador	Tropical moist forest	Macroinvertebrate species richness was considerably lower in palmito monoculture farmlands than in the other two types of land use (pristine montane cloud forest and organic farms).	Genus	8	1	Morabowen et al. (2019)
21	Brazil	Atlantic forest	There was a significant difference in macroinvertebrate composition among riparian buffer widths. This study showed that riparian buffer widths <15 m altered the macroinvertebrate community	Family	9	4 to 5	Moraes et al. (2014)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
22	Brazil	Amazon rainforest	Aquatic insect richness and Ephemeroptera, Plecoptera, and Trichoptera richness were significantly lower in pasture streams, and their taxonomic composition differed significantly from streams in forested areas	Species	20	1 to 3	Nessimian et al. (2008)
23	Brazil	Amazon rainforest	The occurrence of odonate species was strongly associated with the configuration of the riparian vegetation. Agricultural activities appear to have changed in the composition of odonate assemblages and these insects can act as indicators of the ecological consequences of riparian habitat loss and disturbance	Species	50	1 to 3	De Oliveira-Junior et al. (2015)
24	Brazil	Atlantic forest	Invertebrate richness was strongly correlated with land use index	Family	9	4 to 5	Ometo et al. (2000)
25	Brazil	Atlantic forest	This study demonstrated that variables at different scales (stream and riparian zone) structure stream insect assemblages	Genus	18	1 to 2	Ongaratto et al. (2018)
26	Brazil	Savanna (Cerrado)	Six species showed evidence of nonlinear response in sites with a loss of native vegetation loss between 40% and 60%.	Species	98	1 to	Rodrigues et al. (2016)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
27	Brazil	Atlantic forest	Local scale (stream), landscape attributes and large scales (drainage basin and riparian buffer) generated significant effects on the Chironomidae fauna	Genus	18	2	Sensolo et al. (2012)
28	Brazil	Atlantic forest	The results showed that agricultural and forestry land use has a strong negative effect on the structure of Ephemeroptera assemblages	Genus	29	1 to 2	Siegloch et al. (2014)
29	Brazil	Atlantic forest	Aquatic invertebrate diversity has decreased, and community metrics have changed with deforestation	Genus	4	2 to 3	Silva-Araújo et al. (2020)
30	Brazil	Atlantic forest	The study showed that landscape modification by agriculture, pasture, and silviculture reduced beta diversity by limiting the colonization of potential aquatic insect species, and, ultimately, causing taxonomic homogenization	Genus	32	–	Siqueira et al. (2015)
31	Brazil	Savanna (Cerrado)	The abundances of Elmidae, Chironomidae, and total macroinvertebrates increased along the forest remnant, while the abundance of Baetidae, proportion of Ephemeroptera, Plecoptera, and Trichoptera (EPT), rarefied taxonomic richness, and diversity decreased. Taxon richness and EPT abundance did not vary along the forest remnant	Family	12	1	Suga and Tanaka (2013)

(continued)

Table 3.1 (continued)

No.	Nation	Ecosystem	Conclusions	Taxonomic resolution	Sample size	Stream orders	References
32	Brazil	Atlantic forest	The study found higher total nitrogen concentrations and electric conductivity in streams with land use dominated by pasture and narrower riparian forests, higher diversity of macroinvertebrates and dissolved oxygen concentrations in streams with higher cover and width of riparian forests although land use was dominated by sugarcane	Family	12	–	Tanaka et al. (2016)
33	Puerto Rico	Tropical forest	The study found little evidence for an insect aquatic effect on leaf breakdown. Results suggested that land use is an important factor affecting leaf litter processing in streams	Family	9	1 to 3	Torres and Ramírez (2014)
34	Colombia	Rainforest	The results suggested that agricultural activity has a higher impact on the diversity of aquatic insects, which may be associated with the loss of riparian vegetation	Genus	10	–	Villada-Bedoya et al. (2017)

more homogeneous assemblages dominated by tolerant individuals (Macedo et al. 2014; Brito et al. 2019; Firmiano et al. 2019). Such findings are consistent with works conducted elsewhere, suggesting that the ecological impacts of converting natural cover to agriculture are globally consistent. We also found that in many Neotropical streams, total macroinvertebrate abundance often increases following forest cover loss (Buss et al. 2004). Most studies attributed greater abundance to an increase in light that elevated primary production, allowing grazers to thrive (Bojsen and Jacobsen 2003). Unlike in temperate regions, primary production in Neotropical streams in most cases is not limited by low temperatures and seasonal fluctuations in light.

Although agricultural land use conversion consistently alters macroinvertebrate assemblages in Neotropical streams, a notable minority of studies did not detect changes in taxonomic composition or richness along changes in spatial and temporal gradients of agricultural cover. Examples span diverse ecological settings, such as karstic forest streams in Brazil (Corrêa et al. 2018, 2019), high-elevation montane forests of Ecuador (Ordóñez 2011; Bücker et al. 2010), and the coffee-growing region of Colombia (Chará et al. 2007). Although works that do detect richness and diversity loss are more common, findings of resilience are encouraging because they suggest that biodiversity can persist despite land cover conversion. Many watersheds (e.g., karstic streams) or ecological attributes could help to diminish the effects of land use conversion (Omernik and Bailey 1997).

Scientific recommendations have been made to conserve lotic ecosystems and to reduce threats to biodiversity (Azevedo-Santos et al. 2021). Given the high degree of landscape change by agriculture, pasture, and other land uses in the Neotropical region. Such recommendations have emphasized the need to create stream conservation strategies and the rehabilitation of disturbed areas, particularly those altered by agricultural activities and ranching. Studies emphasize that governmental agencies need to enforce environmental laws to ensure that riparian vegetation is preserved, maintenance and rehabilitation of the ecological condition of water bodies, and the conservation of aquatic biodiversity (Noss 1999) as well as national and international efforts to safeguard the freshwater life of this hyperdiverse region.

3.3 Case Study: Bodoquena Plateau, Brazil

To illustrate how stream ecosystem responses can be context-specific and nuanced, we present a brief case study of macroinvertebrate community changes in a karstic watershed of tropical Central-West of Brazil. Study sites typify severe land use change in the region, yet we detected limited community structure changes in macroinvertebrates even within streams with radically altered watersheds. Although the effort was part of a larger study designed to explore how macroconsumers such as fish and shrimp induce trophic cascades (see Correa et al. 2018, 2019), the design also allows for comparisons of macroinvertebrate communities along a gradient of native vegetation in riparian buffers.

The Bodoquena Plateau (19° 45′ e 22° 15′ S, 57° 30′ e 56° 15′ W) has an area of 890,68 km^2 and is located in the transition between Cerrado and Atlantic Forest. The hydrography is partially underground with sinks, calcareous tuff, and cave formations, resulting in clear water with high levels of dissolved calcium and bicarbonate. These karst aquatic systems are extensive in Brazil (Sallun-Filho and Karmann 2007). The rivers of the Bodoquena Plateau drain the karst watersheds into the Miranda River, a subunit of the Upper Rio Paraguay Basin, which includes the Pantanal; one the most biodiverse wetlands in the world (Junk et al. 2011). Native vegetation has been rapidly fragmented by cattle ranching and agriculture with predominance of grain monoculture (soybeans and maize), resulting in a mosaic of land cover that ranges from dense riparian vegetation to deforested pasture (Roque et al. 2016).

In May 2015, we selected seven streams within a gradient of remaining forest cover (20–100% of the remnant forest cover) and were distributed across the Bodoquena region. To investigate potential effects of native vegetation loss on benthic aquatic macroinvertebrates, we deployed ten substrate baskets (20 × 20 × 10 cm with mesh opening of 50 mm) in a single pool along gradients of elevation and vegetation cover among seven karst streams with similar substrate composition. Baskets were filled with limestone to promote colonization.

Most of the chemical water parameters, such as temperature (21.0–22.8 °C) ($p = 0.43$), pH (7.2–8.1) ($p = 0.04$), dissolved oxygen (60.0–77.0 $\mathrm{mg\ l^{-1}}$) ($p = 0.140$) were similar between the sampled sites. Total nitrogen (1.87–0.85 lg/l) ($p = 0.38$), total phosphorous (0.179–0.102 lg/l) ($p = 0.47$), and turbidity (80–100 NTU) ($p = 0.63$) were also not correlated with the vegetation cover gradient.

We found a total of 2465 benthic macroinvertebrates comprising 25 families in the stream sampling along the gradient of vegetation cover. Macroinvertebrate abundance varied more than twofold across sites, with a minimum of 224 individuals found at the Taquaral stream (100% vegetation cover) to a maximum of 600 at the Serra stream (79% vegetation cover). Leptophlebiidae (with 934 individuals), Chironomidae (682), Hydrobiidae (177), and Elmidae (124) were the most abundant families along the gradient cover vegetation. Collector-gatherers-scrapers comprised 56% of total invertebrate abundance, followed by collectors-filterers-gatherers (33%) and predators (11%). Permutational multivariate analyses of variance (PERMANOVA) suggested that benthic macroinvertebrate community composition was unrelated to the vegetation gradient in Bodoquena Plateau.

Our results showed that the vegetational loss gradient had no influence on the macroinvertebrate community composition (Fig. 3.2), in contrast with the results found in other studies involving Neotropical streams (Moretti et al. 2007; Silva-Araujo et al. 2020). Similar studies of multitaxa communities in Bodoquena Plateau streams also did not find detectable responses between terrestrial and aquatic insects across a riparian cover gradient (Roque et al. 2017), and comparisons of fish communities along of the land cover gradient also demonstrated weak or no effects (Casatti et al. 2010). The lack of effect on macroinvertebrates could be attributed to mosaics of vegetation in the Bodoquena Plateau, which may maintain functional connectivity despite land conversion. In karstic systems, the watershed or forest cover delimitation is particularly challenging because surface water does not drain directly into surficial channels. Such a hydrogeomorphic settings likely could decouple the effects of landscape degradation from ecological processes in receiving waters.

Findings from our case study plus collective findings from studies in our qualitative survey suggest that while land use conversion can be expected to impact macroinvertebrate communities in Neotropical streams, observed impacts are likely to be context-specific. Landuse conversion that increases light to stream channels can increase productivity, resulting in elevated macroinvertebrate abundance for grazing

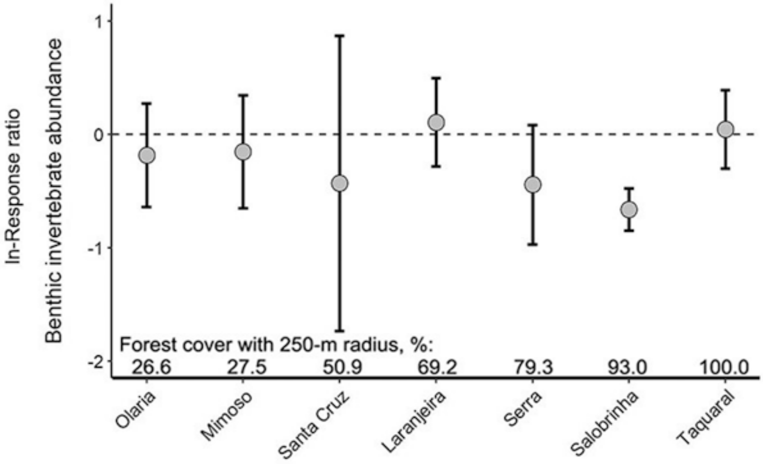

Fig. 3.2 Site-specific ln-response ratio (LRR) of total invertebrates' abundance with respect to the forest cover gradient. Shown are the means of treatment divided by control values ±1 standard error. Sites are ordered from least to most forest cover

taxa (Casatti et al. 2010; Silva-Araújo et al. 2020). Tropical streams are likely to consistently show such patterns because they experience high light and warm temperatures year-round (Boulton et al. 2008). Local hydrogeologic attributes might buffer macroinvertebrate communities from becoming severely degraded, a concept that likely extends beyond tropical regions. Finally, another potential mitigation strategy for minimizing land use effects in streams is maintaining sufficiently wide riparian buffer zones (Azevedo-Santos et al. 2021).

References

Albuquerque LG, Roque FO, Valente-Neto F, Koroiva R, Buss DF, Baptista DF, Hepp LU, Kuhlmann ML, Sundar S, Covich AP, Pinto JOP (2021) Large-scale prediction of tropical stream water quality using rough sets theory. Eco Inform 61:101226

Azevedo-Santos VM, Rodrigues-Filho JL, Fearnside PM, Lovejoy TE, Brito MFG (2021) Conservation of Brazilian freshwater biodiversity: thinking about the next 10 years and beyond. Biodivers Conserv 30:235–241

Barlow J, França F, Gardner TA, Hicks CC, Lennox GD, Berenguer E, Graham NAJ (2018) The future of hyperdiverse tropical ecosystems. Nature 559:517–526

Beuchle R, Grecchi RC, Shimabukuro YE, Seliger R, Eva HD, Sano E, Achard F (2015) Land cover changes in the Brazilian Cerrado and caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. Appl Geogr 58:116–127

Bojsen BH, Jacobsen D (2003) Effects of deforestation on macroinvertebrate diversity and assemblage structure in Ecuadorian Amazon streams. Archiv fur Hydrobiologie 158:317–342

Boulton AJ, Boyero L, Covich AP, Dobson M, Lake S, Pearson R (2008) Are tropical streams ecologically different from temperate streams? Chapter 9. In: Dudgeon D (ed) Tropical stream ecology. Academic, San Diego, pp 257–284

Brito JG, Roque FO, Martins RT, Nessimian JL, Oliveira VC, Hughes RM, de Paula FR, Ferraz SFB, Hamada N (2019) Small forest losses degrade stream macroinvertebrate assemblages in the eastern Brazilian Amazon. Biol Conserv 241:108263

Bücker A, Sondermann M, Frede HG, Breuer L (2010) The influence of land-use on macroinvertebrate communities in montane tropical streams - a case study from Ecuador. Fundam Appl Limnol 177:267–282

Buss DF, Baptista DF, Nessimian JL, Egler M (2004) Substrate specificity, environmental degradation and disturbance structuring macroinvertebrates assemblages in neotropical streams. Hydrobiologia 518:179–188

Casatti L, Romero RM, Teresa FB, Sabino J, Langeani F (2010) Fish community structure along a conservation gradient in Bodoquena Plateau streams, Central West of Brazil. Acta Limnol Bras 22:50–59

Chará J, Pedraza G, Giraldo L, Hincapié D (2007) Efecto de los corredores ribereños sobre el estado de quebradas em la zona ganadera del río La Vieja, Colombia. Agroforestería em las Américas 45:72–78

Chará-Serna AM, Chará J, Giraldo LP, Zúñiga MC, Allan JD (2015) Understanding the impacts of agriculture on Andean stream ecosystems of Colombia: a causal analysis using aquatic macroinvertebrates as indicators of biological integrity. Freshw Sci 34:727–740

Clarivate Analytics (2017) Research in Brazil. pp 1–73. http://www.sibi.usp.br. Accessed 28 Sept 2021

Corbera E, Kosoy N, Martinez-Tuna M (2007) Equity implications of marketing ecosystem services in protected areas and rural communities: case studies from Meso-America. Glob Environ Chang 17:365–380

Corbi JJ, Trivinho-Strixino S (2006) Influence of taxonomic resolution of stream macroinvertebrate communities on the evaluation of different land uses. Acta Limnol Bras 18:469–475

Cornejo A, Tonin AM, Checa B, Tuñon AR, Pérez D, Coronado E, González S, Rios T, Macchi P, Araneda FC, Boyero L (2019) Effects of multiple stressors associated with agriculture on stream macroinvertebrate communities in a tropical catchment. PLoS One. https://doi.org/10.1371/journal.pone.0220528

Corrêa EC, Roque FO, Utz RM, Correa JS, Souza FL, Covich AP (2018) Effects of macroconsumers on benthic communities: rapid increases in dry-season accrual of calcium in a tropical karst stream. PLoS One 13:e0209102

Corrêa EC, Roque FO, Utz RM, da Silva WM, Severo-Neto F, Gido KB (2019) Effects of macroconsumers on benthic communities across a gradient of vegetation loss in tropical karst streams. Hydrobiologia 836:21–34

Dala-Corte R, Melo AS, Siqueira T, Bini LM, Martins RT, Cunico AM, Pes AM, Magalhães ALB et al (2020) Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region. J Appl Ecol. https://doi.org/10.1111/1365-2664.13657

De Castro DMP, de Carvalho DR, Pompeu PS, Moreira MZ, Nardoto GB, Callisto M (2016) Land use influences niche size and the assimilation of resources by benthic macroinvertebrates in tropical headwater streams. PLoS One. https://doi.org/10.1371/journal.pone.0150527

De Castro DMP, Dolédec S, Callisto M (2018) Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. Ecol Indic 84:573–582

De Oliveira-Junior JMB, Shimano Y, Gardner TA, Hughes RM, Júnior PDM, Juen L (2015) Neotropical dragonflies (Insecta: Odonata) as indicators of ecological condition of small streams in the eastern Amazon. Austral Ecol 40:733–744

Encalada AC, Calles J, Ferreira V, Canhoto CM, Graca MAS (2010) Riparian land use and the relationship between the benthos and litter decomposition in tropical montane streams. Freshw Biol 55:1719–1733

Ferreira J, Pardini R, Metzger JP, Fonseca CR, Pompeu PS, Sparovek G, Louzada J (2012) Towards environmentally sustainable agriculture in Brazil: challenges and opportunities for applied ecological research. J Appl Ecol 49:535–541

Ferreira V, Castagneyrol B, Koricheva J, Gulis V, Chauvet E, Graça MAS (2015) A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biol Rev 90:669–688

Ferreira-Peruquetti P, De Marco P Jr (2002) Efeito da alteração ambiental sobre comunidades de Odonata em riachos de Mata atlântica de Minas Gerais, Brasil. Revista Brasileira de Zoologia 19:317–327

Firmiano KR, Ligeiro R, Macedo DR, Juen L, Hughes RM, Callisto M (2017) Mayfly bioindicator thresholds for several anthropogenic disturbances in neotropical savanna streams. Ecol Indic 74:276–284

Firmiano KR, Cañedo-Argüelles M, Gutiérrez-Cánovas C, Macedo DR, Linares MS, Bonada N, Callisto M (2019) Land use and local environment affect macroinvertebrate metacommunity organization in Neotropical stream networks. J Biogeogr:1–13

Guimarães-Souto RM, Facure KG, Jacobucci GB (2021) Do tropical riparian forests in the Cerrado Biome act as a buffer against the impacts of agriculture and livestock on benthic macroinvertebrate communities? Limnetica 40:329–342

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song DX, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052

Hunke P, Mueller EN, Schröder B, Zeilhofer P (2015) The Brazilian Cerrado: assessment of water and soil degradation in catchments under intensive agricultural use. Ecohydrology 8:1154–1180

Iñiguez–Armijos C, Leiva A, Frede HG, Hampel H, Breuer L (2014) Deforestation and benthic indicators: how much vegetation cover is needed to sustain healthy Andean streams? Plos one 9:e105869

Junk WJ, da Silva CJ, Nunes da Cunha C, Wantzen KM (2011) The Pantanal: ecology, biodiversity and sustainable management of a large Neotropical seasonal wetland. Pensoft Publishers, Sofia, p 870

Lammert M, Allan JD (1999) Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ Manag 23:257–270

Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. Trend Ecol Evol 29:107–116

Leal CG, Pompeu PS, Gardner TA, Leitão RP, Hughes RM, Kaufmann PR, Zuanon J, de Paula FR, Ferraz SFB, Thomson JR, Mac Nally R, Ferreira J, Barlow J (2016) Multi-scale assessment of human-induced changes to Amazonian instream habitats. Landsc Ecol. https://doi.org/10.1007/s10980-016-0358-x

Ligeiro R, Hughes RM, Kaufmann PR, Macedo DR, Firmiano KR, Ferreira WR, Oliveira D, Melo AS, Callisto M (2013) Defining quantitative stream disturbance gradients and the additive role of habitat variation to explain macroinvertebrate taxa richness. Ecol Indic 25:45–57

Lima DVM, Please LPM, Silva IHL (2020) Effects of land use on the community of benthic macroinvertebrates in streams of the Iquiri River basin (Acre, Brazil). South Am J 7:160–175

Lorion CM, Kennedy BP (2009) Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams. Freshw Biol 54:165–180

Macedo DR, Hughes RM, Ligeiro R, Ferreira WR, Castro MA, Junqueira NT, ... & Callisto M (2014) The relative influence of catchment and site variables on fish and macroinvertebrate richness in cerrado biome streams. Landsc Ecol 29(6):1001–1016. https://doi.org/10.1007/s10980-014-0036-9

Marcarelli AM, Baxter CV, Mineau MM, Hall RO (2011) Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92(6): 1215–1225. https://doi.org/10.1890/10-2240.1

Martins RT, Couceiro SRM, Melo AS, Moreira MP, Hamada N (2017) Effects of urbanization on stream benthic invertebrate communities in Central Amazon. Ecol Indic 73:480–491

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press, Washington, p 137

Morabowen A, Crespo-Pérez V, Ríos-Touma B (2019) Effects of agricultural landscapes and land uses in highly biodiverse tropical streams of the Ecuadorian Choco. Inland Waters. https://doi.org/10.1080/20442041.2018.1527597

Moraes AB, Wilhelm AE, Boelter T, Stenert C, Schulz UH, Maltchik L (2014) Reduced riparian zone width compromises aquatic macroinvertebrate communities in streams of southern Brazil. Environ Monit Assess 186:7063–7074

Moretti MS, Gonçalves JF Jr, Ligeiro R, Callisto M (2007) Invertebrates colonization on native tree leaves in a neotropical stream (Brazil). Int Rev Hydrobiol 92:199–210

Myers N, Mittermeyer RA, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nessimian JL, Venticinque EM, Zuanon J, Marco P Jr, Gordo M, Fidelis L, Batista JD, Juen L (2008) Land use, habitat integrity, and aquatic insect assemblages in Central Amazonian streams. Hydrobiologia 614:117–131

Noss RF (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. For Ecol Manag 115:135–146

Omernik JM, Bailey RG (1997) Distinguishing between watersheds and ecoregions. J Am Water Resour Assoc 33:935–949

Ometo JPHB, Martinelli LA, Ballester MV, Gessner A, Krusche AV, Victoria RL, Williams M (2000) Effects of land use on water chemistry and macroinvertebrates in two streams of the Piracicaba river basin, south-east Brazil. Freshw Biol 44:327–337

Ongaratto R, Loureiro RC, Restello RM, Hepp LU (2018) Effects of land use and limnological variables on the dissimilarity of common and rare aquatic insects in Atlantic Forest streams. Rev Biol Trop 66:1223–1231

Ordóñez MV (2011) Influencia del uso de suelo y la cobertura vegetal natural en la integridad ecológica de los ríos altoandinos al noreste del Ecuador. MS Thesis, Universidad San Francisco de Quito, Quito

Ratter J, Ribeiro J, Bridgewater S (1997) The Brazilian cerrado vegetation and threats to its biodiversity. Ann Bot 80:223–230

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni F, Hirota MM (2009) Brazilian Atlantic forest: how much is left and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142:1141–1153

Rodrigues ME, Roque FO, Quintero JMO, Pena JCC, Sousa DC, Junior PM (2016) Nonlinear responses in damselfly community along a gradient of habitat loss in a Savanna landscape. Biol Conserv 194:113–120

Roque FO, Ochoa-Quintero J, Ribeiro DB, LSM S, Costa-Pereira R, Lourival R, Bino G (2016) Upland habitat loss as a threat to Pantanal wetlands. Conserv Biol 30:1131–1134

Roque FO, Corrêa EC, Valente-Neto F, Stefan G, Schulz G, Souza PRB, Motta CM, Bavutti LLO, Colzani E, Demétrio MF, Escarpinati SC, Silvestre R, Vaz-de- Mello FZ, Siqueira T, Quintero JMO (2017) Idiosyncratic responses of aquatic and terrestrial insects to different levels of environmental integrity in riparian zones in a karst tropical dry forest region. Aust Entomol 56:459–465

Roque FO, Guerra FA, Johnson M, Padovani C, Corbi J, Covich AP, Eaton D, Tomas WM et al (2021) Simulating land use changes, sediment yields, and pesticide use in the Upper Paraguay River Basin: implications for conservation of the Pantanal wetland. Agric Ecosyst Environ 314:107405

Sallun Filho W, Karmann I (2007) Geomorphological map of the Serra da Bodoquena karst, west-central Brazil. J Maps 3:282–295

Sensolo D, Hepp LU, Decian V, Restello RM (2012) Influence of landscape on assemblages of Chironomidae in Neotropical streams. Ann Limnol Int J Limnol 48:391–400

Siegloch AE, Suriano M, Spies M, Fonseca-Gessner A (2014) Effect of land use on mayfly assemblages structure in Neotropical headwater streams. Ann Brazilian Acad Sci 84:1735–1747

Silva-Araújo M, Silva-Junior EF, Neres-Lima V, Feijó-Lima R, Tromboni F, Lourenço-Amorim C, Thomas SA, Moulton TP, Zandonà E (2020) Effects of riparian deforestation on benthic invertebrate community and leaf processing in Atlantic forest streams. Perspect Ecol Conser 18:277–282

Siqueira T, Lacerda CG-LT, Saito VS (2015) How does landscape modification induce biological homogenization in tropical stream metacommunities? Biotropica 47:509–516

Sponseller RA, Benfield EF, Valett HM (2001) Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshw Biol 46:1409–1424

Strassburg BBN, Brooks T, Feltran-Barbieri R, Iribarrem A, Crouzeilles R, Loyola R, Latawiec AE, Oliveira Filho FJB, Scaramuzza de CAM, Scarano FR, Soares-Filho B, Balmford A (2017) Moment of truth for the cerrado hotspot. Nat Ecol Evol 1:99

Suga CM, Tanaka MO (2013) Influence of a forest remnant on macroinvertebrate communities in a degraded tropical stream. Hydrobiologia 703:203–213

Sweeney BW, Bott TL, Jackson JK, Kaplan LA, Newbold JD, Standley LJ, Hession WC, Horwitz RJ (2004) Riparian deforestation, stream narrowing, and loss of stream ecosystem services. Proc Natl Acad Sci 101:14132–14137

Tanaka MO, De Souza ALT, Mischini LE, De Oliveira AK (2016) Influence of watershed land use and riparian characteristics on biological indicators of stream water quality in southeastern Brazil. Agric Ecosyst Environ 216:333–339

Torres PJ, Ramírez A (2014) Land use effects on leaf litter breakdown in low-order streams draining a rapidly developing tropical watershed in Puerto Rico. Rev Biol Trop 62:129–142

Villada-Bedoya S, Ospina-Bautista F, G-Dias L, Varón JVE (2017) Diversidad de insectos acuáticos en quebradas impactadas por agricultura y minería, Caldas, Colombia. Revista de Biologia Tropical 65:1635–1659

Vörösmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S, Bunn SE, Sullivan CA, Liermann CR, Davies PM (2010) Global threats to human water security and river biodiversity. Nature 46:555–561

Webster JR, Benfield EE (1986) Vascular plant breakdown in freshwater ecosystems. Annu Rev Ecol Evol Syst 17:567–594

Chapter 4
Plant Competition Across Topographic Gradients in Neotropical Cerrado Savannas: An Isotopic Approach

Davi R. Rossatto and Augusto C. Franco

4.1 Introduction

The Cerrado is the second most extensive biome in South America, encompassing a series of plant physiognomies, which normally form gradients of tree cover in the landscape from grasslands with no or little tree cover, through savannas of variable tree density to closed-canopy forests. It is mostly found in the Brazilian territory (from 2° N to 23° S) under a great diversity of climate, soils, and reliefs, showing a mosaic pattern of distribution at, both, landscape and local scales (Ratter et al. 1997). At local scales, different environmental factors can determine the occurrence of the different vegetation types (fire, soils, drought, and herbivory); however, the most elusive example of variations in the abundance of trees and ground layer species is the changes in vegetation structure along topographic gradients of a few hundred meters in the core region of the Cerrado (Eiten 1972). These changes are associated with decreases in species richness, changes on composition, and density of the upper canopy layer from the top to bottom of the topographic gradient, where the ground layer vegetation predominates. Historically, these changes in vegetation structure and composition were thought to be the result of plant competition and variations in edaphic factors (Goodland and Pollard 1973). In this chapter, we

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present the Cerrado and its vegetation gradients, the use of isotopes on plant ecology, and discuss the causes of such drastic variation on plant physiognomies using an isotopic approach ($\delta^{18}O$ and $\delta^{2}H$), to provide new insights on how plant competition aligned with water table level and soil depth caused such structural variations. We show that soil depth, groundwater, water table level, and depth of root water extraction interact on determining the ability of plants to successfully compete under different parts of topographic gradients. At the top of the gradient, soils are deep, with deeper water table, which allows plants with different root depths to thrive, potentially minimizing the effects of belowground competition. At the bottom of the topographic gradient, restricted soil depth and a shallow water table, that remains near or at the soil surface, normally during the wet season, promotes the selection of shallow rooted plants, eliminating woody species with deeper roots or species sensitive to waterlogging.

4.1.1 The Cerrado, Its Abiotic Environment and Vegetation Gradients

The Cerrado vegetation has a wide distribution throughout the Brazilian territory, occurring between latitudes 2° N and 23° S, covering approximately two and half million square km of the national territory, being the second largest vegetation complex in the Neotropics (Ratter et al. 1997). Due to this widespread range, the Cerrado is subjected to different climates, geology, reliefs, and soils, which are associated with a large diversity of plant formations and species (Oliveira-Filho and Ratter 2002). Climate is seasonal with average annual rainfall varying from 800 to 1700 mm annually (Eiten 1972) with a distinct dry season during the winter, while most of the rains are concentrated in spring and summer. The majority of soils are deep, poor nutrient oxisols, with sandy soils appearing at some sites (Eiten 1972; Furley and Ratter 1988), and with altitudes varying from 300 to 1500 m a.s.l. (Eiten 1972). Along with seasonality, fire is an important abiotic driver that normally occurs during the dry season, consuming the dry and dead biomass, influencing vegetation types (Coutinho 1990; Miranda et al. 2002).

Among its diverse vegetation types, the most common and widespread are grasslands, savannas, wet and dry forests, which can form intricate mosaics (Silva et al. 2006). The mosaic appearance within its range allows the Cerrado to attain a great number of biological gradients (Oliveira-Filho et al. 1989; De Castro and Kaufmann 1998; Hoffmann et al. 2005; Ribeiro and Walter 2008), that normally varies within a few hundred meters from grasslands to forests, passing through typical savannas (Eiten 1972). These gradients reflect differences in species composition, density, and plant growth forms (Fig. 4.1): grasslands are treeless open physiognomies where eudicotyledons perennial herbs (3–20 cm height) are scattered within a dominant fire-prone graminoid layer (Fig. 4.1a); in addition to a species-rich ground layer of grasses and herbs, savannas in turn have an upper canopy of thickened shrubs and small trees (2–10 m height) (Fig. 4.1b); and forests are mostly composed

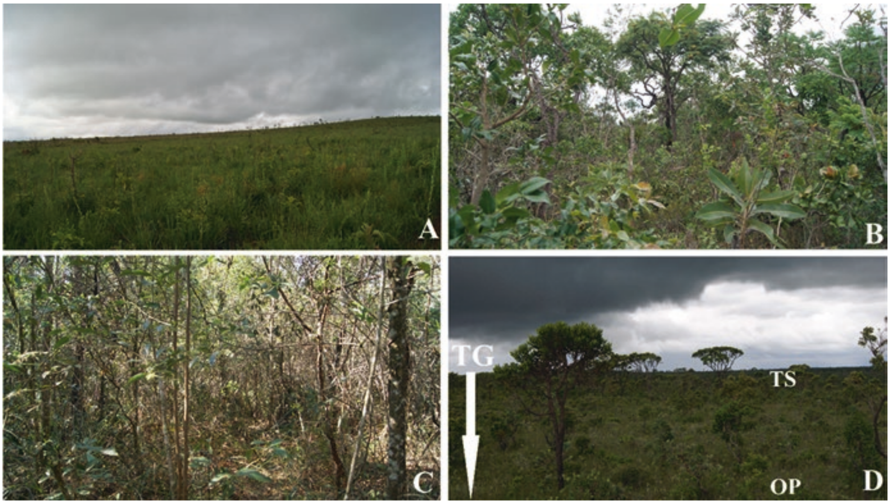

Fig. 4.1 The diversity of vegetation types in the Cerrado of Central Brazil. (**a**) grassland; (**b**) savanna; (**c**) nonflooded gallery forest; and (**d**) a short topographic gradient (TG) showing the variation in tree density from typical savanna (TS) to open savanna (OP). (Photos taken by D.R. Rossatto)

by tree species (8–15 m height) forming a closed canopy (Fig. 4.1c); the ground layer vegetation is not as species-rich and has a scattered distribution (Ribeiro and Walter 2008).

In regions of mostly flat terrain, the presence of such gradients is mainly due to changes in abiotic properties, especially fire frequency, in interactions with water availability and soil nutrients (Goodland and Polard 1973; De Castro and Kauffmann 1998; de Assis et al. 2011). Grassland-savanna-forest gradients can therefore appear by means of differences in fire frequency (Coutinho 1990; Kauffmann et al. 1994; Pivelo and Coutinho 1996; Ruggiero et al. 2006; Gomes et al. 2018), in where grasslands are determined by frequent fires which kill the trees and allow only the persistence of fire-prone grasses and other fire adapted herbaceous species and small shrubs (Simon and Pennington 2012); in contrast, forests remain in regions where fire were excluded for a long period of time (Hoffmann et al. 2012). Soil chemical properties are also pointed out as cause of such gradients at flat regions: grasslands are associated with shallow oxi or sandy soils with higher aluminum content, while forests are mainly reported to occur in deeper soils that can retain more water and naturally have higher amount of nutrients, such as Ca and Mg (Goodland and Polard 1973; Lopes and Cox 1977; Furley and Ratter 1988; Ruggiero et al. 2002; Haridasan 2008; de Assis et al. 2011).

Although very common along the Cerrado distribution domain, the grasslands-savanna gradients are not only determined by fire frequency or soil nutrition (Eiten 1972). In central Brazil, variations on relief and slope along a few hundred meters can provide a great variation on woody species cover (Fig. 4.1d), changing vegetation from dense savanna (with high tree cover) to grasslands (treeless vegetation):

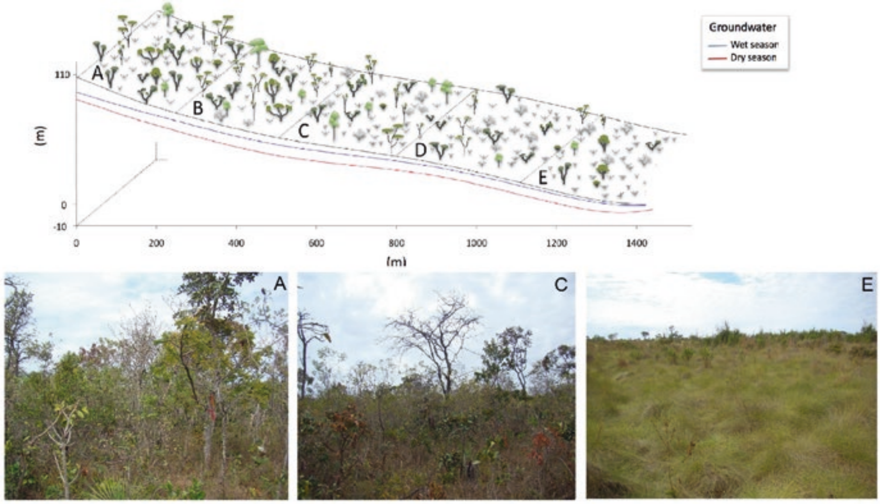

Fig. 4.2 Schematic representation of a topographic gradient of 1500 m spanning an elevation gradient of about 110 m at the RECOR – Reserva Ecológica do IBGE, Brasília – DF, Brazil, and its vegetation types: (**a**) dense savanna; (**b, c**) typical savanna; and (**d, e**) grassland. (Photos taken by D.R. Rossatto at representative locations (A, C, E) along the gradient)

these are the so called topographic gradients in vegetation (Fig. 4.2). Topographic gradients are normally related with great altitudinal differences (Beals 1969; Myster 2017), being commonly studied in mountain ecosystems of subtropical and temperate regions (Fischer et al. 2011) and in the Neotropics, in Amazonian and Atlantic Forest ecosystems along altitudinal gradients (Oliveira-Filho et al. 1998; Sanchez et al. 2013). However, the much shallower topographic gradients in Cerrado are characterized by a great variation of slopes, soil type, water table, and soil depth, which are associated with large changes in plant physiognomy along few hundred meters and with very little changes in elevation (100 m).

At the top of such gradients, the woody component is dominant (Fig. 4.2), with greater density and number of individuals restricting the development of a dense ground layer (Rossatto et al. 2012; Leite et al. 2018). In turn, as we advance a few meters along this gradient, important decreases in the woody component appear, and the ground layer, with eudicotyledonous herbs (thereafter referred as eudicot herbs) and graminoids (Fig. 4.2) becomes more prominent (Pinto et al. 2005; Ruggiero et al. 2006; Rossatto et al. 2012). These variations were thought to be associated with chemical soil properties, such as available Al and Ca (Goodland and Polard 1973; Pinto et al. 2005; Villalobos-Vega et al. 2014), and also soil physical aspects related to water retention, such as the ratios between sand, silt, and clay (Pinto et al. 2005; Júhasz et al. 2006; Ribeiro et al. 2021). However, we demonstrated that such changes in vegetation structure and composition at small scales are not simply explained by variations in chemical and physical properties of the soil, but also involved more complex biotic aspects related to changes in belowground species traits (such as root depth and depth of water uptake), soil depth, and groundwater level.

4.2 The Isotopic Approach

The use of stable isotopes in biology advanced quickly during the latter half of the twentieth century (Ehleringer and Dawson 1992; Newsome et al. 2007), making use of the fact that natural elements possess different stable forms (lighter and heavier forms) and the measurement of abundance ratios of heavier to lighter isotopes can provide information on how biological entities make use of abiotic elements (Rundel et al. 2012). These approaches were mainly performed using the most abundant and important elements for organisms, namely N, C, H, and O (Dawson and Siegwolf 2011). Stable isotopic analysis of elements, as N, can reveal aspects related to animal diet (Robbins et al. 2005), while analysis on C can show water use efficiency and photosynthetic capacity of plants and predominant photosynthetic pathways (O'leary 1988; Farquhar et al. 1989). The analysis of H and O isotopes is mainly used to understand water use in plants (Flanagan and Ehleringer 1991) as well as hydrological processes (Bowen et al. 2019), and in this case, abiotic aspects of plants should be understood based on calculation of depth of water uptake (Rothfuss and Javaux 2017), tracking isotopic signatures of plant tissues with that found in soils (Dawson and Siegwolf 2011). The use of water isotopes in plant ecological studies, mainly focused on the understanding of underground traits such as root depth and depth of water uptake is not relatively new (Ehleringer and Dawson 1992), and brought substantial advances to the theme of plant competition (Dawson 1993). In the past, to have some insight on how plants were using soil water resources, one would have to excavate the entire root system (Rawitscher 1948; Durigan et al. 2012), which is a difficult and laborious task and be a rather complex operation for species with deep root systems that may be as deep as 20 m (Schenk and Jackson 2002), and may require the use of excavation machines or manual excavation. However, root distribution in the soil per se is an indirect evidence of root water extraction patterns. The use of water isotopic ratios proved an easy and relatively quick approach to infer soil water use by plants.

Water is composed by H and O, and both elements can have more than one naturally occurring stable isotope: hydrogen can be found showing mass of 1, 2, and 3, while oxygen can show natural abundances of mass 16, 17, and 18 (Michener and Lajtha 2008). Because there is no significant isotopic fractionation during water uptake by the majority of terrestrial plants, the isotopic composition of plant organs should match those from the soil (Michener and Lajtha 2008), provided tissue evaporation has not occurred, as this phenomenon can enrich the sample with heavier isotopes, destroying the original signature. The first performed studies were focused on understanding how individual plant species take up water along a soil profile and how species can compete for it (Dawson 1993), but quickly, this technique advanced to encompass community and ecosystem ecology studies (Dawson et al. 2002). Many experimental approaches and laboratory methods to extract and measure the isotopic composition of water were developed (Revesz and Woods 1990; Vendramini and Sternberg 2007; Orlowski et al. 2013). These methods aimed to decrease and avoid water evaporation after sample collection, which can drastically affect the natural ratio of isotopes in plant water samples (Vendramini and Sternberg 2007).

The basis for water isotopic approach uses in plant ecology, mainly focusing on understanding root depth and depth of water uptake, consists in the evaluation of soil groundwater, water table, and plant stem water isotopic ratios (Dawson et al. 2002). Natural gradients of hydrogen and oxygen isotopes develop along the soil profile by means of evaporation: on sunny days and under water availability in the soil, evaporation allows heavy isotopes to predominate on soil surface, since lighter elements are more easily evaporated from the soil (Dawson et al. 2002). This results in the formation of a gradient from heavy enriched to lighter enriched isotopes along the soil profile (Fig. 4.3). We can then use the values of isotopic composition of soil water collected at different depths in the soil profile and the isotopic composition of the sap water extracted from plant tissues (mainly lignified branches) to estimate a parameter called average depth of water uptake by a plant. In this regard, many methods are available, but we used the mass balance model developed by Romero-Saltos et al. (2005), which assumes that the bulk of plant water uptake is limited to a 50-cm vertical segment, however, without constraining the depth of the 50-cm segment. In this model, water is taken up by the plant following a normal distribution and the average root depth is at the center of the 50-cm segment. This means that 99.7% of the water taken up by the plant comes from a 50-cm segment of soil (for more details of the model, see Romero-Saltos et al. 2005; Rossatto et al. 2013).

In turn, groundwater in the water table may show a more stable composition for longer periods of time, since is composed by a mix of isotopes that can percolate through the soil (Vogel and Varn Urk 1975). This enrichment process and different isotopic composition of soil layers and water table allows a great opportunity to understand how plants are using and partitioning soil water resources (Michener

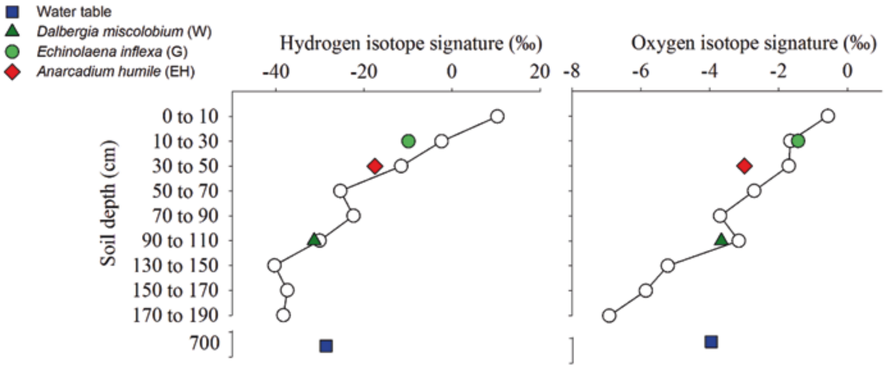

Fig. 4.3 A gradient of hydrogen and oxygen isotopic signatures during the wet season, developed 1 week after the last rainfall event (November 2007) along a soil profile at the upper slope of a topographic gradient in Central Brazil. (Data from Rossatto et al. (2014)). Some examples of isotopic composition for different growth forms and the water table signature are shown. W woody, G grass, and EH eudicot herb

and Lajtha 2008) and whether patterns of soil water use by plants change in time. Since roots of different species may be located at different positions of this enrichment gradient, isotopic composition of the stem water should reflect effective depth of water uptake, which would be the result of several parameters such as root distribution, changes in root conductance and soil water availability, hydraulic redistribution of soil water (Jackson et al. 2000; Goldstein et al. 2008).

The process of collecting samples of water table, groundwater, and extracting water from soil samples and plant stems at the same time are laborious, especially in topographic gradients where groundwater level and soil depth are very variable (Oliveira et al. 2005; Goldstein et al. 2008). For water table groundwater, this requires the installation of wells to access the water table (Fig. 4.4a), which under very depth oxisols such as those found in the Cerrado, these wells may have depths of 12–15 m (Villalobos-Vega et al. 2014) or even more (Rawitscher 1948; Schubart and Rawitscher 1950). For soil samples, collecting is normally performed using a soil auger to collect samples at least to 3–5 m depth (Fig. 4.4b). Plant stems should be collected during nighttime (predawn) to avoid evaporation and isotopic enrichment. Soil and stem water should be extracted on very low temperatures (Fig. 4.4c) under vacuum lines (Vendramini and Sternberg 2007) also to avoid isotopic enrichment followed by analysis of isotope composition generally by mass spectrometry.

With heavy effort these wells can be assembled, and after that water table groundwater depth can be measured periodically. Although this can bring important information on how water table groundwater depth changes along topographic gradients and throughout the year, without information on plant community structure, plant composition, and plant use of soil water resources it is almost impossible to gain any useful insight on how this variation in groundwater levels can affect or determine the observed vegetation gradients (Rossatto et al. 2012; Villalobos-Vega et al. 2014; Leite et al. 2018).

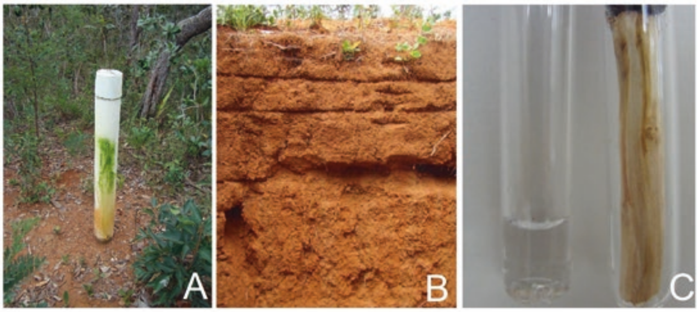

Fig. 4.4 Challenges imposed by the isotopic studies: (**a**) installation of wells to monitor and collect samples from the water table with minimum disturbance to the environment; (**b**) deep clayey soils; and (**c**) correct extraction of water from branch samples. (Photos taken by D.R. Rossatto)

4.3 Topographic Gradients and Plant Competition in Central Brazil

As explained in Sect. 4.1, the Cerrado is characterized by a great diversity of abiotic and biological gradients, with topographic gradients being very common at the core region in Central Brazil. The fact that plant composition and structure gradually change along these gradients in a predictable pattern raised several questions concerning which factors could explain the observed changes in vegetation (Castro and Kauffmann 1998; Henriques 2004). Many hypotheses were proposed as cause-effect relationships between abiotic and biotic components: soil nutrition (Goodland and Pollard 1973), soil depth (Pinto et al. 2005), and groundwater level (Oliveira-Filho et al. 1989). However, these studies did not find a plausible mechanistic explanation, only making general inferences based on correlative results, altought, a study showed differences in leaf and canopy transpiration along the topographic gradient in Cerrado sites (Bucci et al. 2008), which pointed to effects on soil water availability and water table level determining such gradients.

We decided to make use of the isotopic approach to understand if competition for soil water and niche partitioning where the phenomenon behind the occurrence of such changes in vegetation along topographic gradients and why they were so diverse in terms of vegetation types and dominance of certain plant growth forms (Rossatto et al. 2013). We established our field site at the IBGE Ecological Reserve, located south of the city of Brasília, Distrito Federal, in Brazil (15° 56′ S, 47° 53′ W, central point of the reserve). The IBGE reserve is at an average altitude of 1100 m above sea level, showing gentle topographic gradients and encompassing several Cerrado vegetation physiognomies (savannas, grasslands, and forests) (Ribeiro 2011). The annual precipitation is around 1450 mm (historic average between the years of 1990 and 2005), showing a pronounced dry season from May through September. Mean monthly temperature ranges from 19 to 23 °C, with maximum temperatures around 30 °C in summer, and minimum around 6 °C in winter. The predominant soils are deep and well-drained Oxisols (Ribeiro 2011). In November 2007, we set up a transect of 1500 m spanning an elevation gradient of about 110 m (from 1148 to 1038 elevation). The transect was subdivided into five segments from the highest to the lowest elevation. The first two segments were covered by a dense savanna vegetation, a matrix of co-existing woody, herbaceous eudicots and grasses species, with high tree density, that were replaced by typical savanna, a more open shrub-dominated savanna in the following two segments downslope, while the last segment consisted of grasslands, a very open (nearly treeless) physiognomy. To describe vegetation in these segments, we assembled four 4 × 4 m plots in each segment, in which we measured tree diameter, density, basal area, and height. We surveyed all woody species with a minimum stem diameter of 2 cm at 30 cm above ground level.

We started our study at the uppermost segment, where plant density and diversity were higher, and in which a great diversity of growth forms were found. We decided to focus on three different growth forms, adopting a functional group strategy

(Lavorel et al. 2007): grasses (plants with herbaceous stems in the form of culms and slender sheathing leaves), eudicot herbs (small plant around 10–30 cm in height, with herbaceous stems and branches), and trees (a woody plant with a defined stem, generally taller than 2 m) (Rossatto and Franco 2017). We found that at higher elevations, the greater soil depth allowed the presence of a deep water table, which allowed different sets of plants, with distinct kind of root types to co-exist (Table 4.1). In this part of the gradient, grasses are able to explore the most superficial layers (0.1–0.5 m), avoiding competition with trees, which tend to rely mostly on water from relatively deeper soil layers (Fig. 4.3, Table 4.1). Eudicot herbs, which tend to have a great variety of underground organs (De Moraes et al. 2016; Pilon et al. 2021), preferentially extract water from intermediate regions of the soil profile, exploring mostly the region that has less overlap with grasses and trees (Fig. 4.3, Table 4.1). In turn, trees tend to explore deeper regions of the soil profile allowing access to more stable water sources, at least when adults (Rossatto et al. 2013). Such differences were maintained during both, dry and wet seasons despite some seasonal variations in the depth of water uptake, with grasses and herbs having greater overlap in the use of soil water during the dry season. Because most grasses and herbs are partially defoliated or dormant at the peak of the dry season, whole plant transpiration is minimal, which minimizes potential effects of competition for the limited soil water reserves in the upper soil layers that are drier in this time of the year (Rossatto et al. 2013). This vertical partitioning of soil water would lead to a better exploration of water resources through the soil profile, reducing competition in such top regions of the topographic gradient.

Table 4.1 Summary of vegetation properties, water table level, and depth of water uptake for woody and ground layer species along a topographic gradient in Central Brazil

Vegetation type	Distance from first sample point (m)	Altitude (m from sea level)	Lowest water table depth (m)	Wood species density (n°.ha^{-1})	Woody species depth of water uptake (m)	Ground layer species depth of water uptake (m)
Dense savanna	0	1148	7.10 to 7.50	1000	0.5 to 2.10	0.10 to 1.10
Dense savanna	200	1114	3.88 to 4.10	800	0.7 to 1.50	0.10 to 1.00
Typical savanna	500	1091	3.15 to 3.20	600	0.7 to 1.10	0.10 to 0.90
Typical savanna	900	1071	1.02 to 1.80	400	0.5 to 0.70	0.10 to 0.80
Grassland	1300	1038	0.50 to 1.01	300	0.1 to 0.30	0.01 to 0.30

Data compiled from Rossatto et al. (2012), Rossatto et al. (2013), Rossatto et al. (2014), and unpublished data (Rossatto and Franco). Depth of water uptake was estimated according to the mass balance model proposed by Romero-Saltos et al. (2005), which assumes that the bulk of plant water uptake is limited to a 50-cm vertical segment of the soil profile without restricting the depth of the 50-cm segment (see text for more details)

After answering this first question, we assessed how the water uptake and competition may occur~~s~~ along the topographic gradients, from the top to the bottom using woody species alone (Rossatto et al. 2012). For this case, we combined the water table level monitoring with isotopic approach and plant community structure. We were able to show that groundwater level affected plant water uptake patterns and soil water partitioning among savanna woody species. Trees at the top of the gradient had access to a much deeper unsaturated zone which allowed greater variability of water uptake strategies (with plants accessing shallow, < 0.6 m, and deeper, > 1.0 m, soil layers). This great variability on water uptake strategies allowed different species to co-exist, leading to a denser and more complex woody layer (Table 4.1). At the bottom of this topographic gradient downslope, the water table nears the soil surface (Table 4.1) restricting water uptake to the shallower wet season unsaturated zone of the soil profile selecting for a sparsely woody vegetation composed of few species able to produce shallow roots that relied only on superficial water uptake.

Although we provided strong evidence for the effects of water uptake on the structure of woody vegetation, which of course would have implications on ground layer species, we had to confirm if these niche partitioning patterns changed along topographic gradients similarly, to woody and ground layer species. Then, we decided to analyze water isotopic signatures of woody and herbaceous species sampled in the five segments of the transect studied by Rossatto et al. (2012). We showed that woody and herbaceous species indeed display niche partitioning at the top and the center parts of the topographic gradient (Rossatto et al. 2014), with woody species extracting water from deeper soil layers in comparison with the herbaceous species (Table 4.1). At the bottom regions of the gradient, where groundwater is near the soil surface (Table 4.1), soil water extraction by woody and herbaceous plants was constrained to the most superficial soil layers (0–60 cm). Since deep-rooted Cerrado woody species tend to be intolerant to waterlogging (Joly and Crawford 1982; de Oliveira et al. 2015; Ribeiro et al. 2021), tree species diversity and abundance are lower and sometimes non-existent in this part of the topographic gradient (Pinto et al. 2005; Rossatto et al. 2012), while the shallow-rooted herbaceous species would be favored, allowing predominance of a more open vegetation type. Although further studies are necessary, we predict that the scattered shallow-rooted tree species present at the bottom of the gradient would be under strong competition for soil water with the herbaceous component and under severe drought stress, given elevated water table levels.

These three studies, performed along a unique topographic gradient in Central Brazil, provide strong evidence that abiotic factors such as groundwater level and soil depth act in concert as ecological filters, selecting for different water uptake patterns according with plant growth form, reinforcing vegetation gradients by exerting divergent selective pressures across topographic gradients. In fact, after our case study, other papers, performed elsewhere in the Cerrado region, mainly confirmed our findings using other approaches (Villalobos-Vega et al. 2014; Leite et al. 2018; Elias et al. 2019). As the topographic gradients advance a few hundred meters downslope, groundwater tends to be more superficial, restricting the niche space available for roots to grow. In this way, the root systems of woody species tend to be constrained to more superficial soil layers, which increase overlap with herbaceous species in the use of soil water resources. Finally, at the bottom of the gradient downslope, minimum groundwater depth is so low that it reaches soil surface layers in the wet season, making these layers saturated for sufficient time to impair the establishment of most Cerrado woody species that tend to be sensitive to soil waterlogging.

4.4 Final Remarks

When performed alone, the classical techniques of biological (phytosociology, plant growth forms, vegetation analysis) and edaphic (chemical and physical) surveys performed on topographic Cerrado gradients, explained only the effects of abiotic factors on changes in vegetation structure and composition. The use of an isotopic approach allowed us to evaluate the intrinsic relationship between plants and abiotic factors, showing that not only soil properties or soil resources were responsible for the vegetation changes observed along such gradients. In fact, biotic aspects related to competition were determinant to understand vegetation structure and its variation along the topographic gradient. Although yet expensive and not widespread available to scientists in developing countries, the use of isotopes in ecological studies should be encouraged and financed by national government research agencies as a way to address emerging issues in plant ecology especially related to the ecology of abiotic and biotic gradients.

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References

Beals EW (1969) Vegetational change along altitudinal gradients. Science 165(3897):981–985

Bowen GJ, Cai Z, Fiorella RP, Putman AL (2019) Isotopes in the water cycle: regional-to global-scale patterns and applications. Annu Rev Earth Planet Sci 47:453–479

Bucci SJ, Scholz FG, Goldstein G, Hoffmann WA, Meinzer FC, Franco AC et al (2008) Controls on stand transpiration and soil water utilization along a tree density gradient in a Neotropical savanna. Agric For Meteorol 148(6–7):839–849

Castro EA, Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass root mass and consumption by fire. J Trop Ecol 14(3): 263-283.

Coutinho LM (1990) Fire in the ecology of the Brazilian cerrado. In: Fire in the tropical biota. Springer, Berlin/Heidelberg, pp 82–105

Dawson TE (1993) Water sources of plants as determined from xylem-water isotopic composition: perspectives on plant competition, distribution, and water relations. In: Stable isotopes and plant carbon-water relations. Academic, pp 465–496

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable isotopes in plant ecology. Annu Rev Ecol Syst 33(1):507–559

Dawson TE, Siegwolf RTW (2011) Stable Isotopes as Indicators of Ecological Change. Academic Press, New York.

de Assis ACC, Coelho RM, da Silva Pinheiro E, Durigan G (2011) Water availability determines physiognomic gradient in an area of low-fertility soils under Cerrado vegetation. Plant Ecol 212(7):1135–1147

De Castro EA, Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. J Trop Ecol 14(3):263–283

de Moraes MG, de Carvalho MAM, Franco AC, Pollock CJ, Figueiredo-Ribeiro RCL (2016) Fire and Drought: Soluble Carbohydrate Storage and Survival Mechanisms in Herbaceous Plants from the Cerrado. BioScience 66(2):biv178

De Oliveira AS, Ferreira CS, Graciano-Ribeiro D, Franco AC (2015) Anatomical and morphological modifications in response to flooding by six Cerrado tree species. Acta Botanica Brasilica 29(4):478–488

Durigan G, Melo AC, Brewer JS (2012) The root to shoot ratio of trees from open-and closed-canopy cerrado in South-Eastern Brazil. Plant Ecol Divers 5(3):333–343

Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable isotope composition. Plant Cell Environ 15(9):1073–1082

Eiten G (1972) The cerrado vegetation of Brazil. Bot Rev 38(2):201–341

Elias F, Junior BHM, de Oliveira FJM, de Oliveira JCA, Marimon BS (2019) Soil and topographic variation as a key factor driving the distribution of tree flora in the Amazonia/Cerrado transition. Acta Oecol 100:103467

Farquhar GD, Hubick KT, Condon AG, Richards RA (1989) Carbon isotope fractionation and plant water-use efficiency. In: Stable isotopes in ecological research. Springer, New York, pp 21–40

Fischer A, Blaschke M, Bässler C (2011) Altitudinal gradients in biodiversity research: the state of the art and future perspectives under climate change aspects. Waldökologie, Landschaftsforschung und Naturschutz 11:35–47

Flanagan LB, Ehleringer JR (1991) Stable isotope composition of stem and leaf water: applications to the study of plant water use. Funct Ecol 5(2):270–277

Furley PA, Ratter JA (1988) Soil resources and plant communities of the central Brazilian cerrado and their development. J Biogeogr 15(1):97–108

Goldstein G, Meinzer FC, Bucci SJ, Scholz FG, Franco AC, Hoffmann WA (2008) Water economy of Neotropical savanna trees: six paradigms revisited. Tree Physiol 28(3):395–404

Gomes L, Miranda HS, da Cunha Bustamante MM (2018) How can we advance the knowledge on the behavior and effects of fire in the Cerrado biome? For Ecol Manag 417:281–290

Goodland R, Pollard R (1973) The Brazilian cerrado vegetation: a fertility gradient. J Ecol 61(1):219–224

Haridasan M (2008) Nutritional adaptations of native plants of the cerrado biome in acid soils. Braz J Plant Physiol 20(3):183–195

Henrique RPB (2004) Análise fitossociológica em vegetação de cerrado sensu stricto em um gradiente topográfico no Brasil Central. Boletim do Herbário Ezechias Paulo Heringer 13

Hoffmann WA, da Silva ER, Machado GC, Bucci SJ, Scholz FG, Goldstein G, Meinzer FC (2005) Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna. Oecologia 145(2):306–315

Hoffmann WA, Geiger EL, Gotsch SB, Rossatto DR, Silva LCR, Lau OL, Haridasan M, Franco AC (2012) Ecological thresholds at the savanna-forest boundary: how plant traits resources and fire govern the distribution of tropical biomes. Ecol Lett 15(7): 759–768.

Jackson RB, Sperry JS, Dawson, TE (2000) Root water uptake and transport: using physiological processes in global predictions. Trends Plant Scien 5(11): 482–488.

Joly CA, Crawford RMM (1982) Variation in tolerance and metabolic responses to flooding in some tropical trees. J Exp Bot 33(4):799–809

Juhász CEP, Cursi PR, Cooper M, Oliveira TC, Rodrigues RR (2006) Dinâmica físico-hídrica de uma toposseqüência de solos sob Savana Florestada (Cerradão) em Assis SP. Rev Bras Cienc Solo 30(3): 401–412.

Kauffman JB, Cummings DL, Ward DE (1994) Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. J Ecol 82(3):519–531

Lavorel S, Díaz S, Cornelissen JHC, Garnier E, Harrison SP, McIntyre S et al (2007) Plant functional types: are we getting any closer to the Holy Grail? In: Terrestrial ecosystems in a changing world. Springer, Berlin/Heidelberg, pp 149–164

Leite MB, Xavier RO, Oliveira PTS, Silva FKG, Matos DMS (2018) Groundwater depth as a constraint on the woody cover in a Neotropical Savanna. Plant Soil 426(1):1–15

Lopes AS, Cox FR (1977) Cerrado vegetation in Brazil: an edaphic gradient 1. Agron J 69(5):828–831

Michener R, Lajtha K (eds) (2008) Stable isotopes in ecology and environmental science. Wiley-Blackwell, Malden, Massachusetts.

Miranda HS, Bustamante MM, Miranda AC, Oliveira P, Marquis R (2002) The fire factor. In: The cerrados of Brazil: ecology and natural history of a neotropical savanna, vol 51. Columbia University Press, New York, p 68

Myster RW (2017) Gradient (elevation) vs. disturbance (agriculture) effects on primary cloud forest in Ecuador: floristics and physical structure. N Z J For Sci 47:1–7

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5(8):429–436

O'Leary MH (1988) Carbon isotopes in photosynthesis. Bioscience 38(5):328–336

Oliveira RS, Bezerra L, Davidson EA, Pinto F, Klink CA, Nepstad DC, Moreira A (2005) Deep root function in soil water dynamics in cerrado savannas of central Brazil. Funct Ecol 19(4):574–581

Oliveira-Filho AT, Ratter JA (2002) Vegetation physiognomies and woody flora of the Cerrado Biome. In: Oliveira PS, Marquis RJ (eds) The Cerrados of Brazil: ecology and natural history of a neotropical savanna. Columbia University Press, New York, pp 91–120

Oliveira-Filho AT, Curi N, Vilela EA, Carvalho DA (1998) Effects of canopy gaps, topography, and soils on the distribution of woody species in a central Brazilian deciduous dry forest 1. Biotropica 30(3):362–375

Oliveira-Filho AT, Shepherd GJ, Martins FR, Stubblebine WH (1989) Environmental factors affecting physiognomic and floristic variation in an area of cerrado in central Brazil. J Trop Ecol 5(4):413–431

Orlowski N, Frede HG, Brüggemann N, Breuer L (2013) Validation and application of a cryogenic vacuum extraction system for soil and plant water extraction for isotope analysis. J Sens Sens Syst 2(2):179–193

Pilon NA, Cava MG, Hoffmann WA, Abreu RC, Fidelis A, Durigan G (2021) The diversity of post-fire regeneration strategies in the cerrado ground layer. J Ecol 109(1):154–166

Pinto JRR, Oliveira-Filho AT, Hay JDV (2005) Influence of soil and topography on the composition of a tree community in a central Brazilian valley forest. Edinb J Bot 62(1–2):69–90

Pivello VR, Coutinho LM (1996) A qualitative successional model to assist in the management of Brazilian cerrados. For Ecol Manag 87(1–3):127–138

Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian cerrado vegetation and threats to its biodiversity. Ann Bot 80:223–230

Rawitscher F (1948) The water economy of the vegetation of theCampos Cerrados' in Southern Brazil. J Ecol 36(2): 237–268.

Revesz K, Woods PH (1990) A method to extract soil water for stable isotope analysis. J Hydrol 115(1–4):397–406

Ribeiro ML (2011) Reserva Ecológica do IBGE: biodiversidade terrestre. Coordenação de Recursos Naturais e Estudos Ambientais, Rio de Janeiro

Ribeiro JF, Walter BMT (2008) Fitofisionomias do Bioma Cerrado. In: Sano S, Almeida S, Ribeiro JF (eds) Cerrado: Ecologia e flora. EMBRAPA Cerrados, Planaltina

Ribeiro JW, Pilon NA, Rossatto DR, Durigan G, Kolb RM (2021) The distinct roles of water table depth and soil properties in controlling alternative woodland-grassland states in the Cerrado. Oecologia 195(3):641–653

Robbins CT, Felicetti LA, Sponheimer M (2005) The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. Oecologia 144(4):534–540

Romero-Saltos H, Sternberg LDS, Moreira MZ, Nepstad DC (2005) Rainfall exclusion in an eastern Amazonian forest alters soil water movement and depth of water uptake. Am J Bot 92(3):443–455

Rossatto DR, Silva LDCR, Villalobos-Vega R, Sternberg LDSL, Franco AC (2012) Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical savanna. Environ Exp Bot 77:259–266

Rossatto DR, da Silveira Lobo Sternberg L, Franco AC (2013) The partitioning of water uptake between growth forms in a Neotropical savanna: do herbs exploit a third water source niche? Plant Biol 15(1):84–92

Rossatto DR, Silva LCR, Sternberg LSL, Franco AC (2014) Do woody and herbaceous species compete for soil water across topographic gradients? Evidence for niche partitioning in a Neotropical savanna. S Afr J Bot 91:14–18

Rossatto DR, Franco AC (2017) Expanding our understanding of leaf functional syndromes in savanna systems: the role of plant growth form. Oecologia 183(4): 953-962.

Rothfuss Y, Javaux M (2017) Reviews and syntheses: isotopic approaches to quantify root water uptake: a review and comparison of methods. Biogeosciences 14(8):2199–2224

Ruggiero PGC, Batalha MA, Pivello VR, Meirelles ST (2002) Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest. Southeast Brazil Plant Ecol 160(1):1–16

Ruggiero PGC, Pivello VR, Sparovek G, Teramoto E, Pires Neto AG (2006) Relação entre solo, vegetação e topografia em área de cerrado (Parque Estadual de Vassununga, SP): como se expressa em mapeamentos? Acta Botanica Brasilica 20:383–394

Rundel PW, Ehleringer JR, Nagy KA (2012) Stable isotopes in ecological research, vol 68. Springer Science & Business Media, New York.

Sanchez M, Pedroni F, Eisenlohr PV, Oliveira-Filho AT (2013) Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000 m of altitude. Flora-Morphol Distrib Funct Ecol Plants 208(3):184–196

Schenk HJ, Jackson RB (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. J Ecol 90(3):480–494

Schubart O, Rawitscher F (1950) Notas sobre o movimento de água subterrânea de Emas-Pirassununga. Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Botânica. 8(1): 69–74

Silva JF, Fariñas MR, Felfili JM, Klink CA (2006) Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. J Biogeogr 33(3):536–548

Simon MF, Pennington T (2012) Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. Int J Plant Sci 173(6):711–723

Vendramini PF, Sternberg LDS (2007) A faster plant stem-water extraction method. Rapid Commun Mass Spectrom 21(2):164–168

Villalobos-Vega R, Salazar A, Miralles-Wilhelm F, Haridasan M, Franco AC, Goldstein G (2014) Do groundwater dynamics drive spatial patterns of tree density and diversity in Neotropical savannas? J Veg Sci 25(6):1465–1473

Vogel JC, Van Urk H (1975) Isotopic composition of groundwater in semi-arid regions of southern Africa. J Hydrol 25(1–2):23–36

Chapter 5
Diversity of Aquatic Macroinvertebrates Along Altitudinal Gradients in Colombia

Cesar E. Tamaris-Turizo, Gabriel A. Pinilla-A, and Juan David González-Trujillo

5.1 Introduction

Mountains hold fundamental challenges to aquatic macroinvertebrates. As ectotherms, macroinvertebrates are being challenged to adapt or track changes in their environment, either in time through a behavioral shift or in space by an altitudinal shift. Recent evidence shows that such a dynamic, to adapt or to track, is mainly driven by the water temperature and oxygen availability, as well as the metabolic thermal sensitivity of each species (Jacobsen 2020). As such, by considering the interactions of these three modulators, it will be feasible to model diversity patterns along altitudinal gradients across the globe. However, such a generalization is not straightforward, for temperate and tropical macroinvertebrates may exhibit similarly narrow thermal breadths at higher latitudes but contrasting thermal breadths at lower elevations (Shah et al. 2017).

The narrowest thermal breaths in tropical low elevations open a new research agenda on the drivers of community organization in Tropical rivers. In these rivers, other factors are expected to drive the assembly of aquatic communities as species thermal tolerances are not necessarily linked to the variability in water temperature and oxygen (Shah et al. 2017; Jacobsen 2020). For example, in the Colombian Mountain chains, where the variability of environmental factors responds to some degree to the altitudinal shifts (González-Trujillo et al. 2021), it is expected that

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invertebrate diversity responded linearly to the elevation-driven environmental variability. However, mounting evidence is demonstrating that neither the species richness nor species occurrence is linearly correlated to elevation. Recent studies have demonstrated that such nonlinear responses may be partially explained by other factors, such as biogeographical legacies or urbanization intensity.

In this chapter, we review studies assessing the altitudinal distribution shifts of macroinvertebrates communities across tropical Andean streams. We focus on assessing the distribution of the species from different macroinvertebrate orders across the Colombian mountains and how it relates to the elevational-driven changes in the environmental conditions of the streams. Chapter 1 describes how the altitudinal gradient is a modulator of climatic variables (e.g., temperature, precipitation, and relative humidity). Environmental factors of tropical streams present a wide variation across latitudinal (Morales-Castilla and García-Valdés 2014) and altitudinal gradients (Rahbek 2005). These factors are considered as major "engines" that perform structural and functional attributes into aquatic ecosystems (Vannote et al. 1980). Therefore, we explore relations between climatic variables and their relations with structural (e.g., density, biomass, abundance, richness, etc.) and functionals (e.g., energy fluxes) aspects in the communities and ecosystems. We also introduce to alternative explanations to the species turnover among altitudinal ranges which have been proposed in past years.

5.2 Altitudinal Changes in Diversity of Different Taxonomic Groups

A long-standing civil conflict has partially truncated the study of Colombian diversity. Due to social conflict that has affected to Colombia for more than 60 years, the western and the south of the country have been few explored (Sabater et al. 2017), being the Andean and Caribbean regions where more studies have been conducted so far. In this sense, the patterns presented in this section are unavoidable geographically biased. Yet, they provide evidence of non-linear relationships between elevation and macro invertebrate richness.

In the Colombian mountain systems, such as the Sierra Nevada de Santa Marta-SNSM (north of Colombia), we observed two general patterns of altitudinal shifts: (1) the decreasing richness with increasing altitude, and (2) the increase of richness at intermediate altitudes (McCoy 1990; Brehm and Fiedler 2003). The first statement supports the Rappaport rule (Stevens 1992), while the second one supports the idea that "extremes are bad." In the second statement, environmental extremes are thought to occur in altitudinal extremes and then, diversity peaks at intermediate elevations, where environmental conditions are more suitable for organisms' persistence (Jacobsen 2020). Whether one of the two patterns is found depends on the taxonomic group being studied, as responses to elevation-driven constraints of *Leptohyphes* mayflies are different from that of Chironomidae dipterans.

In this section, we provide a brief review of the distributional patterns observed across different taxonomical orders of macroinvertebrates.

Ephemeroptera This order is one of the most widely studied groups in Colombia in two last decades (Roldán et al. 2014). The first works that included elevational gradients were made by Roldán (1980, 1985) in the Antioquia department at Andean Mountain. For rivers of the Tolima Department (Central Mountain Range of the Colombian Andes), genera *Baetodes*, *Camelobaetidius*, *Leptohyphes*, and *Thraulodes* occupy the entire altitudinal range (340–1555 masl) (Vásquez-Ramos and Reinoso 2012). *Leptohyphes* (Ephemeroptera: Leptohyphidae) is a genus well studied in Colombia, especially at the species level (Molineri et al. 2002, 2011; Molineri and Zúñiga 2004, 2006). For this reason, we analyzed the altitudinal distribution of *Leptohyphes* in the SNSM as a model taxon, using presence-absence data of species from 2000 to 2017. The altitudinal tendency of leptohyphids species showed a lower richness in the lower and headstream sections of the gradient, and higher diversity in the middle section (Fig. 5.1a). The unique species reported in the low zone was *L. jodiannae* (60 masl). *L. coconuco* (1700 masl) was present in the high sector, and in the middle section, eight species were found (including the two species mentioned above).

Odonata Tobias-Loaiza and Tamaris-Turizo (2019) reviewed the spatial and temporal distribution of Odonata order in eight rivers of three flanks in the SNSM, finding a wide altitudinal distribution of this order, especially of the genera *Erythrodiplax, Sympetrum* (both of Libellubidae family: 50–2800 masl), and *Hetarerina* (Calopterygidae: 50–1800 masl), being *Archilestes* (Lestidae) genus with lower

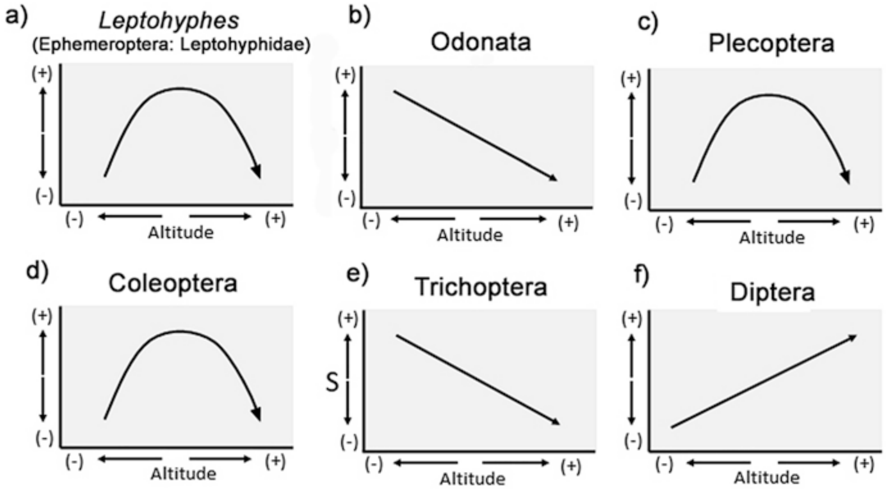

Fig. 5.1 Distribution models of the diversity of some select groups of aquatic insects along of the altitudinal gradient (**a**) *Leptohyphes* (Ephemeroptera: Leptohyphidae), (**b**) Odonata, (**c**) Plecoptera, (**d**) Coleoptera (**e**) Trichoptera (**f**) Diptera

distribution from 600 to 900 masl. The highest richness was found in the lower and middle sections of the basins. *Triacanthagyna*, *Telebasis*, *Micrathyria*, *Miathyria*, *Gynacantha*, *Enallagma*, *Caryphaeshna*, *Archaeogomphus*, and *Agriogomphus* were only reported in the lower zone. As such, evidence suggest that the diversity of Odonata decreases as the altitudinal gradient increases (Fig. 5.1b). This type of distribution, which is commonly observed in this order, is attributed by some authors to the intermediate disturbance hypothesis (Connell 1978), which states that diversity is low after a disturbance when few species have survived, and is high when a disturbance occurs with intermediate frequency or intensity. Human impacts favor the development of favorable environments, such as artificial and temporary ponds and phytotelmata systems, which promote the establishment of Odonata. Similar results were found by Cuellar-Cardozo et al. (2020) in the Paicol River (southwest of Colombia, in the Huila Department), which registered the highest abundances and richness in a heterogeneous area, with the presence of cattle, and near to urban zone and relicts of native forest.

Plecoptera The stoneflies present a variable richness along the altitudinal gradient. In the SNSM, the stoneflies show the higher richness in the middle section of their altitudinal distribution (from 500 to 1800 masl) (Fig. 5.1c). This group of organisms has been little studied, but it is known that *Anacroneuria* is the genus-dominant in Colombia (Rúa-García et al. 2015). In the abundance and distribution of stoneflies, the focus in the altitudinal gradient might be made at the species level. In the Andean zone, their richness has been evaluated from 60 to 2000 masl, with the high zone as the one with the highest richness. In the SNSM, is interesting that endemic species are principally located in the middle and the higher zones, over 1200 masl (e.g., *A. tayrona*, located above 1700 masl) (Tamaris-Turizo et al. 2007). Other species, as *A. caraca* and *A. marta,* have shown a lower altitudinal distribution (20–100 masl) (Unpublished data).

Coleoptera For coleopterans, the altitudinal distributions of the genera are not clear, although they could parallel Plecoptera distributional patterns (Fig. 5.1d). González-Córdoba et al. (2015) carried out a study about the distribution of species of Coleoptera in the Valle del Cauca Department (located in the south-west of Colombia); the organisms corresponded to samples taken from 1991 to 2014, in 63 fluvial systems across an altitudinal range from 0 to 2600 masl of 14 genera; only *Stenhelmoides*, *Xenelmis*, and *Onychelmis* showed a restricted distribution (at 400, 1400, and 1800 masl respectively). These observations could be associated with the wide environmental range of these taxa (González-Córdoba et al. 2020). Despite these studies, it is necessary to develop more work on the altitudinal distribution of coleopterans in Colombia.

Trichoptera A study carried on caddisflies (Trichoptera) of the Gaira River (SNSM) showed that *Amazonatolica*, *Cyrnellus*, *Nectopshyche*, and *Polycentropus* preferred the high part of the basin, in the middle sector the more representative taxa were *Ochotrichia*, *Cerasmatrichia,* and *Metrichia* (reach with the lowest abundance), while in the low basin the organisms more dominant were *Protoptila*, *Mortoniella*, *Oecetis*, and *Chimarra* (Oliveros-Villanueva et al. 2020). Previously, Serna-Macías et al. (2015) studied the distribution of caddisflies in the lower section (60–360 masl) of the Manzanares River (SNSM) and found 14 genera in the higher section, and eight genera in the lower sector. In addition, the abundance decreased with the reduction of the altitudinal gradient (from 1353 to 148 individuals) (Fig. 5.1e). Contrary to these results, González-Vargas and García-García (2021) evaluated the altitudinal distribution of Trichoptera in the Palmar River, located in the Cundinamarca Department (East Andean Mountain), in an altitudinal range from 1090 to 3294, and found a high richness in the headstream and a decrease in diversity according to decline in the altitudinal gradient; *Neotrichia* (Hydroptilidae), *Triplectides* and *Oecetis* (Leptoceridae), and *Contulma* (Anomalopsychidae) were genera with distribution restricted to headwaters. In the Tolima Department, genus *Smicridea* is distributed along the altitudinal gradient (340–1555 masl), but *Culoptila*, *Helicopsyche*, and *Atopsyche* prefer high areas, whereas *Protoptila*, *Neotrichia*, and *Chimarra* are located at low elevation (Vásquez-Ramos and Reinoso 2012).

Diptera Unpublished data of SNSM show some tendencies in genera of Chironomidae (Diptera) related to the altitudinal gradient. The most diverse reaches were located in the middle zones (12 genera), followed by high- (11 genera), and low-altitude zones of the basin (8 genera). In addition, at the subfamily level, Orthocladiinae exhibited the highest abundances and number of species in the high reaches, whereas Tanypodinae in the middle, and Chironominae in the lower sectors of the basin, respectively. However, when considering only individual abundance, low and middle sectors showed higher similarity compared with high-altitude sectors (Fig. 5.1f). Yet, such a pattern may change depending on the location along the Andean chain. In a parallel study performed in the Tolima Department, for instance, Vásquez-Ramos and Reinoso (2012) found that Chironominae, Orthocladiinae, and Tanypodinae did not show preferences for certain altitudinal zones and were recorded in all the stations of the elevation gradient (340–1555 masl).

In Andean streams of the city of Bogotá and other surrounding areas, with an altitudinal range between 2500 and 3200 masl, Buitrago-Guacaneme et al. (2018), Cuadrado et al. (2019), and Rodríguez-Rodríguez et al. (2021) studied the distribution gradients of the aquatic Diptera, especially regarding the black flies of the Simuliidae family. The first of these studies showed that some black fly species, such as *Simulium muiscorum*, had a pattern contrary to dissolved oxygen, temperature, and current velocity so that their distribution seems to increase at the sites with lower elevation and a relatively higher degree of contamination. On the contrary, the species *S. ignescens* was associated with slightly more oxygenated waters of the upper sectors of four streams analyzed (Buitrago-Guacaneme et al. 2018). Complementarily, Cuadrado et al. (2019) found that *S. muiscorum* had a widespread niche and that it can be in high localities, but whose water quality conditions are moderate; for these authors, *S. ignescens* was also common in the middle parts of the streams with medium pollution conditions, while another species (e.g., *Gigantodax ortizi*) were dominant in the high and intermediate sectors of the rivers.

From these investigations, it can be deduced that the different black-flies species prefer some sectors of the altitudinal gradients, but this response interacts with the water quality.

For other groups of Diptera, the study by Rodríguez-Rodríguez et al. (2021) showed that the families Psychodidae, Limoniidae, Pericelididae, and Blephariceridae, and chironomid subfamilies such as Podonominae (which is characteristic of high mountain river systems, Acosta and Prat 2018) and Chironominae are restricted to the upper basin of the Fucha River. Meanwhile, families such as Muscidae, Simuliidae, Dolichopodidae, Ceratopogonidae, and Empididae, and the Orthocladiinae (subfamily of Chironomidae) preferred the middle and lower part of the Bogotá and Fucha river basins. In these fluvial systems, the most polluted are in the lower basin, close to urban influence, which seems to promote the dominance of some genera of the Chironomidae, especially *Corynoneura* and *Cardiocladius*, while genera such as *Larsia*, *Parochlus*, *Podonomus*, *Thienemanniella*, *Riethia*, and *Tanytarsus* have a greater representation in the upper sectors of the rivers (Fig. 5.2). It is important to highlight that these authors found that neither pH nor dissolved oxygen showed a clear association with the presence of Diptera genera along the altitudinal gradients.

Recently, Villamarín et al. (2021) studied the diversity and altitudinal distribution of chironomids in the Ecuadorian Andes. The study was carried out at El Oro Province (Southwestern Ecuador) and the samples were taken in an altitudinal range from 10 to 2427 masl. The results showed that the high-altitude zones had low

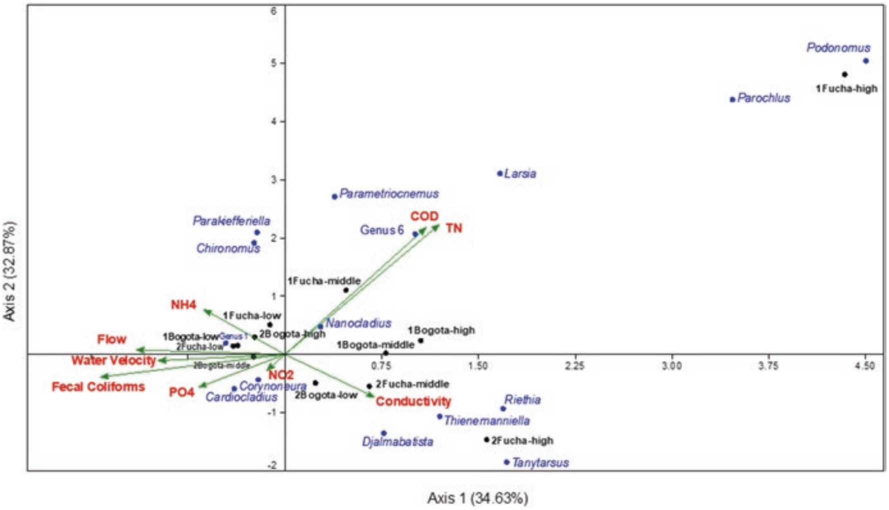

Fig. 5.2 Canonical correspondence analysis of the Chironomidae family genera in the Fucha and Bogotá rivers, Colombian Andes. Number 1 corresponds to the rainy season and number 2 to the dry period; COD chemical oxygen demand, TN total nitrogen, NH_4 ammonium, NO_2 nitrite, PO_4 orthophosphate. (Modified from Rodríguez-Rodríguez et al. 2021). Some genera of clean waters are characteristic of the upper reaches of rivers, while other genera more tolerant to pollution are located in the middle and lower reaches

density of individual of the three principal subfamilies of chironomids (Tanypodinae, Chironomidae, and Orthocladiinae). However, results also showed that such a pattern changes when considering the number of species. Species richness peak at high- and low-altitude zones, and low values in the middle zone. Likewise, both species richness and density of individuals of each subfamily responded differently to the altitudinal gradient.

5.3 Trophic Structure and the Gradient of Elevation

Biotic factors can drive the altitudinal shifts in macroinvertebrate diversity. Differences in climate, soil, and vegetal coverage – linked to altitudinal gradients (Chap. 1), may alter trophic dynamic in freshwater habitats (e.g., Vannote et al. 1980; Luque-Moreno and González-Trujillo 2021) and in turn modify the trophic relationship that are established between the species and the sources of a food web. Changes in the consumption (prey-predator) relationships, for instance, is one of the interspecific relations more studied between organisms, as it could alter the "ecosystem equilibrium" through the local extinctions due to specific relations as the competition (Tokeshi 1999).

The evaluation of trophic networks is based on their attributes or properties, which allow a comprehensive understanding of the community structure based on the relationship of resources with consumers, interactions of top-predators, and the percentage of omnivores. In this section, we review the studies on the food webs of aquatic invertebrates performed along an altitudinal gradient of the Gaira River in the SNSM. These studies showed that changes in the structure of trophic networks are associated with elevation (e.g., Tamaris-Turizo et al. 2018). For example, the link density (L/S), which is a property associated with the complexity and stability of the ecosystem (Dunne et al. 2002), decreased according to elevational gradient (L/S at low: 4.33; middle: 2.17; and high-altitude: 2.48).

Trophic networks may also exhibit some degree of seasonality along altitudinal gradients. In relation to the trophic species richness, Tamaris-Turizo and colleagues found a lower variability along of the altitudinal gradient during the dry season (low basin: 33; middle sector: 32; highwaters: 31); conversely, in the rainy season the values lowered in all sectors (low basin: 22; middle sector: 24; highwaters: 17). The trophic level and the maximum length of the chain had similar values along of gradient (between 2.83 and 3.13). The fraction of top predators (t) displayed a wide variation, so in the lower sector was 0.29 in the rainy seasons and 0.58 in the dry season. In this site, intermediate taxa (mid-network species) had a fraction of 0.27 during the dry season and 0.41 in the rainy season. Diet discontinuity (D_{diet}) is another important property of the trophic networks that permit to know whereas a consumer's diet is constrained by its phylogenetic origin. In the Gaira River, D_{diet} decreased simultaneously with the decrease in the elevational gradient (Table 5.1), which indicates that the taxonomic relations are stronger in the headwater of the fluvial system, which is associated with recent events of divergence. Other attributes

Table 5.1 Trophic networks properties along an altitudinal gradient in the Gaira River, north of Colombia

Property	High	Middle	Low
Frac. Omnivory	0.19	0.12	0.69
D_{diet}	0.10	0.06	0.02
Resource	15	15	14
Consumer	26	27	28

such as the fraction of omnivores and the number of consumers showed higher values in the sectors of middle and lower elevations and low records in the upper river basin. The vulnerability was low in the rainy season in the middle and upper sections, but increased according to the elevation gain. The vulnerability values of the main food resources decreased downstream. The trophic network data of the Gaira River show that the precipitations could be a factor modulator of disturbs that can produce shifts in some trophic properties (Figs. 5.3 and 5.4).

5.4 Anthropogenic Altitudinal Gradients

While the joint effect of the water temperature and oxygen availability explains to a great extent the altitudinal shifts of aquatic insects (see Jacobsen 2020), recent evidence suggests that other factors may also drive community organization in montane streams. In this section, we will discuss two of them: the anthropic drivers linked to land use changes; and the historical drivers linked to past climatic (e.g., temperature oscillation) and geological (e.g., mountain uplift) events.

Human-origin stressors have differential effects on aquatic ecosystems, which make it difficult to identify whether the structure of a certain biotic community is influenced by altitudinal gradients or by human impacts (Forero-Céspedes et al. 2016; de Paiva et al. 2021). As seen in previous sections, in which the altitudinal gradients of some groups of aquatic insects of Andean streams were mentioned, the structural changes in invertebrate communities intersect with the effects derived from human activities. In this way, the gradient of deterioration of the water is overlaid on the altitudinal gradient, which makes it challenging to establish the natural variation of macroinvertebrate communities. In the specific case of dipterans, the works of Cuadrado et al. (2019) and Rodríguez-Rodríguez et al. (2021) showed that the altitudinal gradients of the rivers they studied coincided with the pollution gradients, which means that the higher the elevation, the better the water quality. Therefore, the greater contamination evidenced at the middle section of the basins could function as an isolation mechanism between the high and low sections, and this seems to reduce both the probability of dispersal of taxa between sites and, subsequently, drive species turnover headwaters

Contrasting results have been found in other studies focused on the effects of human activities on aquatic macroinvertebrates. Meza-Salazar et al. (2020) observed

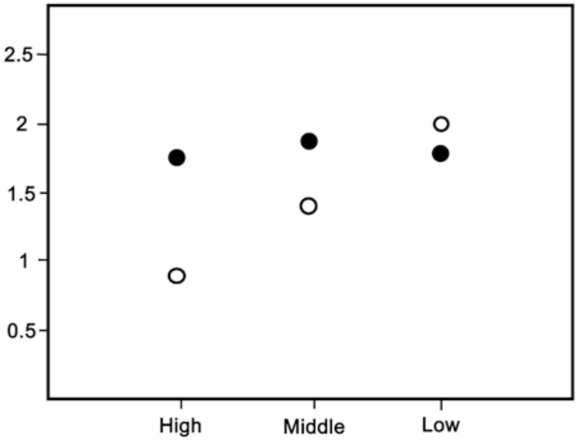

Fig. 5.3 Vulnerability values of a trophic network along their altitudinal gradient during rainy (white circles) and dry seasons (black circles)

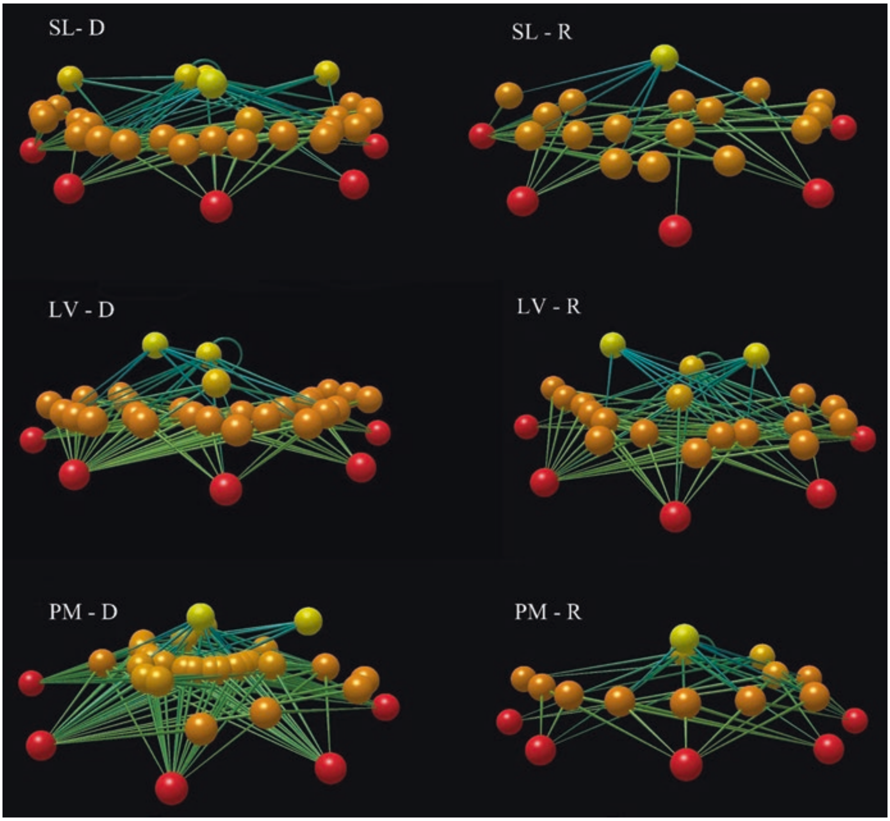

Fig. 5.4 Models of trophic networks at three sites in the Gaira River. Red circles indicate basal resources, orange red intermediate consumer, and yellow circles the top predators. SL San Lorenzo, upper sector; LV La Victoria, middle sector; PM Puerto Mosquito, lower sector; D dry season; R rainy season. (Adapted from Tamaris-Turizo et al. 2018)

in the Caldas Department (Central Mountain Range of Andes) that agriculture has a strong effect on the invertebrate community, causing lower organisms' density and diversity, the dominance of *Simulium*, and the absence of pollution intolerant taxa, such as *Anacroneuria*, *Marilia* (Trichoptera: Odontoceridae), and *Camelobaetidius* (Ephemeroptera: Baetidae). For these authors, this effect of agriculture was even more intense than that produced by livestock or mining. Apparently, in this region of the central Andes of Colombia, mining and agricultural activities are highly variable in their intensity and use of chemical substances, which make it difficult to separate their effects from those dependent on natural hydrological patterns. However, in that study, it was evident that the reference stations, located at a higher elevation (1720 and 2766 masl), and with less anthropic intervention, were more diverse, had a higher abundance of invertebrates, and presented clean water taxa such as *Smicridea* (Trichoptera: Hidropsychidae), *Andesiops* (Ephemeroptera: Baetidae), and *Nanomis* (Baetidae). In addition to the lower degradation by human activities, the presence of riparian forest at these reference sites seems to be one of the reasons for the better conditions of their macroinvertebrate communities.

5.5 Other Drivers Underlying Altitudinal Gradients

As in plant communities, most communities in montane rivers exhibit a high degree of species turnover along elevation gradients (i.e., Wang et al. 2012; Bishop et al. 2015). Such a turnover, as described throughout this chapter, can be explained by the elevation-driven environmental gradients that occur from the bottom to the top of the mountains (Bertuzzo et al. 2016; Nottingham et al. 2018). However, recent evidence has pointed that such a pattern is also shaped by the historical background of the mountain chain (González-Trujillo et al. 2021), at least in the Neotropical region.

In Neotropical basins, past geological and climatic events have a pervasive influence on the contemporary structure of river networks and species distribution (Albert et al. 2018; Bicudo et al. 2019). Andean uplifts and glacier retreats, among others, have shaped unique combinations of river forms and riparian ecosystems at the ecoregional scale in the Orinoco and Amazonas River basins (Rull 2008; Bicudo et al. 2019). Thus, when descending from the Andes to the Amazon, there is a matrix of streams with constrained channels that are surrounded by shrubs in the Paramo, followed by rivers with gorge channels and steep slopes in the Andean-cloud Forest and Piedmont regions, and then meandering rivers surrounded by well-developed rainforest in the Amazonian region. As such, an ecoregional gradient is presented that is coupled with the elevational gradient.

Recent studies have shown that the distribution of diatom and invertebrate taxa partially follows the distribution of ecoregions within the basin (Fig. 5.5) (González-Trujillo et al. 2020a, b). Regardless of their spatial proximity, diatom and invertebrate communities from streams within the same ecoregions were more similar to each other than to those from different ecoregions. Besides, both the environmental features and the species composition of communities in every stream were

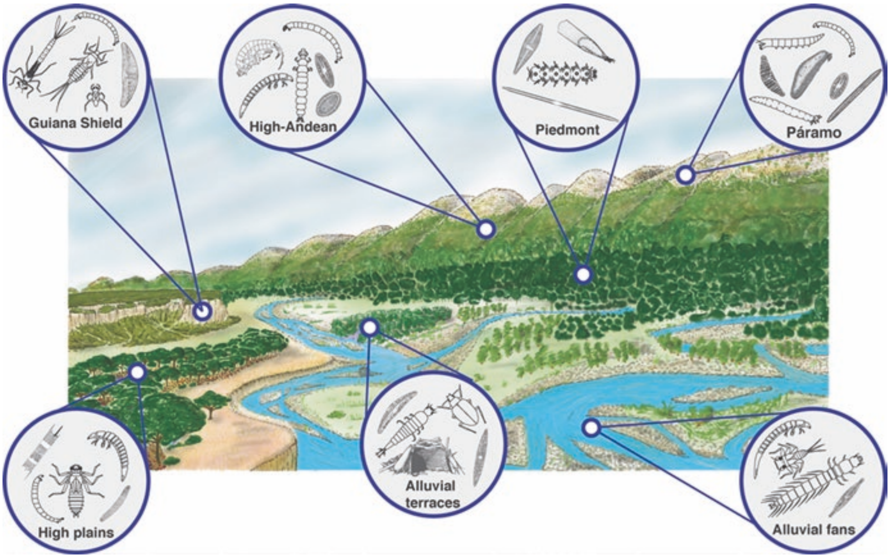

Fig. 5.5 Conceptual scheme representing the ecoregionally constrained distribution of species pools in the Andean mountains

constrained by the type of ecoregion. These patterns suggest the precedence of historical processes over local or regional processes in shaping the contemporary structure of algae and invertebrate metacommunities.

Distributional patterns of diatoms and invertebrates across the Orinoco indicate that knowing the historical background of a region is essential to gain a better understanding of the mechanisms supporting metacommunity-level patterns. Metacommunity ecology needs to embrace biogeography and integrate geological and climatic history with statistical tools. Indeed, a reconstruction of the evolutionary history of the Colombian Andes provides evidence supporting that those past historical events have contributed to shaping the present-day diversity and distribution of benthic communities; and especially, that historical events seemed to be essential in separating lineages (and taxa) in different ecoregions regardless of the long time available for dispersal (thousands or millions of years) (González-Trujillo et al. 2021).

However, historical legacies cannot be fully disentangled from environmental contemporary effects. A different number of present-day factors can also significantly explain the distribution of species along altitudinal gradients (González-Trujillo et al. 2021). While this may serve as evidence supporting that species distributions respond to the environmental changes along the altitudinal gradients, the effect of the environment is not interpretable without considering the historical background of the basin. Historical legacies may constrain the variability of some environmental factors, such as stream water pH, temperature, or substratum mobility. Temperature, for instance, is majorly driven by the altitudinal ranges of

Neotropical mountains (Gill et al. 2016). Substratum mobility, on the other hand, is highly dependent on the fluvial landform (Stallard 1985). Therefore, in line with Perrigo et al. (2019), recent findings emphasize that montane geology sets the stage for speciation and landscape formation, where different ecological and environmental factors co-act to increase biodiversity. As such, altitudinal gradients in the Tropics should be addressed considering both historical and contemporary factors, without excluding the effect that humans have on streams and rivers.

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References

Acosta R, Prat N (2018) Pupas Podonominae (Diptera: Chironomidae) de los ríos altoandinos tropicales. Rev Biol Trop 66(1):6–27

Albert JS, Val P, Hoorn C (2018) The changing course of the Amazon River in the Neogene: center stage for neotropical diversification. Neotrop Ichthyol 16

Bertuzzo E, Carrara F, Mari L, Altermatt F, Rodriguez-Iturbe I, Rinaldo A (2016) Geomorphic controls on elevational gradients of species richness. Proc Natl Acad Sci U S A 113:1737–1742

Bicudo TC, Sacek V, Almeida RP, De Bates JM, Ribas CC (2019) Andean tectonics and mantle dynamics as a pervasive influence on Amazonian ecosystem. Sci Rep 9:1–11

Bishop TR, Robertson MP, van Rensburg BJ, Parr CL (2015) Contrasting species and functional beta diversity in montane ant assemblages. J Biogeogr 42:1776–1786

Brehm G, Fiedler K (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. J Biogeogr 30(3):431–440

Buitrago-Guacaneme A, Sotelo-Londoño A, Pinilla-Agudelo GA, García-García A, Moncada LI, Adler PH (2018) Abundance and diversity of black flies (Diptera: Simuliidae) in rivers of the Andean Eastern Hills of Bogotá (Colombia), and its relationship with water stream physico-chemical variables. Univ Sci 23(2):291–317. https://doi.org/10.11144/Javeriana.SC23-2.aado

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1304–1310

Cuadrado LA, Moncada LI, Pinilla GA, Larrañaga A, Sotelo AI, Adler PH (2019) Black fly (Diptera: Simuliidae) assemblages of high Andean rivers respond to environmental and pollution gradients. Environ Entomol 48(4):815–825. https://doi.org/10.1093/ee/nvz053

Cuéllar-Cardozo JA, Castro-Rebolledo MI, Jaramillo MA (2020) Diversidad y composición de Odonata asociadas con diferentescondiciones de la vegetación riparia a lo largo de un arroyo en Paicol-Huila. Colombia Actualidades Biológicas 42(113):1–11. https://doi.org/10.17533/udea.acbi.v42n113a04

de Paiva CKS, Faria APJ, Calvão LB, Juen L (2021) The anthropic gradient determines the taxonomic diversity of aquatic insects in Amazonian streams. Hydrobiologia 848:1073–1085

Dunne JA, Williams RJ, Martinez ND (2002) Food-web structure and network theory: the role of connectance and size. Proc Natl Acad Sci U S A 99:12917–12922

Forero-Céspedes AM, Gutiérrez C, Reinoso-Flórez G (2016) Composición y estructura de la familia Baetidae (Insecta: Ephemeroptera) en una cuenca andina colombiana. Hidrobiológica 26(3):459–474

Gill BA, Kondratieff BC, Casner KL, Encalada AC, Flecker AS, Gannon DG et al (2016) Cryptic species diversity reveals biogeographic support for the 'mountain passes are higher in the tropics' hypothesis. Proc R Soc B Biol Sci 283(1832):20160553

González-Córdoba M, Zúñiga MDC, Manzo V (2015) Riqueza genérica y distribución de Elmidae (Insecta: Coleoptera, Byrrhoidea) en el departamento del Valle del Cauca. Colombia Biota Colomb 16(2):51–74

González-Córdoba M, Zúñiga MDC, Manzo V (2020) La familia Elmidae (Insecta: Coleoptera: Byrrhoidea) en Colombia: riqueza taxonómica y distribución. Rev Acad Colomb Cienc Ex Fis Nat 44(171):522–553

González-Trujillo JD, Donato-Rondon JC, Muñoz I, Sabater S (2020a) Historical processes constrain metacommunity structure by shaping different pools of invertebrate taxa within the Orinoco basin. Divers Distrib 26:49–61

González-Trujillo JD, Pedraza-Garzón E, Donato-Rondon JC, Sabater S (2020b) Ecoregional characteristics drive the distribution patterns of neotropical stream diatoms. J Phycol 56:1053–1065

González-Trujillo JD, Saito VS, Petsch DK, Muñoz I, Sabater S (2021) Historical legacies and contemporary processes shape beta diversity in neotropical montane streams. J Biogeogr 48:101–117

González-Vargas G, García-García A (2021) Trichopterofauna del río Palmar, Cundinamerca, Colombia. Biologist (Lima) 19(19):41–55. https://doi.org/10.24039/rtb2021191881

Jacobsen D (2020) The dilemma of altitudinal shifts: caught between high temperature and low oxygen. Front Ecol Environ. https://doi.org/10.1002/fee.2161

Luque FJ, González-Trujillo JD (2021) Auto-ecological responses of rainbow trout populations to ecoregional differences in a neotropical Andean river. Limnetica 40(1):43–55. https://doi.org/10.23818/limn.40.04

McCoy E (1990) The distribution of insects along elevational gradients. Oikos 58:313–332

Meza-Salazar AM, Guevara G, Gomes-Dias L, Cultid-Medina CA (2020) Density and diversity of macroinvertebrates in Colombian Andean streams impacted by mining, agriculture and cattle production. PeerJ 8:e9619

Molineri C, Zúñiga MC (2004) *Lumahyphes*, a new genus of Leptohyphidae (Insecta: Ephemeroptera). Aquat Insects 26(1):19–30

Molineri C, Zúñiga MC (2006) New species of Leptophyphidae (Insecta: Ephemeroptera) from Colombia with evidence of reproductive time segregation. Stud Neotropical Fauna Environ 41(2):139–151

Molineri C, Peters J, Zúñiga MC (2002) A new family, Coryphoridae (Ephemeroptera: Ephemerelloidea) and description of the winged and egg stages of *Coryphorus*. Insecta Mundi 15(2):117–122

Molineri C, Cuz PV, Emerich D (2011) A new species of *Asthenopus* (Ephemeroptera: Polymitarcyidae: Asthenopodinae) from Brasil and Colombia. Zootaxa 2750:33–38

Morales-Castilla I, García-Valdés R (2014) Gradientes altitudinales de diversidad inversos, ¿excepciones o prueban la regla? Ecosistemas 23(1):4–12

Nottingham AT, Fierer N, Turner BL, Whitaker J, Ostle NJ, McNamara NP, Bardgett RD, Leff JW, Salinas N, Silman M, Kruuk L, Meir P (2018) Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes. Ecology 99:2455–2466

Oliveros-Villanueva JD, Tamaris-Turizo CE, Serna-Macias DJ (2020) Larvas de Trichoptera en un gradiente altitudinal en un río neotropical. Rev Acad Colomb Cienc Ex Fis Nat 44(171):493–506

Perrigo A, Hoorn C, Antonelli A (2019) Why mountains matter for biodiversity. J Biogeogr. https://doi.org/10.1111/jbi.13731

Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns: scale and species-richness patterns. Ecol Lett 8:224–239

Rodríguez-Rodríguez JF, Pinilla Agudelo GA, Moncada Álvarez LI (2021) Estructura de la comunidad de dípteros acuáticos en tramos de los cursos altos de los ríos Fucha y Bogotá. Acta Biológica Colombiana 26(2):147–159

Roldán G (1980) Estudio limnológico de cuatro ecosistemas neotropicales diferentes con especial referencia a su fauna de efemerópteros. Actual Biol 9(34):103–117

Roldán G (1985) Contribución al conocimiento de las ninfas de efemerópteros en el Departamento de Antioquia. Actual Biol 14(51):3–13

Roldán G, Zúñiga MC, Zamora H, Álvarez LF, Reinoso G, Longo M (2014) Colombia. In: Alonso-Egúa P, Mora JM, Campbell B, Springer M (eds) Diversidad, conservación y uso de los macroinvertebrados duceacuícolas de México, Centroamérica, Colombia, Cuba y Costa Rica. Instituto Mexicano de Tenconología del Agua, Jiutepec, p 444

Rúa-García G, Tamaris-Turizo CE, Zúñiga MC (2015) Composition and distribution of the Ephemeroptera Plecoptera and Trichoptera orders (Insecta) in Rivers of Sierra Nevada de Santa Marta. Colombia Revista de Ciencias 19(2):11–29

Rull V (2008) Speciation timing and neotropical biodiversity: the tertiary-quaternary debate in the light of molecular phylogenetic evidence. Mol Ecol 17:2722–2729

Sabater S, González-Trujillo JD, Elosegi A, Donato-Rondon JCH (2017) Colombian ecosystems at the crossroad after the new peace deal. Biodivers Conserv 26:3505–3507. https://doi.org/10.1007/s10531-017-1415-8

Serna-Macías D, Tamaris-Turizo CE, Gutiérrez L (2015) Distribución espacial y temporal de larvas de Trichoptera (Insecta) en el río Manzanares, Sierra Nevada de Santa Marta (Colombia). Rev Biol Trop 63(2):465–477

Shah AA, Gill BA, Encalada AC (2017) Climate variability predicts thermal limits of aquatic insects across elevation and latitude. Funct Ecol 2017(31):2118–2127

Stallard RF (1985) River chemistry, geology, geomorphology, and soils in the Amazon and Orinoco basins. In: The chemistry of weathering. Springer, Dordrecht

Stevens G (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am Nat 140:893–911

Tamaris-Turizo CE, Turizo-Correa RR, Zúñiga MC (2007) Distribución espacio-temporal y hábitos alimentarios de ninfas de Anacroneuria (Insecta: Plecoptera: Perlidae) en el río Gaira (Sierra Nevada de Santa Marta, Colombia). Caldasia 29(2):375–385

Tamaris-Turizo CE, Pinilla-A G, Muñoz I (2018) Trophic network of aquatic macroinvertebrates along an altitudinal gradient in a Neotropical mountain river. Rev Bras Entomol 62:180–187

Tobias-Loaiza M, Tamaris-Turizo CE (2019) Odonatos de la Sierra Nevada de Santa Marta, Colombia: una lista preliminar. Rev Acad Colomb Cienc Ex Fis Nat 43(167):212–218

Tokeshi M (1999) Species coexistence ecological and evolutionary perspectives. Blackwell Science Ltd., Oxford

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. Can J Fish Aquat Sci 37(1):130–137

Vásquez-Ramos JM, Reinoso-Flórez G (2012) Estructura de la fauna bentica en corrientes de los Andes colombianos. Rev Col Entomol 38(2):351–358

Villamarín C, Villamarín-Cortez S, Salcido DM, Herrera-Madrid M, Ríos-Touma B (2021) Drivers of diversity and altitudinal distribution of chironomids (Diptera: Chironomidae) in the Ecuadorian Andes. Rev Biol Trop 69(1):113–126

Wang J, Soininen J, Zhang Y, Wang B, Yang X, Shen J (2012) Patterns of elevational beta diversity in micro- and macroorganisms. Glob Ecol Biogeogr 21:743–750

Chapter 6
Intraspecific Trait Variability of Emblematic Grass and Tree Species from Venezuelan Savannas Across Extended Physical Gradients

Zdravko Baruch

6.1 Introduction

Research on ecological gradients describe and examine gradual biotic shifts across geographic (elevation, latitude) or physical (irradiance, rainfall, fertility, disturbance). These studies are usually accomplished by surveys and samplings across the gradient of interest and offer significant advantages. For example, they capture environmental variability and detect phenotypic and genetic variation in target species. Also, gradients are proxies for climate and global changes (the space for time approach) and identify climate sensitive ecotypes or the range of intraspecific trait variation (ITV) (Caddy-Retalic et al. 2017). However, the true driver(s) of biotic change may be difficult to discern as many environmental variables (e.g., temperature and rainfall) may covary along single transects (Meirmans 2015).

Studies on ecological gradients in the tropics began with Humboldt's description of altitudinal zones in the Andes of Ecuador. Coincidentally, Humboldt also visited savannas in the Venezuelan Llanos during year 1800 but was unimpressed, referring to them as "being monotonous and with little scientific attraction" (Huber et al. 2006). Research on ecological gradients across Neotropical lowland savannas is scarce. Most studies come from the Brazilian cerrados (317 publications or 84% of total; Web of Science, searched on 18/09/2021) and few from the Venezuelan and Colombian Llanos. They typically discuss ecotones from open savanna to parklands

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"Environmental gradients are Nature's laboratory"

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or forests as well as those caused by fire or waterlogging taking place on a scale of a few kilometers (Araujo et al. 2021; Cassia-Silva et al. 2020; de Oliveira et al. 2021; Neves et al. 2017; Rossatto 2014) among the most recent.

This review of comparative ecology is a contribution to improve the understanding of the quantitative traits and ITVs responses to environmental demands as Neotropical savanna plants are poorly represented in databases (Kattge et al. 2020; Niinemets 2001; Reich et al. 1997; Siefert et al. 2015; Weigelt et al. 2020; Wright et al. 2004). Here, I merge and streamline previous studies to: (i) Characterize the Venezuelan seasonal savanna and its physical gradients; (ii) Portray the grass *Trachypogon spicatus* and the tree *Curatella americana* and establish the scale of their respective ITVs; (iii) Associate species ITVs to savannas physical gradients and; (iv) Discuss ITVs significance for savannas diversity, conservation, and management.

Neotropical savannas, which extend on 2.5 × 10^6 km^2, are warm and seasonally dry, unfertile, frequently burned, and dedicated to extensive cattle ranching (Huber 1987; Medina and Silva 1990; Sarmiento 1983; Solbrig 1996). In northern South America, the major continuous savannas are the Orinoco Llanos, which in Venezuela extend over 220,800 km^2, or 24.5% of the country (Huber and Alarcon 1988). The Andean and Coastal Mountains bound them to the west and north, and the Orinoco River to the south (Fig. 6.1). Physiognomically, the savannas are assembled by an herbaceous matrix of largely C_4 grasses and sedges with a variable proportion of trees (Fig. 6.2). Several sub-types of savanna, replace each other: from treeless grassland to wooded parkland and from drained to seasonally flooded savannas (Ramia 1967; Sarmiento 1983). Contingent on the connotation and area of savannas, they host a considerable floristic richness and diversity represented by either 555 (Ramia 1974) or > 3000 (Huber et al. 2006) Angiosperm species. However, compared to the much larger Brazilian savannas (Cerrados), the Llanos are species

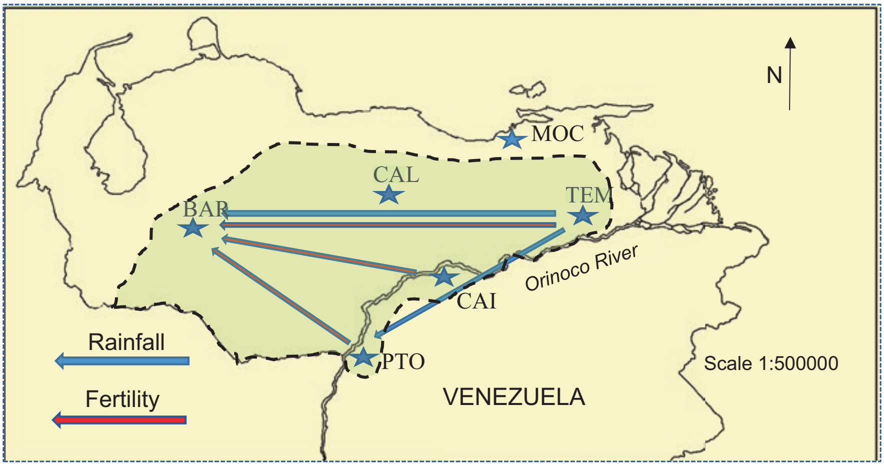

Fig. 6.1 Map of Venezuela displaying population locations and path of rainfall and fertility gradients. Green shaded area corresponds approximately to the Llanos region. Acronyms as in Table 6.1

Fig. 6.2 Vista of a typical savanna with a canopy of *Curatella americana* within a matrix of *Trachypogon spicatus*

poor (Sarmiento 1996). Functionally, nonflooded savannas display a relatively low primary productivity by unit area, attributed to unfertile soils, seasonal droughts, and frequent fires (Medina and Silva 1990).

In Venezuela, lowland savannas overlay recent alluvial and eolian plains resulting from the recess of an ancient inland sea. Most soils are Ultisols or Oxisols, which are acidic, oligotrophic, and low in organic matter (Schargel 2011). Climate is uniformly warm and rainfall is strongly seasonal (from May to November). Within this apparent environmental uniformity, local soil fertility and rainfall vary several fold. Across this extended Llanos landscape, with its significant level of environmental heterogeneity, a group of widespread emblematic plant species offer a first-rate opportunity to study interspecific trait variation of populations from woody and herbaceous species that replace each other across long climatic and edaphic gradients. Savannas are traditionally devoted to cattle ranching, with a mosaic of low-level agriculture in the more fertile sites. Recently, human pressure encouraged deforestation to grow crops or African pasture grasses. Spontaneous invasion of the African grass *Hyparrhenia rufa*, oil exploitation, and Caribbean pine plantations are displacing native savannas (Baruch 1996; Gómez et al. 2008; Ojasti 2001; Rodriguez et al. 2010; Williams and Baruch 2000). Currently and in the near future, Neotropical savannas will also be impacted by hotter and drier climate with increased atmospheric CO_2 (Hoffmann and Jackson 2002) which promotes woody encroachment (Archer et al. 2017) as reported from the CAL site (San Jose and Fariñas 1991; Silva et al. 2001).

From east to west, lowland savanna gradient extends continuously over more than 1000 km that broadens slightly to a narrow strip south of the Orinoco River. Undisturbed populations of both species are named after the nearest inhabited

Table 6.1 Climate and soil physico-chemistry of the research sites

		Rainfall	HI	Sand	Tot. N	P	CEC	O. M.	Fertility	WHC	WAI
Populations (acronyms)	Coordinates	(mm)		(%)	(%)	(ppm)	Meq/100g	(%)	Index	(%)	Index
BARINAS (BAR)	8° 38′ 40″ N 70° 16′ 32″ W	1582	0.79	64.1	0.21	3.33	8.2	4.13	300.0	6.74	106.6
CAICARA (CAI)	7° 35′ 21″ N 66° 08′ 23″ W	1511	0.67	65.1	0.04	1.83	4.5	0.98	150.7	3.61	54.5
CALABOZO (CAL)	8° 51′ 13″ N 67° 22′ 09″ W	1328	0.48	53.1	0.07	1.67	4.4	1.67	165.9	6.27	83.2
MOCHIMA (MOC)	10° 21′ 12″ N 64° 16′ 57″ W	466	0.21	76.5	0.08	0.67	6.6	2.38	135.6	6.57	30.6
PUERTO AYACUCHO (PTO)	5° 41′ 36″ N 67° 34′ 59″ W	2270	1.16	80.5	0.04	1.00	2.0	1.04	96.4	3.10	70.3
TEMBLADOR (TEM)	8°59′ 44″ N 62° 43′ 34″ W	1108	0.51	35.5	0.09	0.83	3.0	2.40	115.8	9.00	99.7

Climate data are from the Venezuelan Ministerio del Ambiente and soils were analyzed with standard laboratory methods

HI Humidity index (Evaporation/Rainfall). Fertility index = Relativized Σ N, P, K, *CEC* Cation exchange capacity, *WHC* Soil water holding capacity, *WAI* Water Availability Index = (Rainfall × ΔH_2O)/100 locality (Fig. 6.1 and Table 6.1). Except the MOC site, populations conform a continuum selected to encompass the range of variation in rainfall and fertility (Fig. 6.1). All sites are below 200 masl and their vegetation was surveyed in another study (Baruch 2005b). Within the savanna warm climate (mean 26.0–27.5 °C), rainfall varies almost fourfold between the wettest (PTO) and the driest (MOC) sites (Table 6.1). There is a gradient of increasing rainfall from east toward the west-southwest (Table 6.1 and Fig. 6.1). The rainy season starts first in the western Llanos at the Andes piedmont and progresses toward the east. The soils are sandy and low in organic matter influencing soil water holding capacity (WHC) that differs up to three times between sites (Table 6.1). By agricultural standards, soil N and P contents are low but large variation exists among sites and their pH is uniformly acidic (4.5–5.2). Soil nutrient content and fertility increase from east to west and it is highest in the piedmont BAR site (Table 6.1 and Fig. 6.1). Vegetation responds to climate and soil gradients with changes in species richness and diversity and with the density of the woody component (Baruch 2005b). As well as rainfall, water available for plants also depends on soil WHC which in turn is reliant on the proportion of sand in the profile. Therefore, the synthetic Water Availability Index [WAI = (Rainfall × WHC)/100] seems to be a better estimator of water availability. The grouping of relative water availability (WAI) and soil fertility (SF) settings generates four population groups: High WA and SF (BAR); High WA and low SF (PTO and CAI); Low WA and high SF (CAL and MOC); Low WA and SF (TEM). Across our study sites, the water availability and soil fertility gradients are not correspondent. For example, the PTO site, with the highest rainfall displays one of the lowest soil N and P contents and fertility due to sandier soils. The opposite example is MOC with the lowest rainfall but relatively fertile soils. In consequence, the effects that both gradients and their interaction have on ITVs are complex and challenging to infer.

6.2 The Emblematic Study Species

Trachypogon spicatus (L.f.)Kuntze, (formerly *T. plumosus* (Humb. and Bonpl. ex Willd.) Nees and henceforth Trachypogon) is a cespitose and perennial C_4 grass of medium height (1.0–1.5 m) dominant in many Neotropical savannas (Ramia 1967; Baruch 2005b; Huber et al. 2006) (Fig. 6.2). Its annual growth cycle starts rapidly with the rains in May, flowers in August- September, and seed dispersal occurs before the dry season (Ramirez 2002) when aerial biomass senesces but remains standing (Baruch and Fernandez 1993; Baruch et al. 1989). In Venezuela, populations of Trachypogon inhabit natural and anthropogenic lowland savannas, but extend to the Guyana plateau in the south-east and to intermediate elevations in the Andes and Coastal Mountains (Baruch 2005b). Although of limited nutritional quality, native savannas dominated by Trachypogon are essential for extensive cattle ranching.

Curatella americana L. (henceforth, Curatella) is an evergreen medium sized (3–5 m high), fire-tolerant tree with twisted and branched trunks, thick bark, and deep roots. Its sclerophyllous leaves last roughly 12 months (Foldats and Rutkis 1975; Goldstein et al. 1986; Medina and Francisco 1994; Sobrado 1996) (Fig. 6.2). Curatella flowers during the dry season, it is insect pollinated with seeds dispersed by frugivores (Ramirez 2002). Curatella is the dominant tree in Venezuelan non-flooded seasonal savannas (San Jose and Fariñas 1991; Silva et al. 2001). As the most abundant savanna tree, Curatella probably controls a large part of the energy, carbon, and water budgets of the savanna (San Jose and Garcia 1981).

By itself, the dominance and widespread distribution of both species in the savanna suggests substantial interpopulation variation.

6.3 Intrapopulation Variability and Responses to Physical Demands

6.3.1 Field Sampling, Trait Assessment, and Analysis

Six populations of both species, identified by the first three letters of their shared localities (Table 6.1) were sampled at the peak growth during the rainy season during several years for ecophysiological and reproductive traits. Except for MOC, which is a patch in the Coastal Mountains, the rest of the populations conform a continuum of savannas. Care was taken to collect enough samples and/or measurements to make meaningful statistically tests following the recommended methods (Pérez-Harguindeguy et al. 2013). In brief, field work started with gas exchange measurements with portable equipment followed by phenology and plant dimensions appraisal. Finally, soil and leaf samples, plant biomass, and seeds were collected and preserved for laboratory analysis. Soil physico-chemistry and water retention capacity were assessed by standard soil methods. Iconic traits such as specific leaf area (SLA), leaf N and P contents, and photosynthetic rate (Amax) (Funk et al. 2017) plus the ^{13}C isotopic signature, as a proxy to water use efficiency, were appraised in both species. Nitrogen use efficiency (NUE) was calculated from SLA, Amax, and leaf N content. For Trachypogon, above ground biomass, awn length of diaspore, seed mass, and germination percentage are also included in the study. Detailed methods are in the respective publications (Baruch 2005a, 2011; Baruch et al. 2004). The relationships between physical variables and population traits are represented by linear models and principal component analysis.

6.3.2 Species Traits

Trachypogon and Curatella differ in growth form, life history, and metabolism routes and diverge in most traits across the entire environmental gradient (Table 6.2). Trachypogon displays higher SLA and Amax and lower leaf N content that are associated to rapid use of resources caused by fast and high growth rate during the rainy season and prompt senescence afterwards. In contrast, Curatella traits display opposite features that are geared to a more conservative use of resources evidenced by much slower growth rate, with long-lived and denser leaves (Foldats and Rutkis 1975; Medina and Francisco 1994; Sobrado 1996). Therefore, they represent opposite ends of the "fast-slow" growth continuum of resource use strategies (Wright et al. 2004). Within each species, trait-trait links are typical of the leaf economics spectrum predictions (Wright et al. 2004) where SLA, Amax, and leaf nutrient content are interdependent and stronger in Trachypogon. The reproductive and ecophysiological traits of Trachypogon populations are also linked such as seed mass is positively linked to Amax and leaf N content. Also, diaspore awns are shorter in late flowering populations that also germinate poorly.

6.3.3 Species Response Across the Physical Gradients

Quantitative traits of both species differed significantly among populations (Table 6.2) and share similar responses to water availability and fertility gradients (Table 6.3). In both species, water availability, either as rainfall or HI, was consistently and positively correlated to SLA, NUE, and the ^{13}C isotopic signature (Table 6.3). Among the fertility variables, soil N was correlated to more Trachypogon traits whereas soil P displayed more links with Curatella traits (Table 6.3). Leaf N and P were positively associated to the respective soil nutrient contents. By itself, Amax was uncorrelated to physical gradients. However, as a component of the NUE variable, it was positively associated to water availability and soil P content (Table 6.3). The ^{13}C isotope signature of both species, as in lieu of water use efficiency, was correlated to water availability showing that in drier sites water is used more efficiently.

The response of Trachypogon reproductive traits to physical gradients mirrors those of the ecophysiological traits. They were correlated to water availability such as that in rainier sites flowering took place earlier in the season ($R^2 = 0.52$), diaspore awns were longer ($R^2 = 0.49$), and germination percentage was higher ($R^2 = 0.80$). On the other hand, seed mass was uncorrelated to physical variables. Soil fertility, mostly soil P content, was only correlated to aerial biomass ($R^2 = 0.44$). The positive correlation of awn length and water availability was unexpected as awn length is associated to depth of seed burial into the soil as an avoidance response to fire damage that is more frequent and severe in the driest sites (Baruch 2005b; Johnson and Baruch 2014).

Although the ecophysiological traits of Trachypogon and Curatella are plainly different, the relationship among populations of both species within the multivariate trait space is alike in regard to responses to physical demands. The populations from the extremes of water availability (MOC and PTO) and fertility gradients (BAR) occupy the ends of both ordination axes (Fig. 6.3). Populations from the intermediate physical ranges (CAL and TEM) are at midway positions along the ordination

Table 6.2 Traits of populations of study species

(a) Ecophysiological traits

	Trachypogon spicatus						*Curatella americana*					
	SLA	Leaf N	Leaf P	Amax	NUE		SLA	Leaf N	Leaf P	Amax	NUE	
Populations	(cm^2g^{-1})	(%)	(ppm)	($\mu mol\ m^{-2}\ s^{-1}$)	($\mu mol\ g^{-1}\ s^{-1}$)	^{13}C	($cm2g^{-1}$)	(%)	(ppm)	($\mu mol\ m^{-2}\ s^{-1}$)	($\mu mol\ g^{-1}\ s^{-1}$)	^{13}C
BARINAS	157.1	0.99	0.08	19.10	30.07	–12.1	103.3	1.22	0.08	14.70	12.45	–29.1
CAICARA	164.5	0.82	0.06	17.38	34.56	–12.5	99.0	0.91	0.08	11.19	12.18	–29.3
CALABOZO	148.9	0.95	0.06	22.18	34.49	–12.1	101.4	1.1	0.05	11.28	10.39	–28.0
MOCHIMA	144.6	0.96	0.07	21.77	32.81	–12.4	79.5	1.18	0.04	14.20	9.56	–27.9
P.AYACUCHO	166.9	0.92	0.05	20.36	36.73	–12.9	98.3	1.36	0.04	17.06	12.33	–29.0
TEMBLADOR	133.0	0.89	0.08	22.14	32.92	–12.6	80.9	1.24	0.07	14.88	9.71	–27.9

(b) Biomass and reproductive traits

	Trachypogon spicatus				
Populations	Aerial biomass	Days to flowering	Awn length	Seed mass	Germination
	(g)	[a]	(mm)	(mg)	(%)
BARINAS	143.2	225	56.1	0.74	41.6
CAICARA	103.3	270	49.3	0.61	44.8
CALABOZO	114.4	225	55.1	0.70	38.4
MOCHIMA	141.1	285	45.7	0.78	54.4
P.AYACUCHO	93.6	180	60.8	0.78	24.8
TEMBLADOR	112.1	210	58.9	0.74	40.0

Acronyms are: *SLA* specific leaf area, *Amax* photosynthesis rate, *NUE* nitrogen use efficiency, *13C* isotopic signature

[a] After January 1st

Table 6.3 Slope (β) and correlation coefficient between physical variables and ITVs of research species

		Physical variables					
Traits	Species	Rainfall	HI	Soil N	Soil P	Fertility	CEC
SLA	*T. spicatus*	**$\beta = 0.016$** **$R^2 = 0.53$**	**$\beta = 28.3$** **$R^2 = 0.52$**	–	**$\beta = 4.9$** **$R^2 = 0.14$**	–	–
	C. americana	**$\beta = 0.012$** **$R^2 = 0.51$**	**$\beta = 20.2$** **$R^2 = 0.37$**	–	**$\beta = 7.99$** **$R^2 = 0.54$**	–	–
Leaf N	*T. spicatus*	–	–	**$\beta = 0.63$** **$R^2 = 0.44$**	–	–	–
	C. americana	–	–	–	–	–	–
Leaf P	*T. spicatus*	–	–	**$\beta = 0.16$** **$R^2 = 0.61$**	–	–	–
	C. americana	–	–	–	**$\beta = 0.01$** **$R^2 = 0.43$**	**$\beta = 0.01$** **$R^2 = 0.31$**	–
Amax	*T. spicatus*	–	–	–	–	–	–
	C. americana	–	–	–	–	–	–
NUE	*T. spicatus*	–	**$\beta = 2.70$** **$R^2 = 0.15$**	–	–	–	–
	C. americana	**$\beta = 0.001$** **$R^2 = 0.67$**	**$\beta = 3.51$** **$R^2 = 0.69$**	–	**$\beta = 0.88$** **$R^2 = 0.40$**	–	–
^{13}C	*T. spicatus*	**$\beta = 0.001$** **$R^2 = 0.13$**	**$\beta = 0.44$** **$R^2 = 0.21$**	**$\beta = -3.2$** **$R^2 = 0.41$**	–	**$\beta = -0.01$** **$R^2 = 0.62$**	**$\beta = -0.10$** **$R^2 = 0.57$**
	C. americana	**$\beta = 0.001$** **$R^2 = 0.49$**	**$\beta = 1.48$** **$R^2 = 0.52$**	–	–	–	–

Acronyms as in Table 6.1

axes whereas CAI, from a site with high water availability but low fertility is set in a peripheral spot. The ordination of Trachypogon populations within the reproductive trait space displays a similar population arrangement except that soil fertility plays a lesser role (Fig. 6.3).

6.4 Recapitulation

Substantive ITV, and the adjustment of functional traits, through structural, biochemical, and physiological adaptations and trade-offs, support and explain the presence and dominance of our savanna emblematic species across long and steep gradients of physical demands. This type of variation is to be expected in populations inhabiting a set of diverse climatic and edaphic environments, like the Venezuelan savannas. Furthermore, the same abilities and capacities may determine species persistence and success in a rapidly changing and unstable planet. At the community level, dominant plant species control vegetation composition, diversity, and interactions. Functionally, plant traits of dominant species regulate energy and mass transfers as well as nutrient cycling of the ecosystems (Chapin 2004; Funk

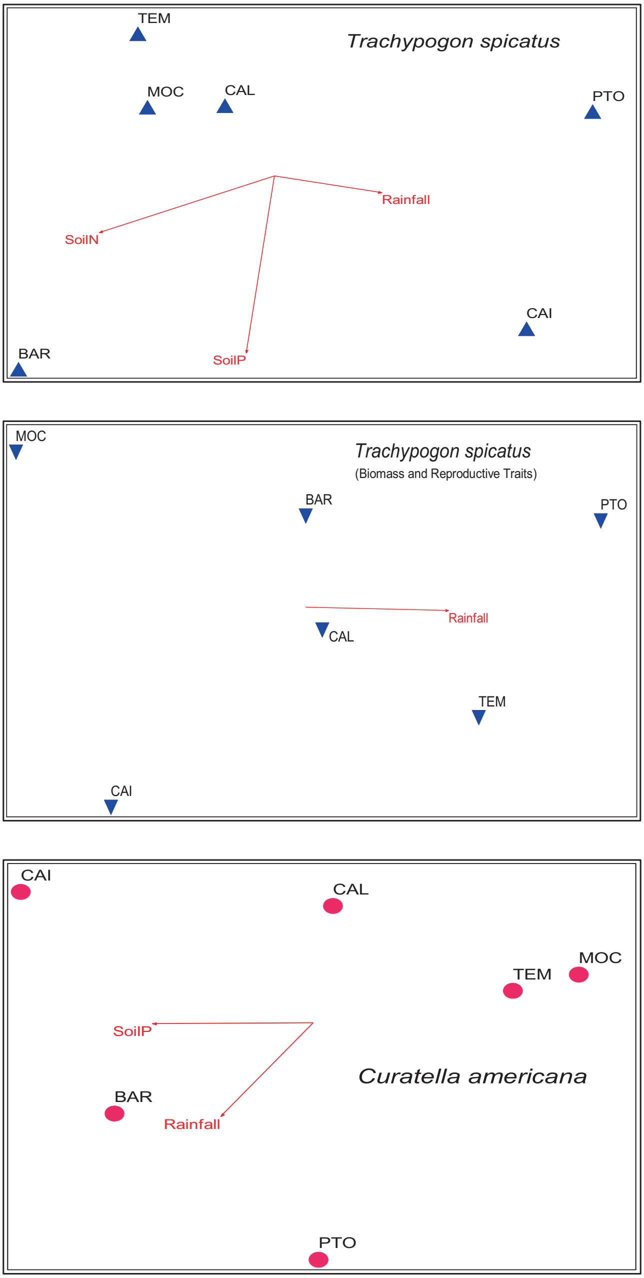

Fig. 6.3 PCA ordination of populations of study species in trait space. Variances explained for X and Y axes: *T. spicatus:* 52.2% and 25.4%; *C. americana*: 50.4% and 33.3%. *T. spicatus* Biomass and reproductive traits: 64.4% and 20.7%. Population acronyms as in Table 6.1

et al. 2017; Westerband et al. 2021). In addition to water and soil fertility limitations, the incidence of frequent fires is another stressor in the Llanos. The responses include rapid regrowth from the basal meristems and increased inflorescence production in Trachypogon (Baruch and Bilbao 1999) and thick cortex protecting the trunk in Curatella (Foldats and Rutkis 1975).

Despite their contrasting life forms, photosynthetic metabolism and with differently scaled ITVs, Trachypogon and Curatella respond similarly to physical demands although at different rates. Trachypogon-high SLA, Amax, and low leaf N content are geared to fast growth and opportunistic responses to resource availability. In contrast, Curatella, with low SLA and Amax, long-lived and high N leaves, grows slowly and uses resources more conservatively. These contrasting traits and responses frame Trachypogon at the fast end and Curatella at the slow end of the leaf economics spectrum (Wright et al. 2004). Genetic variability in Trachypogon differs among populations and their associations across the Llanos are similar to those of its ecophysiological traits (Baruch et al. 2004). Genetic and phenotypic levels of variation could promote selection events and the generation of local ecotypes. The wealth of ITV and genetic variation in Trachypogon represent valuable tools for selection of material to revegetate or restore physically damaged or polluted savanna sites in Venezuela (Rosales et al. 1997).

A plot-based survey of a large portion of Venezuelan savannas found 293 species in the herbaceous stratum and 25% of them inhabit all Venezuelan savanna types (Baruch 2005b). If the patterns of ITVs in most of these species are similar to those shown by Trachypogon and Curatella, then the phenotypic richness of the Llanos should be significantly higher than the relatively low species richness signed for them compared to the much larger Brazilian Cerrados (Sarmiento 1996).

Consequent from the above facts and discussion is the co-existence of Trachypogon and Curatella under the limited offer of savanna resources. Answers to queries such as “Which ITVs are essential for co-existence?” and “Are ITV roles similar under drier or wetter conditions?” are challenging and worth of research.

6.5 Conclusions

- The physical gradients of water availability and soil fertility in the Venezuelan Llanos are long and steep.
- The joint presence and dominance of two species of contrasting growth forms along such physical gradients is unusual.
- The absolute values of all ecophysiological traits are higher in Trachypogon than in Curatella.
- The populations of both species differ significantly across all ecophysiological traits analyzed.
- The populations of both species respond likewise to demands of the physical gradients.

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References

Araujo I, Marimon BS, Scalon MC, Cruz WJA, Fauset S, Vieira TCS, Gloor MU (2021) Intraspecific variation in leaf traits facilitates the occurrence of trees at the Amazonia-Cerrado transition. Flora 279. https://doi.org/10.1016/j.flora.2021.151829

Archer SR, Andersen EM, Predick KI, Schwinning S, Steidl RJ, Woods SR (2017) Woody plant encroachment: causes and consequences. In: Briske DD (ed) Rangeland systems: processes, management and challenges. Springer International Publishing, Cham, pp 25–84

Baruch Z (1996) Ecophysiological aspects of the invasion by African grasses and their impact on biodiversity and function of neotropical savannas. In: Solbrig O, Medina E, Silva J (eds) Biodiversity and savanna ecosystem processes, vol 121. Springer Verlag, Berlin, pp 79–93. (Reprinted from: In File)

Baruch Z (2005a) Trachypogon plumosus (Poaceae), un caso de alta diversidad interpoblacional en sabanas neotropicales. Interciencia 30(8):488–494

Baruch Z (2005b) Vegetation-environment relationships and classification of the seasonal savannas in Venezuela. Flora - Morphol Distrib Funct Ecol Plants 200(1):49–64. https://doi.org/10.1016/j.flora.2004.06.001

Baruch Z (2011) Leaf trait variation of a dominant neotropical savanna tree across rainfall and fertility gradients. Acta Oecol 37(5):455–461. https://doi.org/10.1016/j.actao.2011.05.014

Baruch Z, Bilbao B (1999) Effects of fire and defoliation on the life history of native and invader C-4 grasses in a Neotropical savanna. Oecologia 119(4):510–520

Baruch Z, Fernandez DS (1993) Water relations of native and introduced C4 grasses in a neotropical savanna. Oecologia 96:179–185

Baruch Z, Hernandez AB, Montilla MG (1989) Dinamica del crecimiento, fenologia y reparticion de biomasa en gramineas nativas e introducidas de una sabana neotropical. Ecotropicos 2:1–13

Baruch Z, Nassar JM, Bubis J (2004) Quantitative trait, genetic, environmental, and geographical distances among populations of the C-4 grass Trachypogon plumosus in Neotropical savannas. Divers Distrib 10(4):283–292

Caddy-Retalic S, Andersen AN, Aspinwall MJ, Breed MF, Byrne M, Christmas MJ, Guerin GR (2017) Bioclimatic transect networks: powerful observatories of ecological change. Ecol Evol 7(13):4607–4619

Cassia-Silva C, Cianciaruso MV, Dias PA, Freitas CG, Souza-Neto AC, Collevatti RG (2020) Among cradles and museums: seasonally dry forest promotes lineage exchanges between rain forest and savanna. Plant Ecol Divers 13(1):1–13. https://doi.org/10.1080/17550874.2019.1709103

Chapin FS (2004) Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. Ann Bot 91:455–463

de Oliveira CS, Messeder JVD, Teixido AL, Arantes MRR, Silveira FAO (2021) Vegetative and reproductive phenology in a tropical grassland-savanna-forest gradient. J Veget Sci 32(2). https://doi.org/10.1111/jvs.12997

Foldats E, Rutkis E (1975) Ecological studies of chaparro (curatella americana L.) and m ante co (byrsonima crassifolia h.b.k.) in venezuela. J Biogeogr 2:159–178

Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Wright J (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biol Rev 92(2):1156–1173. https://doi.org/10.1111/brv.12275

Goldstein G, Sarmiento G, Meinzer F (1986) Daily and seasonal patterns of water relations in evergreen tropical savanna tress. Oecol Plant 7:107–120

Gómez Y, Paolini J, Hernández RM (2008) Sustitución de la sabana nativa con plantaciones de Pinus caribaea (Pinaceae) en Venezuela: efecto sobre parámetros indicadores de cambios en el carbono del suelo. Rev Biol Trop 56(4):2041–2053

Hoffmann WA, Jackson RB (2002) Vegetation-climate feedbacks in the conversion of tropical savanna to grassland. J Climate 13:1593–1602

Huber O (1987) Neotropical savannas: their flora and vegetation. Trend Ecol Evol 2:67–71

Huber O, Alarcon C (1988) Mapa de Vegetación de Venezuela. Escala 1:2.000.000. In: M. D. d. V.-T. N. Conservancy. (ed). Caracas, Venezuela

Huber O, de Stefano RD, Aymard G, Riina R (2006) Flora and vegetation of the Venezuelan Llanos: a review. In: Toby Pennington GPLR, Ratter JA (eds) Neotropical savannas and seasonally dry forests. CRC Press, pp 95–120

Johnson EE, Baruch Z (2014) Awn length variation and its effect on dispersal unit burial of Trachypogon spicatus (Poaceae). Rev Biol Trop 62(1):321–326. Retrieved from WOS:000336414800024

Kattge J, Diaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Wright IJ (2020) TRY–a global database of plant traits. Glob Change Biol 17(9):2905–2935. https://doi.org/10.1111/gcb.14869

Medina E, Francisco M (1994) Photosynthesis and water relations of savanna tree species differing in leaf phenology. Tree Physiol 14(12):1367–1381

Medina E, Silva J (1990) Savannas of northern South America: a steady regulated by water-fire interactions on a background of low nutrient availability. J Biogeogr 17:403–413

Meirmans PG (2015) Seven common mistakes in population genetics and how to avoid them. Mol Ecol 24(13):3223–3231. https://doi.org/10.1111/mec.13243

Neves SPS, de Miranda LDP, Rossatto DR, Funch LS (2017) The roles of rainfall, soil properties, and species traits in flowering phenology along a savanna-seasonally dry tropical forest gradient. Braz J Bot 40(3):665–679. https://doi.org/10.1007/s40415-017-0368-1

Niinemets U (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82(2):453–469

Ojasti J (2001) Informe sobre las especies exóticas en Venezuela: Ministerio del Ambiente y de los Recursos Naturales

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61(3):167. https://doi.org/10.1071/bt12225

Ramia M (1967) Tipos de sabanas en los llanos de venezuela. Biol Soc Venezuela Nat Sci 27(112):264–288

Ramia M (1974) Plantas de las sabanas llaneras. Monte Avila Editores, Caracas

Ramirez N (2002) Reproductive phenology, life-forms and habitats of the Venezuelan Central Plain. Am J Bot 89(5):836–842

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Nat Acad Sci 94(25):13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Rodriguez J, Rojas Suarez F, Giraldo Hernandez D (2010) Libro rojo de los ecosistemas terrestres de Venezuela: PROVITA

Rosales J, Cuenca G, Ramirez N, Deandrade Z (1997) Native colonizing species and degraded land restoration in La Gran Sabana, Venezuela. Restor Ecol 5(2):147–155

Rossatto DR (2014) Spatial patterns of species richness and phylogenetic diversity of woody plants in the neotropical savannas of Brazil. Braz J Bot 37(3):283–292. https://doi.org/10.1007/s40415-014-0070-5

San Jose JJ, Fariñas MR (1991) Temporal changes in the structure of a Trachypogon savanna protected for 25 Years. Acta Oecol 12(2):237–247

San Jose JJ, Garcia MJ (1981) Factores operacionales en la produccion de materia organica e n la s sabanas de trachypogon. Biol Soc Venezuela Nat Sci 139:347–374

Sarmiento G (1983) The savannas of tropical America. In: Bourliere F (ed) Tropical savannas, 13th edn. Elsevier, Amsterdam, pp 245–288. (Reprinted from: In File)

Sarmiento G (1996) Biodiversity and water relations in tropical savannas. In: Medina E, Solbrig OT, Silva J (eds) Biodiversity and savanna ecosystem processes: a global perspective. Springer, Berlin, pp 61–78

Schargel R (2011) Una resena de la geografia fisica de Venezuela, con enfasis en los suelos. In: Aymard G (ed) Los Bosques de Venezuela. UNELLEZ, Guanare, pp 11–26. (Reprinted from: In File)

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Wardle DA (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol Lett 18(12):1406–1419. https://doi.org/10.1111/ele.12508

Silva JF, Zambrano A, Fariñas MR (2001) Increase in the woody component of seasonal savanna under different fire regimes in Calabozo, Venezuela. J Biogeogr *28*:977–983

Sobrado MA (1996) Leaf photosynthesis and water loss as influenced by leaf age and seasonal drought in an evergreen tree. Photosyntetica 32(4):563–568

Solbrig OT (1996) Plant traits and adaptive strategies: their role in ecosystem function. In: Schulze ED (ed) Biodiversity and ecosystem function, 99th edn. Springer-Verlag, New York, pp 97–116. (Reprinted from: In File)

Weigelt P, Konig C, Kreft H (2020) GIFT - a global inventory of floras and traits for macroecology and biogeography. J Biogeogr 47(1):16–43. https://doi.org/10.1111/jbi.13623

Westerband AC, Funk JL, Barton KE (2021) Intraspecific trait variation in plants: a renewed focus on its role in ecological processes. Ann Bot 127(4):397–410. https://doi.org/10.1093/aob/mcab011

Williams DG, Baruch Z (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. Biol Invasions 2:123–140

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Villar R (2004) The worldwide leaf economics spectrum. Nature 428(6985):821–827

Chapter 7
Latitudinal Trends in Scorpion Assemblages of Brazilian Atlantic Forest: Do the Rapoport's and Bergmann's Rules Apply?

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7.1 Effects of Latitudinal Gradients in Biodiversity

Considering that species are not evenly distributed across space (Stevens et al. 2013), researchers have attempted to describe and understand broad scale patterns of biodiversity that characterize the world's biota (Darwin 1859; Wallace 1878; LaManna et al. 2017). Few species possess a widespread distribution across habitats, while most species are adapted to a limited range of environmental conditions, referred to as the ecological niche (Peterson 2011). Although niche breadths are generally thought to vary positively with latitude (e.g., Sunday et al. 2011; Papacostas and Freestone 2016; Sexton et al. 2017), a better comprehension of such geographic patterns in species diversity is mandatory for ecological studies with conservation backgrounds (Gaston 2000; Whittaker et al. 2005). In such a context, one of the best-known patterns of species distribution is the latitudinal gradient expressed by an overall increase in species diversity toward the equator (e.g., Brown 2014; Fine 2015; Roll et al. 2017). This geographical trend has been reported for several taxa, including birds, mammals, reptiles, arthropods, and mollusks (Willig et al. 2003; Hillebrand 2004; Kinlock et al. 2018). However, others such as parasitic species and

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taxa with narrow latitudinal ranges may show a positive or non-significant relationship with latitude (Visser et al. 2014; Timms et al. 2016; Brocklehurst et al. 2017).

Different hypotheses have been formulated to explain the effect of latitudinal gradient in biodiversity (reviewed in Pontarp et al. 2019), these hypotheses can be divided into three main categories: (i) ecological limits, (ii) diversification rates, and (iii) time for species accumulation (Mittelbach et al. 2007). In the first, competition for limited resources is a key factor that limits the number of species co-occurring in the same locality (e.g., Mittelbach et al. 2007; Rabosky 2009), and the niche conservatism is often evoked to explain the differential dispersal rates across latitudes (Wiens et al. 2010). In the diversification rate hypothesis, variation in speciation or extinction rates, which may occur faster in the tropics than temperate regions, exert an important role (Allen and Gillooly 2006; Weir and Schluter 2007). Finally, in the third category, historical colonization rates assume an unbalanced diversity dynamic, implying that regions that were colonized first are expected to harbor long periods of diversification, resulting in high levels of species richness (Stephens and Wiens 2003).

Interestingly, the processes behind latitudinal diversity gradients are still under debate (e.g., Fine 2015; Lomolino et al. 2016; Willig and Presley 2018). Several factors may explain the lack of consensus on the relative importance of the processes that generate and maintain such gradients in biodiversity (e.g., Latham and Ricklefs 1993; Willig et al. 2003; Weiser et al. 2017). It is well known, for example, that biodiversity gradients are expected to be driven by spatial ranges in species distribution (e.g., Cardillo et al. 2005; Mittelbach et al. 2007) and the taxonomic resolution (Weiser et al. 2007; Kreft and Jetz 2007). In some cases, latitudinal patterns in species richness are not generally attributed to latitude per se, but to the variation in bioclimatic conditions across latitudinal ranges. In this way, the macroecological approach evokes a set of biotic and abiotic covariables to explain the described patterns of biodiversity (e.g., Currie et al. 2004; Kaspari et al. 2004). For this, explanations for the latitudinal gradient of diversity make implicit assumption that these covariables of latitude are not taxon scale-dependent. For example, the area of a continent or the temperature of a habitat is independent of the taxonomic rank of the focal taxon (Weiser et al. 2018). Therefore, variation in species richness along geographical gradients may help us to understand the evolutionary history of organisms through the interplay between ecological adaptability and dispersal capabilities (Albuquerque et al. 2011; Silveira et al. 2019).

7.2 Rapoport and Bergmann Rules

Species' ecological traits and their tolerance to environmental factors act as a complex interplay constraining their dispersion and thus, determining their geographical ranges (Gaston 2003). In their monograph study, Rapoport (1975) found that latitude correlates with species distribution ranges. This author found that the range size of species was positively correlated with latitude, with smaller ranges for species occurring closer to the equator. Since the description of Rapoport's rule, many studies have tested Rapoport effects in different taxa (e.g., Liu et al. 2020; Murphy et al. 2020; Pie et al. 2021). Ruggiero and Werenkraut (2007) demonstrated that Rapoport's rule was applied particularly for the large, continental landmasses of the Northern Hemisphere and less so in other geographic regions. Applications of Rapoport rule in tropical regions and the Southern Hemisphere appear to be less well defined (Rohde 1996). Many studies in these regions support the existence of complex regional patterns, providing only partial support for Rapoport's rule (e.g., Fortes and Absalão 2004; Pintor et al. 2015; Núñez-Flores et al. 2019).

In addition, species range size is fundamental for understanding of many life sciences disciplines, such as ecology, biogeography, and conservation, and has received significant research attention throughout the decades (e.g., Jablonski and Roy 2003; Böhm et al. 2017). For example, through the determination of drivers of range size we can measure the level of extinction risk of species. Large-ranged species generally possess a large environmental tolerance (Jablonski and Roy 2003) and lower extinction risk than small-ranged species that exhibits a higher environmental specificity, which may result in elevated extinction risks (Purvis et al. 2000; Lee and Jetz 2010; Böhm et al. 2017). Thus, understanding the drivers of range size in species can provide valuable information about appropriate conservation actions for range-restricted species. Therefore, studies at macro-scale are particularly important for testing the universality of latitudinal Rapoport's rule, principally in the Southern Hemisphere.

Furthermore, to richness and range size, latitudinal gradient may affect the ecological traits of species with many of these traits being influenced by body size (Peters and Wassenberg 1983; Smith and Lyons 2013). Body size mediates several aspects of an animal's life history, such as life span, clutch size and growth rate, and its variability across spatial gradients is a prominent topic in biogeography and ecology (Brown et al. 2004; Peters and Wassenberg 1983; Smith and Lyons 2013). The most known ecogeographical rule is the Bergmann's rule (BR), which predicts that closely related endothermic vertebrates increase in body size toward cold environments (Bergmann 1847; Blackburn et al. 1999). The mechanism proposed to explain this pattern toward colder sites is that heat generation capacity increases with body volume, whereas heat loss increases with surface area in endotherms (Blackburn et al. 1999). However, there is increasing evidence pointing that this mechanism is not universal (Blackburn et al. 1999; Meiri 2011). For ectotherm animals, on the other hand, there are comparatively few studies addressing whether variation in body size can be properly represented by latitudinal trends (Blanckenhorn and Demont 2004), with more evidences suggesting mixed indirect effects of latitude on body size variation in arthropods, as an example (Chown and Gaston 2010; Entling et al. 2010; Tseng et al. 2018). For these animals, previous studies have demonstrated that either an increase, or decrease in body size may associate to colder climates, as expected by Bergmann's rule and the so-called converse BR, respectively (Shelomi 2012; ; Scriven et al. 2016). The application of BR to ectotherms is justified by the dependence of environmental temperatures required for these animals to thermoregulatory activities. This implies that thermoregulation in larger ectotherms is expected to be less efficient in cooler climates because they absorb heat more slowly than the smaller ones (Aragon and Fitze 2014). In contrast, the converse BR posits that colder sites limit the time available for foraging and growth, resulting in smaller organisms (Mousseau 1997; Blanckenhorn and Demont 2004). Therefore, these mixed results in the application of BR to ectotherms has been hotly debated, because both geographical patterns have been found (Chown and Gaston 2010).

7.3 Scorpions as Organism Model in Ecological Studies

Scorpions constitute one of the oldest groups of terrestrial arthropods, with their first records dated to the Silurian (Kjelleswig-Waering 1986; Jeram 1998; Dunlop 2010). Due to the long evolutionary period and low modification in the basic *bauplan*, these animals are considered living fossils (Polis 1990). Corresponding to the fifth highest order of Arachnida in terms of species richness, scorpions are currently represented by about 2600 species (Brazil and Porto 2011; Rein 2021), with a total estimated diversity of around 7000 species (Coddington and Colwell 2001). In general, these arachnids present a wide spectrum of ecological requirements, being distributed in a plethora of habitats (e.g., tropical forests, dry forests, mountain tops, deserts, caves, and urban centers) across almost all landmasses (Polis 1990; Lourenço 2015). Scorpion richness seems to be maximized in arid and semiarid environments, with local assemblages being usually represented by an average of 5–6 species (Polis 1990, 1993; Porto et al. 2014), although neotropical forests can eventually harbor a comparable number of species at local scales (Lourenço 1994; Brito and Borges 2015). Despite their wide distribution, scorpions cannot be considered as ecologically generalist, as the vast majority of species have specific requirements regarding habitat and microhabitat (Polis 1990).

Several evidences suggest that scorpion assemblages are, in part, driven by environmental temperature, precipitation, type of substrate (e.g., soil hardness, litter quantity), vegetation structure, as well as by the complex interaction among these factors (Warburg and Ben-Horin 1981; Prendini 2005; Foord et al. 2015; Lira et al. 2019a, 2021a). In some cases, the responses of scorpion assemblages to the environmental variation may be detected even at very small spatial scales (Raz et al. 2009; Foerster et al. 2020). For example, a strong correlation of species composition with climate variation was described by Foord et al. (2015) when investigating the effect of the altitudinal gradient on a mountain system in South Africa. Species of the genus *Hottentotta* Birulla, 1908 and *Parabuthus* Pocock, 1890 were absent in areas where rainfall was above 600 mm. Similar results were described by Prendini (2005) when investigating the scorpion assemblage along a longitudinal gradient in the southern region of Africa, finding that species of *Afroisometrus* Kovarik, 1997, *Lychas* C. L. Koch, 1845, *Cheloctonus* Pocock, 1892, *Pseudolychas* Kraepelin, 1911 and *Opistacanthus* Peters, 1861 were restricted to areas with high rainfall such as montane forests. In a recent study, Lira et al. (2019a) investigated the effects of bioclimatic variables across a longitudinal gradient on Brazilian scorpions. These authors found that variables associated with precipitation and temperature had a strong effect on scorpion distribution.

On a local scale, even within the habitat, scorpions are not randomly distributed within the environment. Different substrates exert different selective pressures on scorpions, resulting in microhabitat-specialist species (Polis 1990; Prendini 2001). In a study carried out in a humid forest enclave in northeastern Brazil, no niche overlap was detected between the three scorpion species (*Tityus brazilae* Lourenço and Eickstedt 1984; *T. neglectus* Mello-Leitão 1932 and *T. pusillus* Pocock 1893) that co-occur in the area with each one collected exclusively in specific microhabitats (Lira and DeSouza 2014). Similarly, when analyzing the use of microhabitat in Colombian species from a dry forest fragment, Álvarez et al. (2013) described that *Opisthacanthus elatus* (Gervais 1844) and *T. tayrona* Lourenço 1991 preferentially use fallen objects (trunks and stones) while *T. ashtenes* Pocock 1893 and *Ananteris columbiana* Lourenço 1991 were frequently found in vegetation and litter, respectively. Such specificity in microhabitat selectivity can be observed even in species that coexist on the same substrate. Lira et al. (2013, 2018) investigating the use of microhabitat in Atlantic Forest scorpions, found a vertical stratification in two litter species, with *T. pusillus* colonizing the upper layers, while *Ananteris mauryi* Lourenço 1982 uses the lower layers of the litter. Due to environmental requirements, whether regional (climate variation) or local (microhabitat specificity), scorpions are responsive to habitat modification. Smith (1995) studying the effect of habitat fragmentation in Australia, reported that larger fragments support higher abundance and richness of scorpions than smaller fragments. Similar results with higher scorpion richness observed in larger fragments have been described for a hyper-fragmented Brazilian Atlantic Forest landscape (Lira et al. 2016). These authors suggested that larger fragments have a greater number of microhabitats available in relation to smaller ones, thus supporting a greater diversity of these arachnids. In a study conducted on locations with different usage histories in the Caatinga, Foerster et al. (2020) corroborates the idea that environmental complexity is crucial for the maintenance of local species pool. In this work, the authors found more species in areas that presented greater environmental complexity than in monotonous landscapes. Therefore, the sensitivity of scorpion species to environmental variations at different scales (regional or local) make these animals good candidates for environmental bioindicators. Polis (1990) argues that scorpions meet a series of criteria that frame them as bioindicators, such as being easily sampled, classified and stored. In addition, Gerlach et al. (2013) point out that these arachnids have a high potential as bioindicators, and may even be used as flagship species, due to their charisma. However, the authors emphasize that the low diversity and abundance in many areas can act as a limiting factor for their potential use as bioindicators. Within this context, scorpions have been used as models for ecological studies that address environmental changes, especially in Neotropics (e.g., Nime et al. 2014; Lira et al. 2020, 2021a).

7.4 The Brazilian Atlantic Forest

As the second largest rainforest biome on the American continent, the Brazilian Atlantic Forest is one of the 36 global hotspots in biodiversity conservation (Conservation International 2009). The exuberant biodiversity contained in Brazilian Atlantic Forest has been continuously threatened by habitat loss and fragmentation due to anthropogenic activities (Laurance 2009; Haddad et al. 2015). Such human activities were (and still are) one of the major drivers affecting the current spatial configuration of the Atlantic Forest, represented today by small islands of vegetation inserted in a matrix of areas converted to the human settlements (Ribeiro et al. 2009; Joly et al. 2014; Haddad et al. 2015; Rezende et al. 2018). These factors, together with other threats to the biome (e.g., hunting and illegal logging), have led to the extinction of numerous species (Marini and Garcia 2005), compromising regions where important centers of endemism are located. Nowadays, the estimated fraction of original vegetation cover in the Atlantic Forest is estimated in only 28%, which includes native forest and non-forest formations (Rezende et al. 2018). Those original formations are extremely important to assure ecological corridors aimed to improve the connectivity among Atlantic Forest patches (i.e., fragments) within the landscape, preventing populations from deleterious effects of genetic isolation and improving their capacity to remain viable over time (Rezende et al. 2018).

High levels of endemism in the Brazilian Atlantic Forest were detected for several taxa, such as bees (Garraffoni et al. 2017), harvestmen (DaSilva et al. 2015), birds (Marini and Garcia 2005; Carvalho et al. 2021), and anuran (Vasconcelos et al. 2014). Different hypotheses have been formulated to explain the causes of the high diversity and endemism in the Atlantic Forest. For example, tectonic activities, marine introgressions, Pleistocene refuges (Martins 2011), and environmental gradients shaped the distribution of lineages in this biome. In the latter case, environmental gradients along the same biome would favor speciation (Silva and Casteleti 2003) and would limit the distribution of species in time and space.

The Atlantic Forest has a wide geographic distribution extending along the entire Atlantic coast of Brazil (Galindo-Leal and Câmara 2003) originally ranged between latitudes 6° S and 30° S and covered approximately 1.1 million km^2. It is characterized by strong environmental gradients, seasonality (Ribeiro et al. 2009), and complex topography. Their latitudinal gradient reveals a biome with a vegetational complex, described below, and climate heterogeneity (Fiaschi and Pirani 2009; Oliveira-Filho et al. 2015). Some researchers have demonstrated the role of climate on floristic differentiation, along altitudinal gradients and between geographic regions in the biome (Oliveira-Filho and Fontes 2000; Joly et al. 2012; Eisenlohr et al. 2013). Temperature and precipitation, for example, varies in a north–south gradient (Oliveira-Filho and Fontes 2000), where the decreasing temperatures toward higher latitudes and altitudes along the coast (Oliveira-Filho et al. 2015) which influence several species. In addition to historical factors, these climatic variations contribute to the high turnover of species in the biome (Condit et al. 2002; Silva et al. 2014; Nogueira et al. 2019).

This complex biome is composed of three forest types influenced by rainfall regime: the Dense Rainforest, the Mixed Rainforest, and the Seasonal Forest (Oliveira-Filho and Fontes 2000). The Dense Rain forests (or ombrophilous forest) are located on the Atlantic coast and are distributed in lowlands (generally the climate is hot and wet) and slopes (climate cold and wetter) from northeastern to southern Brazil (Oliveira-Filho and Fontes 2000), where rainfall is increased by oceanic winds and mountain ranges, especially in the south (Cancello et al. 2014). Associated with the vegetation in lowlands it presents the "*restinga*," characterized by drier climate and sand soil (Marques et al. 2011). Mixed Rain forests, also known as Araucaria forests because of the presence of the conifer *Araucaria angustifolia* (Bertol.) Kuntze, constitute the main forest type on the highland plateau in southern Brazil. The mixed rain forest is characterized by tropical and sub-tropical humid climates without pronounced dry periods. Seasonal forests are characterized by two distinct seasons with marked seasonality (summer with intense rainfalls and winter with low temperatures and scarce precipitation) and extends across the plateau (usually 600 m elevation) in the center and southeastern interior of Brazil (Oliveira-Filho and Fontes 2000) and are influenced by Cerrado biome.

Several mountain ranges and cliffs compose the Atlantic Forest landscape along the latitudinal gradient. Originally, more than 80% of their area occurred at elevations from 200 to 1200 m (Tabarelli et al. 2010). In some high altitudes can be observed an increase in precipitation and humidity (Camara 2003). For example, in southeastern Brazil, the remnants located in "Serra do Mar" and "Serra da Mantiqueira" stand out where the occurrence of orographic rains provides greater humidity in these forests (Por 1992). Due to variations in altitude, we found in Atlantic Forest differences in the phytophysiognomy along its extension that, in addition to lowland forests, montane, and submontane forests. Differences in species composition in relation to the latitudinal gradient in the Atlantic Forest, which are influenced by climate and historical factors, have been the subject of several studies (e.g., Almeida-Neto et al. 2006; Martins et al. 2015; Nogueira et al. 2019; Shimabukuro and Trivinho-Strixino 2021). In this context, this chapter is intended to provide insights into the scorpion assemblages in a latitudinal gradient at Brazilian Atlantic Forest through application of Rapoport effect and Bergmann rule.

7.5 Case Study: Scorpion Assemblage Along Latitudinal Gradient in Brazilian Atlantic Forest

In order to investigate the applicability of Rapoport and Bergman's rules on scorpion assemblages along the latitudinal gradient in the Brazilian Atlantic Forest, we first georeferenced scorpion occurrence data were primarily extracted from public repositories, notably the Global Biodiversity Information Facility (GBIF 2021) and the SpeciesLink platform (CRIA 2021). All georeferenced data available for the order Scorpiones until 18 September 2021 were downloaded from both repositories.

Additional information on scorpion occurrence in Atlantic Forest was also added from scientific literature (Galiano and Maury 1979; Lourenço 2002, 2005; Yamaguti and Pinto-da-Rocha 2003; Lourenço and Giupponi 2004; Dias et al. 2006; Santos et al. 2006; Giupponi et al. 2009; Quintela et al. 2014; Lira et al. 2021a). Combined datasets resulted in a raw amount of 66,976 occurrences, of which, 2429 occurrences were used in downstream analyses as a result of the data cleaning process. This consisted in the exclusion of taxa that were not identified to Linnean species names, as well as those occurrences that fell outside the boundaries of a spatial grid of 0.5° × 0.5° pixel resolution, intersecting the spatial extent of the Brazilian Atlantic forest (Fig. 7.1). The spatial grid was drawn on QGis 3.18 (QGIS Development Team 2021) using a shapefile of the Brazilian Atlantic Forest provided by the MapBiomas project (MaPBiomas Project 2021) as a reference for the delineation of its spatial extent. Spatial operations (i.e., overlapping the spatial grid over the Atlantic Forest boundaries and scorpion occurrences) were performed in the R environment (R Core Team 2021) using the 'sf' (Pebesma 2018) and 'dplyr' (Wickham et al. 2021) packages and assuming the SIRGAS 2000 (EPSG: 4674) map

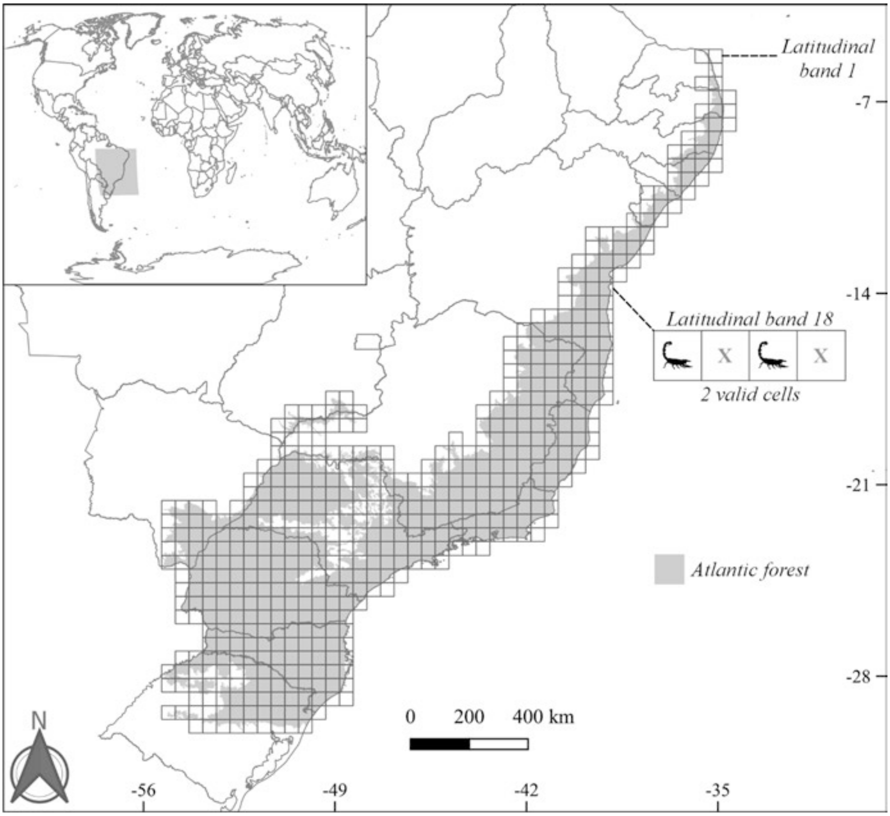

Fig. 7.1 Scheme of grid division applied in each scorpion species from Brazilian Atlantic Forest

projection. Species with dubious distributions within the Atlantic Forest were also excluded from the dataset based on our expertise about their ecological requirements and scientific information from the literature when available. Based on such criteria, the following species were removed from the dataset: *Bothriurus rochai* Mello-Leitão 1932, *Jaguajir rochae* (Borelli 1910), *Physoctonus debilis* (C. L. Koch 1840) – both typical species of Caatinga forests (Foerster et al. 2019; Lira et al. 2020); *Tityus obscurus* (Gervais 1843), *T. metuendus* Pocock 1897, *T. raquelae* Lourenço 1988 – Amazonian species (Martins et al. 2021); *Ananteris franckei* Lourenço 1982 and *B. araguayae* Vellard 1934 commonly found in montane forests of northeastern Brazil and Cerrado formations, respectively (Lourenço 2002; Foerster et al. 2019). The list of scorpion species of the Brazilian Atlantic Forest recovered in this study is presented in Appendix 7.1.

After this, the geographic range of each species was initially calculated as the latitudinal distance (in kilometers) between the northernmost and the southernmost location that each species was found (Lear et al. 2017). To this end, species with a single occurrence (singletons) were excluded from the dataset (Appendix 7.1). As described in the previous section, an average geographic species range per latitudinal band was obtained from the computation of a mean value of the geographic ranges of the species present in each latitudinal band. The average geographic species range per latitudinal band was then adjusted by the number of valid grid cells in each band (thereafter referred to as “latitudinal species range”). Species richness per latitudinal band was obtained by summing the number of species present in each latitudinal band (i.e., latitudinal species richness). The latitudinal species range, latitudinal species richness, and the absolute latitude of each latitudinal band were correlated in a pairwise scheme through the Spearman’s rank correlation coefficient with Holm’s adjustment of *p*-values. Statistical analyses (i.e., mean arithmetic adjustments and Spearman’s rank correlations) were performed in R using the ‘correlation’, dplyr, and ‘base’ (R Core Team 2021) packages.

A second dataset containing the carapace length of scorpion species listed in Appendix 7.1 was assembled based on direct specimen measurements and additional data from the literature. Previous studies have demonstrated that carapace length is a reliable proxy of body size in scorpions (e.g., Outeda-Jorge et al. 2009; Lira et al. 2021b). Moreover, the use of a single corporal structure (carapace) to represent body size in these animals is expected to minimize the error inherent to the measurement process, especially if compared to a more complex metric of body size, such as the total length. This is because total length can be obtained by both measuring the specimen at once – usually a straight line ranging from the anterior tip of the carapace to the distal tip of the telson – or by summing the length of its body parts separately. For the information extracted from the literature, the most recent publications were prioritized (Appendix 7.1) and an average carapace length was calculated when this metric was available for more than one specimen and sex, allowing the incorporation of a potential sexual dimorphism in this character.

To test the presence of latitudinal trends in body size of scorpion species distributed along the Atlantic Forest, the grid cells containing scorpion occurrences were initially identified. After that, those grid cells were consistently grouped according to the latitudinal position of their centroids, resulting in latitudinal bands across the Atlantic Forest (Fig. 7.1). All the species found in each of the latitudinal bands were translated to its measurements of body size, allowing the calculation of an average body size per latitudinal band (c.f. de Menezes et al. 2018). To account for the inevitable difference in the number of grid cells per latitudinal band (Fig. 7.1), the average body size calculated for each latitudinal band was adjusted by the number of valid grid cells (i.e., cells with scorpion occurrence) through the mean arithmetic approach:

$$\frac{\sum_{i=1}^{n} VCi \times BSi}{\sum_{i=1}^{n} VCi} = wBS$$

where, *w*BS corresponds to the mean body size per latitudinal band weighted by the number of valid grid cells in that band (thereafter referred as to “latitudinal body size”); VC*i* is the number of valid grid cells in the latitudinal band *i*; and BS*i* is the mean body size calculated for the latitudinal band *i*. The latitudinal body size was then correlated to the absolute latitude of each latitudinal band through the Spearman’s rank correlation coefficient (ρ), thus, avoiding any assumptions about the shape of the relationship between these two variables or the potential noise due to the presence of skewed data (McDonald 2014; de Menezes et al. 2018). *P*-values for Spearman’s correlation were adjusted using Holm’s correction as implemented in the ‘correlation’ R package (Makowski et al. 2020).

We found a total of 28 species belonging to seven genera and two families (Bothriuridae and Buthidae) for the Atlantic Forest (Appendix 7.1, Fig. 7.2). Buthid scorpions are represented by four genera and 21 species, while bothriurids were represented by eight species grouped into three genera. Buthidae species show a widespread distribution in the Brazilian Atlantic Forest, species from *Tityus* C. L. Koch 1836 genera were found in practically all latitudinal gradient (Fig. 7.3). In contrast, other buthid genera such as *Zabius* Thorell 1893 showed a more limited distribution being found on the southern side of the latitudinal gradient, respectively (Fig. 7.3). Bothriurids scorpions were represented by genera *Bothriurus* Peters 1861, *Thestylus* Simon 1880, and *Urophonius* Pocock 1893, with *Urophonius* represented by one species and *Bothriurus* being more specious with four species. Scorpions from this family are also found throughout the latitudinal gradient (Fig. 7.3).

Species with the highest number of occurrences were also the widest distributed ones in terms of number of occupied grid cells (Fig. 7.4). In terms of genera, *Tityus*, *Bothriurus*, and *Ananteris* Thorell 1891 were the most abundant in number of occurrences, and together with genus *Isometrus* Ehrenberg 1828 presented the wider latitudinal ranges within the Atlantic Forest (Fig. 7.3). The latitudinal range of the scorpion species used to test the Rapoport’s effect in Atlantic Forest ranged from 85.25 to 2625.46 km (Fig. 7.5). Although the largest latitudinal ranges were reported to the genera *Isometrus*, *Tityus*, *Bothriurus*, and *Ananteris* (Fig. 7.3), there was a considerable variation in the latitudinal range sizes among species within these

Fig. 7.2 Representatives of scorpion species found in Brazilian Atlantic Forest. (**a**) *Bothriurus asper* Pocock 1893, (**b**) *Thestylus aurantiurus* Yamaguti and Pinto-da-Rocha 2003, (**c**) *Ananteris mauryi* Lourenço 1982, (**d**) *Tityus adrianoi* Lourenço 2003, (**e**) *Tityus bahiensis* (Perty 1833), (**f**) *Tityus brazilae* Lourenço and Eickstedt 1984, (**g**) *Tityus neglectus* Mello-Leitão 1932 and (**h**) *Tityus pusillus* Pocock 1893. (Photos A, B and G by Dr. Leonardo Carvalho, C, F and H by Dr. Adriano DeSouza and D and E by Dr. Pedro Martins)

genera (Fig. 7.5), except for *Isometrus*, represented here by a single species *I. maculatus* (DeGeer 1778). Latitudinal species range increased toward the equator, as evidenced by the positive correlation ($\rho = 0.390$, $p = 0.016$) found between absolute latitude and latitudinal species range. Yet, there was also a strong positive correlation between the latitudinal species range and the latitudinal species richness ($\rho = 0.787$, $p < 0.001$). To a lesser extent, the latitudinal species richness was positively correlated to the absolute latitude ($\rho = 0.339$, $p = 0.023$), increasing toward the equator. At family level, buthid scorpions from the Atlantic Forest were the most variable in terms of body size (carapace length) than bothriurid species. Most of 50% of Atlantic Forest scorpion assemblage body size was composed by large-mid species (Fig. 7.6). *Tityus* species being overall larger than the species from the other genera in this environment (Fig. 7.6). Nevertheless, body size in Atlantic Forest scorpions was notably conserved among congeneric species (Fig. 7.6) and no latitudinal trends in this trait could be detected, as indicated by the Spearman rank correlation coefficient ($\rho = 0.227$, $p = 0.130$).

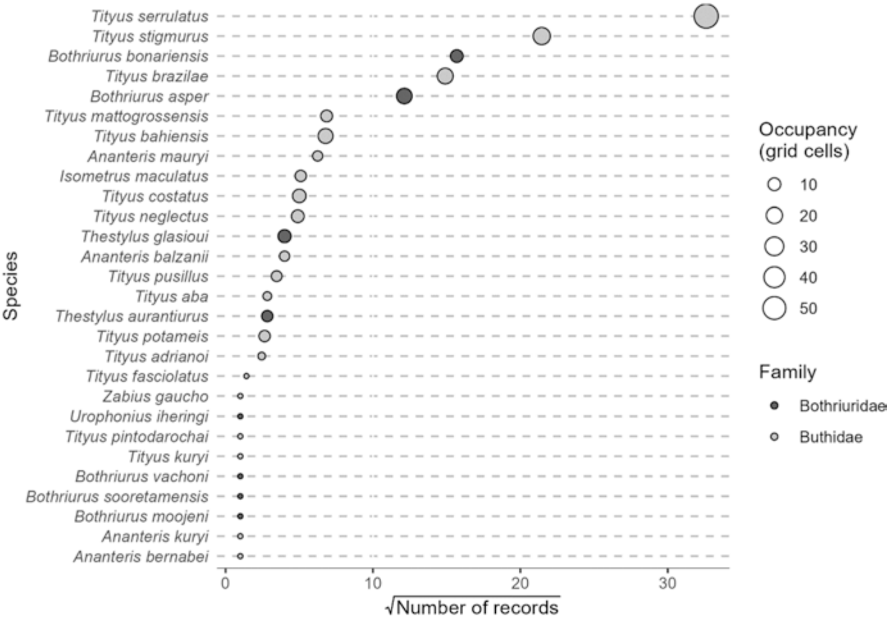

Fig. 7.3 Occupancy in grid cell in Brazilian Atlantic Forest by scorpion species

Our study was a first attempt to help in understanding the patterns behind scorpion diversity in an Atlantic Forest. The scorpions recorded from this biome belong to either Buthidae (70%) or Bothriuridae (30%), the two most diverse scorpion families in the Brazilian fauna (Lourenço 2002). Considering the higher degradation level of this biome (e.g., Ribeiro et al. 2009; Haddad et al. 2015), the Brazilian Atlantic Forest exhibited a greater number of species, corresponding to 20% of the Brazilian scorpion fauna. Most of this fauna is composed of forest-specialist scorpions, such as *T. brazilae*, *T. pusillus*, and *A. mauryi* (Porto et al. 2018; Lira et al. 2020). However, species considered typical of other biomes can occur in ecotonal regions with characteristics of the Atlantic Forest, such as the species *T. fasciolatus*, considered typical of the Cerrado (Savana-like vegetation: Lourenço 2002). We also found records of *I. maculatus*, an Indo-Malayan species, possibly introduced in several coastal regions of the world through ships (Kovařík 2003). In addition, Atlantic Forest scorpion fauna is composed also by species adapted to disturbed environments, such *T. serrulatus* and *T. stigmurus*, considered as synanthropic because of their intimate relationship with urban areas (Amado et al. 2021).

We found that scorpion diversity can be explained by the latitudinal gradient along the Brazilian Atlantic Forest with species richness increasing toward the equator. Although there have been no previous studies on the influence of latitudinal gradient on Atlantic Forest scorpion diversity, studies with other organisms, such as termites (Cancello et al. 2014) and epiphytic lichens (Menezes et al. 2018), indicate effects of latitudinal gradient on species richness similar to those found in this study. In contrast, studies with other animals such as harvestmen (Nogueira et al. 2019), bats (Stevens 2013), and leaf litter ants (Silva and Brandão 2014) described an

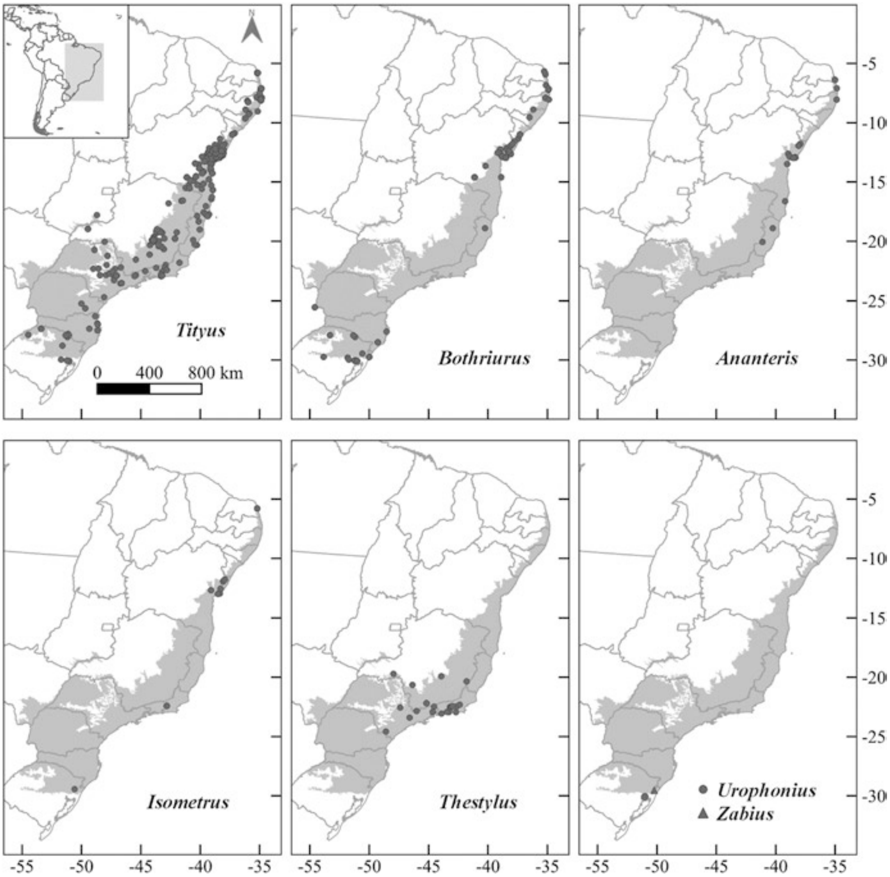

Fig. 7.4 Distribution records of scorpion genus along Brazilian Atlantic Forest

opposite pattern with species richness increasing toward the southern portion of Atlantic Forest. In latitudinal gradients we found a clinal variation in climatic factors, mainly temperature and precipitation, that are the major predictors of floristic structure (Prata et al. 2018). Habitat complexity generated by vegetation structure in a determined area, influencing the habitat structure and providing keystone structure (Tews et al. 2004). Therefore, habitats with greater microhabitat availability are associated with a high species richness once scorpion assemblages are composed of niche specialists, due to aggressive behavior between scorpion heterospecifics (Polis 1990; Lira et al. 2013, 2018). Alternatively, another possible and non-exclusive explanation for the increase in the scorpion species richness toward the equator is related to the species range size. In contrast to the proposed by Rapoport rule, our results pointed up an increase in range size toward the equator. Therefore, the higher species richness found on the north portion of Atlantic Forest may be an artificial artifact resulting from the overlapping distribution of species with a large range size.

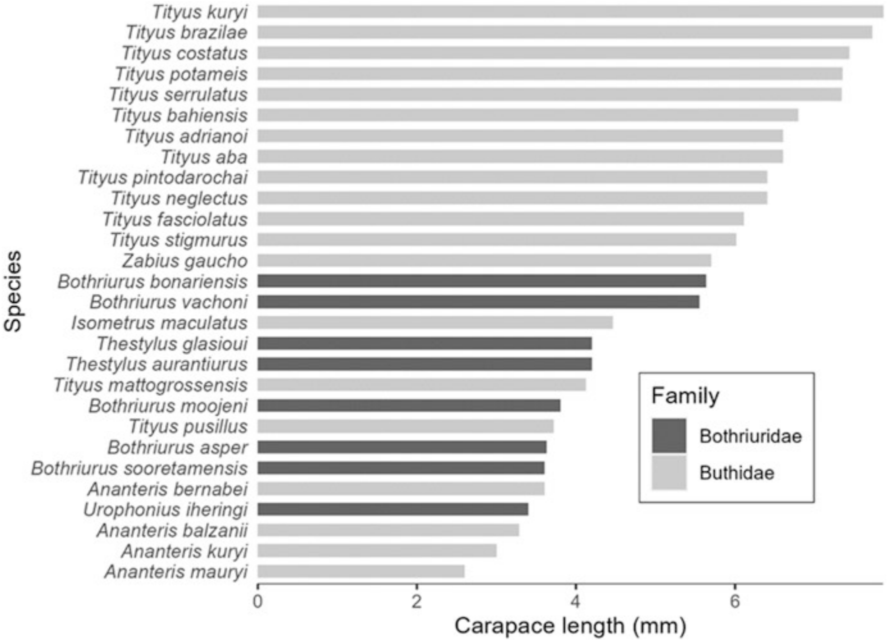

Fig. 7.5 Body size (in mm) of scorpion species from Brazilian Atlantic Forest

Scorpion species range in Atlantic Forest may be related to two main factors: (1) biological traits of these arachnids and (2) historical biome formation. In the first, scorpions are considered invertebrates with poor dispersal capacity (Polis et al. 1985) and dependent on forested habitats (Dionisio et al. 2018; Lira et al. 2019b). For example, Lira et al. (2019b) investigated the scorpion fauna in Atlantic Forest remnants and in their neighboring cropland. These authors found that scorpion species are unable to colonize the croplands being restricted to forested remnants. Although some scorpions may be found in disturbed environments such as urban areas (Brazil et al. 2009; Bertani et al. 2018), these species are exceptions and the majority of Atlantic Forest scorpions are forest-dwelling species (Lira et al. 2021a). In the second main factor, the historical process of Atlantic Forest formation was marked by successive forest reduction during climatic fluctuations and global cooling since the Pliocene or late Miocene (Holbourn et al. 2014; Ravelo et al. 2004). According to Carnaval et al. (2014), the northern portion of Atlantic Forest exhibited a more stable climate. In this way, larger mesic refugia were formed when compared to southern and southeastern portions. This complex process led to the proposal to delimit 12 areas of endemism for the biome, corresponding to two areas in the northern region and ten in the southern region (DaSilva et al. 2015). Therefore, these two main factors may have acted synergistically for the range size pattern found for Atlantic Forest scorpions. Contrary to our expectations, we found any

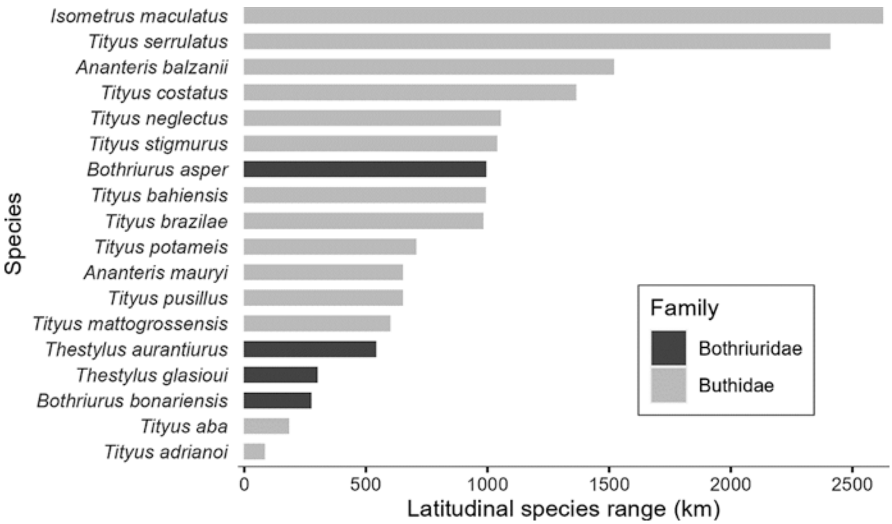

Fig. 7.6 Latitudinal range of each scorpion species from Brazilian Atlantic Forest

effect of latitude on scorpion body size. In addition, the body size of these arachnids seems to be conserved within genus and also within the subgenera (*Tityus* and *Archeotityus*) that subdivide the genus *Tityus* (Lourenço 2006) found in Atlantic Forest. Therefore, in Atlantic Forest, scorpions may be a result of a synergistic interaction encompassing both ancestry and environmental constraints, which, in many cases, may lead to the emergence of ecomorphotypes (Polis 1990; Prendini 2001; Koch et al. 2017).

In summary, this chapter provides a first insight of diversity patterns from Atlantic Forest scorpions. Overall, we found the three main results: (1) the species richness of these arachnids increases toward the equator as postulated in latitudinal diversity gradient hypothesis; (2) species range size follows an inverse that was proposed in the Rapoport rule with range size increasing toward equator; and (3) no latitudinal effects was detected on scorpion body size. These findings may reflect that scorpion natural history traits and historical processes of Atlantic Forest exerts a key role on diversity patterns of these arachnids along a latitudinal gradient in Brazilian Atlantic Forest. However, these findings may be interpreted with some caution as new collection expeditions and taxonomic revisions in progress may alter knowledge about the diversity of Atlantic Forest scorpions.

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Appendix 7.1

Scorpion species listed to the Brazilian Atlantic Forest. The occupancy refers to the number of 0.5° × 0.5° grid cells in which the species were present. "Rapoport" column states if the species were used to test the Rapoport's Effect in the Brazilian Atlantic Forest; all species listed below were used to test the adequacy of Bergmann's rule to the scorpion assemblages in the Brazilian Atlantic Forest. Bergmann's reference states the source of the carapace length was obtained.

Species	Records	Occupancy	Rapoport	Bergmann's reference
Bothriuridae				
Bothriurus asper Pocock, 1893	147	18	yes	Lira et al. (2021a, b)
Bothriurus bonariensis (C.L. Koch 1842)	246	10	yes	Olivero et al. (2012)
Bothriurus moojeni Mello-Leitao, 1945	1	1	No	San Martin (1967)
Bothriurus sooretamensis San Martín, 1966	1	1	No	San Martin (1966)
Bothriurus vachoni San Martín, 1968	1	1	No	San Martin (1968)
Thestylus aurantiurus Yamaguti & Pinto-da-Rocha, 2003	8	7	yes	Yamaguti and Pinto-da-Rocha (2003)
Thestylus glasioui Bertkau, 1880	16	11	yes	Yamaguti and Pinto-da-Rocha (2003)
Urophonius iheringi Pocock, 1893	1	1	No	Pocock (1893)
Buthidae				
Ananteris balzanii Thorell, 1891	16	5	yes	Outeda-Jorge et al. (2009)
Ananteris bernabei Giupponi, Vasconcelos & Lourenço, 2009	1	1	No	Giupponi et al. (2009)
Ananteris kuryi Giupponi, Vasconcelos & Lourenço, 2009	1	1	No	Giupponi et al. (2009)
Ananteris mauryi Lourenço, 1982	39	5	Yes	Lira et al. (2021a, b)
Isometrus maculatus (DeGeer, 1778)	26	7	Yes	Sulakhe et al. (2020)
Tityus aba Candido, Lucas, de Souza, Diaz & Lira-da-Silva, 2005	8	3	Yes	Candido et al. (2005)
Tityus adrianoi Lourenço, 2003	6	2	yes	Lourenço (2003)
Tityus bahiensis (Perty, 1833)	46	16	yes	Outeda-Jorge et al. (2009)
Tityus brazilae Lourenço & Eickstedt, 1984	222	19	yes	Lira et al. (2021a, b)
Tityus costatus (Karsch, 1879)	25	12	yes	Outeda-Jorge et al. (2009)
Tityus fasciolatus Pessôa, 1935	2	1	no	Lourenço (1980)
Tityus kuryi Lourenço, 1997	1	1	no	Outeda-Jorge et al. (2009)

(continued)

Species	Records	Occupancy	Rapoport	Bergmann’s reference
Tityus mattogrossensis Borelli, 1901	47	8	yes	Outeda-Jorge et al. (2009)
Tityus neglectus Mello-Leitao, 1932	24	10	yes	Lira et al. (2021a, b)
Tityus pintodarochai Lourenço, 2005	1	1	no	Lourenço (2005)
Tityus potameis Lourenço & Leao Giupponi, 2004	7	7	yes	Lourenço and Giupponi (2004)
Tityus pusillus Pocock, 1893	12	6	yes	Lira et al. (2021a, b)
Tityus serrulatus Lutz & Mello, 1922	1063	58	yes	Outeda-Jorge et al. (2009)
Tityus stigmurus (Thorell, 1876)	460	24	yes	Lira et al. (2021a, b)
Zabius gaucho Acosta, Candido, Buckup & Brescovit, 2008	1	1	no	Acosta et al. (2008)

References

Acosta LE, Candido DM, Buckup EH, Brescovit AD (2008) Description of *Zabius gaucho* (Scorpiones, Buthidae), a new species from southern Brazil, with an update about the generic diagnosis. J Arachnol 36:491–501

Albuquerque FS, Castro-Díez P, Rueda M, Hawkins BA, Rodríguez MÁ (2011) Relationship of climate, residence time and biogeographical origin with the range sizes and species richness patterns of exotic plants in Great Britain. Plant Ecol 212:1901

Allen AP, Gillooly JF (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecol Lett 9:947–954

Almeida-Neto M, Machado G, Pinto-da-Rocha R, Giaretta AA (2006) Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain Rapoport’s rule? J Biogeogr 33:361–375

Álvarez D, Gómez D, Martínez J, Mendoza H, Ruiz S (2013) Microhabitat use by scorpions in a tropical dry forest relict of the Colombian Caribbean. Revista Colombiana de Entomologia 39:301–304

Amado TF, Moura TA, Riul P, Lira AFA, Badillo-Montaño R, Martinez PA (2021) Vulnerable áreas to acidentes with scorpions in Brazil. Tropical Med Int Health 26:591–601

Aragon P, Fitze PS (2014) Geographical and temporal body size variation in a reptile: roles of sex, ecology, phylogeny and ecology structured in phylogeny. PLoS One 9:e104026

Bergmann C (1847) Ueber die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. Gottinger Studien 1:595–708

Bertani R, Bonini RK, Toda MM, Isa LS, Figueiredo JVA, Santos MR, Ferraz SC (2018) Alien scorpions in the municipality of São Paulo, Brazil: evidence of successful establishment of *Tityus stigmurus* (Thorell, 1876) and first records of *Broteochactas parvulus* Pocock, 1897, and *Jaguajir rochae* (Borelli, 1910). Bioinvasion Rec 7:89–94

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann’s rule. Divers Distrib 5:165–174

Blanckenhorn WU, Demont M (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum. Integr Comp Biol 44:413–424

Böhm M, Kemp R, Williams R, Davidson AD, Garcia A, McMillan KM, Bramhall HR, Collen B (2017) Rapoport’s rule and determinants of species range in snakes. Divers Distrib 23:1472–1481

Brazil TK, Porto TJ (2011) Os escorpiões. Edufba, Salvador

Brazil TK, Lira-da-Silva RM, Porto TJ, Amorim AMD, Silva TFD (2009) Escorpiões de importância médica do estado da Bahia, Brasil. Gazeta Médica da Bahia 79:38–72

Brito G, Borges A (2015) A checklist of the scorpions of Ecuador (Arachnida: Scorpiones), with notes on the distribution and medical significance of some species. J Venom Anim Toxins Incl Trop Dis 21:23–40

Brocklehurst N, Day MO, Rubidge BS, Fröbisch J (2017) Olson's extinction and the latitudinal biodiversity gradient of tetrapods in the Permian. Proc R Soc B Biol Sci 284:20170231

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Brown JH (2014) Why are there so many species in the tropics? J Biogeogr 41:8–22

Câmara IG (2003) Brief history of conservation in the Atlantic Forest. In: Galindo–Leal C, Câmara IG (eds) The Atlantic forest of South America: biodiversity status, threats, and outlook. CABS and Island Press, Washington, pp 31–42

Cancello EM, Silva RR, Vasconcellos A, Reis YT, Oliveira LM (2014) Latitudinal variation in termite species richness and abundance along the Brazilian Atlantic Forest hotspot. Biotropica 46:441–450

Candido DM, Lucas S, Souza CAR, Diaz D, Lira-da-Silva RM (2005) Uma nova espécie de *Tityus* C. L. Koch, 1836 (Scorpiones, Buthidae) do estado da Bahia. Brasil Biota Neotropica 5:193–200

Cardillo M, Orme CDL, Owens IPF (2005) Testing for latitudinal bias in diversification rates: an example using new world birds. Ecology 86:2278–2287

Carnaval AC, Waltari E, Rodrigues MT, Rosauer D, VanDerWal J, Damasceno R, Prates I, Strangas M, Spanos Z, Rivera D, Pie MR, Firkwski CR, Bornschein MR, Ribeiro LF, Moritz C (2014) Prediction of phylogeographic endesmism in na environmentally complex biome. Proc R Soc B Biol Sci 281:20141461

Carvalho CS, Martello F, Galetti M, Pinto F, Francisco MR, Silveira LF, Galetti PM Jr (2021) Environmental heterogeneity and sampling relevance areas in an Atlantic Forest endemism region. Perspect Ecol Conserv 19:311–318

Chown SL, Gaston KJ (2010) Body size variation in insects: a macroecological perspective. Biol Rev 85:139–169

Coddington JA, Colwell RK (2001) Arachnida. In: Levin SC (ed) Encyclopedia of biodiversity. Academic Press, New York, pp 199–218

Condit R, Pitman N, Leigh EG Jr (2002) Beta-diversity in tropical forest trees. Science 295:666–669

Conservation International (2009) Biodiversity hotspots-resources-maps and GIS data. https://www.conservation.org/priorities/biodiversity-hotspots. Accessed 27 Sept 2021.

CRIA (2021) Species link (http://splink.cria.org.br/project?criaLANG=pt). Accessed on 18 Sept 2021

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan J-F, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E, Turner JRG (2004) Predictions and tests of climate-based hypothesis of broad-scale variation in taxonomic richness. Ecol Lett 7:1121–1134

Darwin CR (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. Murray, London

DaSilva MB, Pinto-Da-Rocha R, DeSouza AM (2015) A protocol for the delimitation of areas of endemism and the historical regionalization of the Brazilian Atlantic rain forest using harvestmen distribution data. Cladistics 31:692–705

Dias SC, Candido DM, Brescovit AD (2006) Scorpions from Mata do Buraquinho, João Pessoa, Paraíba, Brazil, with ecological notes on a population of *Ananteris mauryi* Lourenço (Scorpiones, Buthidae). Revista Brasileira de Zoologia 23:707–710

Dionisio-da-Silva W, Lira AFA, Albuquerque CMR (2018) Distinct edge effects and reproductive periods of sympatric litter-dwelling scorpions (Arachnida: Scorpiones) in a Brazilian Atlantic Forest. Zoology 129:17–24

Dunlop JA (2010) Geological history and phylogeny of Chelicerata. Arthropod Struct Dev 39:124–142

Eisenlohr PV, Alves LF, Bernacci LC, Padgurschi MCG, Torres RB, Prata EMB, Santos FAM, Assis MA, Ramos E, Rochelle ALC, Martins FR, Campos MCR, Pedroni F, Sanchez M, Pereira LS, Vieira SA, Gomes JAMA, Tamashiro JY, Scaranello MAS, Caron CJ, Joly CA (2013) Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. Biodiver Conserv 22:2767–2783

Entling W, Schmidt-Entling MH, Bacher S, Brandl R, Nentwig W (2010) Body size-climate relationships of European spiders. J Biogeogr 37:477–485

Fiaschi P, Pirani JR (2009) Review of plant biogeographic studies in Brazil. J Syst Evol 47:477–496

Fine PVA (2015) Ecological and evolutionary drivers of geographic variation in species diversity. Annu Rev Ecol Evol Syst 46:369–392

Foerster SÍA, DeSouza AM, Lira AFA (2019) Macroecological approach for scorpions (Arachnida, Scorpiones): β-diversity in Brazilian montane forests. Can J Zool 97:914–921

Foerster SÍA, Lira AFA, Almeida CG (2020) Vegetation structure as the main source of variability in scorpion assemblages at small spatial scales and further considerations for the conservation of Caatinga landscapes. Neotrop Biol Conserv 15:533–550

Foord SH, Gelebe V, Prendini L (2015) Effects of aspect and altitude on scorpion diversity along an environmental gradient in the Soutpansberg, South Africa. J Arid Environ 113:114–120

Fortes RR, Absalão RS (2004) The applicability of Rapoport's rule to the marine molluscs of the Americas. J Biogeogr 31:1909–1916

Galiano ME, Maury EA (1979) Lista de los ejemplares tipicos de Arachnida (Araneae, Opiliones, Scorpiones y Solifugae) depositados en el Museo Argentino de Ciencias Naturales Bernadino Rivadavia. Revista Del Museo Argentino de Ciencias Naturales Bernadino Rivadavia 5:301–334

Galindo-Leal C, Câmara IG (2003) The Atlantic forest of South America: biodiversity status, threats, and outlook. CABS and Island Press, Washington

Garraffoni AR, Moura FR, Lourenço AP (2017) Areas of endemism in the Atlantic Forest: quantitative biogeography insights from orchid bees (Apidae: Euglossini). Apidologie 48:513–522

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220–227

Gaston KJ (2003) The how and why of biodiversity. Nature 421:900–901

GBIF.org (2021) GBIF home page. Disponible at: https://www.gbif.org. 18 Sept 2021

Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. J Insect Conserv 17:831–850

Giupponi APL, Vasconcelos EG, Lourenço WR (2009) The genus *Ananteris* Thorell, 1891 (Scorpiones, Buthidae) in southeast Brazil, with the description of three new species. ZooKeys 13:29–41

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Cook WM (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1(2):e1500052

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. Am Nat 163:192–211

Holbourn A, Kuhnt W, Lyle M, Schneider L, Romero O, Andersen N (2014) Middle Miocene climate cooling linked to intensification of eastern equatorial Pacific upwelling. Geology 42:19–22

Jablonski D, Roy K (2003) Geographical range and speciation in fossil and living molluscs. Proc R Soc B Biol Sci 270:401–406

Jeram AJ (1998) Phylogeny, classification and evolution of Silurian and Devonian scorpions. In: Brownell P, Polis GA (eds) Scorpion biology and research. Oxford University Press, Oxford

Joly CA, Assis MA, Bernacci LC, Tamashiro JY, Campos MCR, Gomes JAMA, Lacerda MS, Santos FAM, Pedroni F, Pereira LS, Padgurschi MCG, Prata EMB, Ramos E, Torres RB, Rochelle A, Martins FR, Alves LF, Vieira SA, Martinelli LA, Camargo PB, Aidar MPM, Eisenlohr PV, Simões E, Villani JP, Belinello R (2012) Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. Biota Neotrop 12:123–145

Joly CA, Metzger JP, Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytol 204:459–473

Kaspari M, Ward PS, Yuan M (2004) Energy gradients and the geographic distribution of local ant diversity. Oecologia 140:407–413

Kinlock NL, Prowant L, Herstoff EM, Foley CM, Akin-Fajiye M, Bender N, Umarani M, Ryu HY, Sen B, Gurevitch J (2018) Explaining global variation in the latitudinal diversity gradient: meta-analysis confirms known patterns and uncovers new ones. Glob Ecol Biogeogr 27:125–141

Kjelleswig-Waering EN (1986) A restudy of the fossil Scorpionida of the world. Paleontol Res 55:1–287

Koch NM, Ceccarelli FS, Ojanguren-Affilastro AA, Ramirez MJ (2017) Discrete and morphometric traits reveal contrasting patterns and processes in the macroevolutionary history of a clade of scorpions. J Evol Biol 30:814–825

Kovarik F (2003) A review of the genus *Isometrus* Ehrenberg, 1828 (Scorpiones: Buthidae) with description of four new species from Asia and Australia. Euscorpius 10:1–19

Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. Proc Natl Acad Sci U S A 104:5925–5930

LaManna JA, Belote RT, Burkle LA, Catano CP, Myers JA (2017) Negative density dependence mediates biodiversity productivity relationship across scales. Nat Ecol Evol 1:1107–1115

Latham RE, Ricklefs RE (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. Oikos 67:325–333

Laurance WF (2009) Conserving the hottest of the hotspots. Biol Conserv 142:1137

Lear G, Lau K, Perchec A-M, Buckley HL, Case BS, Neale M, Fierer N, Leff JW, Handley KM, Lewis G (2017) Following Rapoport's rule: the geographic range and genome size of bacterial taxa decline at warmer latitudes. Environ Microbiol 19:3152–3162

Lee TM, Jetz W (2010) Unravelling the structure of species extinction risk for predictive conservation science. Proc R Soc B: Biol Sci 278:1329–1338

Lira AFA, DeSouza AM (2014) Microhabitat use by scorpion species (Arachnida: Scorpiones) in the montane Atlantic rainforest, Brazil. Revista Ibérica de Aracnologia 24:107–108

Lira AFA, DeSouza AM, Silva Filho AAC, Albuquerque CMR (2013) Spatio-temporal microhabitat use by two co-occurring Species of scorpions in Atlantic rainforest in Brazil. Zoology 116:182–185

Lira AFA, Araújo VLN, DeSouza AM, Rego FNAA, Albuquerque CMR (2016) The effect of habitat fragmentation on the scorpion assemblage of a Brazilian Atlantic Forest. J Insect Conserv 20:457–466

Lira AFA, DeSouza AM, Albuquerque CMR (2018) Environmental variation and seasonal changes as determinants of the spatial distribution of scorpions (Arachnida: Scorpiones) in Neotropical forests. Can J Zool 96:963–972

Lira AFA, Salomão RP, Albuquerque CMR (2019a) Pattern of scorpion diversity across a bioclimatic dry-wet gradient in Neotropical forests. Acta Oecol 96:10–17

Lira AFA, Pordeus LM, Salomão RP, Badillo-Montaño R, Albuquerque CMR (2019b) Effects of anthropogenic land-use on scorpions (Arachnida: Scorpiones) in Neotropical forests. Int J Trop Insect Sci 39:211–218

Lira AFA, Badillo-Montaño R, Lira-Noriega A, Albuquerque CMR (2020) Potential distribution patterns of scorpion in north-eastern Brazil under scenarios of future climate change. Austral Ecol 45:215–228

Lira AFA, Foerster SÍA, Salomão RP, Porto TJ, Albuquerque CMR, Moura GJB (2021a) Understanding the effects of human disturbance on scorpion diversity in Brazilian tropical forests. J Insect Conserv 25:147–158

Lira AFA, Foerster SÍA, Albuquerque CMR, Moura GJB (2021b) Contrasting patterns at interspecific and intraspecific levels in scorpion body size across a climatic gradient from rainforest to dryland vegetation. Zoology 146:125908

Liu H, Yu R, Huang J, Liu Y, Zang R, Guo Z, Ding Y, Lu X, Li Q, Chen HYH (2020) Latitudinal diversity gradients and Rapoport effects in Chinese endemic woody seed plants. Forests 11:1–9

Lomolino MV, Riddle BR, Whittaker RJ (2016) Biogeography: biological diversity across space and time. Oxford University Press, Oxford

Lourenço WR (1980) Contribution à la connaissance systématique des Scorpions appartenant au "complexe" *Tityus trivittatus* Kraepelin, 1898 (Buthidae). Bulletin Du Muséum National d'Histoire Naturelle Paris 4:793–843

Lourenço WR (1994) Diversity and endemism in tropical versus temperate scorpion communities. Biogeographica 70:155–160

Lourenço WR (2002) Scorpion of Brazil. Les Éditions de I'If, Paris

Lourenço WR (2003) Description of a new species of *Tityus* (Scorpiones, Buthidae) from Serra do Cipo in the State of Minas Gerais, Brazil. Rev Suisse Zool 110:427–435

Lourenço WR (2005) Description of a new species of *Tityus* (Scorpiones, Buthidae) from the Parque Estadual de Vila Velha in the state of Paraná (Brazil). Acta Biológica Paranaense 34:15–26

Lourenço WR (2006) Nouvelle proposition de découpage sous-générique du genre *Tityus* C.L. Koch, 1836 (Scorpiones, Buthidae). Boletín SEA 39:55–67

Lourenço WR (2015) Comments on the Ananterinae Pocock, 1900 (Scorpiones: Buthidae) and description of a new remarkable species of *Ananteris* from Peru. C R Biol 338:134–139

Lourenço WR, Giupponi APL (2004) Description of a new species of "*Tityus*" Koch, 1836 (Scorpiones, Buthidae) from the States of Espirito Santo and Rio de Janeiro in Brazil. Revista Ibérica de Aracnología 10:237–243

Makowski D, Ben-Shachar MSC, Patil I, Ludecke D (2020) Methods and algorithms for correlation analysis in R. J Open Source Softw 5:1–4

MapBiomas Project (2021) Collection of Brazilian land cover & use map series (http://mapbiomas.org/). Accessed on 18 Sept 2021

Marini MA, Garcia FI (2005) Conservação de aves no Brasil. Megadiversidade 1:95–102

Martins FM (2011) Historical biogeography of the Brazilian Atlantic Forest and the Carnaval–Moritz model of Pleistocene refugia: what do phylogeographical studies tell us? Biol J Linn Soc 104:499–509

Martins MA, De Carvalho WD, Dias D, França DDS, De Oliveira MB, Peracchi AL (2015) Bat species richness (Mammalia, Chiroptera) along an elevational gradient in the Atlantic forest of Southeastern Brazil. Acta Chiropterol 17:401–409

Martins JG, Santos GC, Procópio REL, Arantes EC, Bordon KC (2021) Scorpion species of medical importance in the Brazilian Amazon: a review to identify knowledge gaps. J Venom Anim Toxins Incl Trop Dis 27:1–32

Marques MCM, Swaine MD, Liebsch D (2011) Diversity distribution and floristic differentiation of the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest Biodivers Conserv 20:153–168

McDonald JH (2014) Handbook of biological statistics, 3rd edn. Sparky House Publishing, Baltimore

Meiri S (2011) Bergmann's rule – What's in a name? Glob Ecol Biogeogr 20:203–207

Menezes AA, Cáceres MES, Bastos CJP, Lucking R (2018) The latitudinal diversity gradient of epiphytic lichens in the Brazilian Atlantic Forest: does Rapoport's rule apply? Bryologist 121:480–497

Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeek MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol Lett 10:315–331

Mousseau TA (1997) Ectotherms follow the converse to Bergmann's rule. Evolution 51:630–632

Murphy K, Carvalho P, Efremov A, Grimaldo JT, Molina-Navarro E, Davidson TA, Thomaz SM (2020) Latitudinal variation in global range-size of aquatic macrophyte species shows evidence ford a Rapoport effect. Freshw Biol 65:1622–1640

Nime MF, Casanoves F, Mattoni CI (2014) Scorpion diversity in two different habitats in the Arid Chaco, Argentina. J Insect Conserv 18:373–384

Nogueira AA, Bragagnolo C, DaSilva MB, Martins TK, Lorenzo EP, Perbiche-Neves G, Pinto-da-Rocha R (2019) Historical signatures in the alpha and beta diversity patterns of Atlantic Forest harvestman communities (Arachnida: Opiliones). Can J Zool 97:631–643

Núñez-Flores M, Solórzano A, Hernández CE, López-González PJ (2019) A latitudinal diversity gradiente of shallow-water gorgonians (Cnidaria: Octocorallia: Alcyonacea) along the Tropical Eastern Pacific Ocean: testing for underlying mechanisms. Mar Biodivers 49:2787–2800

Oliveira-Filho A, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil, and the influence of climate. Biotropica 32:793–810

Oliveira-Filho AT, Budke JC, Jarenkow JA, Eisenlohr PV, Neves DRM (2015) Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. J Plant Ecol 8:242–260

Olivero PA, Mattoni CI, Peretti AV (2012) Morphometry and geographical variation of *Bothriurus bonariensis* (Scorpiones: Bothriuridae). J Arachnol 40:113–122

Outeda-Jorge S, Mello T, Pinto-da-Rocha R (2009) Litter size, effects of maternal body size, and date of birth in South American scorpions (Arachnida: Scorpiones). Zoologia 26:43–53

Papacostas KJ, Freestone AL (2016) Latitudinal gradient in niche breadth of brachyuran crabs. Glob Ecol Biogeogr 25:207–217

Pebesma E (2018) Simple features for R: standardized support for spatial vector data. R J 10:439–446

Peters RH, Wassenberg K (1983) The effect of body size on animal abundance. Oecologia 60:89–96

Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. J Biogeogr 38:817–827

Pie MR, Divieso R, Caron FS, Siqueira AC, Barneche DR, Luiz OJ (2021) The evolution of latitudinal ranges in reef-associated fishes: heritability limits and inverse Rapoport's rule. J Biogeogr 48:2121–2132

Pintor AFV, Schwarzkpof L, Krockenberger AK (2015) Rapoport's rule: do climatic variability gradients shape range extent? Ecol Monogr 85:643–659

Pocock RI (1893) Notes on the classification of Scorpions, followed by some observations upon synonymy, with descriptions of new genera and species. Ann Mag Nat Hist 12:303–330

Polis GA (1990) The biology of scorpions. Stanford University Press, Stanford

Polis GA (1993) Scorpions as model vehicles to advance theories of population and community ecology: the role of scorpions in desert communities. Mem Queensl Mus 33:401–410

Polis GA, McReynolds CN, Ford RG (1985) Home range geometry of the desert scorpion *Paruroctonus mesaensis*. Oecologia 67:273–277

Pontarp M, Bunnefeld L, Cabral JS, Etienne RS, Fritz SA, Gillespie R, Graham CH, Hagen O, Hartig F, Huang S, Jansson R, Maliet O, Munkemuller T, Pellissier L, Rangel TF, Storch D, Wiegand T, Hurlbert A (2019) The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. Trends Ecol Evol 34:211–223

Por FD (1992) Sooretama - the Atlantic rain forest of Brazil. SPB Academic Publishing, The Hague, p 130

Porto TJ, Carvalho LS, De Souza CAR, Oliveira U, Brescovit AD (2014) Escorpiões da Caatinga: conhecimento atual e desafios. In: Bravo F, Calor AR (eds) Artrópodes do semiárido: biodiversidade e conservação. Printmídia, Feira de Santana

Porto TJ, Pinto-da-Rocha R, Rocha PLB (2018) Regional distribution patterns can predict the local habitat specialization of arachnids in heterogeneous landscapes of the Atlantic Forest. Divers Distrib 24:375–386

Prata BEM, Teixeira AP, Joly CA, Assis MA (2018) The role of climate on floristic composition in a latitudinal gradient in the Brazilian Atlantic Forest. Plant Ecol Evol 151:303–313

Prendini L (2001) Substratum specialization and speciation in southern African scorpion: the effect hypothesis revisited. In: Fet V, Selden PA (eds) Memoriam Gary A. Polis. British Arachnological Society, Burnham Beeches

Prendini L (2005) Scorpion diversity and distribution in southern Africa: pattern and process. In: Hubner BA, Sinclair B, Lampe KH (eds) African biodiversity: molecules, organisms, ecosystems. Springer, New York

Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. Proc R Soc B Biol Sci 267:1947–1952

QGIS Development Team (2021) QGIS geographic information system. Open source geospatial foundation project. http://qgis.osgeo.org

Quintela FM, Iob G, Artioli LGS (2014) Diet of Procyon cancrivorus (Carnivora, Procyonidae) in restinga and estuarine environments of southern Brazil. Iheringia 104:143–149

R Core Team (2021) R: a language and environment for statistical computing. Foundation for Statistical Commuting, Vienna, Austria

Rabosky DL (2009) Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. Ecol Lett 12:735–743

Rapoport A (1975) Toward a redefinition of density. Environ Behav 7:133–158

Ravelo AC, Andreasen DH, Lyle M, Lyle AO, Wara MW (2004) Regional climate shifts caused by gradual global cooling in the Pliocene epoch. Nature 429:263–267

Raz S, Retzkin S, Pavlicek T, Hoffman A, Kimchi H, Zehavi D, Beiles A, Nevo E (2009) Scorpion biodiversity and interslope divergeat evolution canyon, lower Nahal Oren microsite, Mt Carmel, Israel. PLoS One 4:e5214

Rein JO (2021) The scorpion files. Accessed at: https://www.ntnu.no/ub/scorpion-files/

Rezende CL, Scarano FR, Assad ED, Joly CA, Metzger JP, Strassburg BBN, Mittermeier RA (2018) From hotspot to hotspot: an opportunity for the Brazilian Atlantic Forest. Perspect Ecol Conserv 16:208–214

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142:1141–1153

Rohde K (1996) Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. Biodivers Lett 3:10–13

Roll U, Feldman A, Novosolov M, Allison A, Bauer AM, Bernard R, Bohm M, Castro-Herrera F, Chirio L, Collen B, Colli GR, Dabool L, Das I, Doan TM, Grismer LL, Hoogmoed M, Itescu Y, Kraus F, LeBreton M, Lewin A, Martins M, Maza E, Meirte D, Nagy ZT, Nogueira CC, Pauwels OSG, Pincheira-Donoso D, Powney GD, Sindaco R, Tallowin OJS, Torres-Carvajal O, Trape J-F, Vidan E, Uetz P, Wagner P, Wang Y, Orme CDL, Grenyer R, Meiri S (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. Nat Ecol Evol 1:1677–1682

Ruggiero A, Werenkraut V (2007) One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. Glob Ecol Biogeogr 16:401–414

San Martín PR (1966) Escorpiofauna Brasileña III (Bothriuridae). Una nueva forma de "*Bothriurus*" del Brasil. Rev Bras Biol 26:181–190

San Martín PR (1967) Escorpiofauna Brasileña. II. Bothriuridae Redescripcin de *Bothriurus moojeni* Mello-Leitão, 1945. Physis 74:135–141

San Martín PR (1968) *Bothriurus vachoni*, n. sp. del Brasil (Scorpionida, Bothriuridae). Acta Biologica Venezuelica 6:38–51

Santos RL, Almeida EA, Almeida MG, Coelho MS (2006) Biogeography of the Bromeliad-dwelling scorpion *Tityus neglectus* Mello-Leitão (Buthidae) in Rio Grande do Norte, Brazil. J Bromel Soc 56:201–207

Scriven JJ, Whitehorn PR, Goulson D, Tinsley MC (2016) Bergmann's body size rule operates in facultatively endothermic insects: evidence from a complex of cryptic bumblebee species. PLoS One 11:e0163307

Sexton JP, Montiel J, Shay JE, Stephens MR, Slatyer RA (2017) Evolution of ecological niche breadth. Annu Rev Ecol Evol Syst 48:183–206

Shelomi M (2012) Where are we now? Bergmann's rule sensu lato in insects. Am Nat 180:511–519

Shimabukuro EM, Trivinho-Strixino S (2021) Elevational boundaries influence richness patterns at large spatial scales evinced by madicolous insects of the Brazilian Atlantic Forest. Ecol Entomol 46:1036–1046

Silva RR, Brandão CRF (2014) Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. PLoS One 9:e93049

Silva JMC, Casteleti CHM (2003) Status of the biodiversity of the Atlantic forest of Brazil. In: Galindo-Leal C, Câmara IG (eds) The Atlantic forest of South America: biodiversity status, threats, and outlook. CABS and Island Press, Washington, pp 43–59

Silva FR, Almeida-Neto M, Arena MVN (2014) Amphibian beta diversity in the Brazilian Atlantic forest: contrasting the roles of historical events and contemporary conditions at different spatial scales. PLos One 9:e109642

Silveira FAO, Barbosa M, Beiroz W, Callisto M, Macedo DR, Morellato LPC, Neves FS, Nunes YRF, Solar RR, Fernandes GW (2019) Tropical mountains as natural laboratories to study global changes: a long-term ecological research project in a megadiverse biodiversity hotspot. Perspect Plant Ecol Evol Syst 38:64–73

Smith GT (1995) Species richness, habitat and conservation of scorpions in the Western Australian wheatbelt. Rec West Aust Mus 52:55–66

Smith FA, Lyons SK (2013) Introduction. on being the right size: the importance of size in life history, ecology, and evolution. In: Smith FA, Lyons SK (eds) Animal body size. University of Chicago Press, Chicago

Stephens PR, Wiens JJ (2003) Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. Am Nat 161:112–128

Stevens RD (2013) Gradients of bat diversity in Atlantic forest of South America: environmental seasonality, sampling effort and spatial autocorrelation. Biotropica 45:764–770

Stevens RD, Tello JS, Gavilanez SS (2013) Stronger tests of mechanisms underlying geographic gradients of biodiversity: insights from the dimensionality of biodiversity. PLoS One 8:e56853

Sulakhe S, Dandekar N, Padhye A, Bastawade D (2020) Two new cryptic species of *Isometrus* (Scorpiones: Buthidae) from the northern Western Ghats, India. Euscorpius 305:1–24

Sunday JM, Bates AE, Dulvy NK (2011) Global analysis of thermal tolerance and latitude in ectotherms. Proc Royal Soc B 278(1713): 1823–1830. https://doi.org/10.1098/rspb.2010.1295

Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA (2010) Prospects for biodiversity conservation in the Atlantic forest: lessons from aging human-modified landscapes. Biol Conserv 143:2328–2340

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Timms LL, Schwarzfeld M, Sääksjärvi IE (2016) Extending understanding of latitudinal patterns in parasitoid wasp diversity. Insect Conserv Divers 9:74–86

Tseng M, Kaur KM, Pari SS, Sarai K, Chan D, Yao CH, Porto P, Toor A, Toor HJ, Fograscher K (2018) Decreases in beetle body size linked to climate change and warming temperatures. J Anim Ecol 87:647–659

Vasconcelos TS, Prado VH, da Silva FR, Haddad CF (2014) Biogeographic distribution patterns and their correlates in the diverse frog fauna of the Atlantic forest hotspot. PLoS One 9:e104130

Visser V, Clayton WD, Simpson DA, Freckleton RP, Osborne CP (2014) Mechanisms driving an unusual latitudinal diversity gradient for grasses. Glob Ecol Biogeogr 23:61–75

Wallace AR (1878) Tropical nature, and other essays. Macmillan and Company, London

Warburg MR, Ben-Horin A (1981) The response to temperature gradients of scorpions from mesic and xeric habitats. Comp Biochem Physiol 68:277–279

Weir JT, Schluter D (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. Science 315:1574–1576

Weiser MD, Enquist B, Boyle B, Killenn T, Jøgensen P, Fonseca G, Jennings MD, Kerkhoff AJ, Lacher TE Jr, Monteagudo A, Vargas MPN, Phillips OL, Swenson NG, Vasquez Martınez R

(2007) Latitudinal patterns of range size and species richness of New World woody plants. Glob Ecol Biogeogr 16:679–688

Weiser MD, Buzzard V, Deng Y, He Z, Michaletz S, Shen L, Enquist BJ, Waide RB, Zhou J, Kaspari M (2017) Toward a theory for diversity gradients: the abundance-adaptation hypothesis. Ecography 41:255–264

Weiser WD, Swenson NG, Enquist BJ, Michaletz ST, Waide RB, Zhou J, Kaspari M (2018) Taxonomic decomposition of the latitudinal gradient in species diversity of North American floras. J Biogeogr 45:418–428

Whittaker RJ, Araújo MB, Jepson P, Ladle RJ, Watson JE, Willis KJ (2005) Conservation biogeography: assessment and prospect. Divers Distrib 11:3–23

Wickham H, François R, Henry L, Müller K (2021) Dplyr: a grammar of data manipulation. R package version 1.0.7. (1.0.7) [Computer software]. https://CRAN.R-project.org/package=dplyr

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecol Lett 13:1310–1324

Willig MR, Presley SJ (2018) Latitudinal gradients of biodiversity: theory and empirical patterns. Encycl Anthr 3:13–19

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annu Rev Ecol Evol Syst 34:273–309

Yamaguti HY, Pinto-da-Rocha R (2003) Taxonomic review of the genus *Thestylus* Simon, 1880 (Scorpiones: Bothriuridae). Revista Ibérica de Aracnología 7:157–171

Chapter 8
Species Diversity of Three Faunal Communities Along a Successional Cloud Forest Gradient

Juan Manuel Díaz-García, Fabiola López-Barrera, Eduardo Pineda, Jorge Ernesto Valenzuela-González, and Adriana Sandoval-Comte

8.1 Introduction

Forests cover 31% of the global land surface, but only about one-third of this is primary forest because we have lost more than 80 million ha of primary forests since 1990 (FAO and PNUMA 2020). Habitat loss is the main threat to biodiversity; it is estimated that insect populations have decreased by 9% globally every decade since 1980 (van Klink et al. 2020). For vertebrate groups such as mammals, birds, reptiles, amphibians, and freshwater fishes, a population decrease of 68% has been estimated worldwide from 1970 up to the present. This loss is relatively higher in the Neotropical region, where populations of the groups mentioned have been reduced in greater proportion than in other regions of the planet (WWF 2020).

Forest restoration practices have increased worldwide in response to concerns about deforestation and its socio-ecological consequences (Bullock et al. 2011; Gatica-Saavedra et al. 2017). One of the strategies most widely implemented to recover forests is natural regeneration (or passive restoration), which occurs when stressors are eliminated or controlled, and a natural process of secondary succession can begin (Rey-Benayas et al. 2008). It is estimated that 36.2 million ha of secondary forest regrew between 2000 and 2010 in the Neotropics (Aide et al. 2013) as a

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result of land abandonment, exclusion and/or the implementation of restoration practices (Davies et al. 2020).

Species must be able to colonize the successional forests from the regional pool. In this context, Suganuma and Durigan (2021) categorized each plant species according to dispersal syndrome, seed traits, growth rate, shade tolerance, and rarity in the communities. They found that successful colonizers were mostly zoochorous, dispersed by birds or bats, shade tolerant, and of moderate or fast growth. The lack of slow-growing species dispersed by large mammals indicates the absence of certain faunal groups in the secondary forests.

Despite the increase in area of secondary forests, their value in terms of maintaining or recovering animal populations is poorly understood (Thompson and Donnelly 2018; Davies et al. 2020). It has long been assumed that fauna will recolonize naturally in secondary forests once the suitable vegetation and environmental characteristics, such as microclimate or food availability, have re-established (Catterall 2018). However, studying the responses of different groups of fauna to secondary succession is important since animals can significantly modulate the ecological trajectory and the rate of regeneration of forests through their participation in ecological processes such as pollination, seed dispersal, herbivory, and energy flow through trophic webs (Ortega-Álvarez et al. 2013; Fraser et al. 2015; Díaz-García et al. 2017).

To study how the species diversity of faunal communities varies, chronosequences of forest successional processes can be used since they comprise different vegetation conditions that represent a recovery gradient. These recovery gradients should be formed by the following vegetation conditions: a degraded ecosystem, which represents the conditions prior to initiation of natural succession, areas in natural succession of different ages, and an ecological reference ecosystem (Wortley et al. 2013; Marchand et al. 2021). Different ecological and functional attributes can be compared among the vegetation conditions in order to assess the response of faunal communities along the successional and environmental gradients. The components of species diversity, such as species richness, abundance, and composition, are the attributes most commonly used to measure the progress of faunal communities in forest regeneration processes (Gatica-Saavedra et al. 2017).

In studies that have evaluated the response of fauna to restoration strategies, it has been reported that species richness is the first attribute to recover, while this process takes more time for species composition and abundance (Catterall 2018). For example, Hernández-Ordóñez et al. (2015) found that ~25 years of natural succession are sufficient to recover the species richness of amphibians and reptiles, but not the species composition or abundance of these animals. In general, the recovery of species composition and abundance of faunal communities seems to be slower than the recovery of species richness, since they depend on re-establishment of the carrying capacity of secondary forests necessary in order to support stable populations (Chazdon 2008; Catterall 2018).

It has recently been proposed that evaluation of the richness and abundance of faunal communities, considering the habitat specialization type of the species (e.g. forest specialists vs. generalists), can be an effective indicator with which to evaluate changes in forest restoration processes (Díaz-García et al. 2020b). Depending on the ecological traits intrinsic to each habitat specialization type, species can respond differentially to environmental filters generated by the re-establishment of habitat characteristics, including microclimate, refuge and resource availability, and biotic interactions (Catterall 2018; Díaz-García et al. 2020b). To assess the recovery of forest specialist species in particular, it is important to determine the value of secondary forests for the conservation and recovery of vulnerable groups, since these forest specialist species are usually in danger of extinction (Hanski 2011; Pyron 2018; Luther et al. 2020).

The responses of faunal communities to forest regeneration also depend on extrinsic factors of the species, such as land use history, age, and proximity to mature forest (Lamb and Gilmour 2003; Smith et al. 2015). In addition, it has been found that the response may vary within and among taxonomic groups, for which reason the use of multi-taxonomic studies has been recommended (Gatica-Saavedra et al. 2017; Díaz-García et al. 2020b). Amphibians, ants, and dung beetles have been proposed as focal taxa for the evaluation of changes in Neotropical forest regeneration processes (Aguilar-Garavito and Ramírez 2015). Communities of these three faunal groups are highly sensitive to environmental changes and their responses can be detected at the local scale. Furthermore, subsets of species within each group present specific requirements that are positively associated with the heterogeneity and structural complexity of the habitat (Atauri and de Lucio 2001; Brodman et al. 2006; Nichols et al. 2008). Likewise, these taxa perform important functions in the ecosystems. For example, ants favour the flow of nutrients in the soil, promote microbial activity, and efficiently disperse seeds (Del Toro et al. 2012), while dung beetles are involved in nutrient recycling, secondary seed dispersal, and soil aeration (Nichols et al. 2008), and amphibians participate in the control of aquatic algae and herbivorous insects, as well as in energetic exchange between aquatic and terrestrial environments (Cortéz-Gómez et al. 2015). In this chapter, we assessed the species diversity of amphibians, dung beetles, and ants, considering their habitat specialization type, along a successional gradient formed by a cattle pasture, a 13-year-old regenerating secondary forest, a 23-year-old regenerating secondary forest, and a cloud forest remnant located in a mountainous landscape of central Mexico.

8.2 Materials and Methods

8.2.1 Study Area

Fieldwork was carried out in the municipality of Huatusco (19° 11′ 23″ N, 96° 59′ 11″ W, 1300 m a.s.l.) in the mountainous region of central Veracruz, Mexico (Fig. 8.1). The climate of the study site is subhumid with a mean annual temperature of 17.1 °C and mean annual precipitation of 1850 mm (CONAGUA 2016). There are three distinct seasons in the area: cold-dry (November–March), hot-dry (April–May) and hot-humid (June–October). This region currently presents ~10,000 ha of

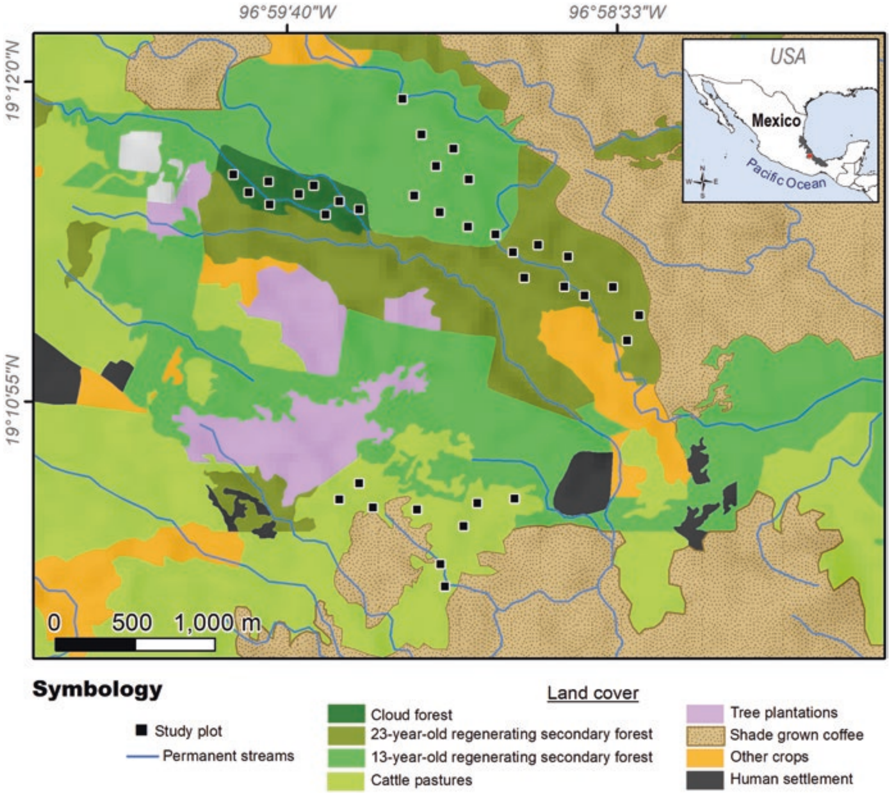


Fig. 8.1 Study area and location of the 36 study plots in four different vegetation conditions studied in the mountainous region of central Veracruz, Mexico. The tree plantations include monoculture plantations of bamboo, avocado, and pine

tropical montane cloud forest but, of these, only 30% are mature patches immersed in a matrix of agricultural crops, agroforestry systems, cattle pastures, and secondary forests (CONABIO 2010).

8.2.2 *Forest Successional Gradient*

To make valid and efficient comparisons of the ecological results generated by forest recovery processes, it is necessary to control certain factors such as the land use history of the intervened areas and their proximity to the reference ecosystem (Reid et al. 2018). In 2018, we determined a secondary successional gradient in a landscape of Huatusco, Mexico, formed by four vegetation conditions: a cattle pasture, a 13-year-old regenerating secondary forest, a 23-year-old regenerating secondary forest, and a mature cloud forest remnant. Both of the secondary forests were adjacent, and presented the same land use history and similar mean distance (~1 km) from the cloud forest remnant (Fig. 8.1, Díaz-García et al. 2020a).

The degraded ecosystem represented by cattle pasture was an open area dominated by exotic grasses, with some isolated trees of native species. The 13-year-old regenerating secondary forest had recovered 47% of the tree density and 87% of the canopy cover values presented in the cloud forest, and had also reduced the value of the exotic grass cover recorded in the cattle pasture by 76%. The 23-year-old regenerating secondary forest had recovered 57% of the tree density and 93% of the canopy cover recorded in the cloud forest, and had reduced the value of the exotic grass cover recorded in the cattle pasture by 82%. The two secondary forest conditions shared similar values of some variables of vegetation structure, such as tree height and basal area. The reference ecosystem, represented by the cloud forest remnant, had the highest values of tree density, basal area, tree height, canopy cover, and leaf litter cover. Finally, the species composition of mature cloud forests is dominated by forest specialist tree species. In contrast, the cattle pasture and both of the regenerating forest sites under natural succession presented a combination of trees from primary forests and secondary succession stages (Table 8.1).

8.2.3 Faunal Sampling

We established nine plots (10 × 50 m) with a north-south orientation in each vegetation condition of the natural succession gradient. All plots were located between 1330 and 1450 m a.s.l. in order to avoid an effect of elevation on the species diversity of the faunal communities. All plots were separated from each other and from other vegetation types by a minimum distance of 100 m (Fig. 8.1).

For the amphibians, we conducted three samplings during June, August, and October (hot-humid season) of 2018. In each sampling, two people searched for amphibians in each plot using a visual encounter survey with manual capture (Crump and Scott 1994) between the hours of 20:00 and 01:00. We identified captured individuals to species level and released them after 24 h at the same site where they had been captured. The sampled area in each vegetation type was 4500 m^2 (500 m^2 × 9 plots) and the total sampling area was 18,000 m^2 (4500 m^2 × 4 vegetation conditions).

We sampled ants and dung beetles once during the hot-dry season (May 2018) and again in the hot-humid season (September 2018). For the ants, we established four sampling stations along the central line of each plot at 0, 17, 34, and 50 m. Each sampling station comprised one pitfall trap (500 ml) buried to ground level, and one trap (200 ml) placed on trees at a height of 2 m from the ground. The two trap types were located at a distance of 10 m apart (the plot width). The resulting eight traps per plot were filled to one quarter of their capacity with soapy water and protected from the rain by plastic plates (García-Martínez et al. 2015). We used different bait types; pitfall traps were either unbaited or baited with ~20 g of tuna. The tree traps were baited with either ~20 g of tuna or honey. Trap and bait types were alternated

Table 8.1 Vegetation structure and composition of a cloud forest successional gradient formed by a cattle pasture, a 13-year-old regenerating secondary forest, a 23-year-old regenerating secondary forest, and a cloud forest remnant located in a mountainous landscape of central Mexico. Mean values ± standard deviation are shown

	Cattle pasture	13-year-old secondary forest	23-year-old secondary forest	Cloud forest
				
Tree density per ha	25 ± 41.8	289 ± 172	350 ± 38.1	614.7 ± 50.3
Tree height (m)	8 ± 12.5	13.5 ± 2.6	13.9 ± 1.2	24.5 ± 1.1
Basal area (m^2/ha)	4.1 ± 8.3	11.1 ± 9.7	11.8 ± 1.3	44.2 ± 4.7
Canopy cover (%)	12.02 ± 14.9	67.5 ± 8.2	72.3 ± 5	77.4 ± 3.7
Leaf litter cover (%)	6.3 ± 8.9	23.1 ± 15.4	44.19 ± 20.8	67.8 ± 13.6
Grass cover (%)	86.2 ± 23.7	20.3 ± 15.9	15.85 ± 8.7	3.5 ± 7.7
Herbaceous plant cover (%)	2.7 ± 6.8	48.8 ± 16.6	34 ± 21.9	16.6 ± 6.3
Shrub cover (%)	1 ± 2.4	22.1 ± 11.6	20.3 ± 11.2	30.8 ± 13.1
Epiphyte cover (%)	7.3 ± 11.45	7.5 ± 8.3	9.5 ± 12.2	49 ± 25.4
Dominant tree species	*Acacia pennatula*, *Psidium guajava*, *Quercus insignis*	*A. pennatula*, *Myrsine coriacea*, *Q. paxtalensis*	*M. coriacea*, *Trema micrantha*, *Q. sapotifolia*	*Q. paxtalensis*, *Q. lancifolia*, *Q. insignis*

from right to left along each plot to avoid traps with the same type of bait being too close to each other or all on the same side of the plot. We checked the traps after 72 h and collected all captured ants. In addition, in the centre of each plot, we collected all leaf litter in 1 m^2 and processed it with Winkler sacks in order to extract the ants contained within (Bestelmeyer et al. 2000). Ant specimens were identified to species level in the laboratory.

For the dung beetles, we established three sampling stations along the central line of each plot at 0.25 and 50 m. Each sampling station comprised two pitfall traps (500 ml) buried to ground level and located at a distance of 10 m apart (the width of the plot). The traps were filled to one quarter of their capacity with soapy water and protected from the rain by plastic plates. We used three different bait types: human faeces, carrion (tilapia fish that had been decomposing for two days), and a mixture of guava and banana (1,1). We used ~20 g of bait placed in a small plastic cup suspended inside the pitfall traps. As with the ant traps, bait type was alternated between pitfall traps from right to left along each plot. We checked the traps after 72 h and collected all captured dung beetles. Specimens were identified to species level in the laboratory.

We grouped amphibian, ant, and dung beetle species into two habitat specialization categories: (1) forest-specialist species; those with populations that thrive better in mature forests and present limited tolerance to environmental changes, and (2) generalist species; those with a broader environmental tolerance, and with thriving populations to be found in a variety of natural and modified habitats (MacArthur and Levins 1964; Devictor et al. 2010). To assign a species to one or the other category, we consulted the specialized literature for each group (see Díaz-García et al. 2020a). Ants not identified to species level were not categorized and not used for analysis.

8.2.4 Data Analysis

To evaluate the efficiency of the inventory and make valid comparisons of the species diversity among the vegetation conditions, we calculated the sample coverage ($\hat{C}_n$) for each vegetation condition, using the formula:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 is the number of singletons, f_2 is the number of doubletons, and n is the number of individuals of the vegetation condition (Chao and Jost 2012). We calculated species richness per habitat specialization category for each faunal group and compared these among vegetation conditions using generalized linear models (GLM) with a Poisson distribution and log link function, and post hoc tests of contrasts. These analyses were conducted with the package 'iNEXT' (Hsieh et al. 2016), 'gmodels' (Warnes et al. 2018), and 'fifer' (Fife 2014) in R version 1.1.383 (R Core Team 2017).

We calculated abundance per habitat specialization category by pooling the number of individuals collected in all samplings for amphibians and dung beetles. To compare abundances between vegetation conditions, we used generalized linear models (GLM) with a Poisson distribution and log link function, and post hoc tests of contrasts. Since ants exhibit social behaviour, we calculated occurrence-frequency as the number of plots in which the species was present and summed the occurrences recorded in each of the two samplings (i.e. maximum occurrence frequency for a species that was present in all plots in every sampling would be 9 × 2 = 18). We used a Chi-square test to evaluate goodness-of-fit and a post hoc test to compare the occurrence-frequency of ants among vegetation conditions. These analyses were conducted with the packages 'gmodels' (Warnes et al. 2018) and 'fifer' (Fife 2014) in R version 1.1.383 (R Core Team 2017).

We constructed a dendrogram using the Bray-Curtis similarity index for each faunal community in order to compare species composition among vegetation conditions. To reduce the influence of the most abundant species, we used the chord transformation on the abundance matrix of amphibians and dung beetles (Legendre and Legendre 2012). We then ran a permutational multivariate analysis of variance (Permanova: 999 permutations) of Bray-Curtis indices. These analyses were conducted with the packages 'vegan' (Oksanen et al. 2016) and 'ggplot2' (Wickham 2016) in R version 1.1.383 (R Core Team 2017). Finally, we compared the structure of each faunal community among vegetation conditions using rank abundance curves (Feinsinger 2001).

8.3 Results

We found a total of 13 amphibian species (7 forest specialists and 6 generalists), 41 ant species (21 forest specialists, 17 generalists, and 3 undefined), and 15 dung beetle species (5 forest specialists and 10 generalists). Since the sample coverage in each vegetation type was >90% for all faunal communities, we were able to compare our variables with the observed values.

8.3.1 Species Richness

For amphibians, the richness of forest specialist species varied among vegetation conditions (Residual Deviance = 30.5, df = 32, $p < 0.001$). The richness of forest specialist amphibian species was similar between the two regenerating secondary forests (13- and 23-year-old), but was lower than in the mature cloud forest. The richness of generalist amphibian species was similar among vegetation conditions (Residual Deviance = 36.5, df = 32, $p = 0.9$; Fig. 8.2a).

For ants, the richness of the forest specialist (Residual Deviance = 23.2, df = 32, $p < 0.01$) and generalist (Residual Deviance = 25.6, df = 32, $p = 0.01$) species varied among vegetation conditions. The richness of forest specialist ants was greater in the cloud forest and 23-year-old regenerating secondary forest than in the other vegetation conditions. The richness of generalist ants was greater in cattle pastures and 13-year-old regenerating secondary forest than in the other vegetation conditions (Fig. 8.2b).

For dung beetles, the richness of forest specialist (Residual Deviance = 16.6, df = 32, $p < 0.001$) and generalist (Residual Deviance = 11.4, df = 32, $p < 0.001$) species varied among vegetation conditions. The richness of forest specialist dung beetles was lower in cattle pasture than in the other vegetation conditions, among which no significant differences were found. The richness of generalist dung beetles was greater in cattle pasture than in the other vegetation conditions, among which no significant differences were found (Fig. 8.2c).

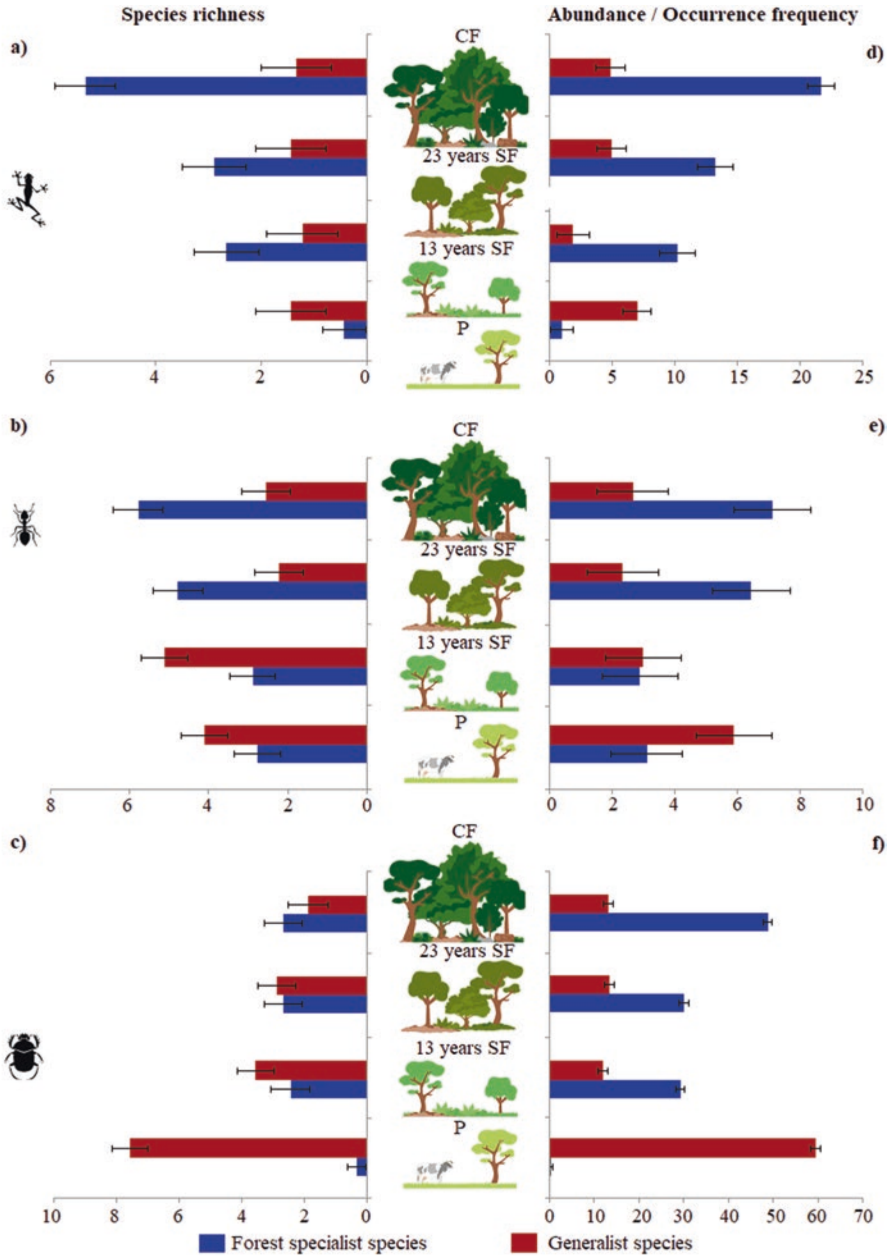


Fig. 8.2 Species richness and abundance or occurrence frequency of amphibians, ants, and dung beetles recorded along a natural succession gradient: P = cattle pasture, 13 years SF = 13-year-old regenerating secondary forest, 23 years SF = 23-year-old regenerating secondary forest, and CF = cloud forest. Mean values and standard error are shown in the graphs

8.3.2 Abundance or Occurrence Frequency

For amphibians, the abundance of forest specialist (Residual Deviance = 120.7, df = 32, $p < 0.001$) and generalist (Residual Deviance = 224.9, df = 32, $p < 0.001$) species varied among vegetation conditions. The abundance of forest specialist amphibians was similar between both secondary forest conditions, but was lower than in the mature cloud forest. The abundance of generalist amphibians was lower in 13-year-old regenerating secondary forest than in the other vegetation conditions, among which no significant differences were found (Fig. 8.2d).

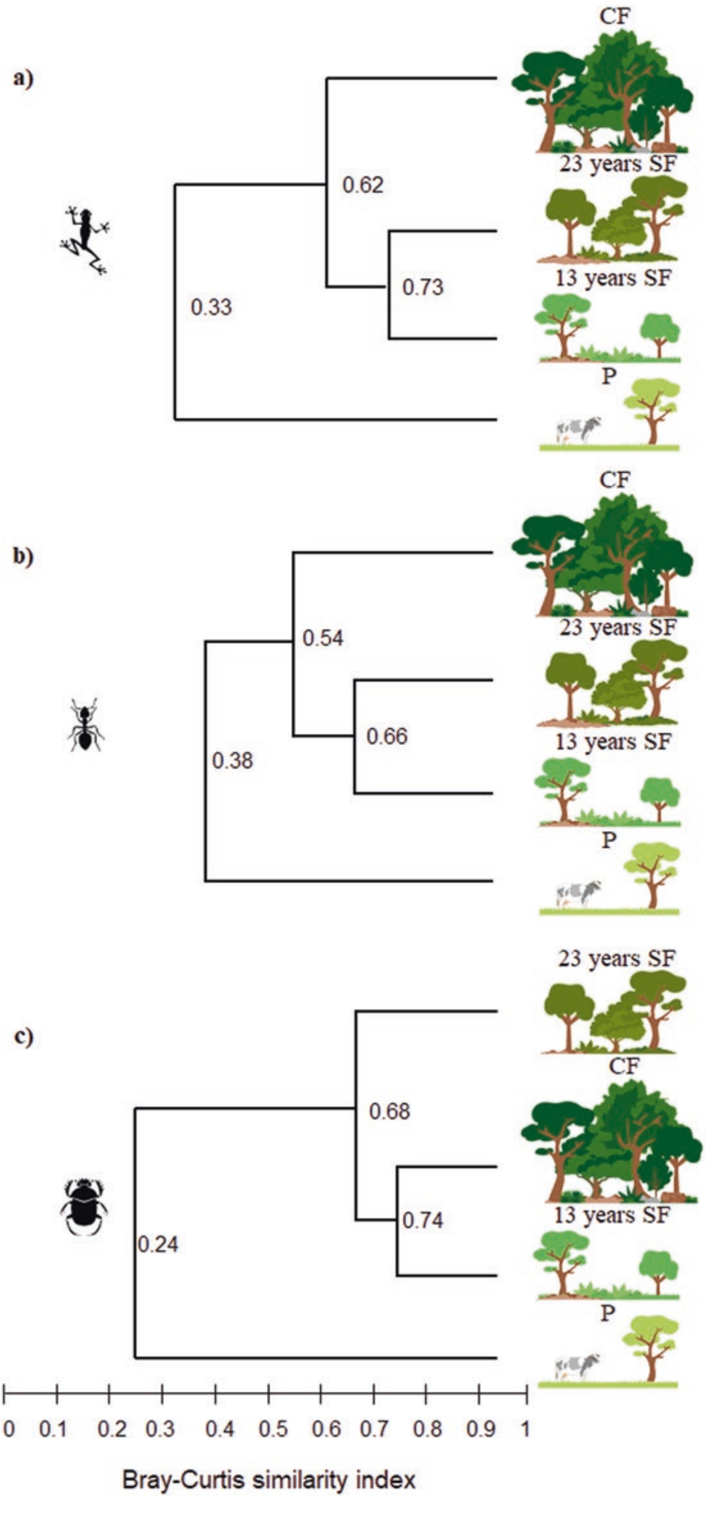
For ants, the occurrence frequency of forest specialist ($X^2 = 25.8$, df = 7, $p < 0.001$) and generalist ($X^2 = 26.1$, df = 7, $p < 0.001$) species varied among vegetation conditions. The occurrence frequency of forest specialist ants was greater in cloud forest and 23-year-old regenerating secondary forest than in the other vegetation conditions. The occurrence frequency of generalist ants was greater in cattle pastures than in the other vegetation conditions, among which no significant differences were found (Fig. 8.2e).

For dung beetles, the abundance of forest specialist (Residual Deviance = 211.5, df = 32, $p < 0.001$) and generalist (Residual Deviance = 273.6, df = 32, $p < 0.001$) species varied among vegetation conditions. The abundance of forest specialist dung beetles was similar between the two secondary forests, but was higher in the mature cloud forest. The abundance of generalist dung beetles was greater in cattle pasture than in the other vegetation conditions, among which no significant differences were found (Fig. 8.2f).

8.3.3 Species Composition

The species composition of amphibians ($F = 12.7$, $p = 0.001$), ants ($F = 10.8$, $p = 0.01$), and dung beetles ($F = 15.3$, $p = 0.001$) varied among vegetation conditions. For all taxa, the similarity in species composition of the two secondary forests was closer to that recorded in the cloud forest (47–62%), than to that of the cattle pasture (24–38%). For the amphibian and ant communities, the highest similarity values were observed between the two secondary forests (Fig. 8.3a, b). For dung beetles, the highest similarity values were observed between the cloud forest and 13-year-old regenerating secondary forest (Fig. 8.3c).

Fig. 8.3 Dendrogram of similarity (Bray-Curtis index) based on amphibian abundance (**a**), ant occurrence frequency (**b**), and dung beetle abundance (**c**) recorded along a natural succession gradient: P = cattle pasture, 13 years SF = 13-year-old regenerating secondary forest, 23 years SF = 23-year-old regenerating secondary forest, and CF = cloud forest. In all dendrograms: 0 = completely different and 1 = completely identical


a)
CF
23 years SF
13 years SF
P
0.62
0.73
0.33
b)
CF
23 years SF
13 years SF
P
0.54
0.66
0.38
c)
23 years SF
CF
13 years SF
P
0.68
0.74
0.24
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Bray-Curtis similarity index

8.3.4 Community Structure

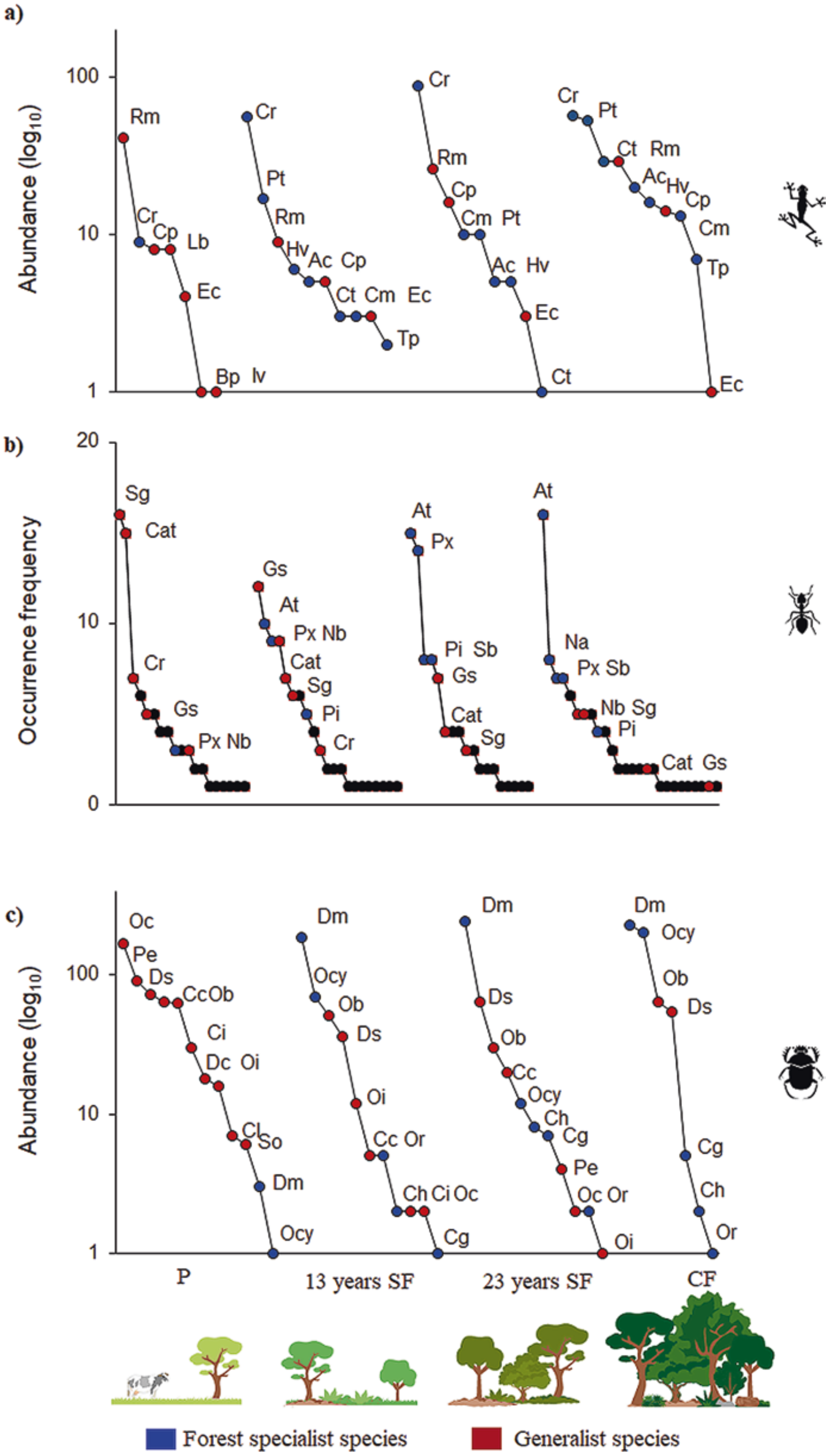
For amphibians, two forest specialist species were dominant in the cloud forest (*Craugastor rhodopis* and *Parvimolge townsendi*). The dominant species in both successional forests was the forest specialist *C. rhodopis*, while the dominant species in the cattle pasture was the generalist species *Rheohyla miotympanum*. Other forest specialist species, such as *Charadrahyla taeniopus*, *Aquiloeurycea cafetalera*, and *Thorius pennatulus* were recorded in both successional forests, but with abundance values lower than those of the cloud forest (Fig. 8.4a).

For ants, the habitat-generalists *Solenopsis geminata* and *Camponotus atriceps* were the dominant species in the cattle pasture, but their abundance decreased in the other vegetation conditions along the successional gradient. In the 13-year-old secondary forest, the dominant species was the habitat-generalist species *Gnamptogenys strigata*. In the 23-year-old secondary forest, the dominant species were the forest specialists *Adelomyrmex tristani* and *Pheidole xyston*. In the cloud forest, the dominant species was the forest specialist *A. tristani*. The abundance of some forest specialist species, such as *A. tristani*, increased from the 13-year-old forest to the cloud forest (Fig. 8.4b).

For dung beetles, the habitat-generalist species *Onthophagus corrosus* and *Phanaeus endymion* were the species with the highest number of individuals in the cattle pasture. However, these species were absent or presented low abundance in the forested sites. In both successional forests, the forest specialist species *Deltochilum mexicanum* was the dominant species. In the cloud forest, the forest specialist species *D. mexicanum* and *Onthophagus cyanellus* were the most abundant. In the vegetation conditions along the successional gradient, the abundance of habitat-generalist species such as *Coprophanaeus corythus* and *Onthophagus incensus* decreased from the cattle pasture to the cloud forest. Some forest specialist species, such as *Canthidium hespenheidei*, *Coprophanaeus gilli*, and *Onthophagus rhinolophus*, were recorded in both regenerating forest sites, but did not reach the values recorded in the mature forest (Fig. 8.4c).

⟶

Fig. 8.4 Rank abundance curves of the amphibian (**a**), ant (**b**), and dung beetle (**c**) communities recorded along a successional gradient: P = cattle pasture, 13 years SF = 13-year-old regenerating secondary forest, 23 years SF = 23-year-old regenerating secondary forest, and CF = cloud forest. For amphibians: Ac *Aquiloeurycea cafetalera,* Bp *Bolitoglossa platydactyla*, Cm *Craugastor mexicanus*, Cp *Craugastor pygmaeus,* Cr *Craugastor rhodopis*, Ct *Charadrahyla taeniopus,* Ec *Eleutherodactylus cystignathoides,* Hv *Hyalinobatrachium viridissimum,* Iv *Incilius valliceps*, Lb *Lithobates berlandieri*, Pt *Parvimolge townsendi*, Rm *Rheohyla miotympanum*, and Tp *Thorius pennatulus*. For ants: At *Adelomyrmex tristani*, Cat *Camponotus atriceps*, Cr *Cyphomyrmex rimosus*, Gs *Gnamptogenys strigata*, Na *Nylanderia austroccidua*, Nb *Nylanderia bourbonica*, Pi *Pheidole insipida*, Px *Pheidole xyston*, Sb *Strumigenys brevicornis*, and Sg *Solenopsis geminata*. For dung beetles: Ch *Canthidium hespenheidei*, Cl *Canthon leechi*, Ci *Copris incertus*, Cc *Coprophanaeus corythus*, Cg *Coprophanaeus gilli*, Dm *Deltochilum mexicanum*, Dc *Dichotomius colonicus*, Ds *Dichotomius satanas*, Ob *Onthophagus belorhinus*, Oc *Onthophagus corrosus*, Ocy *Onthophagus cyanellus*, Oi *Onthophagus incensus*, Or *Onthophagus rhinolophus*, Pe *Phanaeus endymion*, and So *Scatimus ovatus*


a)
Abundance ($\log_{10}$)
100
10
1
Rm
Cr
Cp
Lb
Ec
Bp
Iv
Cr
Pt
Rm
Hv
Ac
Cp
Ct
Cm
Ec
Tp
Cr
Rm
Cp
Cm
Pt
Ac
Hv
Ec
Ct
Cr
Pt
Ct
Rm
Ac
Hv
Cp
Cm
Tp
Ec
b)
Occurrence frequency
20
10
0
Sg
Cat
Cr
Gs
Px Nb
Gs
At
Px Nb
Cat
Sg
Pi
Cr
At
Px
Pi
Sb
Gs
Cat
Sg
At
Na
Px Sb
Nb Sg
Pi
Cat
Gs
c)
Abundance ($\log_{10}$)
100
10
1
Oc
Pe
Ds
Cc Ob
Ci
Dc
Oi
Cl
So
Dm
Ocy
Dm
Ocy
Ob
Ds
Oi
Cc
Or
Ch
Ci
Oc
Cg
Dm
Ds
Ob
Cc
Ocy
Ch
Cg
Pe
Oc
Or
Oi
Dm
Ocy
Ob
Ds
Cg
Ch
Or
P
13 years SF
23 years SF
CF
Forest specialist species
Generalist species

8.4 Discussion

Successional forest gradients could theoretically also impose environmental gradients (i.e. canopy or litter cover, etc.) that gradually change as forest ages. Along our successional gradient, the environmental variation was represented by increased tree density, tree height, canopy cover, and leaf litter cover and decreased grass cover, as the forest ages. There was also a decrease in the variability of these conditions as the forest recovered. It is considered that a large proportion of species may coexist under intermediate conditions along an environmental gradient (Flynn et al. 2009; Bitencourt et al. 2019). In our study, to evaluate species turnover along the natural regeneration gradient, we analysed the response of generalist and forest specialist species separately. In the case of the amphibians and ants, a general trend was found; forest specialist species increased in richness and abundance as the forest ages. However, recovery of the species richness of forest specialist dung beetles occurred in the early successional stages (13 years). Our results show that biodiversity recovery during natural forest regrowth is taxon-specific and depends on the habitat specialization type of the species.

8.4.1 Species Richness and Abundance in Forest Specialists Across Forest Chronosequences

8.4.1.1 Amphibians

Studies that have assessed changes in amphibian communities across forest succession chronosequences in Neotropical landscapes have shown that species richness can be recovered in a relatively short period following agricultural abandonment (5–25 years; Herrera-Montes and Brokaw 2010; Basham et al. 2016). Acevedo-Charry and Aide (2019) conducted a meta-analysis of amphibian recovery along tropical forest succession gradients and found that secondary forests reached the levels of species richness found in the reference forests after 5–30 years of succession. It has been reported that secondary forests can maintain the same abundance of amphibians as mature forests after 10–30 years of natural succession (Hilje and Aide 2012; Hernández-Ordóñez et al. 2015).

Acevedo-Charry and Aide (2019) reported that forest specialist amphibians colonize secondary forests gradually, and only secondary forest of 15–30 years of age reached values similar to those of the mature forests used as a reference. In this study, the species richness and abundance of forest specialist species were still not reached even after 23 years of forest regeneration, probably because the strict habitat requirements of these species had not completely recovered in the secondary forests (Thompson and Donnelly 2018). Studies that have related environmental factors to the recovery of forest specialist amphibians suggest that forest cover and connections between forests appear to help species to colonize sites, regardless of age. Moreover, forests with closed canopy, high humidity, deep leaf litter, and abundant arthropods provide favourable microhabitat conditions and resources for forest specialist amphibians (Hilje and Aide 2012; Smith et al. 2015; Díaz-García et al. 2017). In the study area, proximity to water bodies, as well as high canopy and leaf litter cover, had a strong positive influence on the recovery of forest specialist amphibians [Díaz-García et al. 2020a].

Along the successional gradient, the richness and abundance of amphibian generalist species remained intact, with only a small decrease in their abundance found in the youngest forest. However, it is important to highlight the significant increase in the species richness and abundance of forest specialist amphibians, although, for these species, a period of 23 years is still insufficient to recover the conditions of the mature forest. Given the current state of danger of extinction of the forest specialist amphibians, this result may point to the need to intervene in forests undergoing natural succession with complementary actions based on the particular requirements of the species (i.e. artificial ponds, introduction of tree trunks or translocation of epiphytic plants [Fernandez-Barrancos et al. 2017]).

8.4.1.2 Ants

Studies that have evaluated the response of ant communities to natural regeneration in Neotropical landscapes have obtained contrasting results. It has been found that secondary forests can entirely recover the species richness recorded in mature forests after 30–50 years of natural succession (Dunn 2004; Bihn et al. 2008). Higher species richness has also been found in mid-secondary forest under natural regeneration (25–35 years) compared to that of mature forests (Osorio-Pérez et al. 2007), as well as a decline in species richness with increasing forest age (5–30 years; Hethcoat et al. 2019). Tiede et al. (2017) found similar species richness and occurrence among primary and secondary forests of different ages. However, the increase in forest specialist species with advancing forest succession can be considered a general pattern (Dunn 2004; Hethcoat et al. 2019).

In this study, the species richness and occurrence of forest specialist ants reached values similar to those recorded in the mature forest fragment after 23 years of forest regeneration. It is interesting to note that the 13-year-old regenerating forest and cattle pasture sites had similar values of forest specialist ant species, indicating either that their recovery is faster than that of the forest specialist amphibians and dung beetles, or that there are processes of persistence despite the environmental conditions of the cattle pasture. The persistence or recovery of forest specialist species may be due to the proximity of secondary forests and cattle pastures to the mature forest remnant (Domínguez-Haydar and Armbrecht 2011; Gilroy and Edwards 2017), and also to the re-establishment of microhabitat conditions such as higher canopy cover and fallen trunk density in secondary forests, or the presence of isolated trees and shrubs in cattle pastures (Díaz-García et al. 2020b).

Ant generalist species showed a sharp decrease in the 23-year-old regenerating forest stand. At the beginning of the successional gradient (pasture and early successional forest), it is expected to find generalist and forest specialist species that were able to resist forest transformation due to the existence of forest remnants, availability of nesting resources and favourable soil conditions (Rocha-Ortega and García-Martínez 2018). This latter subset of species is expected to increase in secondary forests in the middle portion of the gradient. This pattern of high species substitution contributes to the β-diversity for different organisms (Hernández-Ordóñez et al. 2019; Bitencourt et al. 2019), particularly in the heterogeneous region of Central Veracruz, where montane cloud forest landscapes present a high β-diversity of woody plants, ants, amphibians, and dung beetles (Arellano and Halffter 2003; Williams-Linera et al. 2013; Meza-Parral and Pineda 2015; García-Martínez et al. 2016, 2017).

8.4.1.3 Dung Beetles

In the Neotropics, it has been reported that the species richness and abundance of dung beetles can be lower in early and mid-secondary forests (0–18 years) than in old-secondary (40 years) and mature forests (Audino et al. 2014). In contrast, Bitencourt et al. (2019) reported a similar species richness of dung beetles in young successional (15–16 years), mid-successional (25–26 years), and mature forests. In addition, Davies et al. (2020) reported similar species richness in secondary (35 years) and primary forest, which was higher than that of cattle pastures. In general, dung beetle abundance has been reported to be lower in secondary forests than in mature forests, even after 18, 26, or 35 years of forest regeneration (Audino et al. 2014; Bitencourt et al. 2019; Davies et al. 2020).

For forest specialist dung beetles in particular, an increase in species richness and abundance has been found after ~10 years of natural succession (Audino et al. 2014). Similarly, the forest specialist dung beetle species richness and abundance in our study reached the mature forest values from 13 years of forest regeneration onwards, demonstrating the resilience of this group and the importance of even young forests stands for this group (Davies et al. 2020; Whitworth et al. 2021). They also found that tree density was the main factor determining the recovery of specialist dung beetles in their study sites. Other important factors that maximize the recovery of forest specialist dung beetles during secondary succession include a closed canopy, and a high cover of leaf litter, fallen trunks, and non-grass herbaceous plants (Díaz-García et al. 2020b).

The values of abundance and richness of generalist dung beetle species were almost two times higher in cattle pasture than in the forested stands, but were similar across the secondary forests. Generalist dung beetle communities can persist in cattle pastures with isolated trees because the livestock present provides sufficient resources for feeding and nesting (Huerta et al. 2018). The different responses between generalist and specialist forest dung beetles in the studied successional gradient may also be due to the fact that both species types have different biogeographic origins (Nearctic and Neotropical), which acts to determine the level of tolerance to habitat modifications (Gómez-Cifuentes et al. 2018).

8.4.2 Composition Similarity and Community Structure Along the Successional Forest Gradient

In several natural regeneration processes in the Neotropical region, species composition is an attribute that presents slower recovery compared to species richness and abundance (Catterall 2018). For amphibians, ants, and dung beetles, most studies have found a transformation from open environment generalist species to forest specialist species along different secondary successional gradients (Dent and Wright 2009; Audino et al. 2014; Thompson and Donnelly 2018; Acevedo-Charry and Aide 2019; Bitencourt et al. 2019; Hethcoat et al. 2019; Díaz-García et al. 2020b).

In the same study area, Trujillo-Miranda et al. (2018) reported that woody plant species composition differed significantly from the adjacent old-growth forests even after 23 years of natural regeneration. Seedling density of late-successional, barochorous-synzoochorous species was much higher in mature forests than in the secondary forests, highlighting the lack of efficient seed dispersal (few seed sources and/or vertebrate seed dispersers) of these species in successional forests (Toledo-Aceves et al. 2021). Biological traits have also been found that can determine the response of faunal groups to habitat modifications. For example, hot climate specialist ants are dominant in open areas and scarce in secondary and primary forests (Gómez and Abril 2011). Forest specialist salamanders from our study (belonging to the Plethodontidae Family) are skin-breathers and depend on the restoration of high levels of atmospheric humidity and a constant temperature (Díaz-García et al. 2020b). Large paracoprid dung beetles decreased with increasing temperature (Gómez-Cifuentes et al. 2017).

Along our studied gradient, a greater similarity of amphibian, ant, and dung beetle composition (66–74%) was recorded between the successional forests (13 and 23 years-old) than when compared to the mature forest (54–68%). The successional forest stands presented similarity in some average values related to vegetation structural variables such as tree density, tree height, basal area, and canopy cover. However, the early secondary forest (13 years) presented higher variation in these attributes than the older (23 years) and mature forests, since forest regeneration is not spatially homogeneous. The highly variable environmental conditions during the early successional stages could act to promote the abundance of generalist species, as occurred for the ant species.

As expected, the active cattle pasture presented a different composition, mostly dominated by generalist species. However, a subset of species was similar to those that occurred in forested stands; similarity varied from 24% in the case of dung beetles to 38% for ants. The studied cattle pasture had an average tree density of 25 trees per ha and presented highly variable canopy cover. This tree density is low compared to forested stands, and the average basal area is about 33% of that recorded in natural regenerated forests. Isolated large and mature trees remain in non-intensive cattle pastures, providing a refuge to several other species such as the taxa studied. When these sites are abandoned, these isolated trees may act as regeneration nuclei, thus assisting forest recovery (Sandor and Chazdon 2014).

The changes from generalist to forest specialist species can also be noted in the place that the species occupied in the community structure of each vegetation condition along the successional gradient studied. Generalist ants, dung beetles, and amphibians were dominant in the cattle pastures, while forest specialist species were abundant in the secondary and reference forests. Moreover, some generalist species were unique to cattle pastures and/or early successional forest, while some forest specialist species appeared with natural regeneration and increased in abundance with forest age. For example, the same forest specialist frog (*Craugastor rhodopis*) was dominant in the forested sites but scarce in the cattle pasture, probably due to that fact that this species requires a high cover of leaf litter in which to lay its eggs and hunt its arthropod prey (Luría-Manzano et al. 2019).

For ants, the habitat-generalist species *Solenopsis geminata* was dominant in the cattle pasture, but its abundance decreased in the other vegetation conditions along the successional gradient. Species of the *Solenopsis* genera are common ants that persist at higher abundances in cattle pastures, and are considered generalist foragers (Hethcoat et al. 2019). This is in contrast to *Adelomyrmex tristani*, the dominant species in the 23-year-old and mature forests, a ground-dwelling specialist predator (Groc et al. 2014). For dung beetles, *Onthophagus corrosus* was the species with the highest number of individuals in the cattle pasture. The diet of *O. corrosus* is based on dung, a resource provided by livestock. In the forested sites, the forest specialist species *Deltochilum mexicanum* was dominant. This is a copro-necrophagous species that can exploit the high availability of faeces and dead animals in the forest (Huerta et al. 2016).

8.5 Perspectives

Forest successional gradients are a useful framework with which to understand how plant and animal communities could recover as forest ages, and to determine which local and landscape factors modulate the recolonization or persistence processes. Exploring the recovery patterns of a range of taxa during secondary forest succession is critical for conservation and restoration strategies.

Few studies include a degraded system as part of their forest successional gradients, to act as a reference system with environmental and land management characteristics similar to those of the historic initial point of the secondary succession process (Reid et al. 2018). Our study demonstrates that, besides the abundance of generalist species in the cattle pasture, this land use harboured a subset of low abundance species that were present in forested ecosystems. Remnant large trees (such as *Quercus insignis* trees) in these modified habitats must be conserved since they could play an important role in facilitating forest recovery once these sites are passively or actively restored. Tree species from the *Quercus* genus provide acorns that are consumed by many insects, birds, and mammals, and their dense canopy creates a favourable microhabitat for many other species (Nsibi et al. 2006; Magee 2019). Oak trunks provide shelter for birds, bats, and a diversity of epiphytic plants (i.e. orchids, bromeliads, ferns, mosses, and lichens; Alzate-Q et al. 2019).

Along forest successional gradients, the gradual gradient of vegetation structure recovery is expected to dictate the fauna recovery. However, this study shows that biodiversity recovery during natural forest regrowth is taxon-specific and depends on the particular habitat specialization of the species. The expected gradual change in environmental gradient across the studied chronosequences does not always take place, since forest regeneration is spatially heterogeneous, especially in the earlier stages. Each animal group therefore responds to the creation of permanent and ephemeral microhabitats according to its own habitat requirements. The three studied fauna groups play crucial roles in ecosystem functioning and the evaluation of their responses in a single study therefore provides us with valuable information regarding the regeneration success of the ecosystem.

This study also highlights the need to complement traditional metrics such as species richness with others such as the richness of forest specialist or functional groups, which can help us to understand the species turnover along these forest successional gradients. The slow recovery of species compositional similarity in several taxa confirms the need to conserve mature forests as a habitat for forest specialists and a potential source for passive forest restoration.

Understanding the factors that modulate fauna recovery is important to the establishment of restoration actions to accelerate the recovery of compositional similarity. In the studied region, the intervention of early successional forest stands by the establishment of artificial ponds and the introduction of broad-leaved tree species in canopy gaps could facilitate fauna colonization and biodiversity recovery. It has been also documented that, at the landscape level, biodiversity recovery through natural forest regrowth varies according to ecological, cultural, and socioeconomic factors (Chazdon et al. 2020; Crouzeilles et al. 2017). In several regions, secondary forests are under tremendous pressure from selective logging, edge effects, grazing, invasive species, etc., which could prevent the recovery of biodiversity (Guariguata and Ostertag 2001). Nevertheless, secondary forests clearly provide important environmental services and habitat for many species, some of which are currently endangered (Chazdon et al. 2020). In this study, both of the secondary forests evaluated are under the protection of the landowners and are located relatively close to the mature forest fragment, and the forest specialist recovery rate could therefore have been higher compared to that of other less well-conserved landscapes.

References

Acevedo-Charry O, Aide M (2019) Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics. Oikos 128(8):1065–1078. https://doi.org/10.1111/oik.06252

Aguilar-Garavito M, Ramírez W (2015) Monitoreo a procesos de restauración ecológica, aplicado a ecosistemas terrestres. Instituto de Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá

Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, Redo D, Bonilla-Moheno M, Riner G, Andrade-Núñez MJ, Muñiz M (2013) Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45:262–271. https://doi.org/10.1111/j.1744-7429.2012.00908.x

Alzate-Q NF, García-Franco JG, Flores-Palacios A, Krömer T, Laborde J (2019) Influence of land use types on the composition and diversity of orchids and their phorophytes in cloud forest fragments. Flora 260:151463. https://doi.org/10.1016/j.flora.2019.151463

Arellano L, Halffter G (2003) Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. Acta Zool Mex 90:27–76

Atauri JA, de Lucio JV (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landsc Ecol 16:147–159. https://doi.org/10.1023/A:1011115921050

Audino LD, Louzada J, Comita L (2014) Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? Biol Conserv 169:248–257. https://doi.org/10.1016/j.biocon.2013.11.023

Basham EW, González del Pliego P, Acosta-Galvis AR, Woodcock P, Medina-Uribe CA, Haugaasen T, Gilroy JJ, Edwards DP (2016) Quantifying carbon and amphibian co-benefits from secondary forest regeneration in the Tropical Andes. Anim Conserv 19(6):548–560. https://doi.org/10.1111/acv.12276

Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WR, Delabie JHC, Silvestre R (2000) Field techniques for the study of ground-dwelling ants, an overview, description, and evaluation. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington/London, pp 122–144

Bitencourt BS, da Silva PG, Morato EF, de Lima YG (2019). Dung beetle responses to successional stages in the Amazon rainforest. Biodivers Conserv 28(10):2745–2761. https://doi.org/10.1007/s10531-019-01791-y

Bihn JH, Verhaagh M, Brändle M, Brandl R (2008) Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. Biol Conserv 141(3):733–743. https://doi.org/10.1016/j.biocon.2007.12.028

Bitencourt BS, da Silva PG, Morato EF, de Lima YG (2019) Dung beetle responses to successional stages in Amazon rainforest. Biodivers Conserv 28:2745–2761. https://doi.org/10.1007/s10531-019-01791-y

Brodman R, Parrish M, Kraus H, Cortwright S (2006) Amphibian biodiversity recovery in a large-scale ecosystem restoration. Herpetol Conserv Biol 2:101–108

Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends Ecol Evol 26:541–549. https://doi.org/10.1016/j.tree.2011.06.011

Catterall CP (2018) Fauna as passengers and drivers in vegetation restoration: a synthesis of processes and evidence. Ecol Manage Restor 19:54–62. https://doi.org/10.1111/emr.12306

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than by size. Ecology 93(12):2533–2547. https://doi.org/10.1890/11-1952.1

Chazdon RL (2008) Beyond deforestation: restoring forest and ecosystem services on degraded lands. Science 320:1458–1460. https://doi.org/10.1126/science.1155365

Chazdon RL, Lindenmayer D, Guariguata MR, Crouzeilles R, Rey-Benayas JR, Lazos-Chavero E (2020) Fostering natural forest regeneration on former agricultural land through economic and policy interventions. Environ Res Lett 15(4):043002. https://doi.org/10.1088/1748-9326/ab97cc

Comisión Nacional del Agua (CONAGUA) (2016). Available from: https://smn.conagua.gob.mx/

Comisión Nacional para el conocimiento y uso de la Biodiversidad (CONABIO) (2010) El bosque mesófilo de montaña en México: amenazas y oportunidades para su conservación y manejo sostenible. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Distrito Federal, México

Cortéz-Gómez AM, Ruiz-Agudelo CA, Valencia-Aguilar A, Ladle RJ (2015) Ecological functions of Neotropical amphibians and reptiles: a review. Univ Sci 20(2):229–245. https://doi.org/10.11144/Javeriana.SC20-2.efna

Crouzeilles R, Ferreira MS, Chazdon RL, Lindenmayer DB, Sansevero JBB, Monteiro L, Iribarrem A, Latawiec A, Strassburg BBN (2017) Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. Sci Adv 3(11):e1701345. https://doi.org/10.1126/sciadv.1701345

Crump ML, Scott NJ (1994) Visual encounter surveys. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS (eds) Measuring and monitoring biological diversity. Standard methods for amphibians. Smithsonian Institution Press, Washington, DC, pp 84–92

Davies RW, Edwards DP, Edwards FA (2020) Secondary tropical forests recover dung beetle functional diversity and trait composition. Anim Conserv 23(5):617–627. https://doi.org/10.1111/acv.12584

Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecol News 17:133–146

Dent DH, Wright SJ (2009) The future of tropical species in secondary forests: a quantitative review. Biol Conserv 142(12):2833–2843. https://doi.org/10.1016/j.biocon.2009.05.035

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S, Mouquet N (2010) Defining and measuring ecological specialization. J Appl Ecol 47:15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x

Díaz-García JM, Pineda E, López-Barrera F, Moreno CE (2017) Amphibian species and functional diversity as indicators of restoration success in tropical montane forest. Biodivers Conserv 26:2569–2589. https://doi.org/10.1007/s10531-017-1372-2

Díaz-García JM, López-Barrera F, Pineda E, Toledo-Aceves T, Andresen E (2020a) Comparing the success of active and passive restoration in a tropical cloud forest landscape: a multi-taxa fauna approach. PLoS One 15(11):e0242020. https://doi.org/10.1371/journal.pone.0242020

Díaz-García JM, López-Barrera F, Toledo-Aceves T, Andresen E, Pineda E (2020b) Does forest restoration assist the recovery of threatened species? A study of cloud forest amphibian communities. Biol Conserv 242:108400. https://doi.org/10.1016/j.biocon.2019.108400

Domínguez-Haydar Y, Armbrecht I (2011) Response of ants and their seed removal in rehabilitation areas and forests at El Cerrejon coal mine in Colombia. Restor Ecol 19(201):178–184. https://doi.org/10.1111/j.1526-100X.2010.00735.x

Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. Conserv Biol 18(2):302–309. https://doi.org/10.1111/j.1523-1739.2004.00151.x

FAO and PNUMA (2020) El estado de los bosques del mundo 2020. Los bosques, la biodiversidad y las personas. Roma, Italy. https://doi.org/10.4060/ca8642es

Feinsinger P (2001) Designing field studies for biodiversity conservation. Island Press, Washington, DC

Fernandez-Barrancos EP, Reid JL, Aronson J (2017) Tank bromeliad transplants as an enrichment strategy in southern Costa Rica. Restor Ecol 25(4):569–576. https://doi.org/10.1111/rec.12463

Fife DA (2014) An introduction to the "fifer" package in R. R package version 1.0. Available at: https://CRAN.R-project.org/package=fifer

Flynn DF, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett 12:22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Fraser LH, Harrower WL, Garris HW, Davidson S, Hebert PDN, Howie R, Moody A, Polster D, Schmitz OJ, Sinclair ARE, Starzomski BM, Sullivan TP, Turkington R, Wilson D (2015) A call for applying trophic structure in ecological restoration. Restor Ecol 23:503–507. https://doi.org/10.1111/rec.12225

García-Martínez MA, Martínez-Tlapa DL, Pérez-Toledo GR, Quiroz-Robledo LN, Castaño-Meneses G, Laborde J, Valenzuela-González JE (2015) Taxonomic, species and functional group diversity of ants in a tropical anthropogenic landscape. Trop Conserv Sci 8(4):1017–1032. https://doi.org/10.1177/194008291500800412

García-Martínez MA, Martínez-Tlapa DL, Pérez-Toledo GR, Quiroz-Robledo LN, Valenzuela-González JE (2016) Myrmecofauna (Hymenoptera: Formicidae) response to habitat characteristics of tropical montane cloud forest in Central Veracruz. Mexico Fla Entomol 99(2):248–256

García-Martínez MA, Valenzuela-González JE, Escobar-Sarria F, López-Barrera F, Castaño-Meneses G (2017) The surrounding landscape influences the diversity of leaf-litter ants in riparian cloud forest remnants. PLoS One 12(2):e0172464. https://doi.org/10.1371/journal.pone.0172464

Gómez C, Abril S (2011). Selective logging in public pine forests of the central Iberian Peninsula: Effects of the recovery process on ant assemblages. For Ecol Manag 262(6):1061–1066. https://doi.org/10.1016/j.foreco.2011.05.043

Gatica-Saavedra P, Echeverría C, Nelson CR (2017) Ecological indicators for assessing ecological success of forest restoration: a world review. Restor Ecol 25(6):850–857. https://doi.org/10.1111/rec.12586

Gilroy JJ, Edwards DP (2017) Source-sink dynamics: a neglected problem for landscape-scale biodiversity conservation in the tropics. Curr Landsc Ecol Rep 2(1):51–60. https://doi.org/10.1007/s40823-017-0023-3

Gómez-Cifuentes A, Munevar A, Gimenez VC, Gatti MG, Zurita GA (2017) Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina. J Insect Conserv 21(1):147–156. https://doi.org/10.1007/s10841-017-9964-4

Gómez-Cifuentes A, Giménez-Gómez VC, Moreno CE, Zurita GA (2018) Tree retention in cattle ranching systems partially preserves dung beetle diversity and functional groups in the semideciduous Atlantic forest: the role of microclimate and soil conditions. Basic Appl Ecol 34:64–74. https://doi.org/10.1016/j.baae.2018.10.002

Groc S, Delabie JHC, Fernández F, Leponce M, Orivel J, Silvestre R, Vasconcelos HL, Dejean A (2014) Leaf–litter ant communities (Hymenoptera: Formicidae) in a pristine Guianese rainforest: stable functional structure versus high species turnover. Myrmecol News 19:43–51

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manag 148(1–3):185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Hanski I (2011) Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio 40:248–255. https://doi.org/10.1007/s13280-011-0147-3

Hernández-Ordóñez O, Urbina-Cardona N, Martinez-Ramos M (2015) Recovery of amphibian and reptile assemblages during old-field succession of tropical rain forests. Biotropica 47:377–388. https://doi.org/10.1111/btp.12207

Hernández-Ordóñez O, Santos BA, Pyron RA, Arroyo-Rodríguez V, Urbina-Cardona JN, Martínez-Ramos M, Parra-Olea G, Reynoso VH (2019) Species sorting and mass effect along forest succession: Evidence from taxonomic, functional, and phylogenetic diversity of amphibian communities. Ecol Evol 9(9):5206–5218. https://doi.org/10.1002/ece3.5110

Herrera-Montes A, Brokaw N (2010) Conservation value of tropical secondary forest: a herpetofaunal perspective. Biol Conserv 143(6):1414–1422. https://doi.org/10.1016/j.biocon.2010.03.016

Hethcoat MG, King BJ, Castiblanco FF, Ortiz-Sepúlveda CM, Prada-Achiardi FC, Edwards FA, Medina C, Gilroy JJ, Haugaasen T, Edwards DP (2019) The impact of secondary forest regeneration on ground-dwelling ant communities in the Tropical Andes. Oecologia 191:475–482. https://doi.org/10.1007/s00442-019-04497-8

Hilje B, Aide TM (2012) Recovery of amphibian species richness and composition in a chronosequence of secondary forests, northeastern Costa Rica. Biol Conserv 146(1):170–176. https://doi.org/10.1016/j.biocon.2011.12.007

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7(12):1451–1456. https://doi.org/10.1111/2041-210X.12613

Huerta C, Arellano-Gámez L, Cruz-Rosales M, Escobar-Sarria F, Martínez-Morales I (2016) Los escarabajos del estiércol en los potreros ganaderos de Xico. Instituto de Ecología, A. C, Xalapa/Veracruz, p 20

Huerta C, Arellano-Gámez L, Cruz-Rosales M (2018) Dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae) and dung removal in Mexican livestock pastures. Rev Mex Biodivers 89:1280–1292. https://doi.org/10.22201/ib.20078706e.2018.4.2495

Lamb D, Gilmour D (2003) Rehabilitation and restoration of degraded forests. IUCN, Gland, Switzerland and Cambridge, UK and WWF, Switzerland

Legendre P, Legendre L (2012) Numerical ecology. Elsevier Press, Amsterdam

Luría-Manzano R, Oropeza-Sánchez MT, Aguilar-López JL, Díaz-García JM, Pineda E (2019) Dieta de la rana de hojarasca *Craugastor rhodopis* (Anura: Craugastoridae): una especie abundante en la región montañosa del este de México. Rev Biol Trop 67(1):196–205. https://doi.org/10.15517/rbt.v67i1.33135

Luther D, Beatty CR, Cooper J, Cox N, Farinelli S, Foster M, Lamoreux J, Stephenson PJ, Brooks TM (2020) Global assessment of critical forest and landscape restoration needs for threatened terrestrial vertebrate species. Glob Ecol Conserv 24:e01359. https://doi.org/10.1016/j.gecco.2020.e01359

MacArthur R, Levins R (1964) Competition, habitat selection, and character displacement in a patchy environment. Proc Natl Acad Sci U S A 51(6):1207–1210. https://doi.org/10.1073/pnas.51.6.1207

Magee R (2019) Effects of leaf litter on amphibian site selection. College of Applied Natural Sciences. Louisiana Tech University. Master's Theses

Marchand L, Castagneyrol B, Jiménez JJ, Rey-Benayas JM, Benot ML, Martínez-Ruiz C, Alday JC, Jaunatre R, Dutoit T, Buisson E, Mench M, Alard D, Corcket E, Comin F (2021) Conceptual and methodological issues in estimating the success of ecological restoration. Ecol Indic 123:107362. https://doi.org/10.1016/j.ecolind.2021.107362

Meza-Parral Y, Pineda E (2015) Amphibian diversity and threatened species in a severely transformed neotropical region in Mexico. PLoS One 10(3):e0121652. https://doi.org/10.1371/journal.pone.0121652

Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME, The Scarabaeinae Research Network (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biol Conserv 141(6):1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011

Nsibi R, Souayah N, Khouja LM, Bouzid S (2006) La régénération naturelle par semis de la subéraie de Tabarka - Aïn Draham face aux facteurs écologiques et anthropiques. Geo-Eco-Trop 30(1):35–48

Oksanen J, Guillaume-Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn, D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016) Community ecology package "Vegan" for R. https://cran.r-project.org/web/packages/vegan/index.html

Ortega-Álvarez R, Lindig-Cisneros R, MacGregor-Fors I, Renton K, Schondube JE (2013) Avian community responses to restoration efforts in a complex volcanic landscape. Ecol Eng 53:275–283. https://doi.org/10.1016/j.ecoleng.2012.12.058

Osorio-Pérez K, Barberena-Arias MF, Aide TM (2007) Changes in ant species richness and composition during plant secondary succession in Puerto Rico. Caribb J Sci 43(2):244–253. https://doi.org/10.18475/cjos.v43i2.a9

Pyron RA (2018) Global amphibian declines have winners and losers. Proc Natl Acad Sci 115:3739–3741. https://doi.org/10.1073/pnas.1803477115

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reid LJ, Fagan ME, Zahawi RA (2018) Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. Sci Adv 4:eaas9143. https://doi.org/10.1126/sciadv.aas9143

Rey-Benayas JM, Bullock JM, Newton AC (2008) Creating woodland islets to reconcile ecological restoration, conservation and agricultural land use. Front Ecol Environ 6:329–336. https://doi.org/10.1890/070057

Rocha-Ortega M, García-Martínez MA (2018) Importance of nesting resources and soil conditions for the recovery of ant diversity during secondary succession in a tropical rainforest. Trop Conserv Sci 11:1–14. https://doi.org/10.1177/1940082918787063

Sandor ME, Chazdon RL (2014) Remnant trees affect species composition but not structure of tropical second-growth forest. PLoS One 9(1):e83284. https://doi.org/10.1371/journal.pone.0083284

Smith GC, Lewis T, Hogan LD (2015) Fauna community trends during early restoration of alluvial open forest/woodland ecosystems on former agricultural land. Restor Ecol 23:787–799. https://doi.org/10.1111/rec.12269

Suganuma MS, Durigan G (2021) Build it and they will come, but not all of them in fragmented Atlantic Forest landscapes. Restor Ecol:e13537. https://doi.org/10.1111/rec.13537

Thompson ME, Donnelly MA (2018) Effects of secondary forest succession on amphibians and reptiles: a review and meta-analysis. Copeia 106(1):10–19. https://doi.org/10.1643/CH-17-654

Tiede Y, Schlautmann J, Donoso DA, Wallis CIB, Bendix J, Brandl R, Farwig N (2017) Ants as indicators of environmental change and ecosystem processes. Ecol Indic 83:527–537. https://doi.org/10.1016/j.ecolind.2017.01.029

Toledo-Aceves T, Trujillo-Miranda A, López-Barrera F (2021) Tree regeneration in active and passive cloud forest restoration: functional groups and timber species. For Ecol Manag 489(1):119050. https://doi.org/10.1016/j.foreco.2021.119050

Trujillo-Miranda AL, Toledo-Aceves T, López-Barrera F, Gerez-Fernandez P (2018) Active versus passive restoration: recovery of cloud forest structure, diversity and soil condition in abandoned pastures. Ecol Eng 117:50–61. https://doi.org/10.1016/j.ecoleng.2018.03.011

van Klink R, Bowler DE, Gongalsky KB, Swengel AB, Gentile A, Chase JM (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368:417–420. https://doi.org/10.1126/science.aax9931

Warnes GR, Bolker B, Lumley T, Johnson RC (2018) Package ‘gmodels’: various R programming tools for model fitting for R. Available at: https://CRAN.R-project.org/package=gmodels

Whitworth A, Beirne C, Flatt E, Froese G, Nuñez C, Forsyth A (2021) Recovery of dung beetle biodiversity and traits in a regenerating rainforest: a case study from Costa Rica’s Osa Peninsula. Insect Conserv Divers 14:439–454. https://doi.org/10.1111/icad.12470

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York, p 260

Williams-Linera G, Toledo-Garibaldi M, Gallardo-Hernández C (2013) How heterogeneous are the cloud forest communities in the mountains of central Veracruz, Mexico? Plant Ecol 214(5):685–701. https://doi.org/10.1007/s11258-013-0199-5

Wortley L, Hero JM, Howes M (2013) Evaluating ecological restoration success: a review of the literature. Restor Ecol 21:537–543. https://doi.org/10.1111/rec.12028

WWF (2020) In: Almond REA, Grooten M, Petersen T (eds) Living planet report 2020 - bending the curve of biodiversity loss. WWF, Gland

Chapter 9
Ecohydrological Gradient in Neotropical Montane Ecosystems: From Tropical Montane Forests to Glacier

Conrado Tobón, Erick Castro, and Jorge Luís Ceballos

9.1 Introduction

Neotropical montane ecosystems are diverse and complex, ranging from glaciers, on top of highest mountains (above 4500 masl), with no vegetation at all, to páramo ecosystems with short vegetation (between 3000 and 4500 masl), mostly herbaceous and shrubs, and to montane forest with larger tree size and abundant epiphytes hanging from tree branches and attached to tree trunks (Tobón et al. 2010). Climate conditions affect these ecosystems in a different manner, which determines their soils (e.g. weathering, physical and chemical composition), vegetation and functioning, notably, the ecohydrological one (Tobón 2022a; Aparecido et al. 2018; Beck et al. 2008; Beck et al. 2008; Bruijnzeel and Lu 2001). Although Neotropical montane ecosystems are well known for their specific climate conditions, only until the last decades they are recognized by their importance as ecosystem service provider, mainly of fresh water and the large carbon storage in soils (Tobón 2022b; Bruijnzeel and Lu 2001). Albeit several hydrological and climate studies have been carried out in Neotropical regions (Tobón 2022a; Aparecido et al. 2018; Beck et al. 2008; Bendix et al. 2008; Wilcke et al. 2008), they concentrated on a specific individual ecosystem, but almost non comprised all ecosystems in the gradient of tropical montane forest to glaciers, where this gradient is characterized by changes on

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vegetation and environmental variables connected to the altitudinal decrease in precipitation and temperature, and the increase on air humidity and fog frequency. This environmental stratification may control plant diversity, ecosystem dynamics and functioning, with their partial contribution to water supply.

Retreat of tropical glaciers, through ice ablation and snowmelt, is one the most common processes occurring worldwide in the last decades (Veettil and Kamp 2019; Rabatel et al. 2013, 2018; Vuille et al. 2018; Buytaert et al. 2017; Zemp et al. 2015; Poveda and Pineda 2009; Ceballos et al. 2006), as these are very sensitive to global warming (Veettil and Kamp 2019; Chevallier et al. 2011; Thompson et al. 2011; Ruiz et al. 2008), consequently, most of them have already disappeared or are disappearing (Vuille et al. 2018), with an apparent consequence on water yield and water supply reduction, especially from tropical mountains where downwards ecosystems are dry (Veettil and Kamp 2019; Mark et al. 2017; Marulanda Aguirre et al. 2016; Rabatel et al. 2013; Kaser et al. 2010; Vuille et al. 2018; Bradley et al. 2006). However, in some tropical mountains, as those in Colombia, glaciers are not the main source of water for downstream population, as downwards ecosystems like paramos and montane forests also provide water for people living in the Andes (Tobón 2009, 2022a). Nevertheless glacier melt could affect in different ways downstream ecosystems, as paramos and montane forests (Rabatel et al. 2017), but this is still unknown.

Gradients in the Neotropics are found for several physical and ecological variables, which provide a spectrum of landscapes and biomes that may comprise worldwide tendencies. Most outstanding ones are: (i) the climate conditions (Tobón and Cárdenas 2023; Aparecido et al. 2018; Bendix et al. 2008; Martin et al. 2007), where rainfall varies from 750 to 3500 mm y^{-1} (Tobón and Cárdenas 2023; Bendix et al. 2008; Bruijnzeel and Lu 2001; Cavelier et al. 1996), and in several sites this increases through horizontal precipitation and fog inputs (Tobón 2009, 2022c; Bruijnzeel and Lu 2001), (ii) soils and their hydraulic and physical properties (Tobón 2022b; Wilcke et al. 2008a, b) and (iii) vegetation, with a general tendency to decrease in tree height and density with altitude, ranging from an average of 15 m height trees in tropical montane (Crausbay and Martin 2016; Prada and Stevenson 2016; Apaza-Quevedo et al. 2015; Martin et al. 2007), to around 1 meter height and herbaceous vegetation in paramos (Peyre et al. 2022, 2015).

Last but not the least are the ecohydrological gradients in these tropical montane ecosystems, where changes in environmental conditions controls some processes as evapotranspiration, rainfall interception (Tobón 2022d), and thus, water yield from these ecosystems (Aparecido et al. 2018; Morán-Tejeda et al. 2018; Marulanda Aguirre et al. 2016; Kaser et al. 2010; Wilcke et al. 2008a, b; Bradley et al. 2006). Nowadays, it is well known that disappearance of tropical glaciers may generate water scarcity, or at least considerably decrease the amount of water flowing from existent glaciers (Veettil and Kamp 2019; Morán-Tejeda et al. 2018; Buytaert et al. 2017; Marulanda Aguirre et al. 2016; Kaser et al. 2010; Vergara et al. 2007; Bradley et al. 2006). Adding to this, paramos and montane forest are widely known as large water yield Neotropical ecosystems (Tobón 2022a; Aparecido et al. 2018; Buytaert et al. 2011; Célleri and Feyen 2009). However, up to now, there are no ecohydrological studies that comprise these Neotropical ecosystems in a single one, which allows the understanding of the total ecohydrological contribution of these Neotropical montane ecosystems to total water yield.

Accordingly, in this study, we analyse the specific climatic and ecohydrological conditions of the three main Neotropical montane ecosystems in Colombia: glaciers, paramos and montane forests, and disclose the key parameters that control the ecohydrological functioning of these Neotropical montane ecosystems. Collected data from an entire elevational gradient at Río Claro basin within Los Nevados Natural Park (Colombia) allowed us for a comprehensive description of altitudinal climate and ecohydrological gradient and provides evidence of the role of climate, soils and vegetation drivers on ecosystem ecohydrological functioning, their specific role in Neotropical montane water cycle and ecosystem water yield.

9.2 Methodology

9.2.1 Study Sites

This study includes three ecosystems located above 2700 masl.: (i) tropical montane forest, also called cloud forest (Bruijnzeel 2004), (ii) paramos and (iii) glacier ice caps, in the uppermost headwaters of the Rio Claro basin (Fig. 9.1), which flows

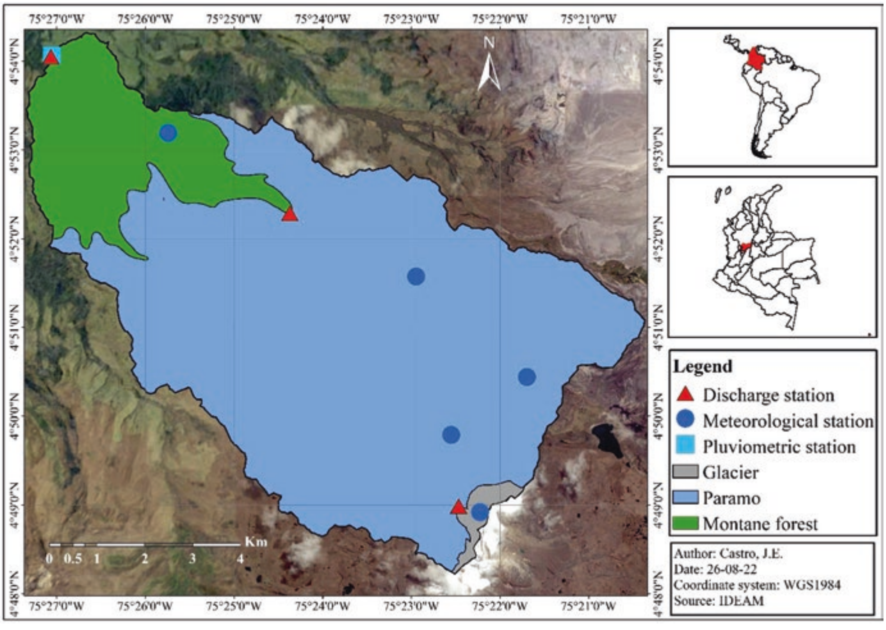

Fig. 9.1 Gradient of Neotropical ecosystems in Claro river basin of Colombia: glacier, paramo and montane forest areas and meteorological and hydrological stations are indicated

down through the three ecosystems and originates in the snowfields of the Conejeras glacier, as part of the Nevado Santa Isabel, located on the West flank of the Central Cordillera of Colombia, as part of the Nevados National Park (Fig. 9.1). The Santa Isabel glacier has been retreating since the nineteenth century, with an intensification of deglaciation since the middle of the twentieth century, and as a result, the glacier is now a set of separated ice fragments instead of a continuous ice mass, as it was two decades ago (IDEAM 2012). One of the fragments, located at the northeast sector of the glacier, is the Conejeras glacier, which is studied here, as being part of the Rio Claro basin, and whose elevation ranges between 4700 and 4895 m. In 2006, at the glacier terminus, hydro-meteorological stations were installed in order to measure weather conditions, glacier contribution to runoff and rainfall. Automatic weather and hydrological stations were also installed in the paramo and montane forest, following an altitudinal gradient (Fig. 9.1). The total area of the basin with studied gradient of ecosystems comprises an area of 71,5619 km^2, (0,8559 km^2 correspond to glacier, 51,0487 km^2 to paramo and 19,6573 to montane forest) (Fig. 9.1).

The part of the Claro river basin studied here comprises ecosystems located at altitudinal gradient between 2700 and 4895 m and, from highest to lowest part included in this study, presents a succession of typical Andean ecosystems: glacier and periglacial (4300–4894), paramo biome (3200–4300 m) and montane tropical forest ecosystem (2700–3200 m). The first step was to determine the basin area, and separately for each ecosystem considered in this study. Therefore, a detail high-resolution watershed area for the entire Claro river was created using cartography on a 1:25.000 scale, from where the specific delimitation of the basin was made and ecosystem areas were separated (Fig. 9.1).

9.2.2 Collected Data

Meteorological and hydrological data used in the present work have been collected by the Institute for Hydrological, Meteorological and Environmental Studies of Colombia (IDEAM) and Universidad Nacional de Colombia. Data on meteorological and hydrological variables, as precipitation, temperature and air humidity were collected through a network of automatic weather stations, located at different altitudes within the Rio Claro basin, from 2010 until 2021 (Fig. 9.1, Table 9.1). These data were collected on an hourly basis, from where daily, seasonally and yearly data were calculated. From meteorological data, actual evapotranspiration (ETa) was calculated for the paramo and montane ecosystems by using the Penman-Monteith (PM) equation and parameters values deduced for the paramo and montane forest vegetation (Tobón and Castro 2023). There are no lysimeter measurements of evaporation/sublimation ($Ls = 2.834 \times 10^6 \text{ J kg}^{-1}$) available for the studied glacier, therefore this was calculated from the latent heat of sublimation for snow/ice at zero degrees (Armstrong and Brun 2008; Wagnon et al. 1999). Data on stream discharge

Table 9.1 Meteorological and hydrological stations to measure weather conditions and stream discharge gradients in Neotropical basin (Río Claro), between 2010 and 2021

Ecosystem	Station type	Location	Altitude (m)	Average annual rainfall (mm)	Average annual temperature (°C)	Average annual relative humidity (%)
Glacier	Meteorological (MMA)	4° 48′ 59″ N 75°22′ 25″ W	4759	754.2 ± 36.6	0.10 ± 2.7	95.6 ± 9.1
Glacier	Meteorological (Conejeras)	4°48′59.16″N 75°22′28.02″W	4699	887.2 ± 40.8	1.09 ± 1.5	94.9 ± 8.6
Paramo	Meteorological (Sendero Laguna Verde)	4°50′26.4″N 75°21′41.76″W	4325	978.9 ± 209.2	3.8 ± 2.6	88.6 ± 12.0
Paramo	Meteorological (Conejeras)	4°49′47.4″N 75°22′33″W	4304	1211.10 ± 204.4	3.4 ± 1.9	ND
Paramo	Meteorological (PNN Los Nevados)	4°51′34.5″N 75°22′56.7″W	3637	972.3 ± 424.2	7.8 ± 2.5	84.9 ± 12.5
Montane forest	Meteorological (San Antonio)	4°53′11.46″N 75°25′44.52″W	3052	1406.8 ± 475,7	10.5 ± 3.0	92.9 ± 7.9
Montane forest	Pluviometric (Río Claro)	4°54′3,18″N 75°27′3,96″W	2714	1387.30 ± ND	ND	ND
Glacier[a]	Discharge (Conejeras)	4°48′59,16″N 75°22′28,02″W	4699			
Paramo[a]	Discharge (Sietecuerales)	4°51′34″N 75°22′56″W	3450			
Montane forest[a]	Discharge (Río Claro)	4°54′3.18″N 75°27′3.96″W	2714			

[a] Stations to measure discharge only

were collected at three elevations along the Claro river within the basin, by installing Parshall gauges in the main stream of Claro river, equipped with OTT Hydromet equipment (OTT Hydromet Co.) to measure the water level (Table 9.1) each minute, and average data was recorded every 15 minutes since 2010 until 2021. Data was converted to a water volume ($m^3\ s^{-1}$) and water depth (mm) through in situ calibration by volumetric discharge measurements and the construction of a flow rate curve for each station.

In this study we concentrated on analysing the measured discharge from each studied ecosystem, which is, the amount of water flowing down from the three different ecosystems in this Neotropical gradient: glacier, paramo and montane forest, and compare the water outputs with inputs in each ecosystem. This was done by calculating the different hydrological indices (Table 9.2) to characterize streamflow responses of individual ecosystem to rainfall events.

Table 9.2 Hydrological indices to evaluate streamflow responses to rainfall events

Index	Equation	Description
Runoff ratio	$Wy = \frac{Q}{P}$	It is the ratio between the total discharge (Q) and precipitation (P), both in mm (Chang 2013)
Runoff coefficient (%)	$\mathrm{Rc} = \frac{\mathrm{Qr}}{P} \times 100$	It is the ratio between stormflow or fast runoff (Qr) and precipitation (P) in mm. This coefficient indicates how fast an ecosystem responds to rainfall events (Singh and Eng 2017)
Base flow index (%)	$\mathrm{BFI} = \frac{\mathrm{Qb}}{\mathrm{Qt}} \times 100$	It is the ratio of daily base flow discharge (Qb) and the daily total discharge (Qt) in mm (Stoelzle et al. 2020)
R-B flashiness index	$R - Bi = \frac{\sum_{i=1}^{n} \lvert q_i - q_{i-1} \rvert}{\sum_{i=1}^{n} q_i}$	It provides a meaningful characterization of the way a given basin converts rainfall into streamflow (Baker et al. 2004)
Water regulation index (%)	$\mathrm{IRH} = \frac{\Sigma Q_{Q<50}}{\Sigma Q}$	This is the volume of water below the 50th percentile (Q50) in the flow duration curve divided by total volume (Qt) (IDEAM 2014)
1st quartile of the distribution of de FDC	$Q25 = \frac{\sum_{i=1}^{Q25} q_i}{N_{q<Q25}}$	It is the average of discharge occurring during 25% of the time from the Flow Duration Curve (FDC), and it describes the mean discharge with less probability of exceedance
3rd quartile of the distribution of the FDC	$Q75 = \frac{\sum_{i=1}^{Q75} q_i}{N_{q<Q75}}$	It is the average of discharge occurring under 75% of the time from the FDC

9.2.3 Data Analysis

For a better understanding of gradient distribution of discharge, measured rainfall at the different sites was spatialized separately for the glacier, paramo and montane forest. This was carried out through Invers Distance Weight (IDW method), which is a deterministic method based on the assumption that the depth of rainfall at unmeasured sites is equal to the distance weighted average of data points occurring within a neighbourhood of measured sites (Albert et al. 2014; Di Piazza et al. 2011). Thus, through this method, the total rainfall for every point at each ecosystem was calculated using Eq. (9.2) $z(x) = \sum_{i=1}^{N} w_i z_i$

Where $z(x)$ is the estimated value of rainfall for the total area at issue, w_i is the weight expressed as function of distance. The function of distance is determined by the Eq. (9.3):

$$w_i = \frac{\frac{1}{d_{ik}}}{\Sigma_i^n \frac{1}{d_{ik}}}.$$

Where d_{ik} is the distance of every point (station) to the centroid of the zone or catchment, and n is the number of stations. From the annual amounts of precipitation and discharge measurements made at each gauge station (Table 9.1), annual and average water yield was calculated as the relationship between annual discharge and annual rainfall, from which standardized water yield ($\text{m}^3\ \text{ha}^{-1}\ \text{year}^{-1}$) was deduced, using the area occupied by each ecosystem in the studied basin. Discharge measurements also allowed for the calculations of daily discharge (mm d^{-1}) and average daily streamflow ($\text{m}^3\ \text{s}^{-1}$). To determine the hydrological gradient as the responses of individual ecosystems to rainfall events, two approaches were followed: (1) the separation of streamflow flowing down from each ecosystem and (2) the hydrological response analysis through hydrological indices (Table 9.2). Streamflow separation was carried out for individual events, as the direct response of ecosystem to rainfall events or stormflow and delay fluxes of water or base flow. To this purpose, a specific technique was carried out by means of *Recursive Digital Filter technique* proposed by Lyne and Hollick (1979): $\text{Qb} = \propto q_{t-1} + \frac{(1+\propto)}{2}(Q_t - Q_{t-1})$,

Where Qb is the filtered quick response at kth sampling instant, $qt - 1$ is the filtered quick response at the previous instant ($t - 1$), α is a filer parameter (dimensionless), Q_t is the original streamflow and Q_{t-1} is the total discharge at the previous instant ($t - 1$).

As glacier melting seems to be the most important process worldwide, mainly in the tropics (Cepeda Arias et al. 2022; de Vries et al. 2022; Thompson et al. 2021; Xin et al. 2021; Braun et al. 2019; da Rocha et al. 2019; Dussaillant et al. 2019; Seehaus et al. 2019; Veettil and Kamp 2019; Morán-Tejeda et al. 2018; Wu et al. 2015; Zhang et al. 2011; Fujita et al. 2006), therefore a relationship between discharge from the glacier and air temperature was searched by means of regression analysis. The regression model (Eq. 5) estimated the daily discharge (dependent variable, y) in function of temperature (independent variable, x).

$$y = \beta o + \sum_{i}^{N} a_i X_i \,,$$

where a_i is the ith regression model parameter and X_i is the daily temperature.

9.3 Results

Climate in the entire gradient is normally inter-tropical and it is mainly characterized by small fluctuations in inter-annual temperatures but large daily temperature fluctuations. In studied gradient, rainfall displays a bimodal regime during the year due to the influence of the intertropical convergence zone (ITCZ) and the mountainous terrain of the region, with two seasons with higher rainfall (March to June and October to December) and two with lower rainfall amounts (December to early March and July to early September). The climate gradient in these Neotropical montane ecosystems is characterized by a gradual decrease in temperature as altitude increases, which is related to the adiabatic process undergone by air masses, which tend to expand and decrease in temperature with altitude, which in turn controls cloud formation and thus precipitation, partly determining the water entering and the supply from these ecosystems (Tobón and Cárdenas 2023). In addition, there is a low thermal oscillation on an annual scale, but a considerable wide range on a daily scale (Tobón and Cárdenas 2023), with sudden changes in meteorological conditions, which are determined by the presence of low clouds or fog, which cover these ecosystems and temporarily modify the atmospheric weather conditions. Average values for annual rainfall, air temperature and relative humidity of air are presented in Table 9.1 for the studied ecosystems.

In the studied Neotropical gradient, rainfall presents a large spatial variability between individual events, despite the fact that all rain gauges were located with the same exposure within the studied basin (towards the west side). Moreover, there were statistically significant differences ($p < 0.05$) in annual rainfall inputs to the three ecosystems located at different altitudes, showing a decrease on total annual rainfall as altitude increases (Table 9.3). In table 3 we present the average, maximum and minimum values of annual rainfall, and the rainiest day during the studied period, and for the entire gradient ecosystems. For all ecosystems, during the study period, 2013 was the wettest year and 2015 the year with the lowest precipitation. Similarly, most of the events were of low intensity and magnitude (most with rainfall between 0.2 and 0.8 mm being the lowest in the glacier and paramo ecosystems, respectively). Completely dry days, with no precipitation events are uncommon in the entire gradient, but dry days (with rainfall lower than 0.8 mm) normally occur between December to March and August to September, among which, January is on average the month with the highest number of dry days, followed by February.

Table 9.3 Maximum, minimum, and mean values for rainfall, temperature, relative air humidity and evaporation/evapotranspiration occurring at the Neotropical gradient of ecosystems in Colombia

Variable	Glacier	Paramo	Montane forest
Maximum annual rainfall (mm)	1157.3 (2011)	1583.8 (2011)	2064.4 (2011)
Mean annual rainfall (mm)	870.2 ± 43	1296 ± 106	1580 ± 206
Minimum annual rainfall (mm)	750.3 (2015)	948.9 (2015)	1387.3 (2015)
Rainiest day (mm day^{-1})	9.8 (2014)	58.5 (2010)	58.4 (2010)
Maximum daily temperature °C	11.3 (12:00 hours)	21.7 (13:00 hours)	24.9 (14:00 hours)
Mean daily temperature °C	0.33 ± 1.6	5.4 ± 3.1	10.58 ± 2.98
Minimum daily temperature °C	−9.3 – at night time	−2.6 – at night time	2.3 at night time
Maximum relative humidity (%)	100 (at least once a day)	100 (at least once a day)	100 (at last once a day)
Mean relative humidity (%)	94.8 ± 10.4	85.1 ± 11.7	92.93 ± 7.40
Minimum relative humidity (%)	60 (13:00 hours)	50 (15:00 hours)	40 (15:00 hours)
Maximum annual evaporation/ evapotranspiration (mm)	245.6 (2015)	443.3 (2015)	789.1 (2015)
Mean annual evaporation/ evapotranspiration (mm)	170.6 ± 21.5	378.6 ± 41.2	567.7 ± 72.3
Minimum annual evaporation/ evapotranspiration (mm)	148.7 (2011)	315.4 (2011)	498.7 (2011)

9.3.1 Temperature

Annual average temperature for the different sites in studied Neotropical gradient is presented in Table 9.1. Differences among sites within the same ecosystem were not significant ($p \geq 0.05$); however, annual average values were significantly different among ecosystems ($p < 0.05$), but also in the maximum and minimum values registered at each one (Table 9.3). Except for the glacier, in studied Neotropical ecosystems, temperature decreases at a rate of 0.89 °C at each 100 m of altitude, and the greatest amplitude of diurnal variation of temperature was observed in the paramo (a difference of 18.9 °C in the same day), as compared with the other two biomes (Table 9.3). Maximum, minimum and annual average values of daily temperature at the studied gradient of ecosystems are presented in Table 9.3. During the studied period and for the entire gradient, the warmer years were 2015 and 2016, respectively, in which the number of warm nights (temperatures above 5 °C) increased considerably compared to the overall average, which appeared to be related to the ENSO phenomena occurring between 2015 and 2016 (IDEAM 2016). In general, in the entire gradient, the maximum extreme temperature values occurred in January and eventually, in September. In contrast, the coldest ones were 2011 and 2019, but lowest temperature tended to occur annually between December and February. For the glacier, negative temperatures are normal throughout the year, but almost not for the montane forest (Table 9.3). As a general tendency, in the studied Neotropical gradient, there is a daily tendency of having low temperatures between 00:00 and 5:00 hours, which increases during early mornings, reaching a maximum around 12:00 hours for the glacier, 13:00 hours for the paramo and around 14:00 hours in the montane forest (Table 9.3).

9.3.2 Relative Air Humidity

Relative air humidity in studied Neotropical ecosystems does not have a gradient in any direction: lowest relative air humidity in time was registered in the glacier and the highest, through the time, occurred in the paramo; moreover, some very high air humidity, close to saturation (above 98%) was common at all ecosystems, and almost every day (Table 9.3). This variable has a negative asymmetric distribution or negative bias, which indicates that there is a greater possibility of finding values above the mean (87.8 ± 9.4%) in studied ecosystems. Predominantly, increases in air humidity in this Neotropical gradient of ecosystems were related to the presence of rain, fog or both, reaching saturation conditions in most cases and exhibiting stability conditions for several hours, independently of diurnal or nocturnal hours. Nonetheless, the stability was longer during the night and early morning. Air humidity ranged from 60% to 100% in the glacier, from 50% to 100% in the paramo and between 60% and 100% in montane forest. The averages of maximum, mean and minimum annual values are presented in Table 9.3. The largest range of variation of relative humidity in a single day was 61%, occurring in the paramo and the lowest was 5%, occurring both, in the paramo and montane forest, mainly between April and July and in November of each year, except at the end of 2015 and first months of 2016, when air humidity was the lowest, which could be related to the effects of the ENSO phenomenon (2015) on the national territory (IDEAM 2016). Although

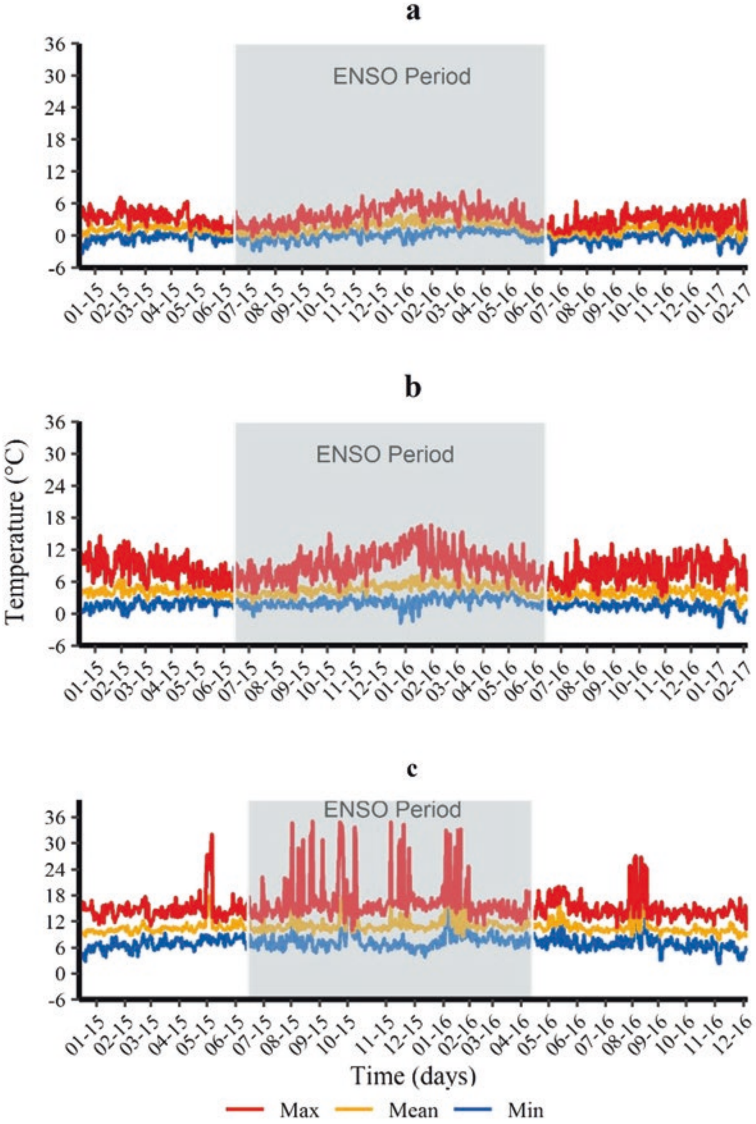

Fig. 9.2 Temporal behaviour of maximum, minimum and average values of temperature in studied gradient of Neotropical ecosystems in Colombia ((**a**) glacier, (**b**) paramo, (**c**) montane forest), during the ENSO phenomena occurring from 2015 to 2016

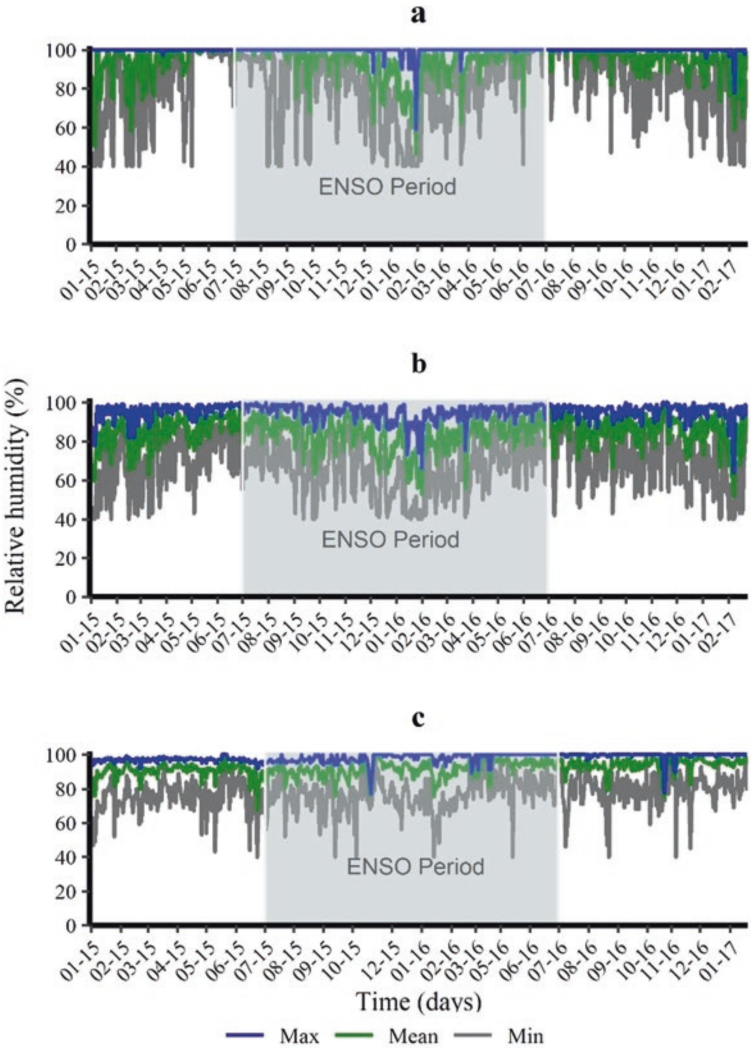

Fig. 9.3 Temporal dynamics of maximum, minimum and average values of relative air humidity in a gradient of Neotropical ecosystems in Colombia ((**a**) glacier, (**b**) paramo, (**c**) montane forest), during the ENSO phenomena occurring from 2015 to 2016

temperature showed a seasonal behaviour, with the highest temperature normally between December to March, for the three ecosystems studied here, the ENSO phenomenon introduces a noise, which considerably increases on air temperature (Fig. 9.2), and decreases slightly on relative air humidity (Fig. 9.3) between August 2015 and April 2016, with maximum temperatures in December (2015) and March (2016) in the three ecosystems. Minimum temperatures and air humidity values also increased on the average, resulting in less frequent negative temperatures mainly in the paramo.

9.3.3 Evaporation and Evapotranspiration

In Table 9.3, we present the annual average, maximum and minimum values of evaporation (sublimation) calculated for the icecap of Conejeras, according to Armstrong and Brun 2008; Wagnon et al. 1999) and field measurements of radiation. Values for evapotranspiration calculated for the paramo and montane forest are shown in Table 9.1. Statistically significant differences ($p < 0.05$) were found for average values encountered in the three ecosystems. Moreover, results indicate that there is a gradient on water losses through evaporation/evapotranspiration in studied ecosystems, where montane forest presents the largest water losses through evapotranspiration and the glacier the lowest by calculated sublimation.

9.3.4 Streamflow

Found values of streamflow responses of each ecosystem to rainfall events, as water yield, baseflow and stormflow. Runoff ratio and coefficient and discharge indices are shown in Table 9.4. The hydrological response of the glacier is significantly different from the other two ecosystems ($p < 0.05$), given that its streamflow generation was constantly above total entering rainfall (larger than 100% rainfall inputs), which is indicated by the Runoff coefficient (Table 9.4), while in the paramo, the value for this parameter is less than 4% (Table 9.4), implying that about 96% of total rainfall infiltrates in the soil. This different behaviour is also evidenced in the Base Flow index, which shows that the lowest value was found for the glacier, as compared with the other two ecosystems (Table 9.4). During the study period, the largest annual water yield per hectare was observed from the glacier, as compared with the other two ecosystems in studied gradient (Table 9.4). However, it is important to

Table 9.4 Average values of streamflow parameters and indices found for the biomes studied in a gradient of Neotropical montane ecosystems in Colombia

Hydrological response index	Glacier	Paramo	BAA
Water yield (m^3 ha^{-1} $year^{-1}$)	29,624.3	4905.4	5050.6
Base flow water yield (m^3 ha^{-1} $year^{-1}$)	9883.0	4467.2	4177.8
Stormflow water yield (m^3 ha^{-1} $year^{-1}$)	20,055.6	438.2	872.8
Mean daily discharge (mm d^{-1})	8.66 ± 6.5	1.46 ± 0.2	2.56 ± 1.2
Mean daily streamflow (m^3 s^{-1})	0.02 ± 0.02	0.28 ± 0.04	1.87 ± 1.1
Runoff ratio	1.2	0.8	0.5
Runoff coefficient (%)	215.6	3.4	15.4
Base flow index (%)	36.0	96.0	86.8
R-B Flashiness Index	0.3	0.03	0.1
Water regulation index, IRH (%)	30.7	96.5	85.2
Q25 (mm d^{-1})	12.29 ± 5.6	1.67 ± 0.2	4.03 ± 1.7
Q75 (mm d^{-1})	8.73 ± 6.5	1.51 ± 0.2	2.82 ± 1.3

understand from Fig. 9.1 that the actual area of this glacier is less than 15 ha, which renders a very low value for total water yield. Moreover, most of this water yield flowed out of the glacier as a stormflow, during rainfall events (Table 9.4). In contrast, most of the total water yield from the paramo and montane forest ecosystems flowed out as base flow.

According to the results for the R-b Flashiness index, there was large variation in the daily discharge among studied ecosystems, where values range between 0.3 and 0.03. Largest values indicate high variation of discharge amounts, while low ones are an expression of stability in the discharge regimes, and values close to 0 indicate the permanence of stable discharges (e.g. paramo biome). To illustrate these dynamics, we deduced a flow duration curve for the three ecosystems (Fig. 9.4). Differences among ecosystems are evident from the 10% of the total daily flow distribution (decile). Despite the flow duration curve bringing similar quantities on the first decile (10%) for studied ecosystems, it does not mean the same moment of occurrence. It is worth noting that the glacier protrudes a shape of “false” high-water regulation, as the daily discharge values remained higher during more than 60% of the time, whereas the rest of the time, it descends to the lower values of discharges, meaning nothing but that base flow or the permanent flow is highly contrasting with the flows with low probability of exceedance. It is important to stress that in the glacier, the base flow belongs exclusively to the ice and snow melting, since there is no evidence for soil presence under the ice. In contrast, paramo and montane forest present a constant slope throughout their daily discharge distribution, but the last presents a greater slope and a lower magnitude of daily discharges (Fig. 9.4).

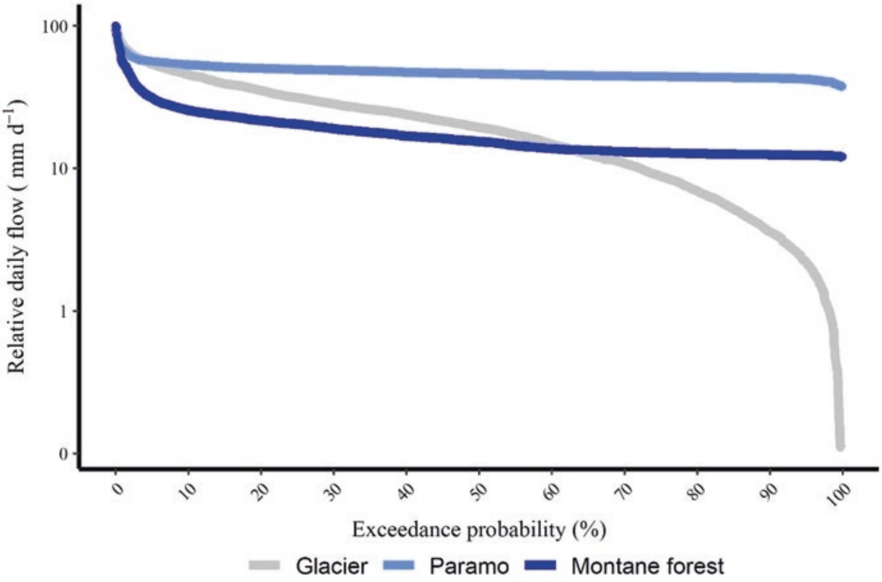

Fig. 9.4 Curves for the probability of exceedance of the daily water flow from the gradient of studied Neotropical montane ecosystems

Results of mean daily streamflow from each ecosystem indicate that the largest value is observed from the glacier, being four to six times larger than ones from montane forest and paramo, respectively (Table 9.4, Fig. 9.5), but the probability of exceeding this streamflow is lower from the glacier (16.4%) as compared from the other two ecosystems, which present a similar probability between them (39.7% and 34.2% from the paramo and montane forest, respectively). Noticeable, the glacier presents the highest amount of water by unit of area during the first and third quartile of the of the total distribution of the FDC (Q25 and Q75), as compared to the Paramo and the High Andean Forest ecosystems (Fig. 9.5), which is the result of snow and ice melting throughout the studied time, as indicated above. However, we

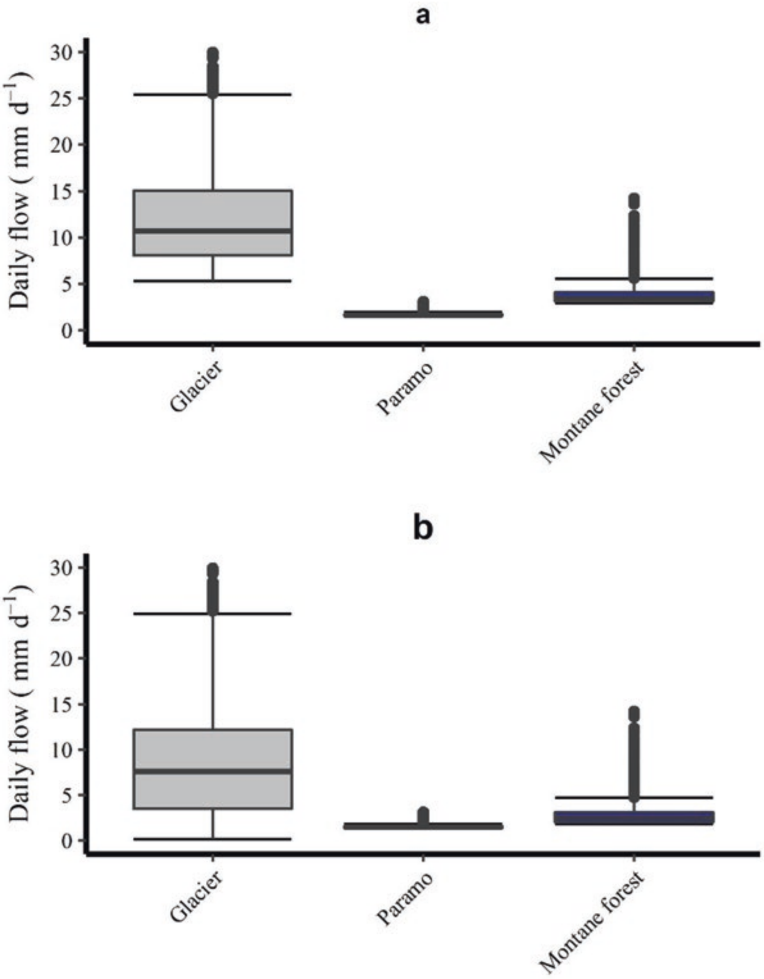

Fig. 9.5 Temporal behaviour of water flow from studied ecosystems located in an altitudinal gradient in the Neotropical environment. (**a**) Q1 (25%) and (**b**) Q3 (75%)

may take into account that some of past snow and ice coming to the glacier, accumulated on top of these mountains, which in fact acted as a regulation system for water yield today, when local environmental conditions are changing. Nevertheless, the distribution of this water yield presents low variation in the paramo, as it is illustrated in the small change in the interquartile range (Fig. 9.5), whereas the glacier changes meaningfully. The aforementioned brings a perception of stability of the discharges at the Paramo zone.

Figure 9.6 shows the temporal dynamics of daily discharge from studied gradient of ecosystems during the studied period. Daily discharge distribution from each ecosystem presented a large variability, the largest being the one from the glacier (Fig. 9.6). Average daily discharge from the glacier was about 0.02 ± 0.02 m^3 s$^{-1,}$ with a range between 0.00013 m^3 s^{-1} and 0.1 m^3 s^{-1}. The Paramo presented a mean discharge of 0.28 ± 0.04 m^3 s^{-1}, with values ranging from 0.18 m^3 s^{-1} and 0.62 m^3 s^{-1}, while mean daily discharge from the montane forest was 1.87 ± 1.08 m^3 s^{-1} with a range varying from 0.98 m^3 s^{-1} and 11.53 m^3 s^{-1} (Table 9.3). Discharge responses during the ENSO period (El Niño and La Niña South Oscillation) is highlighted in Fig. 9.6. According to the National Unity for the Disaster Risk Management (UNGRD), El Niño phenomenon was presented chiefly between July 2015 and July 2016 at Colombia, and La Niña between July 2010 and May 2011 (UNGRD 2016). During these events, discharge observed a distinctive behaviour through the gradient, as compared with average time conditions (Fig. 9.6). During El Niño time, there was clearly an increase in daily discharge from the glacier, with values 1.5 to 2.3 times higher than during times of average conditions. Moreover, the largest increase of discharge in studied gradient were observed from October 2010 until the half of 2011, with increments up to 2.3 times the average discharge, the largest being the one from the glacier (Table 9.3). It is important emphasize that one of the streamflow sources is the glacier melt, and during the augmentation of temperature that El Niño generates, and the evident response on discharge behaviour is evident from the glacier. Results from the regression analysis between air temperature and discharge from the glacier, as the result of ice and snow melting due to air temperature, indicated that there is a significant relationship between the discharges of the glacier and the temperature ($p < 0.05$) with a Pearson's coefficient of 0.34 (Table 9.5).

9.4 Discussion

Most ecohydrological studies in the Neotropics, as well in other latitudes, were done in a specific ecosystem (Tobón 2022a; Tobón and Bruijnzeel 2021; Rodríguez-Morales et al. 2019; Aparecido et al. 2018; Buytaert et al. 2017; Tobón 2009; Beck et al. 2008; Bendix et al. 2008; Wilcke et al. 2008a, b, Bruijnzeel and Lu 2001), although some included different ecosystems in a given gradient (Buytaert et al. 2011; Beck et al. 2008; Martin et al. 2007; Bendix et al. 2004; Cavelier 1996), but not including the three uppermost ecosystems in the Neotropics. This study allowed us to reveal the ecohydrological role of each one of these ecosystems, thus

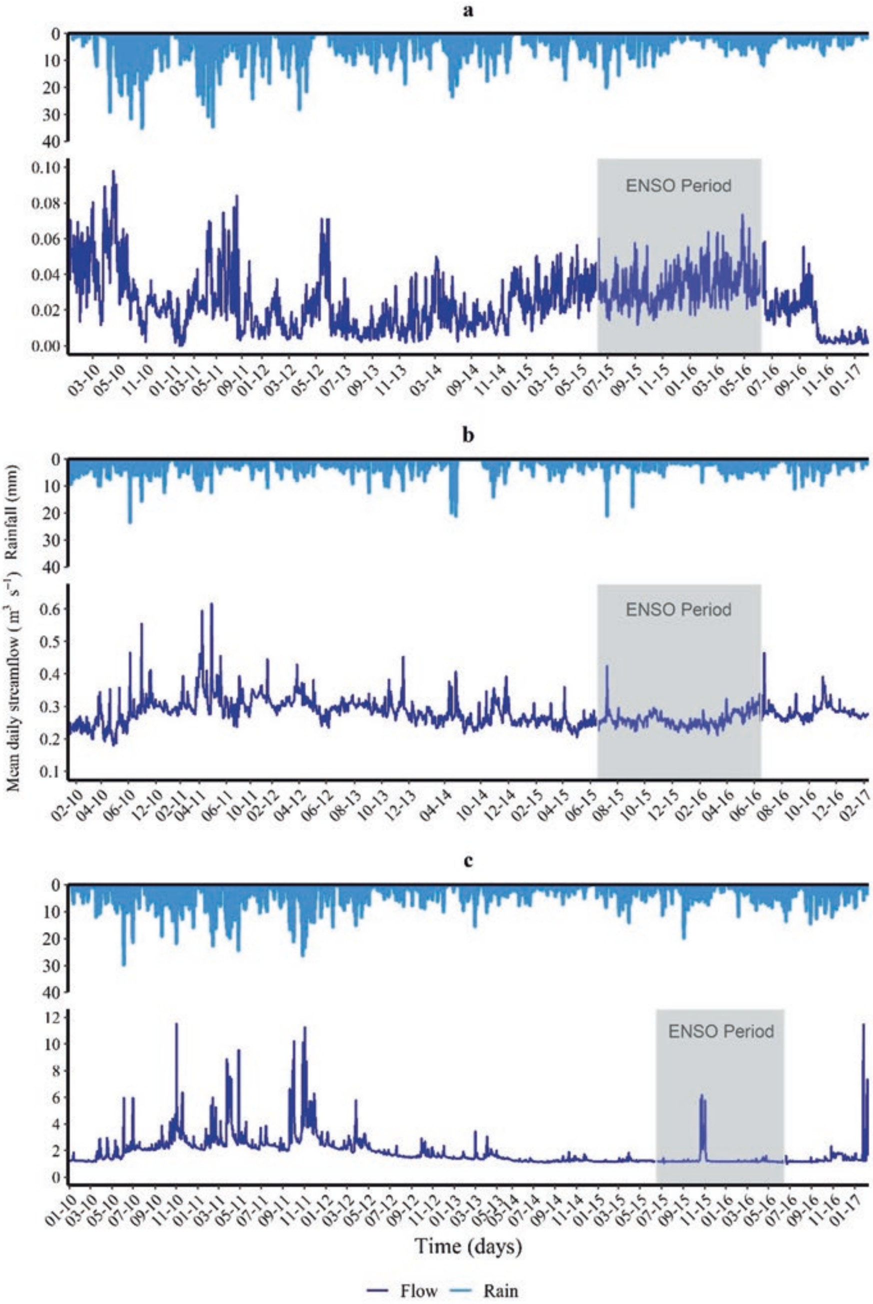

Fig. 9.6 Temporal dynamics of discharge from the Neotropical gradient of montane ecosystems, during the ENSO period, 2015–2016. Glacier (**a**), paramo (**b**) and montane forest (**c**)

Table 9.5 Results from the regression model analysis between air temperature and discharge from the glacier in the studied Neotropic gradient of ecosystems

Correlation coefficient	*t*	Degrees of freedom	*P* value	Confidence interval
0.34	14.79	1660	<2e-16	0.30–3.38

clarifying the real hydrological effects of glacier extinction on water yield, and the specific ecohydrological contribution of neighbouring ecosystems.

Based on measured weather variables, the studied ecosystems present a gradient on rainfall annual amounts and temperature conditions, both decreasing with altitude. This is similar to that described in other gradient analysis in the tropics (Sierra et al. 2015; Cavalcanti and Shimizu 2012; Buytaert et al. 2011; Poveda et al. 2011; Beck et al. 2008; Bendix et al. 2004; Cavelier 1996). Nonetheless, a clear shift on rainfall amounts occurs in studied altitudinal gradient, decreasing from the montane forest to the glacier, implying that the higher the ecosystem in the altitudinal gradient, the lower the inputs by rainfall and air temperature. Nevertheless, the fog and low clouds covering the ecosystems may contribute differently to inputs at each ecosystem according to their frequency and density (Berrones et al. 2022; Tobón 2022c; Cárdenas et al. 2017). Fog is a common feature in studied ecosystems; however, depending on its frequency, and therefore its contribution to total water inputs to the ecosystems, it seems to be higher in paramos than to other Neotropical montane ecosystems (Berrones et al. 2021, 2022; Tobón 2022c; Cárdenas et al. 2017), but there is no data available for fog inputs in Neotropical gradient, and existing studies for fog inputs to cloud forest (montane forest) may indicate the contrary (Aparecido et al. 2018; Tobón 2009; Bendix et al. 2004; Bruijnzeel and Lu 2001; Bruijnzeel and Veneklaas 1998). In any case, its contribution, as an extra water input to these ecosystems, is known worldwide (Tobón 2022a; Bruijnzeel et al. 2010; Bruijnzeel and Lu 2001).

From the glacier discharge measurements, we observed a daily streamflow cycle, which seems to be related with the ablation and accumulation dynamics presented in the Conejeras glacier (Morán-Tejeda et al. 2018). Nevertheless, these cycles were not observed at the other two measurement sites (Sietecuerales and Rio Claro stations), which implies that amounts of water added from the last mask the one from the glacier, given their larger magnitudes. Temporal dynamics of discharge from studied ecosystems normally responds to rainfall dynamics (Fig. 9.6), as it does in other ecosystems (Tobón and Castro 2023; López-Ramírez et al. 2020; Zhai et al. 2020; Guan et al. 2016; Penna et al. 2016; Crespo et al. 2011; Poveda et al. 2011). However, glaciers seem to have a differential hydrological functioning as ice and snow melting contribute considerably to the discharge (Veettil and Kamp 2019; Morán-Tejeda et al. 2018; Vuille et al. 2018; Buytaert et al. 2017; Mark et al. 2017; Chevallier et al. 2011; Marulanda Aguirre et al. 2016; Penna et al. 2016; Rabatel et al. 2013; Kaser et al. 2010; Bradley et al. 2006; Gutiérrez et al. 2006).

Although the glacier zone is capable of producing the highest quantity of water by unit of area both 25% and 75% of the time compared to the Paramo and montane forest, its very small area protrudes in a very low contribution to total streamflow in the studied gradient of ecosystems. Moreover, results here indicate that the discharge from the glacier is mostly related to snow and ice melting, according to the large values for mean daily discharge (8.66 mm d^{-1}), which is 4–5 times larger than the one in paramo and montane forest ecosystems, even during no rainfall events (Table 9.4), but also the large runoff ratio above the unit (Table 9.4), implying either a melting contribution or an extra water input to the basin. The last must not be the case, as rainfall inputs to the glacier are lower than to the other two ecosystems (Table 9.1). Moreover, a considerable discharge is flowing down from the glacier, even during the dry periods, a process that is more common in recent decades and has been widely explained by several authors, and is to be connected to ice and snow melting (Cepeda Arias et al. 2022; de Vries et al. 2022; Thompson et al. 2021; Xin et al. 2021; Braun et al. 2019; da Rocha et al. 2019; Dussaillant et al. 2019; Seehaus et al. 2019; Veettil and Kamp 2019; Morán-Tejeda et al. 2018; Wu et al. 2015; Chevallier et al. 2011; Zhang et al. 2011; Fujita et al. 2006). Moreover, ice and snow melting from the studied Conejeras glacier has been observed by different authors (de Vries et al. 2022; Braun et al. 2019; Morán-Tejeda et al. 2018; Johansen et al. 2018; Albert et al. 2014; Rabatel et al. 2013; Ceballos et al. 2006), which explains the high runoff ratio of 1.2 found from the glacier discharge, despite its very low mean daily streamflow, as compared with that from the paramo and montane forest (Table 9.4).

Results here show that the studied glacier is melting throughout the years, which explains its current large discharge as compared to rainfall annual inputs, indicating that if the trend continues as it is occurring now, this glacier will disappear soon (Morán-Tejeda et al. 2018; Rabatel et al. 2018; Vuille et al. 2018; Poveda and Pineda 2009; Ceballos et al. 2006), with important consequences for water supply to the local population, as concluded by several authors (Cepeda Arias et al. 2022; Veettil and Kamp 2019; Morán-Tejeda et al. 2018; Johansen et al. 2018; Vuille et al. 2018; Marulanda Aguirre et al. 2016; Chevallier et al. 2011; Vergara et al. 2007; Bradley et al. 2006; Gutiérrez et al. 2006), whose studies comprise the glaciers only, without considering the ecohydrological functioning of neighbouring ecosystems.

Contrary to those findings, after including the entire gradient of Neotropical montane ecosystems in an ecohydrological survey, this study demonstrates that disappearance of small glaciers, such as the Conejeras one, located in humid gradients (e.g. Claro river basin), the extinction of a glacier will not threaten the water supply, nor water availability for people downstream. The found low values for streamflow indices (Table 9.4) and the very small area of the glacier (0.8559 km^2) clearly indicates that in this gradient of ecosystems, paramos and montane forest are the main water source in the studied basin, mainly due to their large rainfall inputs and large exposed areas. Although runoff alterations are expected to occur once this glacier disappears (whose actual values are shown in Table 9.4), glacier streamflow magnitudes will be masked by downward ecosystems. However, this must not be the case, for a glacier located in dry environments, where downward ecosystems do not receive considerable precipitation, thus does not have an important contribution to streamflow, and people depend on glacier water, as happens in Peru and Chile (Escanilla-Minchel et al. 2020; Seehaus et al. 2019; Vuille et al. 2018; Baraer et al. 2012;

Gascoin et al. 2011; Vuille et al. 2018; Kaser et al. 2003) and other dry zones of the world (Frans et al. 2018; Carey et al. 2017; Sorg et al. 2012; Kaser et al. 2010; Tandong et al. 2007). Notably, in this gradient analysis, the water regulation capacity of each ecosystem becomes an important issue to study, as this capacity can be used as an indicator of the level of risk for water supply to people depending on water from Neotropical ecosystems.

Concerning the paramo ecosystem, the runoff ratio is 0.8, which implies that at least 20% of rainfall inputs is converted to evapotranspiration and deep water percolation. However, according to the results here, evapotranspiration from the paramo represents 29% of average rainfall inputs (Table 9.4), which suggest that there are extra water inputs to the paramo ecosystem. According to Tobón (2022c), annual fog inputs to this paramo range from 142 to 219 mm, which represent 18% of mean annual rainfall. Fog water inputs to the paramo ecosystem in Northern Andes are well documented (Berrones et al. 2021; Ochoa-Sánchez et al. 2018; Cárdenas et al. 2017; Tobón et al. 2008), with values up to 340 mm y^{-1}; however, larger numbers have been reported for montane forest (Bittencourt et al. 2019; Ramirez et al. 2017; Domínguez et al. 2017; Pryet et al. 2012; García-Santos and Bruijnzeel 2011; Rollenbeck et al. 2011; Tanaka et al. 2011; Holwerda et al. 2010; Gomez-Peralta et al. 2008; Villegas et al. 2008; Holder 2003).

Lastly, to highlight the hydrological attributes and as part of the flow duration curve within studied ecosystems, paramo stands out as the highest water regulation, as is indicated by the largest IRH value, which is closely followed by montane forest (see Table 9.4). This implies a homogeneity in discharge distribution, where the average volume of this discharge is similar to the total volume of water that these ecosystems generate. These results also indicate that the Glacier has a high heterogeneity in the distribution of its discharges, with large values depending either on temperature conditions or rainfall events.

9.5 Conclusion

The climate and ecohydrological gradient of Neotropical ecosystems in the Claro river basin was studied, which gives an insight into the partial contribution of each ecosystem to total water yield from the basin and ecohydrological functioning of Neotropical ecosystems. Temperature and rainfall decrease with increase in altitude, while relative air humidity did not present a clear trend. Rainfall–runoff responses from each ecosystem showed that although the actual contribution of glacier is relatively high, its net contribution is considerably low when considering the contribution of other ecosystems, such as the paramo and montane forest, which showed to be connected to rainfall amounts and exposed area of each ecosystem.

This study demonstrates that the extinction of small Neotropical glacier may not threaten the water supply to the local population. The specific humid conditions of ecosystems surrounding the studied glacier makes a great difference on the hydrological consequences of glacier retreat and its disappearance, as the contribution from those ecosystems to water yield is considerably larger than the one from the small glacier. This highlights the ecohydrological importance of paramos and montane forests for water supply to the local population, notably their large capacity for water regulation.

References

Albert T, Klein A, Kincaid JL, Huggel C, Racoviteanu AE, Arnaud Y, Ceballos JL (2014) Remote sensing of rapidly diminishing tropical glaciers in the northern Andes. In: Global land ice measurements from space. Springer, Berlin, pp 609–638

Aparecido LMT, Teodoro GS, Mosquera G, Brum M, Barros FDV, Pompeu PV, Mulligan M (2018) Ecohydrological drivers of Neotropical vegetation in montane ecosystems. Ecohydrology 11(3):e1932

Apaza-Quevedo A, Lippok D, Hensen I, Schleuning M, Both S (2015) Elevation, topography, and edge effects drive functional composition of woody plant species in tropical montane forests. Biotropica 47(4):449–458

Armstrong RL, Brun E (2008) Snow and climate: physical processes, surface energy exchange and modeling. Cambridge University Press, Cambridge

Baker DB, Richards RP, Loftus TT, Kramer JW (2004) A new flashiness index: characteristics and applications to midwestern rivers and streams 1. JAWRA J Am Water Resour Assoc 40(2):503–522

Baraer M, Mark BG, McKenzie JM, Condom T, Bury J, Huh KI, Rathay S (2012) Glacier recession and water resources in Peru’s Cordillera Blanca. J Glaciol 58(207):134–150

Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (2008) Gradients in a tropical mountain ecosystem of Ecuador, vol 198. Springer, Berlin

Bendix J, Fabian P, Rollenbeck R (2004). Gradients of fog and rain in a tropical montane cloud forest of southern Ecuador and its chemical composition. In: Paper presented at the proceedings of the 3rd international conference on fog, fog collection and dew

Bendix J, Rollenbeck R, Fabian P, Emck P, Richter M, Beck E (2008) Climate variability. In: Gradients in a tropical mountain ecosystem of. Springer, Berlin, pp 281–290

Berrones G, Crespo P, Wilcox BP, Tobón C, Célleri R (2021) Assessment of fog gauges and their effectiveness in quantifying fog in the Andean páramo. Ecohydrology 14(6):e2300

Berrones G, Crespo P, Ochoa-Sánchez A, Wilcox BP, Célleri R (2022) Importance of fog and cloud water contributions to soil moisture in the Andean Páramo. Hydrology 9(4):54

Bittencourt PR, Barros FDV, Eller CB, Müller CS, Oliveira RS (2019) The fog regime in a tropical montane cloud forest in Brazil and its effects on water, light and microclimate. Agric For Meteorol 265:359–369

Bradley RS, Vuille M, Diaz HF, Vergara W (2006) Threats to water supplies in the tropical Andes. Science 312(5781):1755–1756

Braun MH, Malz P, Sommer C, Farías-Barahona D, Sauter T, Casassa G, Seehaus TC (2019) Constraining glacier elevation and mass changes in South America. Nat Clim Chang 9(2):130–136

Bruijnzeel LA, Lu J (2001) Hydrology of tropical montane cloud forests: a reassessment. Land Use Water Resour Res 1(1732-2016-140258):1.1–1.18

Bruijnzeel L, Veneklaas EJ (1998) Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. Ecology 79(1):3–9

Bruijnzeel L, Kappelle M, Mulligan M, Scatena FN (2010) Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world. In: Tropical montane cloud forests science for conservation and management

Buytaert W, Cuesta-Camacho F, Tobón C (2011) Potential impacts of climate change on the environmental services of humid tropical alpine regions. Glob Ecol Biogeogr 20(1):19–33

Bruijnzeel LA (2004) Hydrological functions of tropical forests: not seeing the soil for the trees?. Agriculture, Ecosystems & Environment, Volume 104, Issue 1, Pages 185–228, ISSN 0167-8809, https://doi.org/10.1016/j.agee.2004.01.015.

Buytaert W, Moulds S, Acosta L, De Bievre B, Olmos C, Villacis M, Verbist KM (2017) Glacial melt content of water use in the tropical Andes. Environ Res Lett 12(11):114014

Cárdenas MF, Tobón C, Buytaert W (2017) Contribution of occult precipitation to the water balance of páramo ecosystems in the Colombian Andes. Hydrol Process 31(24):4440–4449

Carey M, Molden OC, Rasmussen MB, Jackson M, Nolin AW, Mark BG (2017) Impacts of glacier recession and declining meltwater on mountain societies. Ann Am Assoc Geogr 107(2):350–359

Cavalcanti IFA, Shimizu MH (2012) Climate fields over South America and variability of SACZ and PSA in HadGEM2-ES, 01, 132

Cavelier J (1996) Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains. In: Tropical forest plant ecophysiology. Springer, pp 399–439

Cavelier J, Solis D, Jaramillo MA (1996) Fog interception in montane forests across the Central Cordillera of Panama. J Trop Ecol 12(3):357–369

Ceballos JL, Euscátegui C, Ramírez J, Cañon M, Huggel C, Haeberli W, Machguth H (2006) Fast shrinkage of tropical glaciers in Colombia. Ann Glaciol 43:194–201

Célleri R, Feyen J (2009) The hydrology of tropical Andean ecosystems: importance, knowledge status, and perspectives. Mt Res Dev 29(4):350–355

Cepeda Arias, E., Cañon Barriga J., & Salazar, J.F. (2022) Changes of streamflow regulation in an Andean watershed with shrinking glaciers: implications for water security, Hydrological Sciences Journal, 67:11, 1755-1770, https://doi.org/10.1080/02626667.2022.2105650

Chang M (2013) Forest Hydrology: An Introduction to Water and Forests, Third Edition (3rd ed.). CRC Press. https://doi.org/10.1201/b13614

Chevallier P, Pouyaud B, Suarez W, Condom T (2011) Climate change threats to environment in the tropical Andes: glaciers and water resources. Reg Environ Change 11(1):179–187

Crausbay SD, Martin PH (2016) Natural disturbance, vegetation patterns and ecological dynamics in tropical montane forests. J Trop Ecol 32(5):384–403

Crespo PJ, Feyen J, Buytaert W, Bücker A, Breuer L, Frede HG, Ramírez M (2011) Identifying controls of the rainfall–runoff response of small catchments in the tropical Andes (Ecuador). J Hydrol 407(1–4):164–174

da Rocha NS, Veettil BK, Grondona A, Rolim S (2019) The influence of ENSO and PDO on tropical Andean glaciers and their impact on the hydrology of the Amazon Basin. Singap J Trop Geogr 40(3):346–360

de Vries M, Carchipulla-Morales D, Wickert AD, Minaya VG (2022) Glacier thickness and ice volume of the Northern Andes. Sci Data 9(1):1–16

Di Piazza A, Conti FL, Noto LV, Viola F, La Loggia G (2011) Comparative analysis of different techniques for spatial interpolation of rainfall data to create a serially complete monthly time series of precipitation for Sicily, Italy. Int J Appl Earth Obs Geoinf 13(3):396–408

Domínguez CG, García Vera MF, Chaumont C, Tournebize J, Villacís M, d'Ozouville N, Violette S (2017) Quantification of cloud water interception in the canopy vegetation from fog gauge measurements. Hydrol Process 31(18):3191–3205

Dussaillant I, Berthier E, Brun F, Masiokas M, Hugonnet R, Favier V, Ruiz L (2019) Two decades of glacier mass loss along the Andes. Nat Geosci 12(10):802–808

Escanilla-Minchel R, Alcayaga H, Soto-Alvarez M, Kinnard C, Urrutia R (2020) Evaluation of the impact of climate change on runoff generation in an andean glacier watershed. Water 12(12):3547

Frans C, Istanbulluoglu E, Lettenmaier DP, Fountain AG, Riedel J (2018) Glacier recession and the response of summer streamflow in the Pacific Northwest United States, 1960–2099. Water Resour Res 54(9):6202–6225

Fujita K, Thompson LG, Ageta Y, Yasunari T, Kajikawa Y, Sakai A, Takeuchi N (2006) Thirty-year history of glacier melting in the Nepal Himalayas. J Geophys Res: Atmos 111(D3)

García-Santos G, Bruijnzeel L (2011) Rainfall, fog and throughfall dynamics in a subtropical ridge top cloud forest, National Park of Garajonay (La Gomera, Canary Islands, Spain). Hydrol Process 25(3):411–417

Gascoin S, Kinnard C, Ponce R, Lhermitte S, MacDonell S, Rabatel A (2011) Glacier contribution to streamflow in two headwaters of the Huasco River, Dry Andes of Chile. Cryosphere 5(4):1099–1113

Gomez-Peralta D, Oberbauer SF, McClain ME, Philippi TE (2008) Rainfall and cloud-water interception in tropical montane forests in the eastern Andes of Central Peru. For Ecol Manag 255(3–4):1315–1325

Guan M, Sillanpää N, Koivusalo H (2016) Storm runoff response to rainfall pattern, magnitude and urbanization in a developing urban catchment. Hydrol Process 30(4):543–557

Gutiérrez M, Zapata P, Ruiz D (2006) Understanding the signals of climate change and climate variability on the water supply of high mountain watersheds. In: Environmental engineering program, school of engineering, Antioquia, Colombia

Holder CD (2003) Fog precipitation in the Sierra de las Minas biosphere reserve, Guatemala. Hydrol Process 17(10):2001–2010

Holwerda F, Bruijnzeel L, Muñoz-Villers L, Equihua M, Asbjornsen H (2010) Rainfall and cloud water interception in mature and secondary lower montane cloud forests of central Veracruz, Mexico. J Hydrol 384(1–2):84–96

IDEAM (2014) Estudio Nacional del Agua

IDEAM (Instituto de Hidrología, Meteorlogia y Estudios Ambientales). (2012). Glaciares de Colombia, más quemontañas con hielo. Bogotá, DC, 344.

IDEAM. (2016). Impacto del fenómeno “El Niño” 2015-2016 en los nevados y en la alta montaña en Colombia. Obtenido de Instituto de Hidrología Meteorología y Estudios Ambientales: http://www.ideam.gov.co/documents/11769/132669/Impacto+de+El+Ni%C3%B1o+en+la+alta+monta%C3%B1a+colombiana.pdf/dd41d158-0944-41d5-917e44fdb524e8ea

Johansen KS, Alfthan B, Baker E, Hesping M, Schoolmeester T, Verbist K (2018) The Andean glacier and water atlas: the impact of glacier retreat on water resources. UNESCO Publishing, Paris

Kaser G, Juen I, Georges C, Gómez J, Tamayo W (2003) The impact of glaciers on the runoff and the reconstruction of mass balance history from hydrological data in the tropical Cordillera Blanca, Peru. J Hydrol 282(1–4):130–144

Kaser G, Großhauser M, Marzeion B (2010) Contribution potential of glaciers to water availability in different climate regimes. Proc Natl Acad Sci 107(47):20223–20227

López-Ramírez SM, Sáenz L, Mayer A, Muñoz-Villers LE, Asbjornsen H, Berry ZC, Gómez-Aguilar LR (2020) Land use change effects on catchment streamflow response in a humid tropical montane cloud forest region, Central Veracruz, Mexico. Hydrol Process 34(16):3555–3570

Lyne V, Hollick M (1979) Stochastic time-variable rainfall-runoff modelling. In: Paper presented at the institute of engineers Australia national conference

Mark BG, French A, Baraer M, Carey M, Bury J, Young KR (2017) Glacier loss and hydro-social risks in the Peruvian Andes. Glob Planet Change 159:61–76

Martin PH, Sherman RE, Fahey TJ (2007) Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. J Biogeogr 34(10):1792–1806

Marulanda Aguirre A, Fonseca Tobasura OA, Vélez Upegui JJ, Arboleda OD (2016) Hydrological study of the potential effects of the melting of Nevado del Ruiz glacier on urban growth zones in Manizales, Colombia. Hydrol Sci J 61(12):2179–2192

Morán-Tejeda E, Ceballos JL, Peña K, Lorenzo-Lacruz J, López-Moreno JI (2018) Recent evolution and associated hydrological dynamics of a vanishing tropical Andean glacier: Glaciar de Conejeras, Colombia. Hydrol Earth Syst Sci 22(10):5445–5461

Ochoa-Sánchez A, Crespo P, Célleri R (2018) Quantification of rainfall interception in the high Andean tussock grasslands. Ecohydrology 11(3):e1946

Penna D, van Meerveld HJ, Zuecco G, Dalla Fontana G, Borga M (2016) Hydrological response of an Alpine catchment to rainfall and snowmelt events. J Hydrol 537:382–397

Peyre G, Balslev H, Martí D, Sklenář P, Ramsay P, Lozano P, Font X (2015) VegPáramo, a flora and vegetation database for the Andean páramo. Phytocoenologia 45(1–2):195–201

Peyre GP, Bottin M, Sanchez A (2022) Flora y vegetación de paramo. In: Tobón C (ed) Los Páramos de Colombia. Características biofísicas, Ecohidrología y Cambio climático. Universidad Nacional de Colombia, Editorial UN, Bogotá, pp 143–178

Poveda G, Pineda K (2009) Reassessment of Colombia's tropical glaciers retreat rates: are they bound to disappear during the 2010–2020 decade? Adv Geosci 22:107–116

Poveda G, Alvarez DM, Rueda OA (2011) Hydro-climatic variability over the Andes of Colombia associated with ENSO: a review of climatic processes and their impact on one of the Earth's most important biodiversity hotspots. Clim Dyn 36(11):2233–2249

Prada CM, Stevenson PR (2016) Plant composition associated with environmental gradients in tropical montane forests (Cueva de Los Guacharos National Park, Huila, Colombia). Biotropica 48(5):568–576

Pryet A, Dominguez C, Tomai PF, Chaumont C, d'Ozouville N, Villacís M (2012) Quantification of cloud water interception along the windward slope of Santa Cruz Island, Galapagos (Ecuador). Agric For Meteorol 161:94–106

Rabatel A, Francou B, Soruco A, Gomez J, Cáceres B, Ceballos JL, Huggel C (2013) Current state of glaciers in the tropical Andes: a multi-century perspective on glacier evolution and climate change. Cryosphere 7(1):81–102

Rabatel A, Ceballos JL, Micheletti N, Jordan E, Braitmeier M, González J, Zemp M (2018) Toward an imminent extinction of Colombian glaciers? Geogr Ann Ser A 100(1):75–95

Rabatel A, Sirguey P, Drolon V, Maisongrande P, Arnaud Y, Berthier E, Davaze L, Dedieu J-P, Dumont M (2017) Annual and Seasonal Glacier-Wide Surface Mass Balance Quantified from Changes in Glacier Surface State: A Review on Existing Methods Using Optical Satellite Imagery. Remote Sens. 9, 507. https://doi.org/10.3390/rs9050507

Ramírez BH, van der Ploeg M, Teuling AJ, Ganzeveld L, Leemans R (2017) Tropical montane cloud forests in the Orinoco river basin: the role of soil organic layers in water storage and release. Geoderma 298:14–26

Rodríguez-Morales M, Acevedo-Novoa D, Machado D, Ablan M, Dugarte W, Dávila F (2019) Ecohydrology of the Venezuelan páramo: water balance of a high Andean watershed. Plant Ecol Divers 12(6):573–591

Rollenbeck R, Bendix J, Fabian P (2011) Spatial and temporal dynamics of atmospheric water inputs in tropical mountain forests of South Ecuador. Hydrol Process 25(3):344–352

Ruiz D, Moreno HA, Gutiérrez ME, Zapata PA (2008) Changing climate and endangered high mountain ecosystems in Colombia. Sci Total Environ 398(1–3):122–132

Seehaus T, Malz P, Sommer C, Lippl S, Cochachin A, Braun M (2019) Changes of the tropical glaciers throughout Peru between 2000 and 2016–mass balance and area fluctuations. Cryosphere 13(10):2537–2556

Sierra JP, Arias PA, Vieira SC (2015) Precipitation over northern South America and its seasonal variability as simulated by the CMIP5 models. Adv Meteorol 2015:1

Singh VP, Eng D (2017) Handbook of applied hydrology. McGraw-Hill Education, New York

Sorg A, Bolch T, Stoffel M, Solomina O, Beniston M (2012) Climate change impacts on glaciers and runoff in Tien Shan (Central Asia). Nat Clim Change 2(10):725–731

Stoelzle M, Schuetz T, Weiler M, Stahl K, Tallaksen LM (2020) Beyond binary baseflow separation: a delayed-flow index for multiple streamflow contributions. Hydrol Earth Syst Sci 24(2):849–867

Tanaka N, Kuraji K, Tantasirin C, Takizawa H, Tangtham N, Suzuki M (2011) Relationships between rainfall, fog and throughfall at a hill evergreen forest site in northern Thailand. Hydrol Process 25(3):384–391

Tandong Y, Pu J, Lu A, Wang Y, Yu W (2007) Recent glacial retreat and its impact on hydrological processes on the Tibetan Plateau, China, and surrounding regions. Arct Antarct Alp Res 39(4):642–650

Thompson LG, Mosley-Thompson E, Davis ME, Brecher HH (2011) Tropical glaciers, recorders and indicators of climate change, are disappearing globally. Ann Glaciol 52(59):23–34

Thompson LG, Davis ME, Mosley-Thompson E, Porter SE, Corrales GV, Shuman CA (2021) The impacts of warming on rapidly retreating high-altitude, low-latitude glaciers and ice core-derived climate records. Glob Planet Change 203:103538

Tobón C (2009) Los bosques andinos y el agua

Tobón C, Bruijnzeel LA, Frumau, KFA, Calvo JC (2010) Changes in soil hydraulic properties and soil water status after conversion of tropical montane cloud forest to pasture in northern Costa Rica. In: LA Bruijnzeel, FN Scatena, LS Hamilton (editors), Tropical MontaneCloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, UK. 765–778

Tobón C (2022a) Los Páramos de Colombia. Características biofísicas, Ecohidrología y Cambio climático. Universidad Nacional de Colombia, Editorial UN, Bogotá. 629 p

Tobón C (2022b) Los suelos de los páramos de Colombia y sus propiedades hidrofísicas. In: Tobón C (ed) Los Páramos de Colombia. Características biofísicas, Ecohidrología y Cambio climático. Universidad Nacional de Colombia, Editorial UN, Bogotá, pp 93–142

Tobón C (2022c) Contribución de la niebla a la ecohidrología de los páramos en Colombia. In: Tobón C (ed) Los Páramos de Colombia. Características biofísicas, Ecohidrología y Cambio climático. Universidad Nacional de Colombia, Editorial UN, Bogotá, pp 308–348

Tobón C (2022d) Interceptación de la precipitación por la vegetación de los páramos. In: Tobón C (ed) Los Páramos de Colombia. Características biofísicas, Ecohidrología y Cambio climático. Universidad Nacional de Colombia, Editorial UN, Bogotá, pp 272–307

Tobón, C., & Bruijnzeel, L. A. (2021). Near-surface water fluxes and their controls in a sloping heterogeneously layered volcanic soil beneath a supra-wet tropical montane cloud forest (NW Costa Rica). Hydrological Processes, 35 (11), e14426. https://doi.org/10.1002/hyp.14426

Tobón C, Castro E (2023) Funcionamiento ecohidrológico de los páramos en Colombia. In: Colombia UN d (ed) Los Páramos de Colombia, vol 1, Colombia

Tobón C, Cárdenas MF (2023) El clima de los páramos en Colombia. En: Tobón, C. (Ed). Los Páramos de Colombia. Características biofísicas, Ecohidrología y Cambio climático. Universidad Nacional de Colombia, Editorial UN, Bogotá. Pag. 61–94.

Tobón C, Gil G, Villegas CJ (2008) Aportes de la niebla al balance hídrico de los bosques alto-andinos

UNGRD (2016) Fenómeno El Niño-Análisis Comparativo 1997–1998 y 2014–2016. Retrieved from Colombia

Veettil BK, Kamp U (2019) Global disappearance of tropical mountain glaciers: observations, causes, and challenges. Geosciences 9(5):196

Vergara W, Deeb A, Valencia A, Bradley R, Francou B, Zarzar A, Haeussling S (2007) Economic impacts of rapid glacier retreat in the Andes. Eos Trans AGU 88(25):261–264

Villegas JC, Tobón C, Breshears DD (2008) Fog interception by non-vascular epiphytes in tropical montane cloud forests: dependencies on gauge type and meteorological conditions. Hydrol Process 22(14):2484–2492

Vuille M, Carey M, Huggel C, Buytaert W, Rabatel A, Jacobsen D, Timm OE (2018) Rapid decline of snow and ice in the tropical Andes–Impacts, uncertainties and challenges ahead. Earth-Sci Rev 176:195–213

Wagnon P, Ribstein P, Kaser G, Berton P (1999) Energy balance and runoff seasonality of a Bolivian glacier. Glob Planet Change 22(1–4):49–58

Wilcke W, Yasin S, Fleischbein K, Goller R, Boy J, Knuth J, . . . Zech W (2008) Water relations. In Gradients in a Tropical Mountain Ecosystem of Ecuador (pp. 193–201): Springer.

Wilcke W, Yasin S, Fleischbein K, Goller R, Boy J, Knuth J, Zech W (2008a) Water relations. In: Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 193–201

Wilcke W, Yasin S, Schmitt A, Valarezo C, Zech W (2008b) Soils along the altitudinal transect and in catchments. In: Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 75–85

Wu F, Zhan J, Wang Z, Zhang Q (2015) Streamflow variation due to glacier melting and climate change in upstream Heihe River Basin, Northwest China. Phys Chem Earth A/B/C 79:11–19

Van Wyk de Vries M, Carchipulla-Morales D, Wickert AD, Minaya VG (2022) Glacier thickness and ice volume of the Northern Andes. Sci Data 9(1):1–16

Xin J, Sun X, Liu L, Li H, Liu X, Li X, Xu Z (2021) Quantifying the contribution of climate and underlying surface changes to alpine runoff alterations associated with glacier melting. Hydrol Process 35(3):e14069

Zemp M, Frey H, Gärtner-Roer I, Nussbaumer SU, Hoelzle M, Paul F, Anderson B (2015) Historically unprecedented global glacier decline in the early 21st century. J Glaciol 61(228):745–762

Zhai Y, Wang C, Chen G, Wang C, Li X, Liu Y (2020) Field-based analysis of runoff generation processes in humid lowlands of the Taihu Basin, China. Water 12(4):1216

Zhang M, Ren Q, Wei X, Wang J, Yang X, Jiang Z (2011) Climate change, glacier melting and streamflow in the Niyang River Basin, Southeast Tibet, China. Ecohydrology 4(2):288–298

Chapter 10
Communities of Small Terrestrial Arthropods Change Rapidly Along a Costa Rican Elevation Gradient

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10.1 Elevational Gradients

The abundance and diversity of life changes with elevation. Indeed, because of the interactions between climate and elevation that produce environmental heterogeneity (Körner 2004, 2007), mountains are hotspots for diversity (Rahbek et al. 2019a). Numerous specific mechanisms have been proposed to explain why changes in diversity would track changes in elevation, including area, geometric constraints,

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and abiotic factors such as temperature and precipitation. Perhaps the simplest of those mechanisms is the species-area relationship. Larger areas at the base of a mountain have more space for immigration and evolution in ecological and evolutionary time-scales than do the smaller areas towards the peak (Rosenzweig 1995). In the absence of other changes along an elevational gradient, the species-area relationship predicts greater diversity in the larger downslope habitats than in the smaller upslope peaks. Another possible explanation is the geometric constraints (or the mid-domain effect [Colwell et al. 2004]), which predict diversity peaks at mid-elevations through the greatest accumulation of overlapping elevational ranges. The mid-domain effect is essentially a null model (Colwell et al. 2005) and the lack of independence between other factors may demonstrate support for this model (e.g. if area and ideal habitat peak at mid-elevations, it would produce the same pattern) (Currie and Kerr 2008). Diversity-elevation patterns have been mechanistically linked to abiotic factors such as temperature and precipitation. Changing levels of precipitation across elevation could drive changes in animal abundance and diversity if they change plant diversity or productivity (Antonelli et al. 2018). Precipitation

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can increase with elevation (McCain and Grytness 2010), though in the tropics, this pattern can be extremely variable. Temperature changes with elevation, often in a linear fashion called the lapse rate (Barry 2008), and this change is a frequent predictor of diversity and abundance. Combining the effect of temperature and precipitation through time, Janzen (1967) made the observation that where these abiotic conditions are less variable (low seasonality) as in the neotropics (Myster in press), communities should be characterised by high turnover with increasing elevation. Because of this stability, neotropical species should be characterised by narrow physiological tolerances and experience large costs of dispersal across climatic gradients, resulting in low gene flow among populations, and high rates of allopatric speciation across that elevational gradient (Smith 2018).

Janzen's observations produced a mini-industry of ecological inquiry in the following 50+ years (Ghalambor et al. 2006; Sheldon et al. 2018b). This is perhaps not surprising considering that since von Humboldt's famous recounting of his exploration of Ecuadorian mountains, elevational gradients have intrigued biologists – in particular for how rapidly the animal and plant species changed as one moved up or down slope. The apparent vertical stacking of species' ranges results in a situation where one might expect ranges that span hundreds of kilometres across latitude or longitude to reach across only hundreds of vertical metres. Janzen's 1967 "mountain passes" observation was that the particularly dense strata along tropical elevational gradients were likely due to the relative stability (compared to temperate

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elevational gradients) of abiotic factors. Densely packed and rapidly changing ranges have bestowed tropical mountains with some of the greatest diversity on the planet (Antonelli et al. 2018; Rahbek et al. 2019a; Perrigo et al. 2020). Tropical mountains are thus home to an enormous proportion of global diversity, much of it endemic to these elevational "islands" (Myers et al. 2000; Rahbek et al. 2019a), because they can act as both a pump (or a cradle) for novel diversity (Chown and Gaston 2000; Camacho et al. 2021) or a museum for diversity to persist within, or retreat to, as habitat shrinks (Rahbek et al. 2019b), or all of the above.

As with many ecological phenomena, much of what is known about how diversity changes along elevation is known through, or extrapolated from, vertebrates. In a series of influential meta-analyses, Dr. Christy McCain described four predominant patterns, varying in frequency across vertebrate taxa: with increasing elevation (i) decreasing diversity; (ii) low-elevation plateau in diversity; (iii) low-elevation plateaus with mid-elevation peaks; and (iv) unimodal mid-elevational peak in diversity. Birds tended to be equally distributed amongst the trends (McCain 2009). Reptiles predominantly declined with elevation (McCain 2010). Small mammals displayed either mid-elevational diversity peaks (nonvolant; McCain 2005), or a combination of decreasing and mid-elevational peaks (bats; McCain 2007).

We have learned much from vertebrate-described patterns of macroecology. However, most organisms are invertebrates, most of these are arthropods, most of these are insects and most of these are unknown to science (Odegaard 2006; Basset et al. 2012). This enormous taxonomic impediment frames how incompletely we understand the relationship between diversity and elevation for the most diverse taxonomic group (terrestrial arthropods), in the most species-rich regions (the tropics). While there are examples of insect taxa for which we have a good taxonomic understanding (including moths – [Beck et al. 2017], and some beetle taxa such as the Carabidae [Zou et al. 2014]), for most taxa, we simply do not have the data and elevation-diversity patterns are inferred or unclear. This is most prevalent in the tropics, where, up to 90% of taxa may await formal description (Raven et al. 2021). In spite of the impediment of their enormous diversity; when diversity and elevation relationships of different insects has been investigated we have seen all of mid-elevational peaks, declines, and increases (McCoy 1990). Brehm et al. (2007) found much variation within moth taxa along a Costa Rican elevational transect with many following a mid-elevational peak. Janzen found many arthropod taxa showed mid-elevation peaks in diversity and abundance in Costa Rica (Janzen 1973) and Venezuela (Janzen et al. 1976). He postulated that this was due to a higher number of consumable small niches of plants because days were warm enough days for full photosynthesis, but colder nights so that the plants did not burn off what they made in the day. This has likely long been the cause of higher agricultural yields at mid-elevations in the tropics and was suggested to him by old agricultural discussions and considerations of plant metabolism.

Faced with this uphill battle through the morass of diversity and underfunded and unappreciated taxonomy, in many cases, we resort to a strategy of surrogacy, where a better known or understood taxon is considered to predict and hold for the unknown species or taxa. Unfortunately, efforts to use patterns elucidated for these surrogate umbrella taxa have often failed to predict and explain patterns of less charismatic organisms (Fiedler et al. 2008; Peters et al. 2016).

10.2 Expectations in the Study of High Elevation Tropical Forest Communities: Past and the Future

In temperate environments, high elevation localities are often thought to experience greater variation in abiotic conditions and therefore, high-elevation taxa are expected to show greater physiological tolerances (Mamantov et al. 2021). However, along tropical mountains, as in Costa Rica's Área de Conservación Guanacaste (ACG), the greatest variability in abiotic factors occurs in the low elevation dry forest. Here, forests may experience months with no appreciable precipitation and then effectively become rain forests during the wet season. In fact, the arthropod species in high-elevation tropical environments, such as cloud forests, are often thought to be specialised to the invariably cold and wet conditions found there. Thus, while diversity often declines with elevation, such specialisation can lead to disproportionately high biodiversity per unit area in high-elevation environments.

While high elevation cloud forest may have lower biodiversity than associated areas downslope, they also likely host higher biodiversity than one would expect based on area and history alone. Furthermore, selection for lineages able to survive in the prevalent cold-wet conditions may result in environmental filtering of the species present in a community resulting in a pattern of phylogenetic clustering (e.g. Smith et al. 2014). This is to be expected if biological feature (or function) and phylogeny were coupled (Faith 2018) such that taxa from a restricted part of the phylogeny possessed some (suite of) morphological or physiological trait(s) that fostered their success in the hostile environment. How well supported is this reasonable initial assumption of functional and phylogenetic coupling? What is known regarding how insects and arthropods tolerate extreme high and low temperatures?

Counter to this expectation for greater physiological tolerance in high vs. low variability environments, a recent and exhaustive meta-analysis found that thermal tolerance did not vary with elevation for terrestrial ectotherms (Sunday et al. 2019). However, in truth, our current conclusions about "ectotherms" or "insects" to date are in no way complete, and although the literature may contain statements regarding macroecological trends for insects or arthropods, these may be misleading due to various taxonomic biases of what taxa have been described (large-bodied) and where (the global North). Indeed, when global data are synthesised, these evident biases are apparent. For example, large meta-analyses regarding how ectotherms are affected by elevation (Freeman et al. 2018; Sunday et al. 2019) show this literature bias towards species living in the global north and toward certain taxa. Estimates of one common measure of thermal tolerance (in this case of high temperature extremes or CT_{max}) were dominated by studies on one taxon; ants (Sunday et al. 2019). There were 185 cases of thermal tolerance (CT_{max}) associated with elevation for terrestrial arthropods, and of these, 123 (66%) were from species of ants. Since these data were derived from one taxon where the individuals tested are not the unit of selection (in social species, the colony is also the unit of selection) a bias is introduced. Although there have been several comprehensive reviews of late, it is important to note there were fewer than 150 reports regarding insect range changes with elevation and of these, 2/3rds were moth species from one study and no study occurred in the neotropics (Freeman et al. 2018).

However exhaustive, and needed, analyses like Sunday et al. (2019) and Freeman et al. (2018) are, from the perspective of the terrestrial invertebrate they are only as comprehensive or predictive as the existing data allow. Indeed, one of the stated goals for the publication of such synthetic datasets like GlobalTherm is to call attention to the gaps such that we can identify and fill them (Bennett et al. 2018). Tropical terrestrial invertebrates represent such a gap. To understand how thermal tolerance changes with elevation requires more data and testing of those taxa about which we know the least. Our intent is not to criticise the authors of syntheses. We acknowledge the dearth of information for the majority of life which share their planet with us. But best to minimise such generalisations when so much remains unknown – and to resolve the so-called "taxonomic impediment" is critical to this problem. How insects will respond across elevation during climate change (or other perturbations such has drought, landslides, entomological or food pandemics, etc.) is largely not understood. In part, this is because of the scale of the problem – it is not possible to yet be comprehensive when insect diversity is overwhelmingly large and perhaps as little as 10% of species are described (Raven et al. 2021). In this slice of the world's biodiversity, using transparent proxies for formally described species hypotheses, such as DNA barcodes, may provide the greatest benefit.

Janzen's observation that mountain passes act "higher" in the tropics than their elevation would suggest, and that therefore there are predictable differences between tropical and temperate elevational gradients prompted much ecological inquiry in the intervening years (Ghalambor et al. 2006; Sheldon et al. 2018a). One example involved changes in aquatic insects across elevation in Ecuador and Colorado (Polato et al. 2018; Smith 2018). Aquatic insect species may change more rapidly than terrestrial species because they may be limited by lower oxygen levels in warm water temperatures more rapidly than terrestrial insects would be by air temperatures changes (Shah et al. 2020). Furthermore, arthropods in the terrestrial environment may be able to move in space (e.g. microhabitats such as deeper in leaf litter, etc.) to avoid these fluctuations and buffer them from the warming (Antão et al. 2020; Shah et al. 2020). However, terrestrial arthropods will be exposed to more rapid temperature fluctuations in air than in water, and so we might expect them to be more dramatically affected than aquatic systems. Because of these competing processes, it is unclear whether the patterns observed in aquatic insects will be as strong, or evident, for the diverse and abundant taxa in the forest leaf-litter.

Here we describe our ongoing work within this taxonomic impediment amongst terrestrial arthropods of the forests (and principally the leaf litter of those forests) in a neotropical hotspot of global biodiversity and conservation – the Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (Janzen and Hallwachs

2016). We describe results of this work gathered in more than a decade of sampling this biodiversity using DNA barcodes as a preliminary identification of the units of diversity by including it with what is known about ecology and morphology. Interim names are a necessary step since most of the taxa we work with have no formal scientific name. We will begin by describing the ACG terrestrial environment along three volcanoes in broad strokes (to do this description justice would require many large volumes alone) followed by temperature and precipitation data collected in the past decade along one of the specific elevation gradients present within the park: Volcan Cacao.

10.3 Case Study: Elevation Gradients on the Volcanoes of the Área de Conservación Guanacaste (Costa Rica)

Área de Conservación Guanacaste (ACG) in northwestern Costa Rica is a 169,000 hectare UNESCO World Heritage Preserve that, in addition to a 43,000 hectare marine area, has a terrestrial environment that contains several isolated stratovolcanoes that create elevational gradients from sea-level to ~1800 m. Along these volcanoes, ACG contains 11 Holdridge life zones (Holdridge 1967). Upslope from the Pacific Ocean, the principal changes are from tropical dry forest to rain forest and then to cloud forest (Fig. 10.1). Of course, within these elevation gradients, there are multiple anthropogenic gradients in and around ACG associated with a long history of human habitation, including farming and ranching (Janzen and Hallwachs 2016, 2020). In ACG, there is no páramo, although in some cases (such as the active

Fig. 10.1 The ACG contains 11 Holdridge life and as you move upslope from the Pacific Ocean, the principal changes you would observe is a change from tropical dry forest to rain forest and then to cloud forest. We captured these high-resolution panoramic images (GigaPans) in our field work across this ~1500 m elevational gradient. Dry forest (near the Area Administrativa in late April): http://gigapan.com/galleries/10092/gigapans/207958, Rain forest (1200 m elevation in late April): http://gigapan.com/galleries/10092/gigapans/207933, Cloud forest (1500 m elevation in late November): http://www.gigapan.com/galleries/6817/gigapans/94235. This images and others are included in a gallery of multiple sites through time is here: http://www.gigapan.com/galleries/10092

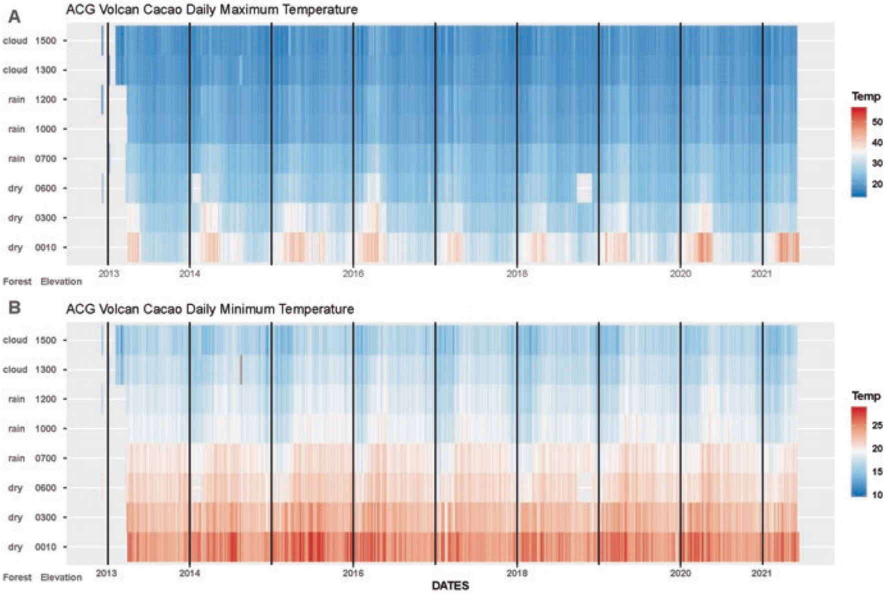

Fig. 10.2 Elevational Warming Stripes through time and space: this is a plot of more than two million temperature recordings at eight elevations across the Volcan Cacao elevational gradient in ACG between December 2012 and June 2021. At each location, temperature dataloggers recorded the temperature each 15 minutes. The maximum and minimum of these daily 96 recordings at each elevation is presented at a vertical bar along the x-axis that coloured according to the temperature scale bar for each panel. Going from left to right through time, you can see the evident seasonality of hot temperatures associated with the dry season and the comparative cooler temperatures in the rainy season. Going up the y-axis, in the mid-high elevation sites, moving from left to right through time, you can see the comparative stability in maximum temperatures

volcano Rincon de la Vieja), there are areas near the peak of the volcano that are without forest owing to recent eruptions. There is no classical "tree line" largely because the "trees" are eventually replaced with shrubs with increasing elevation.

While an ecologist working on temperate mountains may expect that high elevation communities experience the greatest variation in abiotic conditions like temperature and precipitation. However, on the ACG volcanoes, it is the low-elevation seasonal dry forest that has the greatest annual and daily variation in temperature and precipitation compared to the (historically – pre-climate change) stable cool and wet of the high elevation cloud forest (Fig. 10.2).

The forests that are vertically stratified across the ACG elevational gradient looked markedly different during the time that many of its extant resident species likely evolved or moved there as the high elevation glaciers retreated perhaps 20,000–30,000 years ago. The region has been subject to tens of thousands of years of violent volcanic change – some of which would have led to the eradication of whatever forests and communities were there previously. For example, a powerful explosion ~1.5 million years ago, where the Rincon de la Vieja volcanic complex stands today, filled a lake and destroyed forests that that had extended from Nicaragua to the city of Liberia (Janzen and Hallwachs 2020). The modern day volcanoes (Volcan Rincon de la Vieja, Cacao, and Orosi) emerged roughly 50,000, 30,000, and 20,000 years ago, respectively (Janzen and Hallwachs 2020). Forests colonised these emerging and cooling slopes during periods of Pleistocene cooling (Janzen and Hallwachs 2016). During these times, the cloud forest that we see today, restricted to the very highest elevations of the volcanoes, likely extended all the way to their base and connected them (Ramirez-Barahona and Eguiarte 2013). The massive diversity of life that calls these gradients home today would only have had a chance to evolve in situ if their speciation occurred >1.5 million years ago – and since then, their home was volcanically razed to the ground and re-erected. It is more useful to consider that the taxa we observe today have, by and large, arrived from elsewhere. Niche diversification across elevation would certainly have played a role in this long-term diversification – but the diversity of live resident here is the product of multiple processes (Antonelli 2022).

On smaller, or isolated mountains or volcanoes, as occur in ACG, the transition from rain forest to cloud forest appears at lower elevations compared to larger massifs farther south in Costa Rica due to the so called Massenerhebung Effect (Grubb 1971) (also called the mountain mass elevation effect [Flenley 1995], mountain elevation effect [McCain 2005], or Merriam Effect [Martin 1963]). Here, forest types typically seen at higher elevations on large mountains occur at lower elevations on isolated peaks (like ACG stratovolcanoes) due to the reduced capacity to reflect heat and that block the prevailing moisture laden winds than a smaller mountain has compared to a larger mountain (range) and the subsequent formation of clouds at these lower elevations. One consequence of the climate crisis is that the time covered in clouds, that any mountain would have experienced historically, will be reduced (the "lifting cloud base hypothesis" – [Pounds et al. 1999]), whereas the base height of orographic clouds formation will increase (Lawton et al. 2016) – an effect is particularly pronounced on small, isolated mountains in northwestern Costa Rica (Karmalkar et al. 2008). Indeed, the proportions of times that the peaks of the ACG volcanoes are observed to be imbedded in clouds has reduced dramatically in the past two decades (Janzen and Hallwachs 2020). Because of the high rate of endemicity in cloud forest taxa (Still et al. 1999), this consequence of the climate crisis has a dramatically negative effect on endemic biological diversity (Freeman et al. 2018) – preceded ironically by an increase in diversity as downslope taxa from the rain and dry forest move upward as occurs in numerous taxa (Warne et al. 2020; Edwards et al. in review).

A brief aside about the terms, "elevation" and "altitude." Altitude is vertical distance between two points not in contact. Elevation is the vertical distance between a point on the land's surface and a reference point (i.e. sea level) and so our data are elevational, not altitudinal. See Körner (2007) and McVicar and Körner (2013) for a concise explanation of the difference between altitude and elevation as it pertains to ecologists.

10.3.1 Sampling Leaf Litter Arthropods and Temperature Along Elevation Gradients on the Volcanoes of the Área de Conservación Guanacaste (Costa Rica)

To capture and quantify elevational, seasonal, and temporal changes in temperature and precipitation, we initiated air temperature measurements in ACG across the Volcan Cacao elevation gradient in late 2012 – and after some technical difficulties – all monitoring sites were active by March 2013. We measured air temperature using Hobotemp HOBO 64 K Pendant (Waterproof) Data Loggers and the HOBO Rain Gauge (Metric) RG3M Data Loggers set to record air temperature (every 15 minutes) and precipitation. Each monitoring site hosts two dataloggers (set on a tree trunk approximately 1 metre off the ground) in case one experiences battery failure. While there were some small interruptions (for example, at the 600 m site, both dataloggers failed for a period in 2018), these eight sites have been continuously monitoring air temperature since early 2013, resulting in >2.6 million data points over ~3500 days. These dataloggers are not contained within a solar radiation shield, but the setup at each elevation was comparable. Thus, comparisons of specific temperatures to other elevational gradients may be difficult (as direct solar radiation may cause intense microclimatic spikes), but do permit comparisons between these monitoring sites along this gradient and through time. To display the trends across elevation and through time, we adapted the "Warming Stripes" approach pioneered by Ed Hawkins (Hawkins 2018) into a vertical mountain of space, time, and temperature. For each day and each elevation, we determined the average maximum and minimum temperatures. These were then plotted through time on the x-axis where each day is a vertical bar, and across elevation on the y-axis (labelled with elevation and forest type). The shade of the daily vertical bar represents the temperature (deeper blue = colder and deeper red = hotter). The resulting visualisation (Fig. 10.2) captures the elevational, seasonal, and temporal trends in daily maximum and minimum temperature. For example, consider the dry season–rainy season periodicity in the dry forest up to ~600 m elevation. At these low elevation localities, the dry season extends from ~November to mid-May, which is reflected in the deep red the daily bars of the daily maximum temperature (Fig. 10.2a). The daily minimum temperatures show the trend during the rainy season of cooler conditions associated with the return of the rain (Fig. 10.2b). At the rain forest localities (~700–1200 m), there is reduced seasonality in the daily maximum temperatures, although one can see a slight increase in the daily maximum temperature during the dry season. The lower elevation rain forest locations bear much similarity to the down slope dry forests with respect to the daily minimum temperature – they do not cool off proportionally as much from the heat of the day (Fig. 10.2b). The cloud forest locations (1300 and 1500 m) show the low temperatures and limited variability in daily minimum or maximum temperature that still characterise these high elevation/high precipitation and low temperature forests.

These >2 million data points, are the raw data for lapse rates for daily maximum, minimum, and average temperature (Fig. 10.3). The expected change of average

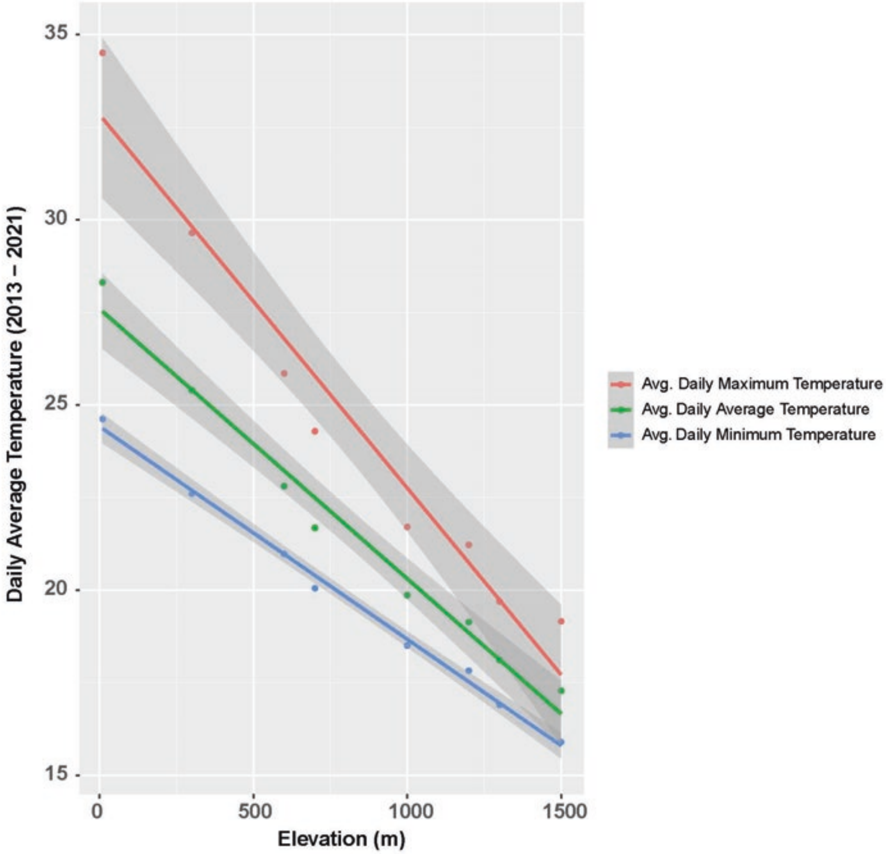

Fig. 10.3 Lapse rate for daily average (green), maximum (red), and minimum (blue) temperature across the Volcan Cacao elevation gradient. Calculated between March 2013 and June 2021, the average temperature changes 0.73 °C with 100 m elevational change, the average daily maximum temperature changes 1.0 °C with every 100 m change in elevation, and the daily average minimum changes 0.57 °C with every 100 m of elevational change

temperature is 0.7 °C/100 m elevation for the daily average, 1 °C change/100 m in daily maximum, and 0.5 °C/100 m for the daily minimum.

These vertical and seasonal changes, have all been recorded in the hottest decade that Costa Rica has endured since the start of the twentieth century. Hawkins' warming stripes for Costa Rica (https://showyourstripes.info/c/centralamerica/costarica) display this pattern dramatically. The elevational patterns from this 9-year period would have been even more pronounced if we had been able to capture the previous records with this precision. As we move farther into the climate-crisis, we are seeing more seasonality in the low-elevation dry forests (longer hot dry conditions as were evident during the 2015/2016 El Nino event) and an increased frequency with which this pulsing seasonality extends upslope into today's rain and cloud forest. When

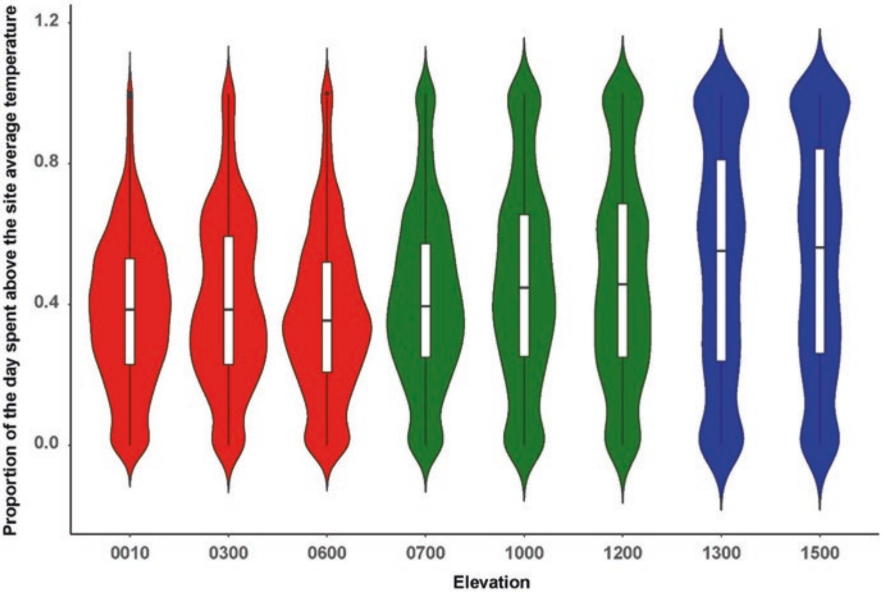

Fig. 10.4 The proportion of the day, at each site, that the temperature recorded was above the average daily temperature for that site. Cloud forest locations (blue), while cooler, with lower average temperatures – spend a greater proportion of the day above that average. Thus, while they are colder, they exist near a tipping point that makes them more vulnerable to coming changes associated with the climate crisis (increasing heat and dryness)

DHJ arrived in Liberia in 1963 the dry season was roughly 4 months long – and today it is six. A foreshadowing was during the 2015/2016 El Nino event. During this severely dry period, daily maximum temperatures, much hotter than average, can be seen leaking into the rain and cloud forest, while in addition, the expected cooling of the dry forest never occurred.

One additional way to consider the stability and therefore climate change vulnerability of the high-elevation forests in ACG is to examine the proportion of the day that each site spends above its average temperature (Fig. 10.4). The pattern is that the hot dry forests spend less than half the day above the site average, while the colder and wetter cloud forest sites spend much more of the day above the average. This is driven by the marked diurnal temperature spikes in the dry forest in the dry season, and the comparative diurnal stability in the cloud forest in the same months. The forest is on a precipice – cloud forest average temperatures are already being exceeded and the coming regularity of spikes and dryness will only serve to accelerate the rate at which these forests surpass historic average values – and in doing so – likely remove habitat for their species.

The patterns of precipitation collected using the tipping bucket rain gauge RG3M remain to be analysed. In the interim, we present a single temporal snapshot (March to September 2013) of data across the elevational gradient to demonstrate the marked differences in amounts of precipitation that each site receives during the last 3 months of the dry season and the first 3 months of the rainy season. While incomplete, we prefer this to using the WorldClim (Fick and Hijmans 2017) data because the ACG elevational gradient is steep enough that several sites occur within the same grid square of the WorldClim dataset and as such, sites that experience marked differences in precipitation would be lumped together.

The standardised sampling regime of the ACG leaf-litter organisms has been detailed elsewhere (Smith et al. 2014) and is covered in detail in the associated supplementary material (Appendix ECOG-00631 at http://www.ecography.org/readers/appendix). Briefly, we have adjusted the ALL ant protocol (Agosti and Alonso 2000) to be carried out by a single person. At each sample elevation, a representative 50 m long transect is actively sampled for 1–2 hours while six pairs of bait and pitfall traps collect for 5 hours. Three 0.5 m^2 samples of leaf litter are sifted and collected in the field using a Davis sifter, and that siftate is then placed in a mini-Winkler for approximately 48 hours. Each site has a Townes-style Malaise trap (Townes 1972) that runs continuously throughout the year and its insects collected weekly. The result is a standardised and replicated combination of six different collection methods that have been ongoing since 2008. While the protocol was initiated with the goal of sampling ants – it is efficient at collecting many leaf-litter taxa, and in the intervening 12–15 years, we have taken every available opportunity to sort, categorise, image, and DNA barcode other exemplar taxa of the leaf-litter including rove beetles (Staphylinidae: Coleoptera), spiders (Araneae: Arachnida), springtails (Collembola: Hexapoda), and pillbugs (Isopoda: “Crustacea”). In addition, we have included in this analysis one group of parasitoid wasps (Microgastrinae, Braconidae, Hymenoptera) that were captured exclusively using Townes style Malaise traps (Townes 1972) within a subset of the same gradient (300–1500 m) and at the same locations (Rodriguez 2009).

To better understand the distributions, causes, and consequences of biodiversity and elevation in the tropics, we used these resilient and standardised collection methods across the ACG elevational gradient multiple times per year intensively (and continuously throughout the year for the Malaise trap method). However, most of the tens of millions of species of multi-cellular animal on the planet weigh less than a gram, are less than a centimetre long, have never been sampled and are not named; so, conducting pragmatic or theoretical biodiversity science within this kind of taxonomic impediment is at best difficult, at worst, impossible. Certainly, without names and methods to identify samples, future comparisons across localities will be impossible. Indeed, names are critical to nearly all downstream biology (Patterson et al. 2010). Therefore, to identify and describe species, we augmented traditional taxonomic methods by DNA barcoding (Smith 2012) the samples collected here. Samples from the six taxa we include here were then either randomly sub-sampled from the total collected to equally represent samples across elevation (Formicidae, Araneae, Collembola, and Isopoda) or all collected members of the family or sub-family were analysed (Staphylinidae and Microgastrinae). All DNA sequences, trace files, collection details, and specimen images associated with the

10, 330 samples from 1243 species analysed here can be accessed on the Barcode of Life Datasystem (BOLD – [Ratnasingham and Hebert 2007]) via this DOI: https://doi.org/10.5883/DS-ASACGART.

In each of the six taxa, we used a specific molecular operational taxonomic unit (Blaxter et al. 2005) called the Barcode Index Number (or BIN) derived from the BOLD applied RESL algorithm (Ratnasingham and Hebert 2013) to estimate diversity. These BINS represent our species hypotheses. We calculated abundance and incidence matrices for each of the eight monitoring sites across Volcan Cacao. To create phylogenies for each taxon, we used a single representative high-quality sequence for each species (longest read length with the fewest ambiguities), calculated the best model for DNA substitution using MEGAX (Kumar et al. 2018), and then created a Maximum Likelihood method and General Time Reversible model (Nei and Kumar 2000). With the incidence matrix and phylogeny, we then used the picante (Kembel et al. 2010), and vegan (Oksanen et al. 2018) packages in R (Team 2021) to calculate indices of alpha diversity (phylogenetic diversity [Faith 2018], richness), betadiversity (phylobetadiversity [comdistnt]), and then to visualise community dissimilarities using Nonmetric Multidimensional Scaling (NMDS). Relationships between elevation, temperature (daily average maximum temperature [Fig. 10.2a]), and precipitation were then plotted using ggplot2 (Wickham 2016) and ggord (Beck 2017). The relationships of alpha diversity with elevation, temperature, precipitation, and area were visualised with either linear regression (lm) if the relationship was monotonic or loess (Cleveland and Loader 1996) or gam (Hastie 1992) if there were evident non-linear trends across elevation, temperature, area, or precipitation. To determine whether betadiversity exhibited spatial turnover across elevation or was nested, we used the R packages vegan and betapart (Baselga and Orme 2012).

To determine if the changes in abiotic conditions associated with elevation could influence a morphological feature (so called functional morphospace) – we estimated the length of the propodeal spines of ants in the diverse genus *Pheidole*. Here, we measured an indicator for total ant body length (Weber's length [Weber 1938]), and the length of the propodeal dorsal spine (the measurement was modified as per Sarnat et al. (2017) as beginning at the point directly dorsal to the propodeal spiracle and ending at the tip of the propodeal dorsal spine) of each specimen from images archived in BOLD using ImageJ (Schneider et al. 2012). To test whether body size and spine length were phylogenetically correlated, we calculated Blomberg's K (Blomberg et al. 2003) and Pagel's Lambda (Pagel 1999) using the R package phytools (Revell 2012). Since body size and spine length were phylogenetically correlated, we used phylogenetic independent contrasts (Felsenstein 1985) to correct for this statistical lack of independence using phytools. The highest quality sequence for each *Pheidole* BIN was then selected (as above) and then a Maximum Likelihood phylogeny was created using the General Time Reversible model (Nei and Kumar 2000). We then compared how this morphological trait varied across elevation in raw measurements and phylogenetically corrected.

10.3.2 Formicidae

Ants are the most numerous and species-rich of the social insects (Hölldobler and Wilson 1990). They have an enormous effect on the ecosystems where they live – often being called ecosystem engineers (Folgarait 1998). Their dominance extends to nearly all terrestrial environments, except Antarctica, the high latitude Arctic above the tree line, and extremely high-elevation environments such as páramo (Ward 2006). The systematics of ants, at the sub-family or generic level, is understood and well supported (Moreau et al. 2006; Borowiec et al. 2021). Within these subfamilies, there are more than 13,500 described species. However, as with most arthropod groups, there remain many species to be described. Globally, ant diversity is greatest in the tropics. For example, some have estimated that there are 900 species of ants in Costa Rica alone (a total that exceeds the United States and Canada combined [Borowiec et al. 2021]). In fact, 900 Costa Rican species is certainly an underestimate for Costa Rica, as in the ACG alone we estimate there to be at least that many species. It is well known that tropical arthropod communities change with elevation (Janzen 1973; Janzen et al. 1976; Wolda 1987; McCoy 1990; Hodkinson 2005), and ant communities conform to this trend. Ant communities become less diverse with elevation (Brühl et al. 1999; Glaser 2006; Lessard et al. 2007) or exhibit mid-elevation peaks in diversity (Andersen 1997; Samson et al. 1997; van der Hammen and Ward 2005; Longino and Branstetter 2019). These two principal patterns are not aligned with latitude (i.e. tropical and temperate elevational gradients have each been found to support each trend [Smith 2015]). One supported latitudinal comparison is that between site dissimilarity across elevation (betadiversity) changes much more rapidly in tropical rather than in temperate sites (Smith 2015).

A word about Malaise traps and ants. In the process of collecting and DNA barcoding both workers and reproductive ants collected using the standardised array of traps in ACG, we have learned much about ant species that were previously hidden. This routine explicitly includes Malaise traps, a common entomological passive intercept trap whose contents are often not used by ant biologists because it tends to catch winged males and females – the least taxonomically labile life history stages of the ant (Longino and Colwell 1997; Yoshimura and Fisher 2012). However, DNA barcodes can be used to reconcile workers and reproductive of the same species. For example, combining all trapping methods with DNA barcoding, we were able to identify males and queens of a genus of ant common in neotropical cloud forest – *Adelomyrmex* (Smith et al. 2015). Prior work had not identified these life history stages despite workers of *Adelomyrmex* being one of the more commonly encountered cloud forest ant taxa. In the dry forest, we uncovered the first known occurrence of a species from the genus *Acanthostichus* in Costa Rica (Smith et al. 2020). Before this discovery, it was a mystery as to why the distribution of species from this genus extended from Argentina to Texas without including Costa Rica, perhaps the most well-studied country in Central America for ants. *Acanthostichus* ants are subterranean termite feeders. Most survey techniques will miss them; however, reconciling queens and males via DNA barcodes of Malaise-trapped individuals

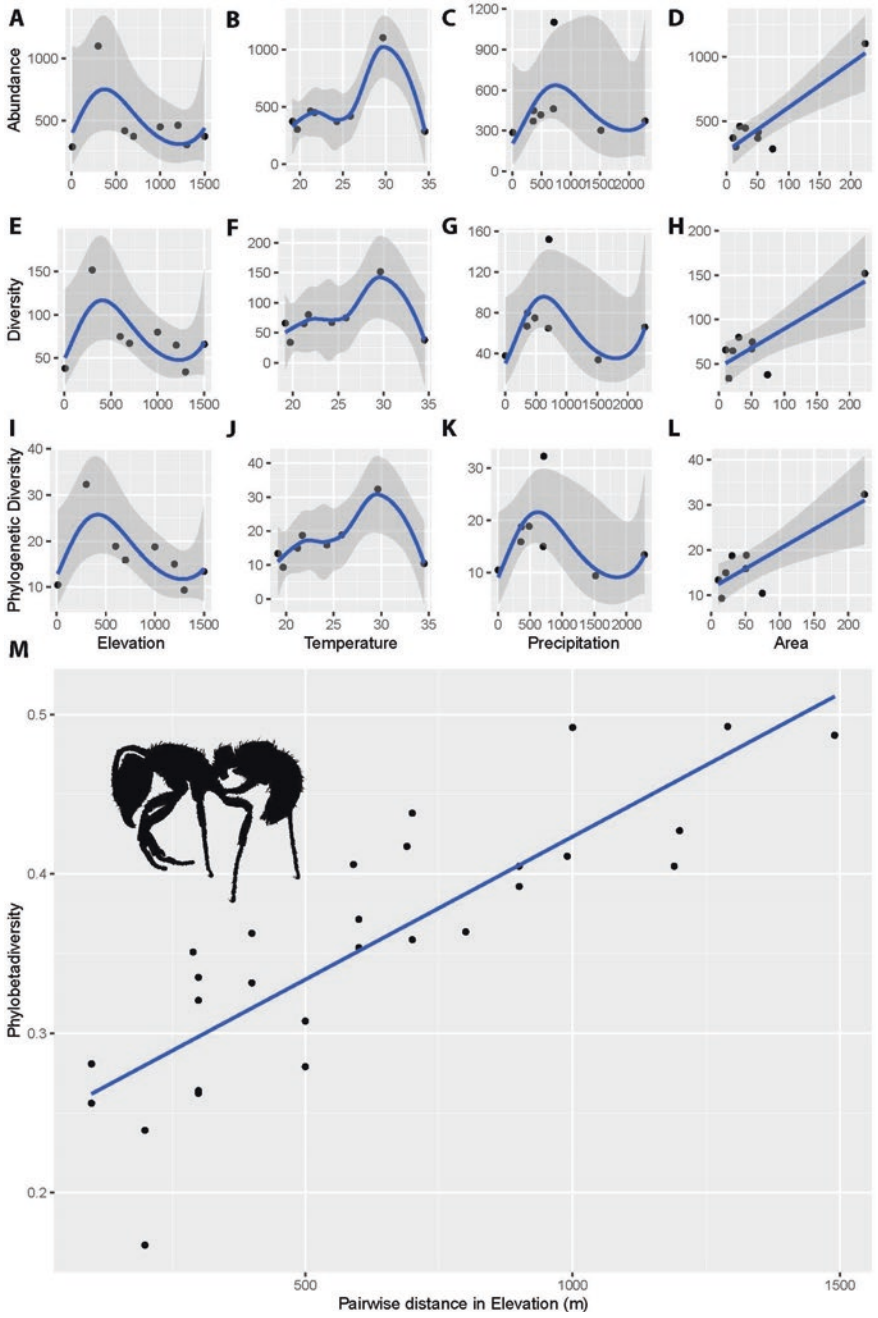

Fig. 10.5 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Formicidae (ants). Ants in ACG (Smith et al. 2014) exhibit a peak in abundance and diversity at mid-elevations (**a**, **e**, **i**) or temperature (**b**, **f**, **j**). Ant diversity and

enabled the taxa to be captured in the brief window when they are above the surface for their nuptial flight. Interestingly, despite large investments in ACG into barcoding Malaise trap contents (Janzen et al. 2020), we have not seen this genus again since it's discovery. We have also documented the creep of lower elevation dry and rain forest taxa into the cloud forest in ACG by DNA barcoding older Malaise trap contents that were maintained in a freezer for a decade before our current sampling regime was initiated in 2008 (Warne et al. 2020). Barcoding Malaise trapped samples in the tropics may provide a map to reconciling parallel taxonomies that exist amongst army ant lineages (Longino 2021). Worker and male army ants are rarely found together, and parallel taxonomies have arisen as the morphologically disparate castes have been named independently. Barcoding reproductive and worker ants will help to synonymise the dual naming.

In ACG we found that ant diversity and abundance were greatest at mid-elevations, temperatures, and amounts of precipitation (Fig. 10.5; Smith et al. 2014). Diversity and abundance tended to increase with area (Fig. 10.5) and phylogenetic dissimilarity increased rapidly with increasing elevational distance between sites. Betadiversity changed rapidly with elevation (Fig. 10.12) with very little overlap between sites other than those immediately adjacent (Fig. 10.13). The community of ant species did not change via a nested process (less diverse areas being a subset of species from the more diverse areas), but rather changed via turnover where the composition of the community changed along the elevational gradient.

In the high-elevation forests of ACG, we have previously demonstrated significant phylogenetic clustering compared to lower elevation forests (Smith et al. 2014). Phylogenetic clustering is a potential signal of an "environmental filter" on the regional species pool whereby only taxa with certain morphological or physiological traits are capable of passing through the strict abiotic "filter" to be found in the "stressful" environment (cold, wet cloud forest in this case). This hypothesis of clustering and inferred abiotic filtering suggests that phylogenetic and feature diversity are coupled. Indeed, phylogenetic measures of diversity are appealing tools for the study of diverse taxa most exposed to the taxonomic impediment if they are coupled with measures of feature diversity (Owen et al. 2019). The data we have collected for the arthropod taxa of the ACG leaf-litter allow us to test this hypothesis. If phylogenetic distance and functional dissimilarity are uncoupled, as is the case when traits have evolved convergently, this would confound the phylogenetic pattern. One might predict that the localities experiencing the greatest variation in

Fig. 10.5 (continued) abundance declined with precipitation after an initial increase (**c**, **g**, **k**). Ant diversity and abundance increased with area (**d**, **h**, **l**). Community dissimilarity (here measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 300 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities) abiotic conditions would exhibit greater physiological tolerances (Chick et al. 2020; Mamantov et al. 2021) and/or variation in morphologies associated with survival. As an example of this extension from phylogenetic to functional patterns in diversity, we offer a case study of spine length across elevation in one diverse ant genus, *Pheidole*.

Interspecific competition among ants is so prevalent that propodeal dorsal spines have been hypothesised to serve as a protection mechanism from invertebrate attack (Dornhaus and Powell 2010). Sarnat et al. (2017) tested several mechanisms that might promote a diversity in dorsal spine length. They found evidence supporting a relationship between the length of the propodeal dorsal spine and defence against invertebrate predators (Dornhaus and Powell 2010) – those with a greater risk of predation have longer propodeal spines (Sarnat et al. 2017). They also proposed that the abiotic and biotic factors of high elevation habitats could influence the spine length of *Pheidole* but found little supporting evidence. This too is logical, since ants are ectotherms, their ability to thermoregulate is related to their microenvironment as well as their own behaviour in it (Hodkinson 2005). Ectotherms often conserve heat or prevent overheating via morphological features (Hodkinson 2005; Bishop et al. 2016) that alter the exposed surface area. Spinesence ("the elongation and proliferation of dorsal spines" [Sarnat et al. 2017]) may have evolved as a method of adjusting surface area ratios to better dissipate or absorb heat, in hot or cold environments, respectively.

We found that the relationship between *Pheidole* spine length and elevation varied among species. For example, the propodeal dorsal spine of minor *Pheidole* ants was as little as 3% and as much as 24% of the total length of the individual's mesosoma. While *Pheidole* spine length appeared to decrease with increasing elevation (Fig. 10.6a), this relationship was not significant when both the spine length and elevational range of the species were phylogenetically controlled (Fig. 10.6b). This suggests that rather than abiotic factors like temperature and precipitation that covary with elevation representing the underlying mechanism behind spine length; other factors, such as competition and predation, may affect this trait. In presenting this example, we are calling attention to the importance of testing patterns that one might consider apparent, or intuitively appealing, with data. In this case, phylogenetic corrections removed any significance to the relationship that we might have expected between a morphological trait and elevation. The capacity to conduct such phylogenetic corrections is another useful by-product of DNA barcoding a fauna since the barcodes themselves, though not accurately portraying a phylogeny; can approximate phylogenies.

10.3.3 Staphylinidae

The rove beetles (Coleoptera, Staphylinidae) are one of the largest families of insects, and eukaryotic animals worldwide (Irmler et al. 2018). They are present in an enormous range of terrestrial habitats and ecosystems (Brunke et al. 2011; Irmler et al. 2018). Staphylinid diversity is large (more than 63,000 described staphylinid

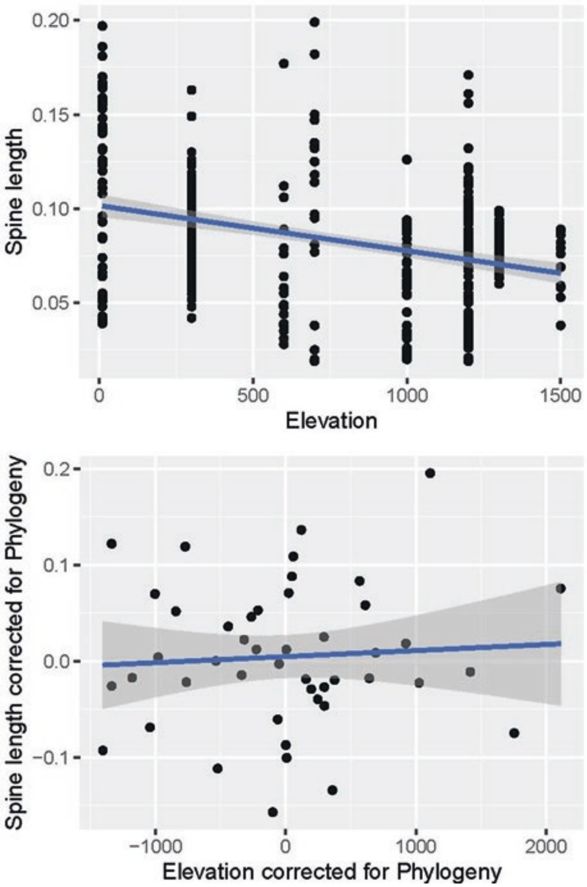

Fig. 10.6 Functional measures of diversity can change with elevation. Estimating these changes while accounting for phylogeny is important. For example, in the hyperdiverse ant genus *Pheidole*, any evident decrease in the length of propodeal spines associated with elevation (as one might expect if "spinesence" (or the elongation and proliferation of dorsal spines" [Sarnat et al. 2017]) evolved as a method of adjusting surface area ratios to better dissipate heat, in environments) (top), is removed when both spine length and elevational distribution are phylogenetically corrected (lower). In this case, removing this potential relationship (or abiotic driver) allows one to examine the likely biotic factors that could drive spinesence (such as predation)

species) and even a conservative estimate suggests there are more staphlylinid species than all vertebrate species (Irmler et al. 2018). Staphylinid species exhibit a great diversity of feeding strategies (functional groups) and occupy almost all terrestrial microhabitats (Thayer 2005). With such great diversity and so many undescribed species, much about their natural history and ecology remains unknown. Despite this, some generalisations can be made: staphylinids tend to be abundant in moist habitats (Newton and Thayer 1992; Qodri et al. 2016), their diversity is positively influenced by microhabitat diversity (Irmler and Gurlich 2007). Pohl et al.

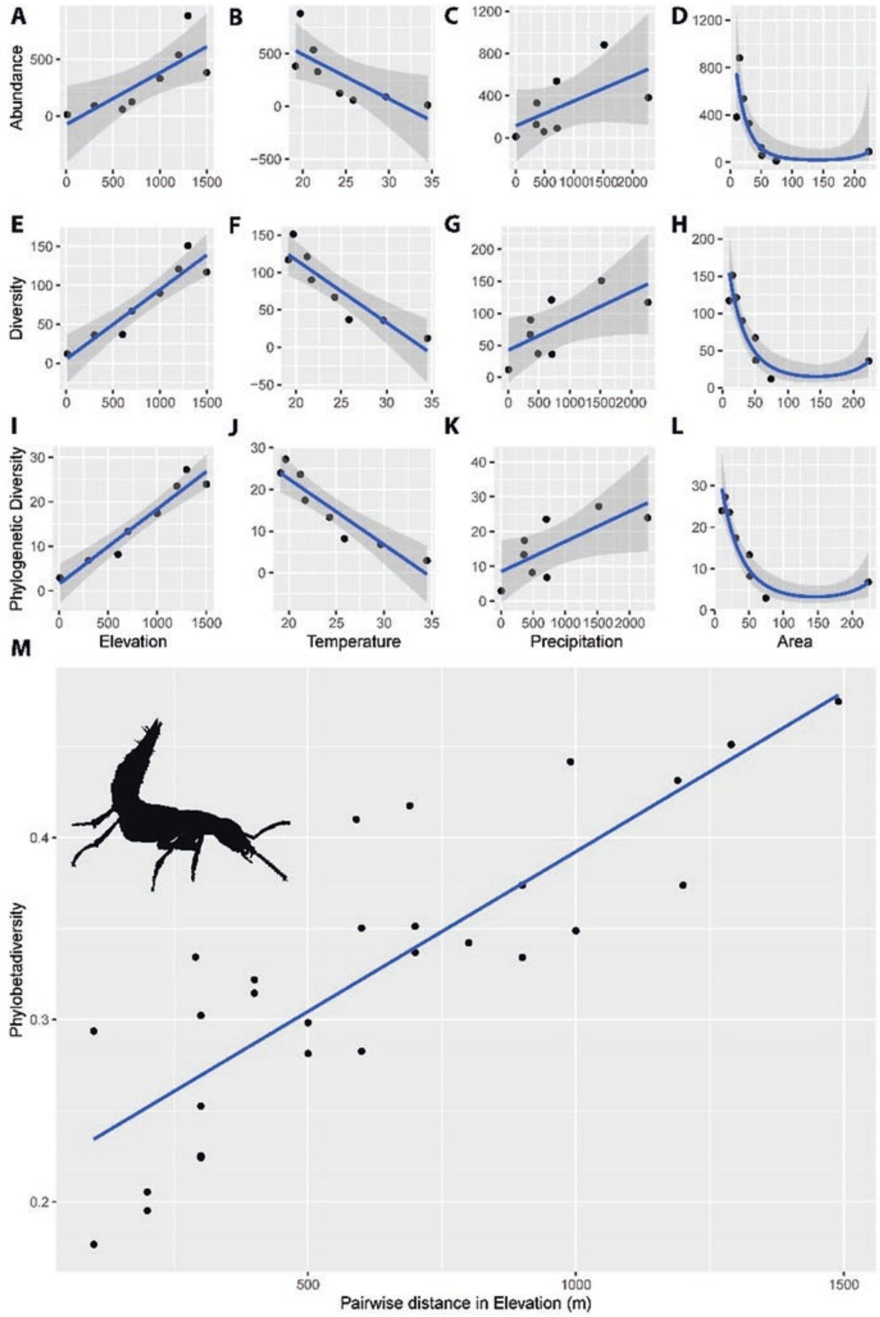

Fig. 10.7 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Staphylinidae (rove beetles). Staphylinids in ACG (Dolson et al. 2021) increase in abundance and diversity with elevation (**a**, **e**, **i**), decrease with temperature (**b**, **f**, **j**) and

(2008) and Bohac (1999) showed that staphylinid diversity is also influenced by disturbance. Because staphylinids are present in most terrestrial ecosystems, some have proposed that they would be a useful indicator taxon when developing conservation priorities (Bohac 1999; Anderson and Ashe 2000; Cajaiba et al. 2017). While hyperdiverse and omnipresent, relatively few studies have examined how they relate to elevation. This is likely due to the enormous diversity of staphylinids that remain to be described (Gutiérrez-Chacon et al. 2009; Irmler et al. 2018). In particular, much remains to be known regarding how staphylinid communities change with elevation in the tropics (Irmler and Lipkow 2018).

In ACG, we found the surprising pattern that staphylinid diversity (taxonomic and phylogenetic) and abundance increased with elevation and precipitation while decreasing with increasingly hot air temperatures (Dolson et al. 2021) (Fig. 10.7). Betadiversity changed rapidly with elevation (Fig. 10.12) with very little overlap between sites outside of those immediately adjacent (Fig. 10.13). The community of staphylinid species changed between sites via turnover more than a nested process (in which less diverse areas were not a subset of species from the more diverse areas).

10.3.4 Araneae

Spiders are a dominant predator in terrestrial ecosystems (Symondson et al. 2001). Across elevational gradients, spider species and communities have exhibited both direct and indirect sensitivity to the associated changing abiotic conditions. However, spider diversity does not change uniformly across elevation. Spiders have been observed to decline (Greenstone 1984; Yanoviak et al. 2003; Binkenstein et al. 2017; González-Reyes et al. 2017; Müller et al. 2022), increase (Uetz 1976; Nogueira et al. 2021), peak at mid-elevations (McCoy 1990; Chatzaki et al. 2005; Jimenez-Valverde and Lobo 2007; Peters et al. 2016), or exhibit no change at all (Reta-Heredia et al. 2018) with elevational change.

In ACG, we examined the diversity of leaf-litter spiders across elevation and found high turnover across the entire gradient (Dolson et al. 2020). While phylogenetic- or richness-based indices weakly appeared to decline after reaching a moderate mid-elevation peak, neither the diversity nor the abundance of spiders was significantly correlated with precipitation or area (Fig. 10.8).

Fig. 10.7 (continued) increase with precipitation (**c**, **g**, **k**). Diversity and abundance declined rapidly with area (**d**, **h**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 300 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are based on a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

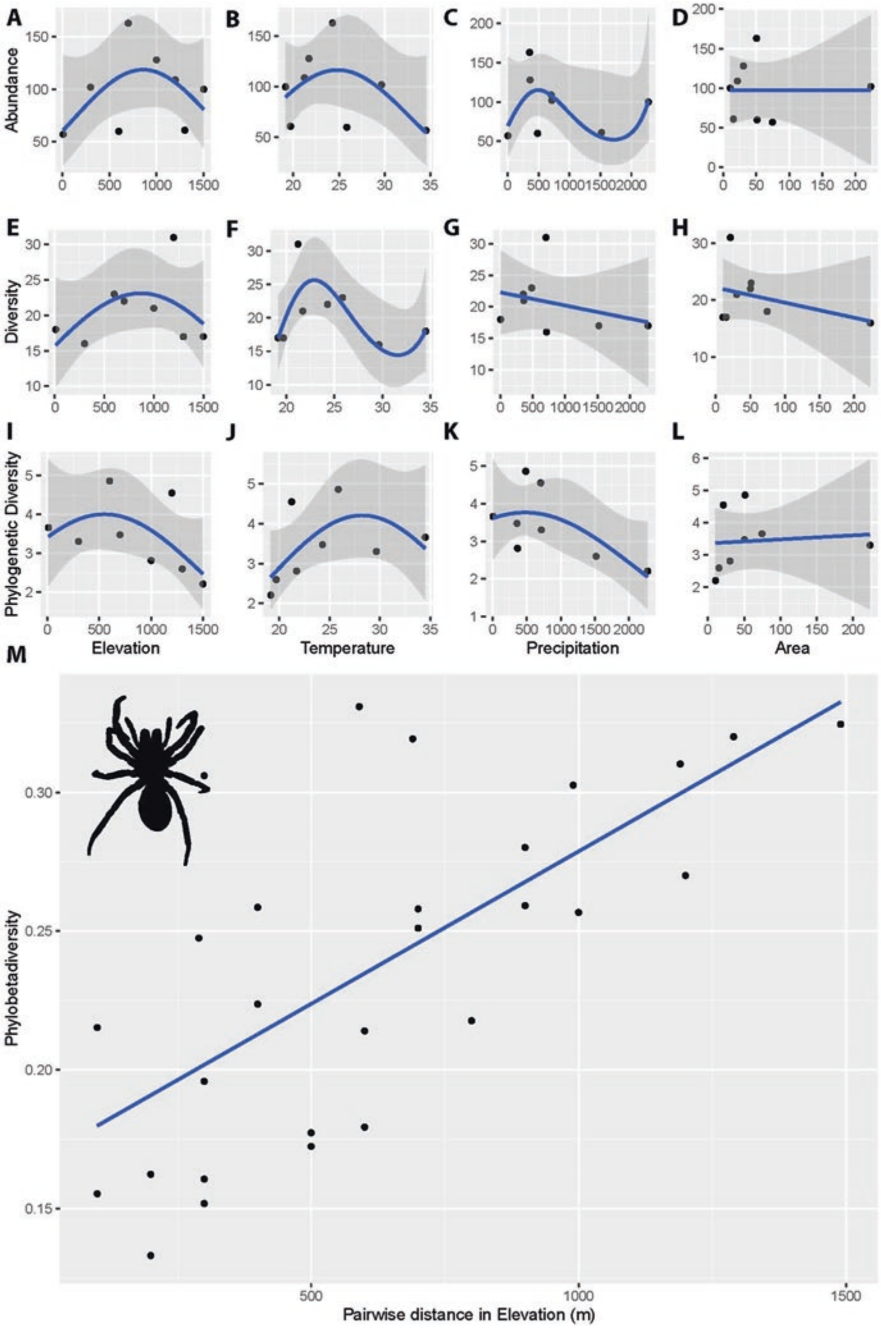

Fig. 10.8 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Araneae (spiders). Spiders in ACG (Dolson et al. 2020) display a slight intermediate peak in abundance and diversity with elevation (**a**, **e**, **i**), and temperature (**b**, **f**, **j**) and

Spiders are the dominant predators in many terrestrial environments (Turnbull 1973) and have been used by others as an indicator taxon (Marc et al. 1999). However, on Cacao, we found no prominent change with elevation for indices of alpha diversity. Malumbres-Olarte et al. (2018) also found no relationship between spider diversity and elevation in Tanzania. They proposed that if niche availability was equivalent at different elevations then richness ought not to vary across the apparent gradient.

10.3.5 Collembola

Collembola (springtails) are a class of small, wingless hexapods that live within the top 10–15 cm of soil (Whalen and Sampedro 2010), in leaf litter, and on vegetation (Illig et al. 2010). Here, they are one of the most abundant taxa (Potapov et al. 2020); they are often found in large densities in most terrestrial ecosystems and on every continent, including Antarctica, (Plowman 1979; Rusek 1998; Whalen and Sampedro 2010; Fiera and Ulrich 2012). Due to their high abundance, Collembola can influence ecological processes such as the mechanical breakdown of organic matter, soil aggregation, plant establishment, and plant diversity (Rusek 1998; Siddiky et al. 2012; Caravaca and Ruess 2014). Furthermore, Collembola grazing can change the soil microbial community by spreading fungal spores (Poole 1959; Parkinson et al. 1979; Hanlon 1981; Newell 1984).

Collembola species show preference in their habitat selection; and distinct forest types differ in their species diversity and composition (Bolger et al. 2013). The majority of species within Collembola communities are only represented by a few individuals, while the majority of individuals in the community belong to just a few species (Bolger et al. 2013). Collembola are sensitive to conditions that change with elevation, especially desiccation (Pflug and Wolters 2001). Drought can cause some species to stop molting and reproducing and can reduce Collembola diversity and species richness (Waagner et al. 2011; Xu et al. 2012). Despite their abundance, they are a morphologically cryptic group (Cicconardi et al. 2013) and, particularly in the tropics, are exposed to a taxonomic impediment (Smith 2012; Potapov et al. 2020) that leaves them frequently understudied.

As a result of their tight association with water/humidity, one might expect that there would be evident associations between abundance and diversity across

Fig. 10.8 (continued) appear to decrease slightly with precipitation (**c**, **g**, **k**). Diversity and abundance have no apparent change with area (**d**, **h**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 300 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

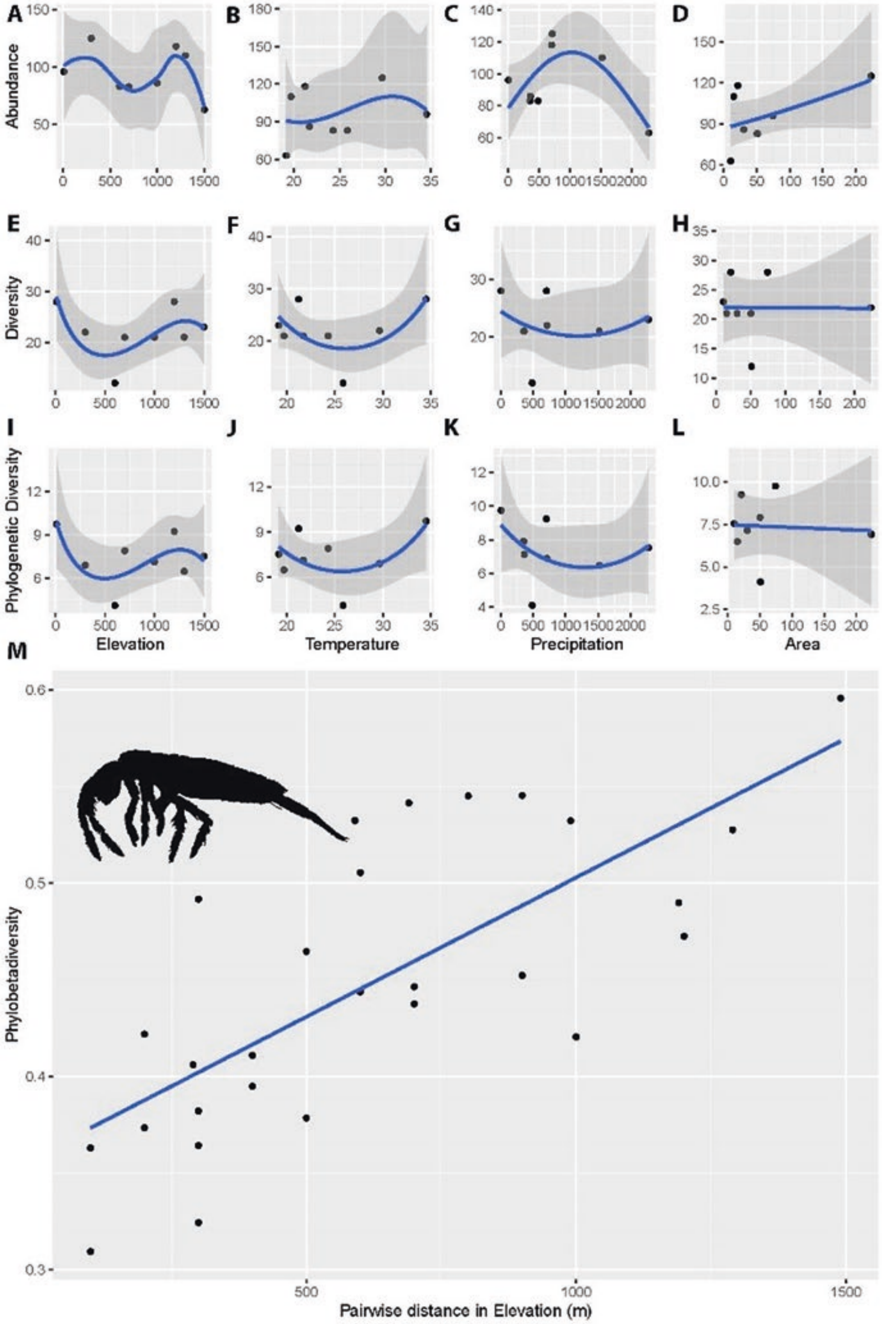

Fig. 10.9 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Collembola (springtails). As a Class, the ACG springtails display no

neotropical elevation. Indeed, in some localities, their diversity (often estimated as morphospecies) declined with elevation (Cutz-Pool et al. 2010; Sun et al. 2020); however, mid-elevation peaks in diversity have also been observed (García-Gómez et al. 2009; Greenslade and Kitching 2011; Xie et al. 2022). The relationship between Collembola abundance and elevation is also variable among mountains. Abundance has been shown both to increase (Sadaka and Ponge 2003) and decrease (Jing et al. 2005; Sun et al. 2020) with elevation.

In ACG, we found that abundance displayed two apparent peaks with elevation, no clear trend with temperature, a mid-value peak with precipitation, and an increase with area (Fig. 10.9a–d). Collembola richness and phylogenetic diversity displayed a mid-elevation trough with elevation and temperature, and no clear relationship to precipitation or temperature (Fig. 10.9e–l). Collembolan patterns of betadiversity across elevation were steep (communities changed rapidly [Fig. 10.12]), had little overlap other than among adjacent sites, and patterns were principally based on turnover and not nesting (Fig. 10.13).

Interestingly, there was some indication of competing elevational patterns of diversity amongst the orders within the taxon as a whole – a mid-elevation peak in Poduromorpha, an elevational trough in Symphypleona, and a negative relationship between diversity and elevation for the Entomobryomorpha (Pare 2015). Similar patterns of taxonomic discontinuity across elevation have been uncovered in other taxa. For example, Fiedler et al. (2008) found multiple elevation/diversity patterns within multiple moth families across an Ecuadorian elevation gradient. We found two peaks in collembola abundance across the ACG elevational gradient. Xie et al. (2022) also found a secondary peak in abundance at a higher elevation site than the peak that corresponded with their mid-elevation diversity peak. They associated their second peak with the large number of individuals associated with taxa adapted to the harsh and cold conditions. Further sampling and sequencing of these abundant and charismatic groups will be needed to elucidate these relationships in ACG.

◄

Fig. 10.9 (continued) clear relationship between diversity or abundance with elevation, temperature, or precipitation. Abundance is only idiosyncratically related to elevation and temperature (**a**, **b**), displays a mid-value peak with elevation (**c**), and is positively related to area (**d**). Diversity appears to show a mid-elevation trough (**e**, **f**, **i**, **j**) and no apparent trend with precipitation or area (**g**, **h**, **k**, **l**). While ambiguous as a class, there are apparently conflicting patterns within the class at the Ordinal level (Pare 2015). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation. Sites separated by more than 300 m shared few species (**m**). Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

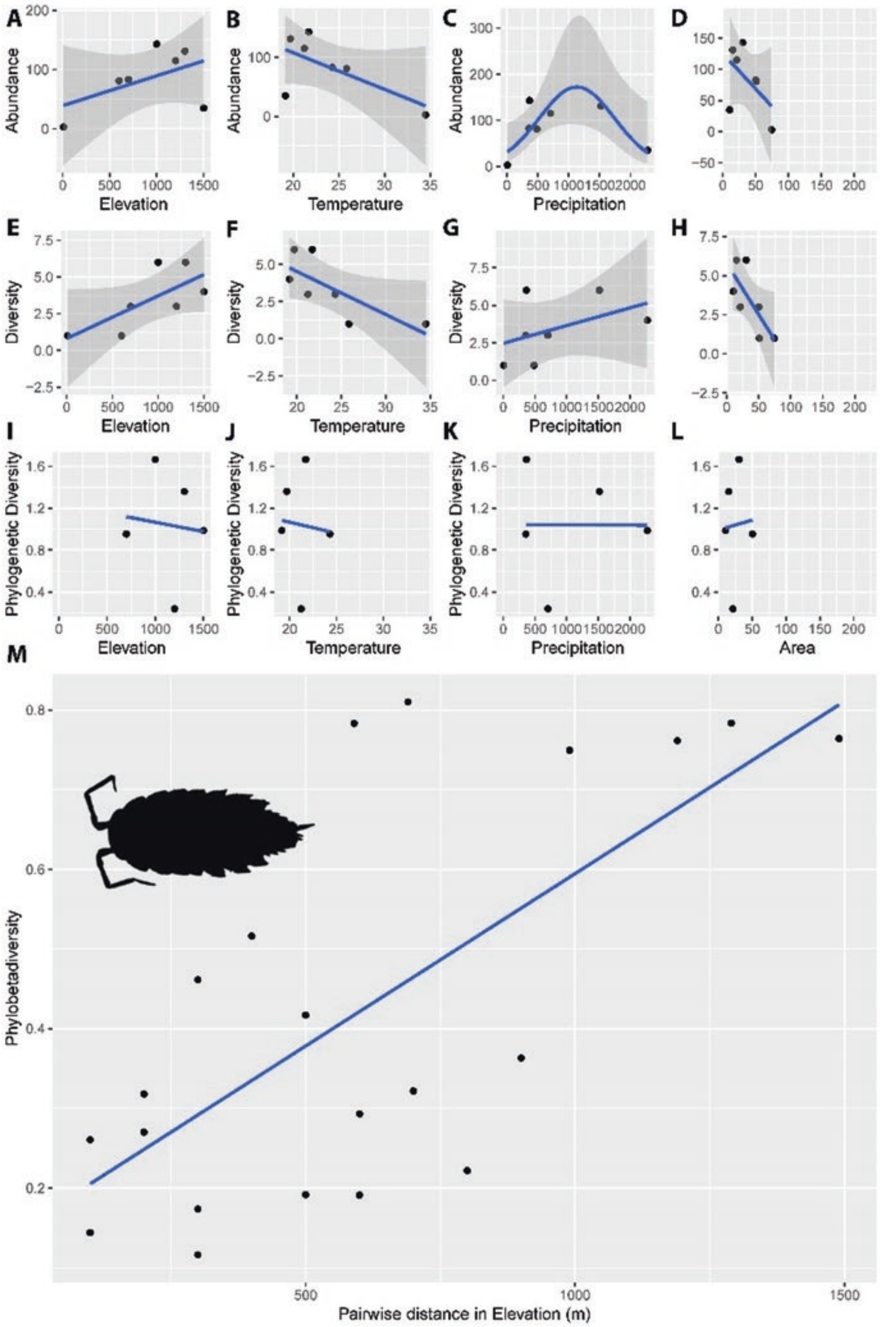

Fig. 10.10 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Isopoda (pill bugs). ACG isopods increased in abundance and

10.3.6 Isopoda

Terrestrial isopod crustaceans are omnivorous detritivores that can be omnipresent in and on leaf-litter. As their cuticle is relatively thin (compared to other arthropods in the leaf-litter), they tend to exhibit a marked dependence on high temperature and humidity (Sfenthourakis 1992; Sfenthourakis and Hornung 2018). However, despite these tight associations, isopod abundance and diversity does not change uniformly with elevation (Sfenthourakis 1992; Sfenthourakis et al. 2005; Khila et al. 2018). For example, in Greece, Sfenthourakis (1992) found that diversity decreased with elevation, while in Tunisia, (Khila et al. 2018) reported that isopod diversity peaked at mid-elevations. Although there are taxonomic and phylogenetic descriptions of terrestrial isopods in Costa Rica (e.g. Leistikow 2000), much remains to be learned regarding the distribution and diversity of terrestrial isopods – in Costa Rica and in the tropics in general (Sfenthourakis and Hornung 2018) (Fig. 10.10).

Isopod abundance may already have changed from a historical norm. DHJ and WH remember sampling in the cloud forest of Volcan Cacao in the mid-1980s, where all exposed surfaces were covered with active isopods. This is not the case today when Smith samples in the same forests. We found that isopod abundance in the ACG peaked at mid-elevations and was not highest in the wettest environments at the highest elevations. Though isopod betadiversity shows a pattern of spatial turnover with elevation, it also showed the strongest component of nestedness of all the taxa we observed. In addition, the relationship between dissimilarity and elevational separation is the steepest compared to the other taxa. While this may suggest that the isopods are more isolated between elevational bands (as their dependence on moist and humid conditions and lack of areal dispersal might suggest), these results may be impacted by the comparatively sparse specimen sampling and barcoding. More work on these crustaceans is required to determine whether the relationship between their betadiversity and elevational separation are in fact different from the other taxa we have examined here.

Fig. 10.10 (continued) diversity with elevation (**a**, **d**) and decreased with temperature (**b**, **e**). Diversity increased with precipitation (**g**), while abundance showed a mid-value peak (**c**). Both diversity and abundance declined with area (**d**, **h**). Because of the presence of only one taxon in the lowest elevation forests recovered to date, phylogenetic patterns of diversity are available across only the mid-high elevation part of the volcano and patterns are ambiguous (**i**, **j**, **k**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 1–200 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

10.3.7 Microgastrinae Parasitoid Wasps

Parasitoid insects (those whose larvae develop by feeding on a single arthropod host, killing it in the process [Godfray 1994]) may be the most species-rich group of insects in the world (Forbes et al. 2018). With extreme taxonomic and functional diversity, perhaps it is not surprising that there is no uniform elevational pattern exhibited by parasitoid insects. One family of parasitoid fly (Tachinidae) was shown to have a negative relationship between diversity and elevation, and a positive relationship with temperature (Corcos et al. 2018). Ichneumonidae in Honduras, Guatemala, and Nicaragua were found to peak in diversity at mid-elevations (Veijalainen et al. 2014). Another family of Hymenopteran parasitoids (Encyrtidae) exhibited a positive relationship between diversity and elevation (Veijalainen et al. 2014). Gauld (1988) reported that diversity declined between the lowland dry forest and higher cloud forest in northwestern Costa Rica for the Ophioninae (a subfamily of Ichneumonidae), while for another subfamily (the Pimplinae) diversity increased (Gaston and Gauld 1993) as collected by Malaise traps – which catch enormous numbers of species, but conspicuously catch a very small proportion of other parasitoid species and higher taxa, known to be in the same forest by rearing them. Also working in Costa Rica, Aguirre et al. (2018) found that one subfamily of Braconidae exhibited a negative relationship between diversity and elevation, while another displayed two peaks of diversity before declining at high elevations. McCoy found that parasitoid abundance increased with elevation (1990). Janzen found that parasitoid abundance exhibited a mid-elevation plateau and then declined in high elevations in the Venezuelan Andes (Janzen et al. 1976). While there may be a diversity of relationships to elevation within the hyperdiverse parasitoid insects, one common deterministic driver is likely to be the diversity of actual or potential hosts that these predators can consume.

The Microgastrinae are a subfamily of braconid (Hymenoptera) parasitoid wasp. They are globally hyperdiverse, ubiquitous obligate endoparasitoids of larval Lepidoptera (butterflies and moths) (Rodriguez et al. 2013; Whitfield et al. 2018; Fernandez-Triana et al. 2020). Global diversity of the group may be as high as 40–50,000 species (Rodriguez et al. 2013; Whitfield et al. 2018; Fernandez-Triana et al. 2020). Within the ACG, our understanding of this group has been dramatically altered by DNA barcoding of parasitoids derived from the rearing of caterpillar hosts and the Malaise trapping of adult wasps in the same forests (Smith et al. 2008). In many cases, what were previously thought to be host generalists were better understood as complexes of morphologically cryptic complexes of host specialists. Indeed, in one case, a specimen initially identified by specialists on the family Braconidae as belonging to a single previously described species, *Apanteles leucostigmus,* was eventually formally split into 39 different species based on host taxon, genetic differences, and morphological discontinuities (Fernandez-Triana et al. 2014b). Many, many more new species of microgastrine wasp remain to be described in ACG.

We used microgastrine wasps Malaise-trapped between 300 and 1500 m on Volcan Cacao that had been DNA barcoded (including some that have been used in the description of new species (e.g. Fernandez-Triana et al. 2014a; Carolina Arias-Penna et al. 2019) to determine whether the diversity and abundance of these important predators changed with elevation. These sites represent a subset (four sites between 300 and 1500 m) of the total elevational gradient considered for the other taxa described here (eight sites between 10 and 1500 m); however, this comparison includes all three forest types and is not a subset of the animals trapped (i.e. all microgastrine wasps collected in the traps–1565 specimens from 165 species) that were DNA barcoded (Rodriguez 2009).

In ACG, we found that the relationship between the diversity and abundance of micrograstrines exhibited an apparent trough with elevation and diversity was higher in dry forest and cloud forest than in rain forest (Fig. 10.11). This relationship was more strongly associated with area and temperature than precipitation (Fig. 10.11). Microgastrine patterns of betadiversity across elevation were steep (communities changed rapidly Fig. 10.12), with little overlap outside of adjacent sites and patterns were principally based on turnover and not nesting (Fig. 10.13). Interestingly, the trough revealed here with Malaise-trapped microgastrines is very similar to what Malaise traps at nearly the same locations captured for another subfamily of parasitoids (Pimplinae, Ichneumonidae) in terms of diversity and abundance (Gaston and Gauld 1993). The similar pattern suggests perhaps a common mechanism underlying the pattern, but current ongoing sampling from rearing and Malaise trapping are showing that all of these Microgastrinae data are far too preliminary to be used for generalisations at this time. There is as little as 15–20% overlap between the species reared in these forests and the species Malaise trapped in them.

Does the trough of microgastrine diversity track diversity and/or abundance of host taxa? Host use by a parasitoid species is intimate and important information. However, since a large proportion of described taxa are from intercept traps like the Malaise, host-use is unknown for more than half the described species of Micrograstrinae (Fernandez-Triana et al. 2020). For those species for which it is known, they come predominantly from ten families of Lepidoptera (Noctuidae, Tortricidae, Pyralidae, Crambidae, Geometridae, Gracillariidae, Depressariidae, Hesperiidae, Gelechiidae, and Nymphalidae [Fernandez-Triana et al. 2020]). Is there a trend of similar host use with the parasitoid groups where Gauld may also have found rain forest diversity to be lower than dry or cloud forests? The Pimplinae are also predominantly parasitoids of Lepidoptera larvae and pupae (although some are parasitoids of spiders [Gauld and Dubois 2006]). Based on the Pimplinae reared from the Janzen-Hallwachs caterpillar rearing program in ACG that have been DNA barcoded – the top four Lepidopteran host familes represented are Saturniidae, Sphingidae, Hesperiidae, and the Erebidae. Between the two parasitoid taxa, we see limited taxonomic overlap with one of the two taxa (the Pimplinae) tending towards larger host species. If there is a common mechanism underlying these patterns that is related to host use, it is not discernable at a coarse taxonomic level. More study is required to unravel the potential relationship between parasitoid diversity and host

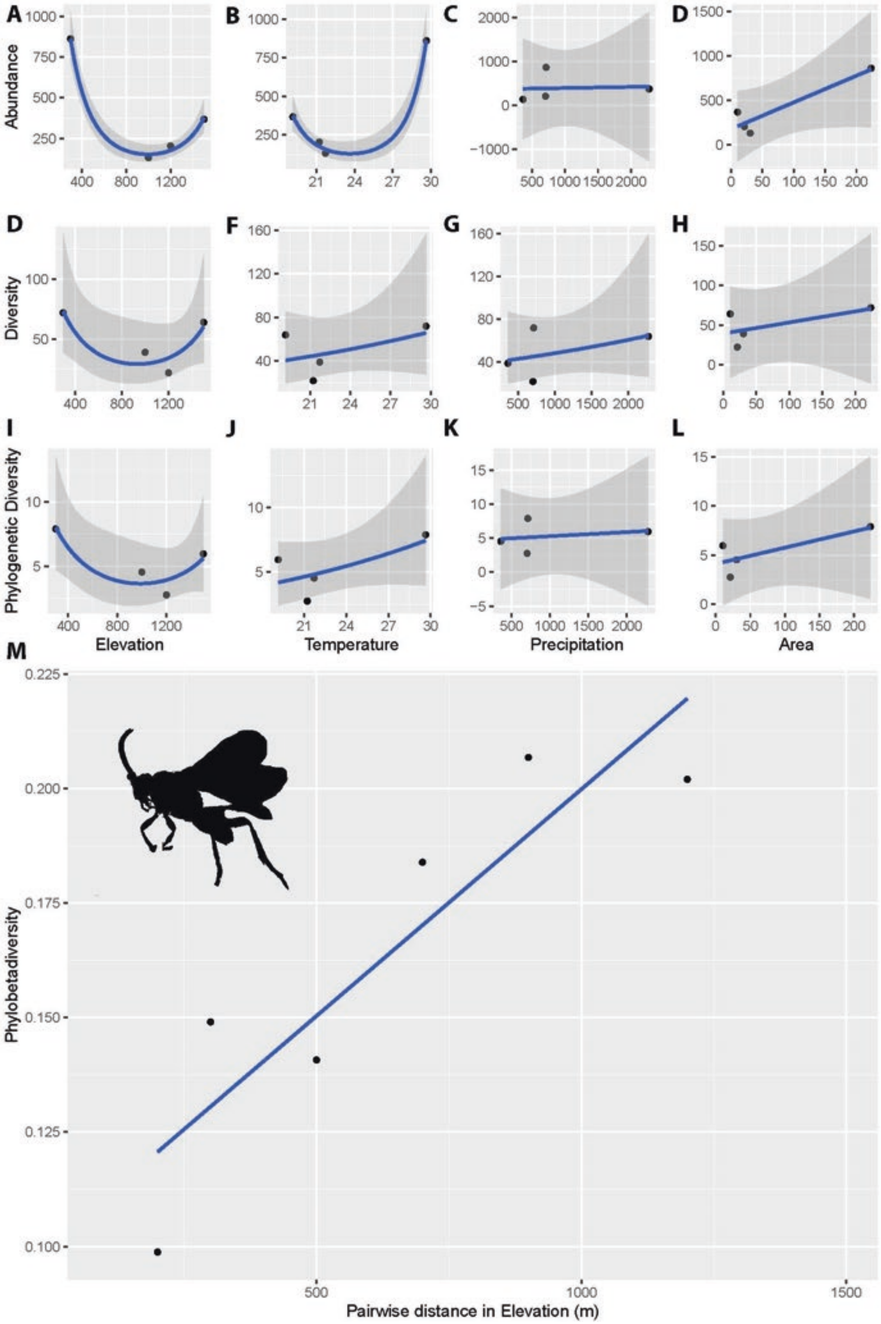

Fig. 10.11 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, precipitation, and area: Microgastrinae (parasitoid wasps). ACG microgastrine (Rodriguez 2009) decline with elevation, exhibiting a mid-elevation trough in abundance and

diversity across elevation in ACG other than there are obviously many fewer species at higher elevations than lower elevations, and that with only Malaise trapping, it cannot be known which species are seasonal migrants passing the lowland dry season refuging in moist cool cloud forest, before returning to the lowlands when the rains begin (Hunt et al. 1999).

10.4 Conclusions and Next Steps

Stable bands of temperature along this small volcano in northwestern Costa Rica present a significant boundary to some of the most abundant and diverse taxa of leaf-litter invertebrates across elevation. Although separated by only hundreds of meters, community change across this elevational gradient occurs with dramatic speed (Fig. 10.14). The cold, historically invariant cloud forests are rapidly heating and drying. Declines in cloud immersion frequency may remove up to 80% or more of Neotropical cloud forests (Helmer et al. 2019). Species will track this phenomenon and move upslope (Feeley et al. 2013; Pecl Gretta et al. 2017; Warne et al. 2020), but there is no more "top." Most species of cloud forest trees are unable to invade higher or lower elevations (Rehm and Feeley 2015), and it will be the same for their resident arthropod communities. It is very likely that many downslope taxa will establish successfully upon arrival; and many endemics to these cold wet places will soon become locally extinct. For some taxa that can get there, the wet Caribbean slopes to the east of our study transect may be accessible as a refuge from the dry warmth of the lower elevation Pacific slope marching into what used to be cloud forest. For the others (for the majority?), to whom such a distance or habitat represents an impossible dispersal, there will be local extirpations and even extinctions. It has become increasingly clear that many of the unnamed insect taxa in these tropical mountains are smaller, more regionally restricted, and/or more host-specific than had been imagined (Bickford et al. 2007; Scheffers et al. 2012; Hood et al. 2015), and many of the taxa in these sky islands are likely endemic (Myers et al. 2000; Dirnböck et al. 2011; Rahbek et al. 2019a), so in many of these cases, an

Fig. 10.11 (continued) diversity between dry forest and rain forest and then increase towards the cloud forest (**a**, **d**, **i**). Microgastrine diversity and abundance increased with temperature (**b**, **f**, **j**), showed no apparent relationship with precipitation (**c**, **j**, **k**) and increased with area (**d**, **h**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 1–200 m shared few species. Collection of microgastrine wasps differed from the other invertebrates analysed here. Parasitoids were captured exclusively using Malaise traps (Townes 1962) maintained at four elevation sites between 1998–2000, 2008, and 2012/2013. Temperature presented here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

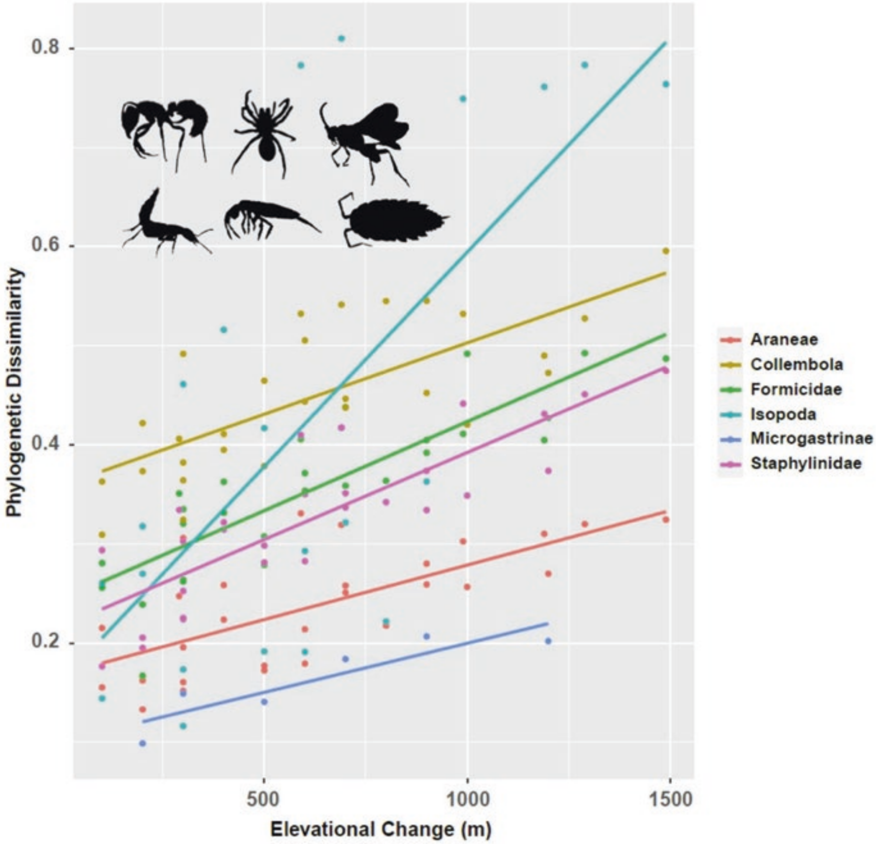

Fig. 10.12 Changes in community dissimilarity (betadiversity) across the ACG elevational gradient. Betadiversity (measured here as phylogenetic dissimilarity) changes rapidly for all taxa examined here. What does this rapid change look like on the ground? Of the nearly 1300 species examined here, sites that are 3–400 m apart share less than 0.5% species. Outside of the taxa with the least intense sampling (Isopoda), the slopes of the relationships are nearly identical, differing only in intercept

extirpation is an extinction and represents a global loss. These, "escalators to extinction" (Marris 2007; Urban Mark 2018), are occurring on elevational gradients around the world, but due to the greater diversity and ecophysiologically sensitive lifestyles on tropical mountains, the climate-driven population extinctions have been higher in tropical than on temperate mountains (Parmesan et al. 2022). Thus, while the largest amplitude changes in temperature are occurring in high-latitude locales – the most rapidly changing environments are tropical high-elevation communities. Here, long-term temperature stability has resulted in both high diversity and small species ranges – each highly vulnerable to changes in temperature and precipitation.

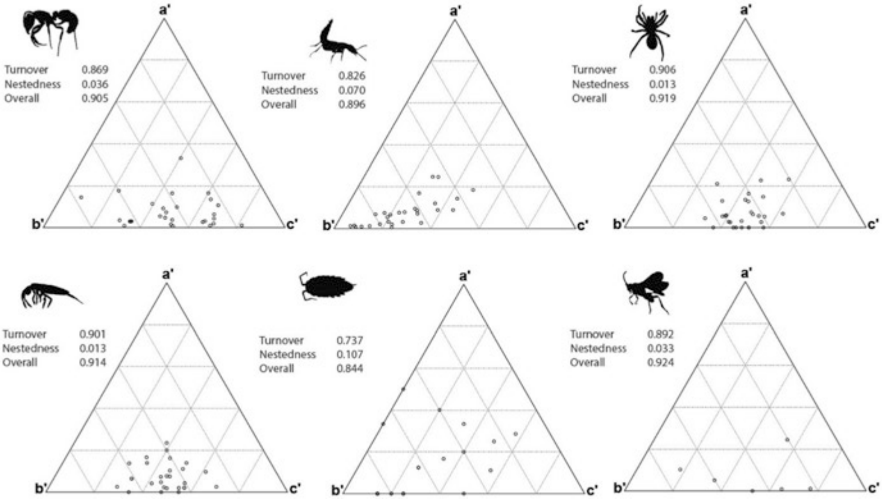

Fig. 10.13 Triangular ternary plots where points of the triangle represent (a′) the % of species shared, (b′) the % of species present exclusively in the neighbouring site, and (c′) the % species present only in the focal site (Koleff et al. 2003). Statistics describing betadiversity partitioning derived from betapart (Baselga and Orme 2012) where turnover (or spp. replacement) is beta.SIM, nestedness (spp. loss) is beta.SNE and overall betadiversity is beta.SOR. While elevational patterns in alpha diversity change in taxon-specific manners, patterns in betadiversity are markedly similar (Fig. 10.12). Change between sites separated by elevation is based on turnover (i.e. species are replaced) and not nested (where species present at the least diverse site are a subset of a larger pool present at other elevations). All taxa exhibit very few shared taxa where, if shared with other sites, they tend to be adjacent, or not at all

10.4.1 Insect Decline

Discussions about the global loss of insect diversity and abundance (a so-called insect apocalypse [Jarvis 2018]) have exploded into the scientific literature (Hallmann et al. 2017; Leather 2018; Lister and Garcia 2018; Forister et al. 2019; Goulson 2019; Sánchez-Bayo and Wyckhuys 2019; Wagner 2020; Kehoe et al. 2021; Uhler et al. 2021; Wagner David et al. 2021; Wilson and Fox 2021; Milman 2022; New 2022; Outhwaite et al. 2022). However, the unambiguous loss of insect species and abundance in both low- and high-elevation forest of ACG has been apparent for years (Janzen and Hallwachs 2019, 2021). In most of the world, the likely traditional explanations are habitat destruction and degradation (Sánchez-Bayo and Wyckhuys 2019). In ACG, habitat destruction occurred in the 400 years following European colonisation (Janzen and Hallwachs 2016). While the focus of these efforts was principally on the easier to access low-elevation dry forest areas of Guanacaste that were deforested and converted to agriculture or ranching – the efforts were opportunistic and nearly comprehensive (Janzen and Hallwachs 2016). Higher elevation forests (rain and cloud forests), which could have been cut for

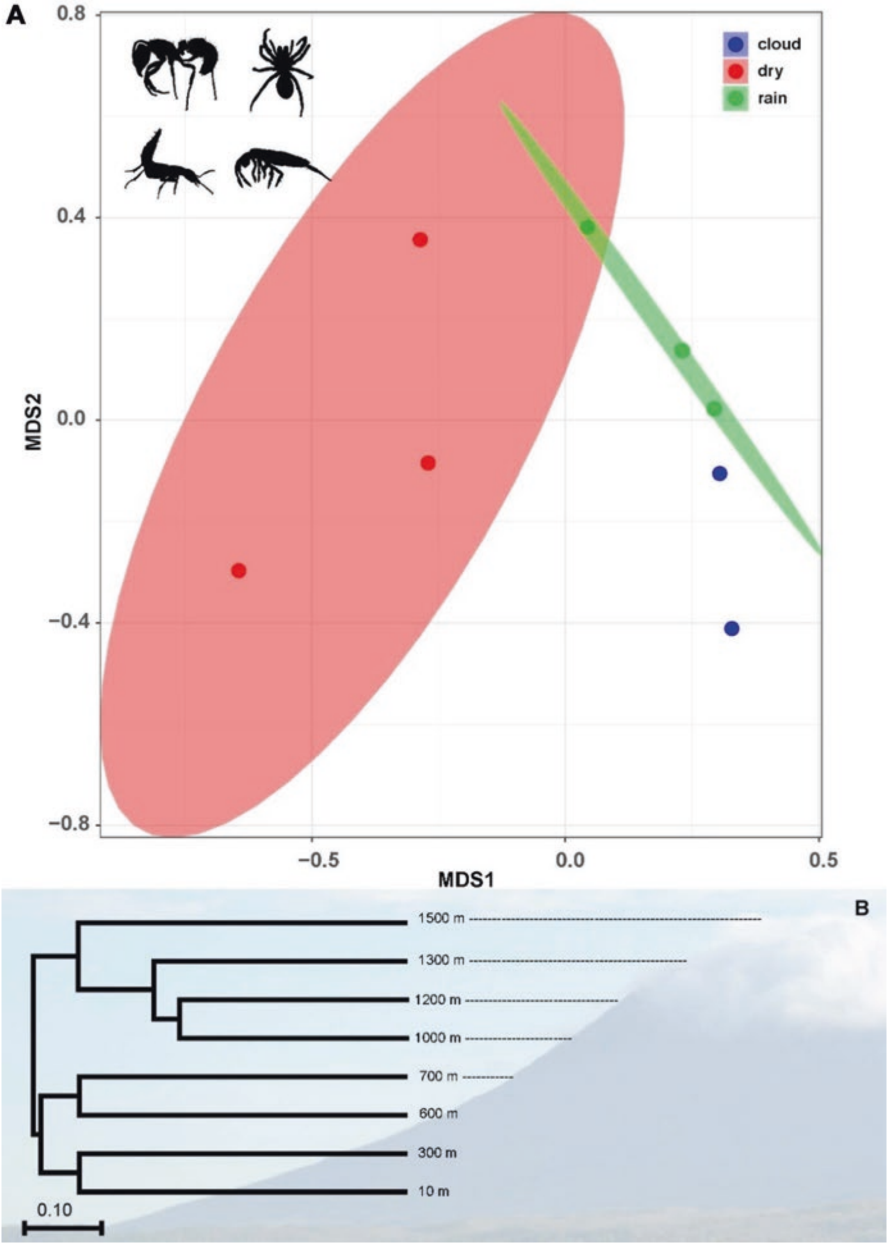

Fig. 10.14 Visualising community structure across forest types associated with elevation on Volcan Cacao (ACG) using non-metric multi-dimensional scaling (NMDS) based on the 1078 species from four leaf-litter taxa (Staphylinidae, Formicidae, Araneae, and Collembola) sampled at all eight locations. (**a**) The first NMDS dimension is largely an expression of temperature, while the second is of precipitation and elevation. The communities in the three forest types are significantly different (ANOSIM statistic $R = 0.537$, $p = 0.027$). (**b**) the Bray-Curtis dissimilarity index between communities clustered using UPGMA projected on the elevational gradient of Cacao's northern neighbour volcano – Volcan Orosi. Communities in similar forest types are more similar. As these forests change with elevation, this can result in nearby communities exhibiting markedly different communities (e.g. 600–700 m) or extreme similarity (1000–1200 m)

coffee plantations, avoided deforestation largely due to the inconvenient distance from Guanacaste to the Central Valley (Janzen and Hallwachs 2016). While there has always been some small-scale agriculture on the mid-elevation slopes of Guanacaste, the cloud forest peaks were likely too inhospitable and difficult to access to be thoroughly deforested. In recent times, the creation of the ACG from Santa Rosa National Park has seen the amount of total habitat protected increase from 9900 ha in 1971 to 169,000 ha in 2022 (Pringle 2017). So, in ACG, where the most dramatic deforestation events are decades (several or many) in the past – what is driving insect decline? The answer appears to be anthropogenic climate change and the associated changes in temperature and precipitation (Janzen and Hallwachs 2021). Warm temperatures are moving upslope, variation in temperatures exceeding levels experienced historically, precipitation levels and predictability are changing. These mechanisms have effects across the ACG elevational gradient – but likely manifest differently at different elevations. While the cloud forest peaks on the ACG stratovolcanoes avoided historic deforestations – they are not avoiding the changes in amount, variation, and predictability of temperature and precipitation. Thus, species here that may be specialised to an existence in such a refrigerator-like environment (Smith et al. 2014) will be at a disadvantage in the warmer and drier future. There is nowhere colder, wetter, and higher up to migrate to – and thus they are likely to go locally extinct. Dry forest species live in the warm lowland forests with the highest variance in temperature and precipitation – and so one might expect them to have the greatest resilience to a changing climate. However, they are likely already living at their environmental thermal optima (Deutsch et al. 2008), and so increases in the temperature extremes and averages that the dry forests experience will also result in species loss here. Colwell et al. (2008) referred to these respectively as high-elevation extinction and low elevation attrition – but we prefer to think of them each as thermal tolerance extinctions.

10.4.2 Thermal Tolerance

How insects regulate their temperature intimately affects their local and global distributions (Parmesan 2006; Sinclair et al. 2016; González-Tokman et al. 2020). Tropical insects already live close to their thermal optima and so are most likely to be negatively affected by the climate crisis (Deutsch et al. 2008; Duffy et al. 2015), both by absolute values and by the obvious asynchronies among seasonal and biological cues brought on by the changes. Indeed, despite the comparatively smaller changes in temperature forecast for the tropics (compared to the polar regions), there is likely to be a disproportionately large effect of climate change on tropical ectotherms (Dillon et al. 2010). While such a disproportionately large effect is likely – we also predict it from a profoundly uninformed position. Uninformed simply due to the scale of the problem(s) of social disinterest, the taxonomic impediment, and competition with other human agendas. There are many species of arthropods – and for most of these we know nothing about their existence, let alone their thermal tolerance (and of course knowing it will not change the impact of climate change). In the tropics is where this trend of "unknown" is felt most keenly. For example, while there have been nearly 50 years of studies examining the thermal tolerance for the soil hexapod taxon, the collembola, there are nearly no tolerance estimates of for tropical species (Escribano-Álvarez et al. 2022). Moreover, given that staphylinids are the most diverse beetle family, with over 60,000 described species (Betz et al. 2018), there is surprisingly little known regarding their thermal tolerance – in fact, to date, only one record of staphylinid thermal tolerance exists in the literature (Slabber and Chown 2005). The thermal breadth of ants has been better studied than many other insects (see Roeder et al. 2021; Nascimento et al. 2022), however, even in what may be the best studied insect taxon (for thermal limits) there are a conspicuous lack of tropical studies (Nascimento et al. 2022). In one recent example, a small period of experimental warming (2 years) resulted in changes in community composition that resulted in more ant taxa with moderate thermal tolerance and invasive qualities moving into the newly warmed environments (Bujan et al. 2022). While there is variation, across elevations of different absolute intensity, in the abiotic values changing with elevation (like temperature, clouds humidity, solar radiation, etc.), in general, it appears that species in lower elevations have higher thermal tolerances than do mountaintop species (García-Robledo et al. 2016). These low-elevation species with higher thermal tolerances are moving upslope and replacing species with lower thermal tolerance (Warren et al. 2016). More generally, a recent review found that species living across gradients of anthropogenic change were exposed to a wider thermal envelope in more disturbed areas (Williams et al. 2020). However, estimating the thermal envelope in the tropics for most taxa remains elusive as estimates of cold tolerance (chill coma recovery time or critical minimum temperature [CT_{min}]) are infrequently studied in tropical insects (Roeder et al. 2021). The relationship between an individual's fitness and temperature represents a multidimensional envelope of history (how many exposures to extreme high or low values), life history (variation between life-history stages), taxon and additive effects, including biotic ones (Sinclair et al. 2016). The response of any one taxon may be idiosyncratic, making predictions complicated (Sinclair et al. 2016). To begin to better understand how these knowledge gaps (taxonomic, high tolerance, and low tolerance) affect the species of ACG, we have initiated experiments to estimate ACG leaf-litter arthropod thermal tolerance (higher and lower). Preliminary results suggest that high temperature thermal tolerance does change across the ACG elevation gradient.

10.4.3 Upslope Migration

High elevation insect taxa may be pushed out of their habitat and driven locally extinct as the arriving higher temperatures exceed their thermal tolerances (Shah et al. 2020). These species may endure an increase in temperatures (Muhlfeld et al. 2020) or they may experience the re-wiring of seasonal events such that formerly predictable elements of their phenology (such as the return of the rains in the lower elevations) is no longer a dependable signal. For example, there are many species of insect characteristic of drier, low elevation ACG forests which seasonally migrate upslope in ACG to escape the heat, dryness, and lack of prey of the dry season (Janzen 1993, 2004; Hunt et al. 1999; John and Post 2021). As higher temperatures move upslope and precipitation is reduced and less predictable, these seasonal migrants will be without a reprieve from the violent dry-season furnace below (Janzen and Hallwachs 2021). Some taxa may escape the direct effects of the new normal hot temperatures by altering their activity patterns into the night. While this strategy will not be available to all, the trends in temperature we see within years and across elevation (Fig. 10.2) are indeed more amplified for daily maximums achieved during the daytime and more muted overnight (when the daily minimum temperatures are typically achieved). Some terrestrial taxa will have, at least a temporary, opportunity for small scale spatial retreats into more amenable micro-habitats (Duffy et al. 2015). While habitat heterogeneity (and associated micro-climates) is likely to be important for insects impacted by climate change-caused temperature extremes (Harvey et al. 2020; McCain and Garfinkel 2021), they will not provide sanctuary for the long term (or through extreme events).

10.4.4 Idiosyncratic Changes in Alpha Diversity – Consistent Changes in Betadiversity

One clear message from examining the species richness (alpha diversity) of the ACG leaf-litter fauna across elevation is the absence of any one single pattern that captures all taxa. The taxonomically idiosyncratic relationship between richness and elevational variables reinforces what others have found across elevation with different taxonomic combinations (Fiedler et al. 2008; Peters et al. 2016; Corcos et al. 2018). Fiedler et al. (2008) found that examining the relationship between diversity and elevation at high taxonomic levels for Ecuadorian moths concealed differences evident at smaller systematic scales. Working with 25 plant and animal taxa on Mt. Kilimanjaro, Peters et al. (2016) found that approximately half the taxa displayed declines in richness with elevation, while the other half displayed more complex (hump shaped or multiple peaks) relationships. In the European Alps, Corcos et al. (2018) reported variable trends across elevation for the diversity parasitoid and predatory insects. Our work in ACG and the observations of others suggests that the desire to extrapolate from one taxa to others as indicator (Kremen 1992) or umbrella strategies (Noss 1990), will not work (Prendergast et al. 1993; Prendergast and Eversham 1997). However, while we have documented extremely variable influences of elevation on alpha diversity in taxa of the ACG leaf litter – there is one strikingly uniform response that was not dependent on the taxon – all communities were increasingly dissimilar with increasing elevational separation. While elevationally adjacent sites may share a small subset of species, most species were found in only one or two elevational sites. Betadiversity changes across elevation were never nested – but instead, exhibited turnover as one travelled up- or downslope. The homogeneity of the relationship between betadiversity and elevational separation exhibited here suggests a similar mechanism may be behind the pattern – and we feel that it is likely the bands of stable temperature that stack upslope across these volcanos. While the absolute distance between locations is small, the stable differences in temperature have selected for taxa that do not move easily across these bands (Janzen 1967). In examining multiple lepidopteran taxa in Ecuador, Fiedler et al. (2008) found support for the same pattern of increasing dissimilarity with increasing elevational separation. They concluded that this concordance supported the dominant role for temperature in determining community composition. When considering a surrogate in questions of montane diversity, our results suggest that approaches based on alpha diversity are to be avoided. They do, however, suggest that analyses of betadiversity may itself provide a measure of surrogacy, suggesting the degree of connection/isolation between various elevational bands and how those change into the future. A recent, non-terrestrial example found that the betadiversity patterns of one taxon of benthic coral reef denizens was a significant predictor for other taxa (McDevitt-Irwin et al. 2021). While suggestive for gradients of elevation, betadiversity surrogacy across taxa will not provide a total panacea. For example, in examining how alpha and betadiversity changed across a gradient of land use intensity in Colombia, Cabra-García et al. (2012) found little congruence between patterns of betadiversity and more congruence in patterns of alpha diversity. In the end, the use of a subset of taxa as surrogates for others will be fraught with problems (Westgate et al. 2014) and likely the best strategy is the most work – a range of taxa rather than a subset. In this regard, our work suggests that phylogenetically expressed patterns of diversity (alpha and beta), rather than taxon-specific strategies, may be a surrogacy measure that frees resources. Phylogenetic measures of alpha (PD) and beta (comdistnt) diversity, in particular those derived from a standardised gene region like a DNA barcode, permit one to examine patterns of community similarity across a gradient without necessarily being exposed to the taxonomic impediment particularly prevalent among small tropical invertebrates (Smith et al. 2009, 2014; Swenson 2012, 2019; Brehm et al. 2016; García-Robledo et al. 2016; Dolson et al. 2020, 2021).

10.4.5 Beyond Abiotic Factors

We have measured abiotic factors here that change with elevation (temperature, precipitation, and area). We could certainly improve the scale at which we measure these factors (e.g. microclimatic conditions vary dramatically from the measures we have captured as coarse descriptions of these locations [Duffy et al. 2015]). As well as the traits of the organisms – pill bugs are not rove beetles.

One potential mechanism that might help explain some of the alpha diversity idiosyncrasy is habitat complexity. For several of the taxa we examined here, others have documented that habitat complexity was positively correlated with richness. In the Collembola, Loranger et al. (2001) found that any effect of elevation on diversity was coincident with changes in soil chemistry, nutrient availability, and soil food webs. Staphylinids are known to live in numerous microhabitats (Thayer 2005) – and thus a reasonable supposition would be that sites with a greater diversity of microhabitats would host a greater diversity of staphylinids. Finally, for spiders, others have shown that the number of available microhabitats and three-dimensional structure both positively influence spider diversity as much or more than those abiotic factors associated with elevation alone (Jimenez-Valverde and Lobo 2007; Malumbres-Olarte et al. 2018). In ACG, we envision utilising the high-resolution panoramic photographs we have collected through time and across elevation to provide a gross estimate of forest complexity. When used in temperate forests, we found that this technique was an efficient predictor of spider diversity (Ho and Smith 2015; Ho 2019).

In addition, another potentially important driver untouched in our investigation is the role that biotic effects (competition, predation, parasitism, etc.) may play in community assembly across this gradient. Quite frankly, the intimate, species-specific knowledge that is required to estimate biotic factors remains qualitatively or quantitatively out of reach for most taxa in the neotropical leaf-litter (90% of which perhaps remains undescribed). However, as we uncover the taxa and their distribution across this ACG gradient, what roles might we expect biotic interactions to play? Hargreaves et al. (2014) found that the low elevation ranges of a species' distribution were better described by biotic than abiotic effects. In a recent meta-analysis, Paquette and Hargreaves (2021) supported this observation and suggested that biotic interactions are more important at "warm" range edges than "cold" range edges. Their analysis predicts that as climate change alters the forests across neotropical elevational gradients, the changes in the hot low-elevation dry forests will be associated with competition and parasitism as opposed to the cloud forests where exceeded thermal tolerances may best predict the coming losses. What kinds of significant biotic changes might the high-elevation cloud forest expect? Consider the role that predators such as army ants may have in the cloud forests. *Eciton* species are now found across the elevation gradient on Volcan Cacao, in a frequency with which they were not in the late twentieth century (Janzen and Hallwachs 2016). Interestingly, *Eciton* themselves are a key architect of neotropical biodiversity – upon whom numerous other taxa depend and live symbiotically, including entire systematic radiations of staphylinid beetles that live cryptically inside *Eciton* colonies (Parker and Kronauer 2021) as well as having lineage-specific prey concentrations (Hoenle et al. 2019). These kinds of far-reaching relationships have led some to propose that army ant taxa can serve as an umbrella for neotropical conservation (Pérez-Espona 2021). Army ants are voracious, carnivorous predators – and their move upslope may perhaps provide a contrast to the patterns shown by Hargreaves et al. (2019) that showed seed predation decreases with elevation. What is clear, is that as the abiotic factors continue to change and challenge the tight belts of environmental conformity across elevation, biotic factors will play a role in determining which species can survive. These effects may be most visible at warm range edges.

However, as these warm edges move upslope, what we eventually observe may include both the loss of specialised endemic high-elevation taxa to increased and efficient predation via army ants and then the eventual loss of taxa specialised to live within/depend upon those army ant species as conditions eventually become so eroded that their resilience is broken. Tracking the interaction diversity (Gaüzère et al. 2022) through time and across elevation would be a useful way to track these changes as we better understand the “players in the play” of this ecological and evolutionary drama.

10.4.6 Going Forward

Stroud and Feeley wrote that “neglect of the tropics is widespread in ecology and evolution” (2017). To us, it seems that the neglect is much more widespread and extends to conservation biology and management; particularly to the knowledge, understanding, and protection of the most diverse of terrestrial taxa; the invertebrates. If we wish to better understand the causes and consequences of diversity and elevation patterns in the neotropics (and to protect what we understand), then we need to lift the veil on cryptic tropical arthropod species biology. What species live where? What is the thermal tolerance of these species (García-Robledo et al. 2016)? How do the species deal with the heat and dryness of low elevation dry forest and the cold and wet of high elevation cloud forest? How is this changing through time? Who cares about these questions and how to make more people care more? And many other things as well. Which are more important? Is it the ones we are equipped already to deal with or the ones that matter to the audience with their jillions of competing agendas? Unpacking these questions will result in better delineation of elevational ranges for tropical arthropod species resulting in a more thorough understanding of evolution and ecology for ectotherms, a baseline toolkit of predictions regarding which species will be most affected by hot temperatures on their relentless march upslope and, finally, a description of many tropical species which frees them into the scientific literature for future work. Ultimately, however, further study of these questions will not provide solutions to the underlying problem. While the climate and biodiversity crises are linked, and while tropical forests themselves are considered a “natural climate solution” (Malhi et al. 2020), what is needed are two local strategies and one global. Locally, when possible, increase the size of the protected area in order to permit more chances for climate refugees to attempt their range-shifting (Thomas Chris et al. 2012; Bates et al. 2014; Lehikoinen et al. 2021), and maintain/expand long-term monitoring and expertise, such as the experienced biodiversity managers of the ACG already do. Long-term trends and baseline data will be critical to understanding the continuing biological context of the climate crisis as well as helping us in the future to evaluate the efficacy of specific management decisions (Malhi et al. 2020). This baseline is particularly important if we find evidence of decline within protected areas (Pollock et al. 2022) as already documented and encountered all over the tropics. Globally, and most importantly, is to accelerate and entrench strategies to reduce greenhouse gas emissions as rapidly as possible and transition the global economy to a sustainable, low-carbon future (Pettorelli et al. 2021). If this does not happen, the long-term narrative for the species across elevational gradients of the ACG, as with the majority of the tropics, will be of the loss of diversity and the degradation of its forests.

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References

Agosti D, Alonso LE (2000) In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants. standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC, pp 204–206

Aguirre H, Shaw SR, Rodríguez-Jiménez A (2018) Contrasting patterns of altitudinal distribution between parasitoid wasps of the subfamilies Braconinae and Doryctinae (Hymenoptera: Braconidae). Insect Conserv Diver 11(3):219–229

Andersen AN (1997) Functional groups and patterns of organization in North American ant communities: a comparison with Australia. J Biogeogr 24:433–460

Anderson R, Ashe J (2000) Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae). Biodivers Conserv 9(5):617–653

Antão LH, Bates AE, Blowes SA, Waldock C, Supp SR, Magurran AE, Dornelas M, Schipper AM (2020) Temperature-related biodiversity change across temperate marine and terrestrial systems. Nat Ecol Evol 4(7):927–933

Antonelli A (2022) The rise and fall of Neotropical biodiversity. Bot J Linn Soc 199(1):8–24

Antonelli A, Kissling WD, Flantua SGA, Bermúdez MA, Mulch A, Muellner-Riehl AN, Kreft H, Linder HP, Badgley C, Fjeldså J, Fritz SA, Rahbek C, Herman F, Hooghiemstra H, Hoorn C (2018) Geological and climatic influences on mountain biodiversity. Nat Geosci 11:718–725

Barry RG (2008) Mountain weather and climate. Cambridge University Press, Cambridge

Baselga A, Orme CDL (2012) Betapart: an R package for the study of beta diversity. Methods Ecol Evol:808–812

Basset Y, Cizek L, Cuénoud P, Didham RK, Guilhaumon F, Missa O, Novotny V, Ødegaard F, Roslin T, Schmidl J, Tishechkin AK, Winchester NN, Roubik DW, Aberlenc H-P, Bail J, Barrios H, Bridle JR, Castaño-Meneses G, Corbara B, Curletti G, Duarte Da Rocha W, De Bakker D, Delabie JHC, Dejean A, Fagan LL, Floren A, Kitching RL, Medianero E, Miller SE, Gama De Oliveira E, Orivel J, Pollet M, Rapp M, Ribeiro SP, Roisin Y, Schmidt JB, Sørensen L, Leponce M (2012) Arthropod diversity in a tropical forest. Science 338(6113):1481–1484

Bates AE, Barrett NS, Stuart-Smith RD, Holbrook NJ, Thompson PA, Edgar GJ (2014) Resilience and signatures of tropicalization in protected reef fish communities. Nat Clim Chang 4(1):62–67

Beck J, Mccain CM, Axmacher JC, Ashton LA, Bärtschi F, Brehm G, Choi SW, Cizek O, Colwell RK, Fiedler K, Francois CL, Highland S, Holloway JD, Intachat J, Kadlec T, Kitching RL, Maunsell SC, Merckx T, Nakamura A, Odell E, Sang W, Toko PS, Zamecnik J, Zou Y, Novotny V (2017) Elevational species richness gradients in a hyperdiverse insect taxon: a global meta-study on geometrid moths. Glob Ecol Biogeogr 26:412

Beck MW (2017) ggord: ordination plots with ggplot2. R package version 1.0.0.: https://zenodo.org/badge/latestdoi/35334615

Bennett JM, Calosi P, Clusella-Trullas S, Martínez B, Sunday J, Algar AC, Araújo MB, Hawkins BA, Keith S, Kühn I, Rahbek C, Rodríguez L, Singer A, Villalobos F, Ángel Olalla-Tárraga M, Morales-Castilla I (2018) GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. Sci Data 5(1):180022

Betz O, Irmler U, Klimaszewski J, Gusarov VI, Chatzimanolis S, Asenjo A, Brunke AJ, Clarke DJ, Lipkow E, Buffam J, Work TT, Venier L, Koerner L, Dettner K, Jałoszyński P, Naomi S-I (2018) Biology of rove beetles (Staphylinidae): life history, evolution, ecology and distribution. Springer, Cham

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends Ecol Evol 22(3):148–155

Binkenstein J, Klein A-M, Assmann T, Buscot F, Erfmeier A, Ma K, Pietsch KA, Schmidt K, Scholten T, Wubet T, Bruelheide H, Schuldt A, Staab M (2017) Multi-trophic guilds respond differently to changing elevation in a subtropical forest. Ecography 40:1–10

Bishop T, Robertson M, Gibb H, Van Rensburg B, Braschler B, Chown S, Foord S, Munyai T, Okey I, Tshivhandekano P, Werenkraut V (2016) Ant assemblages have darker and larger members in cold environments. Glob Ecol Biogeogr 25(12):1489–1499

Blaxter M, Mann J, Chapman T, Thomas F, Whitton C, Floyd R, Abebe E (2005) Defining operational taxonomic units using DNA barcode data. Philos Trans R Soc B Biol Sci 360(1462):1935–1943

Blomberg SP, Garland J, Theodore R, Ives A (2003) Testing for phylogenetic signal in comparative data: behavoral traits are more labile. Evolution 57(4):717–745

Bohac J (1999) Staphylinid beetles as bioindicators. Agric Ecosyst Environ 74:357–372

Bolger T, Kenny J, Arroyo J (2013) The Collembola fauna of Irish forests–a comparison between forest type and microhabitats within the forests. Soil Org 85:61–67

Borowiec ML, Moreau CS, Rabeling C (2021) In: Starr CK (ed) Encyclopedia of social insects. Springer, Cham, pp 52–69

Brehm G, Colwell RK, Kluge J (2007) The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. Glob Ecol Biogeogr 16(2):205–219

Brehm G, Hebert PDN, Colwell RK, Adams M-O, Bodner F, Friedemann K, Möckel L, Fiedler K (2016) Turning up the heat on a hotspot: DNA barcodes reveal 80% more species of geometrid moths along an Andean elevational gradient. PLoS One 11(3):e0150327

Brühl CA, Mohamed M, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. J Trop Ecol 15:265–277

Brunke A, Newton A, Klimaszewski J, Majka C, Marshall S (2011) Staphylinidae of Eastern Canada and adjacent United States. Key to subfamilies; Staphylininae: tribes and subtribes, and species of Staphylinina. Can J Arthropod Identif 12

Bujan J, Nottingham AT, Velasquez E, Meir P, Kaspari M, Yanoviak SP (2022) Tropical ant community responses to experimental soil warming. Biol Lett 18(4):20210518

Cabra-García J, Bermúdez-Rivas C, Osorio AM, Chacón P (2012) Cross-taxon congruence of α and β diversity among five leaf litter arthropod groups in Colombia. Biodivers Conserv 21(6):1493–1508

Cajaiba RL, Périco E, Caron E, Dalzochio MS, Silva WB, Santos M (2017) Are disturbance gradients in neotropical ecosystems detected using rove beetles? A case study in the Brazilian Amazon. For Ecol Manag 405:319–327

Camacho GP, Loss AC, Fisher BL, Blaimer BB (2021) Spatial phylogenomics of acrobat ants in Madagascar—Mountains function as cradles for recent diversity and endemism. J Biogeogr 48(7):1706–1719

Caravaca F, Ruess L (2014) Arbuscular mycorrhizal fungi and their associated microbial community modulated by Collembola grazers in host plant free substrate. Soil Biol Biochem 69:25–33

Carolina Arias-Penna D, Whitfield JB, Janzen DH, Hallwachs W, Dyer LA, Smith MA, Hebert PDN, Fernández-Triana JL (2019) A species-level taxonomic review and host associations of Glyptapanteles (Hymenoptera, Braconidae, Microgastrinae) with an emphasis on 136 new reared species from Costa Rica and Ecuador. ZooKeys 890:1–685

Chatzaki M, Lymberakis P, Markakis G, Mylonas M (2005) The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. J Biogeogr 32(5):813–831

Chick LD, Lessard J-P, Dunn RR, Sanders NJ (2020) The coupled influence of thermal physiology and biotic interactions on the distribution and density of ant species along an elevational gradient. Diversity 12(12):456

Chown SL, Gaston KJ (2000) Areas, cradles and museums: the latitudinal gradient in species richness. Trends Ecol Evol 15(8):311–315

Cicconardi F, Fanciulli PP, Emerson BC (2013) Collembola, the biological species concept and the underestimation of global species richness. Mol Ecol 22(21):5382–5396

Cleveland WS, Loader CL (1996) In: Haerdle W, Schimek MG (eds) Statistical theory and computational aspects of smoothing. Springer, New York, pp 10–49

Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322(5899):258–261

Colwell RK, Rahbek C, Gotelli NJ (2004) The mid-domain effect and species richness patterns: what have we learned so far? Am Nat 163(3):1–23

Colwell RK, Rahbek C, Gotelli NJ (2005) The mid-domain effect: there's a baby in the bathwater. Am Nat 166(5):E149–E154

Corcos D, Cerretti P, Mei M, Vigna Taglianti A, Paniccia D, Santoiemma G, De Biase A, Marini L (2018) Predator and parasitoid insects along elevational gradients: role of temperature and habitat diversity. Oecologia 188(1):193–202

Currie DJ, Kerr JT (2008) Tests of the mid-domain hypothesis: a review of the evidence. Ecol Monogr 78(1):3–18

Cutz-Pool LQ, Palacios-Vargas JG, Cano-Santana Z, Castaño-Meneses G (2010) Diversity patterns of Collembola in an elevational gradient in the NW slope of Iztaccíhuatl Volcano, State of Mexico, Mexico. 121(3):249–261

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci U S A 105:6668–6672

Dillon ME, Wang G, Huey RB (2010) Global metabolic impacts of recent climate warming. Nature 467(7316):704–706

Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob Chang Biol 17(2):990–996

Dolson S, Mcphee M, Vizquez C, Hallwachs W, Janzen D, Smith MA (2020) Diversity, abundance, and phylogenetic structure of spiders (Araneae) across a Costa Rican elevation gradient. Biotropica 52:1092–1102

Dolson SJ, Loewen E, Jones K, Jacobs SR, Solis A, Hallwachs W, Brunke AJ, Janzen DH, Smith MA (2021) Diversity and phylogenetic community structure across elevation during climate change in a family of hyperdiverse neotropical beetles (Staphylinidae). Ecography 44(5):740–752

Dornhaus A, Powell S (2010) In: Lach L, Parr C, Abbott K (eds) Ant ecology. Oxford University Press, Great Britain

Duffy GA, Coetzee BWT, Janion-Scheepers C, Chown SL (2015) Microclimate-based macrophysiology: implications for insects in a warming world. Cur Opin Insect Sc 11:84–89

Edwards AW, Smith MA, Chavarria MM, Sasa M, Janzen DH, Hallwachs W, Chaves G, Fernandez R, Palmer C, Wilson C, Puschendorf R (in review) Changes in amphibian diversity and distribution across four interconnected and protected ecosystems in Costa Rica. J Trop Ecol, JTE-21-091

Escribano-Álvarez P, Pertierra LR, Martínez B, Chown SL, Olalla-Tárraga MÁ (2022) Half a century of thermal tolerance studies in springtails (Collembola): a review of metrics, spatial and temporal trends. Curr Res Insect Sci 2:100023

Faith DP (2018) In: Scherson RA, Faith DP (eds) Phylogenetic diversity: applications and challenges in biodiversity science. Springer, Cham, pp 1–26

Feeley KJ, Hurtado J, Saatchi S, Silman MR, Clark DB (2013) Compositional shifts in Costa Rican forests due to climate-driven species migrations. Glob Chang Biol 19(11):3472–3480

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125(1):1–15

Fernandez-Triana J, Shaw MR, Boudreault C, Beaudin M, Broad GR (2020) Annotated and illustrated world checklist of Microgastrinae parasitoid wasps (Hymenoptera, Braconidae). ZooKeys 920:1–1089

Fernandez-Triana JL, Janzen DH, Hallwachs W, Whitfield JB, Smith MA, Kula R (2014a) Revision of the genus Pseudapanteles (Hymenoptera, Braconidae, Microgastrinae), with emphasis on the species in Area de Conservacion Guanacaste, northwestern Costa Rica. ZooKeys 446:1–82

Fernandez-Triana JL, Whitfield JB, Rodriguez JJ, Smith MA, Janzen DH, Hallwachs WD, Hajibabaei M, Burns JM, Solis MA, Brown J, Cardinal S, Goulet H, Hebert PDN (2014b) Review of Apanteles sensu stricto (Hymenoptera, Braconidae, Microgastrinae) from Area de Conservacion Guanacaste, northwestern Costa Rica, with keys to all described species from Mesoamerica. ZooKeys 383:1–565

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37(12):4302–4315

Fiedler K, Brehm G, Hilt N, Süßenbach D, Häuser CL (2008) Gradients in a tropical mountain ecosystem of Ecuador. Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds). Berlin: Springer, pp 167–179

Fiera C, Ulrich W (2012) Spatial patterns in the distribution of European springtails (Hexapoda: Collembola). Biol J Linn Soc 105(3):498–506

Flenley JR (1995) Tropical montane cloud forests. Hamilton LS, Juvik JO, Scatena FN (eds). New York: Springer, pp 150–155

Folgarait P (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers Conserv 7:1221–1244

Forbes AA, Bagley RK, Beer MA, Hippee AC, Widmayer HA (2018) Quantifying the unquantifiable: why Hymenoptera, not Coleoptera, is the most speciose animal order. BMC Ecol 18(1):21

Forister M, Pelton E, Black S (2019) Declines in insect abundance and diversity: we know enough to act now. Conserv Sci Pract 2019(e80)

Freeman BG, Lee-Yaw JA, Sunday JM, Hargreaves AL (2018) Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. Glob Ecol Biogeogr 27(11):1268–1276

García-Gómez A, Castaño-Meneses G, Palacios-Vargas JG (2009) Diversity of springtails (Hexapoda) according to a altitudinal gradient. Pesq Agrop Brasileira 44(8):911–916

García-Robledo C, Kuprewicz EK, Staines CL, Erwin TL, Kress WJ (2016) Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. Proc Natl Acad Sci 113(3):680

Gaston KJ, Gauld ID (1993) How many species of pimplines (Hymenoptera: Ichneumonidae) are there in Costa Rica? J Trop Ecol 9(4):491–499

Gauld ID (1988) A survey of the Ophioninae (Hymenoptera: Ichneumonidae) of tropical Mesoamerica with special reference to the fauna of Costa Rica Bulletin of the British Museum (Natural History). Entomology 57(1):1–309

Gauld ID, Dubois J (2006) Phylogeny of the Polysphincta group of genera (Hymenoptera: Ichneumonidae; Pimplinae): a taxonomic revision of spider ectoparasitoids. Syst Entomol 31(3):529–564

Gaüzère P, O'connor L, Botella C, Poggiato G, Münkemüller T, Pollock LJ, Brose U, Maiorano L, Harfoot M, Thuiller W (2022) The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity. Curr Biol 32:2093

Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integr Comp Biol 46(1):5–17

Glaser F (2006) Biogeography, diversity and vertical distribution of ants (Hymenoptera: Formicidae) in Vorarlberg, Austria. Myrmecol News 8:263–270

Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, NJ

González-Reyes AX, Corronca JA, Rodriguez-Artigas SM (2017) Changes of arthropod diversity across an altitudinal ecoregional zonation in Northwestern Argentina. PeerJ 5:2–29

González-Tokman D, Córdoba-Aguilar A, Dáttilo W, Lira-Noriega A, Sánchez-Guillén RA, Villalobos F (2020) Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. Biol Rev 95(3):802–821

Goulson D (2019) The insect apocalypse, and why it matters. Curr Biol 29(19):R967–R971

Greenslade P, Kitching R (2011) Potential effects of climatic warming on the distribution of Collembola along an altitudinal transect in Lamington National Park, Queensland, Australia. Memoirs Qld Museum Nat 55:333–347

Greenstone MH (1984) Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. Oecologia 62(3):299–304

Grubb PJ (1971) Interpretation of the 'Massenerhebung' effect on tropical mountains. Nature 229:44–45

Gutiérrez-Chacon C, Zúniga MDC, Van Bodegom PM, Chará J, Giraldo LP (2009) Rove beetles (Coleoptera: Staphylinidae) in Neotropical riverine landscapes: characterising their distribution. Insect Conserv Diver 2:106–115

Hallmann C, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12(109):e0185809

Hanlon R (1981) Influence of grazing by Collembola on the activity of senescent fungal colonies grown on media of different nutrient concentration. Oikos 36(3):362–367

Hargreaves AL, Germain RM, Bontrager M, Persi J, Angert AL (2019) Local adaptation to biotic interactions: a meta-analysis across latitudes. Am Nat 195(3):395–411

Hargreaves AL, Samis KE, Eckert CG (2014) Are species' range limits simply niche limits writ large? a review of transplant experiments beyond the range. Am Nat 183(2):157–173

Harvey JA, Heinen R, Gols R, Thakur MP (2020) Climate change-mediated temperature extremes and insects: from outbreaks to breakdowns. Glob Chang Biol 26(12):6685–6701

Hastie TJ (1992) Statistical models. Chambers JM, Hastie TJ (eds). Wadsworth & Brooks Cole

Hawkins E (2018) Show your stripes

Helmer EH, Gerson EA, Baggett LS, Bird BJ, Ruzycki TS, Voggesser SM (2019) Neotropical cloud forests and páramo to contract and dry from declines in cloud immersion and frost. PLoS One 14(4):e0213155

Ho C (2019) Impacts of forestry on spider (Araneae) diversity, abundance, and community structure. University of Guelph

Ho C, Smith MA (2015) Impacts of anthropogenic disturbance on arthropod biodiversity and community structure. Adamowicz SJ (ed). Genome, pp 163–303

Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. Biol Rev 80(3):489–513

Hoenle PO, Blüthgen N, Brückner A, Kronauer DJC, Fiala B, Donoso DA, Smith MA, Ospina Jara B, Von Beeren C (2019) Species-level predation network uncovers high prey specificity in a Neotropical army ant community. Mol Ecol 28(9):2423–2440

Holdridge R (1967) Life zone ecology. Tropical Science Center, San José, CR

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, MA

Hood GR, Forbes AA, Powell THQ, Egan SP, Hamerlinck G, Smith JJ, Feder JL (2015) Sequential divergence and the multiplicative origin of community diversity. Proc Natl Acad Sci U S A 112. https://doi.org/10.1073/pnas.1424717112

Hunt JH, Brodie RJ, Carithers TP, Goldstein PZ, Janzen DH (1999) Dry season migration by Costa Rican lowland paper wasps to high elevation cold dormancy sites. Biotropica 31(1):192–196

Illig J, Norton RA, Scheu S, Maraun M (2010) Density and community structure of soil-and bark-dwelling microarthropods along an altitudinal gradient in a tropical montane rainforest. Exp Appl Acarol 52(1):49–62

Irmler U, Gurlich S (2007) What do rove beetles (Coleoptera: Staphylinidae) indicate for site conditions? Experimental C-enrichment of tropical agricultural soil View project. Faun Ökol Mitt 8:439–455

Irmler U, Klimaszewski J, Betz O (2018) Biology of rove beetles (Staphylinidae): life history, evolution, ecology and distribution. Springer, Cham, pp 1–4

Irmler U, Lipkow E (2018) In: Betz O, Irmler U, Klimaszewski J (eds) Biology of rove beetles (Staphylinidae). Springer, Cham

Janzen D, Hallwachs W (2020) Área de Conservación Guanacaste, northwestern Costa Rica: converting a tropical national park to conservation via biodevelopment. Biotropica 52:1017–1029

Janzen D, Hallwachs W, Pereira G, Blanco R, Masis A, Chavarria MM, Chavarria F, Guadamuz A, Araya M, Smith MA, Valerio J, Guido H, Sanchez E, Bermudez S, Perez KHJ, Manjunath R, Ratnasingham S, St. Jacques B, Milton MA, Dewaard JR, Zakharov EV, Naik S, Hajibabaei M, Hebert PDN, Hasegawa M (2020) Using DNA-barcoded Malaise trap samples to measure impact of a geothermal energy project on the biodiversity of a Costa Rican old-growth rain forest. Genome 63(9):407–436

Janzen DH (1967) Why mountain passes are higher in the tropics. Am Nat 101:233–249

Janzen DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54(3):687–708

Janzen DH (1993) In: Stamp NE, Casey TM (eds) Caterpillars: ecological and evolutionary constraints on foraging. Chapman and Hall, New York, pp 448–477

Janzen DH (2004) Biodiversity conservation in Costa Rica: learning the lessons in a seasonal dry forest. Gordon WF, Alfonso M, Vinson SB (eds). University of California Press, Berkeley

Janzen DH, Ataroff M, Farinas M, Reyes S, Rincon N, Soler A, Soriano P, Vera M (1976) Changes in the arthropod community along an elevational transect in the Venezuelan Andes. Biotropica 8(3):193–203

Janzen DH, Hallwachs W (2016) Costa Rican ecosystems. University of Chicago Press

Janzen DH, Hallwachs W (2019) Perspective: where might be many tropical insects? Biol Conserv 233:102–108

Janzen DH, Hallwachs W (2021) To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. Proc Natl Acad Sci 118(2):e2002546117

Jarvis B (2018) The insect apocalypse is here, New York

Jimenez-Valverde A, Lobo JM (2007) Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. Ecol Entomol 32(1):113–122

Jing S, Solhøy T, Huifu W, Vollan TI, Rumei X (2005) Differences in soil arthropod communities along a high altitude gradient at Shergyla Mountain, Tibet, China. Arct Antarct Alp Res 37(2):261–266

John C, Post E (2021) Seasonality, niche management and vertical migration in landscapes of relief. Ecography 2022. https://doi.org/10.1111/ecog.05774

Karmalkar AV, Bradley RS, Diaz HF (2008) Climate change scenario for Costa Rican montane forests. Geophys Res Lett 35:L11702

Kehoe R, Frago E, Sanders D (2021) Cascading extinctions as a hidden driver of insect decline. Ecol Entomol 46(4):743–756

Kembel S, Cowan P, Helmus M, Cornwell W, Morlon H, Ackerly D, Blomberg S, Webb C (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464

Khila M, Zaabar W, Achouri MS (2018) Diversity of terrestrial isopod species in the Chambi National Park (Kasserine, Tunisia). Afr J Ecol 56(3):582–590

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence–absence data. J Anim Ecol 72(3):367–382

Körner C (2004) Mountain biodiversity, its causes and function. AMBIO J Human Environ 33(sp13):11–17

Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22(11):569–574

Kremen C (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. Ecol Appl 2(2):203–217

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35(6):1547–1549

Lawton RO, Lawton MF, Lawton RM, Daniels JD (2016) Costa Rican ecosystems. University of Chicago Press

Leather SR (2018) "Ecological Armageddon" – more evidence for the drastic decline in insect numbers. Ann Appl Biol 172(1):1–3

Lehikoinen P, Tiusanen M, Santangeli A, Rajasärkkä A, Jaatinen K, Valkama J, Virkkala R, Lehikoinen A (2021) Increasing protected area coverage mitigates climate-driven community changes. Biol Conserv 253:108892

Leistikow A (2000) The terrestrial isopod genus ischioscia in Costa Rica: new species and records, and an analysis of its phylogeny (Crustacea, Isopoda, Oniscidea). Zoosystematics Evol 76(1):19–49

Lessard J-P, Dunn RR, Parker CR, Sanders NJ (2007) Rarity and diversity in forest ant assemblages of Great Smoky Mountains National Park. Southeast Nat 6:215–228

Lister BC, Garcia A (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. Proc Natl Acad Sci 115(44):E10397–E10406

Longino JT (2021) Army ants take the stage. Curr Biol 31(4):R164–R165

Longino JT, Branstetter MG (2019) The truncated bell: an enigmatic but pervasive elevational diversity pattern in Middle American ants. Ecography 42:272–283

Longino JT, Colwell RK (1997) Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecol Appl 7(4):1263–1277

Loranger G, Bandyopadhyaya I, Razaka B, Ponge JF (2001) Does soil acidity explain altitudinal sequences in collembolan communities? Soil Biol Biochem 33(3):381–393

Malhi Y, Franklin J, Seddon N, Solan M, Turner MG, Field CB, Knowlton N (2020) Climate change and ecosystems: threats, opportunities and solutions. Philos Trans R Soc B Biol Sci 375(1794):20190104

Malumbres-Olarte J, Crespo L, Cardoso P, Szűts T, Fannes W, Pape T, Scharff N (2018) The same but different: equally megadiverse but taxonomically variant spider communities along an elevational gradient. Acta Oecol 88:19–28

Mamantov MA, Gibson-Reinemer DK, Linck EB, Sheldon KS (2021) Climate-driven range shifts of montane species vary with elevation. Glob Ecol Biogeogr 30(4):784–794

Marc P, Canard A, Ysnel F (1999) Spiders (Araneae) useful for pest limitation and bioindication. Agric Ecosyst Environ 74(1):229–273

Marris E (2007) The escalator effect. Nat Climate Change 1(712):94–96

Martin PS (1963) The last 10,000 years, A fossil pollen record of the American South-West. University of Arizona Press, Tucson, AZ

Mccain C, Grytness J-A (2010) Elevational gradients in species richness. In: Encyclopedia of life sciences, pp 1–10

Mccain CM (2005) Elevational gradients in diversity of small mammals. Ecology 86(2):366–372

Mccain CM (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Glob Ecol Biogeogr 16(1):1–13

Mccain CM (2009) Global analysis of bird elevational diversity. Glob Ecol Biogeogr 18:346–360

Mccain CM (2010) Global analysis of reptile elevational diversity. Glob Ecol Biogeogr 19(4):541–553

Mccain CM, Garfinkel CF (2021) Climate change and elevational range shifts in insects. Curr Opin Insect Sci 47:111–118

Mccoy ED (1990) The distribution of insects along elevational gradients. Oikos 58(3):313–322

Mcdevitt-Irwin JM, Kappel C, Harborne AR, Mumby PJ, Brumbaugh DR, Micheli F (2021) Coupled beta diversity patterns among coral reef benthic taxa. Oecologia 195(1):225–234

Mcvicar TR, Körner C (2013) On the use of elevation, altitude, and height in the ecological and climatological literature. Oecologia 171(2):335–337

Milman O (2022) The insect crisis: the fall of the tiny empires that run the world. WW Norton, New York

Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE (2006) Phylogeny of the ants: diversification in the age of angiosperms. Science 312(5770):101–104

Muhlfeld CC, Cline TJ, Giersch JJ, Peitzsch E, Florentine C, Jacobsen D, Hotaling S (2020) Specialized meltwater biodiversity persists despite widespread deglaciation. Proc Natl Acad Sci 117(22):12208–12214

Müller J, Brandl R, Cadotte MW, Heibl C, Bässler C, Weiß I, Birkhofer K, Thorn S, Seibold S (2022) A replicated study on the response of spider assemblages to regional and local processes. Ecol Monogr e1511. https://doi.org/10.1002/ecm.1511

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858

Myster RW (in press) Neotropical gradients. Myster RW (ed). Berlin: Spring

Nascimento G, Câmara T, Arnan X (2022) Critical thermal limits in ants and their implications under climate change. Biol Rev 97:1287. https://doi.org/10.1111/brv.12843

Nei M, Kumar S (2000) Molecular evolution and Phylogenetics. Oxford University Press, New York

New TR (2022) Insect diversity, declines and conservation in Australia. New TR (ed). Springer, Cham, pp 83–97

Newell K (1984) Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. Soil Biol Biochem 16(3):235–239

Newton AF, Thayer MK (1992) Current classification and family-group names in Staphyliniformia (Coleoptera). Field Museum of Natural History, Chicago, IL

Nogueira ADA, Brescovit AD, Perbiche-Neves G, Venticinque EM (2021) Spider (Arachnida-Araneae) diversity in an amazonian altitudinal gradient: are the patterns congruent with mid-domain and rapoport effect predictions? Biota Neotrop 21(4):e20211210

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Conserv Biol 4(4):355–364

Odegaard F (2006) Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama. Biodivers Conserv 15:83–105

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) Vegan: community ecology package: R package version 2.5–2

Outhwaite CL, Mccann P, Newbold T (2022) Agriculture and climate change are reshaping insect biodiversity worldwide. Nature 605:97–102

Owen NR, Gumbs R, Gray CL, Faith DP (2019) Global conservation of phylogenetic diversity captures more than just functional diversity. Nat Commun 10(1):859

Pagel M (1999) Inferring the historical patterns of biological evolution. Nature 401(6756):877–884

Paquette A, Hargreaves AL (2021) Biotic interactions are more often important at species' warm versus cool range edges. Ecol Lett 24(11):2427–2438

Pare K (2015) Patterns in Neotropical Collembola diversity and morphology along an elevation gradient. University of Guelph, Guelph

Parker J, Kronauer DJC (2021) How ants shape biodiversity. Curr Biol 31(19):R1208–R1214

Parkinson D, Visser S, Whittaker J (1979) Effects of collembolan grazing on fungal colonization of leaf litter. Soil Biol Biochem 11(5):529–535

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Ann Rev Ecol Evol Syst 37:637–669

Parmesan C, Morecroft MD, Trisurat Y, Adrian R, Anshari GZ, Arneth A, Gao Q, Gonzalez P, Harris R, Price J, Stevens N, Talukdarr GH (2022) Climate change 2022: impacts, adaptation, and vulnerability. In: Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (eds) Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change. Cambridge University Press

Patterson DJ, Cooper J, Kirk PM, Pyle RL, Remsen DP (2010) Names are key to the big new biology. Trends Ecol Evol 25(12):686–691

Pecl Gretta T, Araújo Miguel B, Bell Johann D, Blanchard J, Bonebrake Timothy C, Chen IC, Clark Timothy D, Colwell Robert K, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia Raquel A, Griffis Roger B, Hobday Alistair J, Janion-Scheepers C, Jarzyna Marta A, Jennings S, Lenoir J, Linnetved Hlif I, Martin Victoria Y, Mccormack Phillipa C, Mcdonald J, Mitchell Nicola J, Mustonen T, Pandolfi John M, Pettorelli N, Popova E, Robinson Sharon A, Scheffers Brett R, Shaw Justine D, Sorte Cascade JB, Strugnell Jan M, Sunday Jennifer M, Tuanmu M-N, Vergés A, Villanueva C, Wernberg T, Wapstra E, Williams Stephen E (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355(6332):eaai9214

Pérez-Espona S (2021) Eciton army ants—umbrella species for conservation in Neotropical Forests. Diversity 13(3):136

Perrigo A, Hoorn C, Antonelli A (2020) Why mountains matter for biodiversity. J Biogeogr 47(2):315–325

Peters MK, Hemp A, Appelhans T, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Haas M, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Mwangomo E, Ngereza C, Otte I, Röder J, Rutten G, Schellenberger Costa D, Tardanico J, Zancolli G, Deckert J, Eardley CD, Peters RS, Rödel MO, Schleuning M, Ssymank A, Kakengi V, Zhang J, Böhning-Gaese K, Brandl R, Kalko EKV, Kleyer M, Nauss T, Tschapka M, Fischer M, Steffan-Dewenter I (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nat Commun 7:1–11

Pettorelli N, Graham NAJ, Seddon N, Maria Da Cunha Bustamante M, Lowton MJ, Sutherland WJ, Koldewey HJ, Prentice HC, Barlow J (2021) Time to integrate global climate change and biodiversity science-policy agendas. J Appl Ecol 58(11):2384–2393

Pflug A, Wolters V (2001) Influence of drought and litter age on Collembola communities. Eur J Soil Biol 37(4):305–308

Plowman KP (1979) Litter and soil fauna of two Australian subtropical forests. Aust J Ecol 4(1):87–104

Pohl G, Langor D, Klimaszewski J, Work T, Paquin P (2008) Rove beetles (Coleoptera: Staphylinidae) in northern Nearctic forests1. Can Entomol 140(4):415–436

Polato NR, Gill BA, Shah AA, Gray MM, Casner KL, Barthelet A, Messer PW, Simmons MP, Guayasamin JM, Encalada AC, Kondratieff BC, Flecker AS, Thomas SA, Ghalambor CK, Poff NL, Funk WC, Zamudio KR (2018) Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. Proc Natl Acad Sci 115(49):12471–12476

Pollock HS, Toms JD, Tarwater CE, Benson TJ, Karr JR, Brawn JD (2022) Long-term monitoring reveals widespread and severe declines of understory birds in a protected Neotropical forest. Proc Natl Acad Sci 119(16):e2108731119

Poole T (1959) Studies on the food of Collembola in a Douglas fir plantation. Proc Zool Soc London 132:71–82

Potapov A, Bellini BC, Chown SL, Deharveng L, Janssens F, Kováč Ľ, Kuznetsova N, Ponge JF, Potapov M, Querner P, Russell D, Sun X, Zhang F, Berg MP (2020) Towards a global synthesis of Collembola knowledge: challenges and potential solutions. Soil Org 92(3):161–188

Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. Nature 398(6728):611–615

Prendergast JR, Eversham BC (1997) Species richness covariance in higher taxa: empirical tests of the biodiversity indicator concept. Ecography 20(2):210–216

Prendergast JR, Quinn RM, Lawton JH, Eversham BC, Gibbons DW (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365(6444):335–337

Pringle RM (2017) Upgrading protected areas to conserve wild biodiversity. Nature 546(7656):91–99

Qodri A, Raffiudin R, Noerdjito WA (2016) Diversity and Abundance of Carabidae and Staphylinidae (Insecta: Coleoptera) in Four Montane Habitat Types on Mt. Bawakaraeng, South Sulawesi. J Biosci 23(1):22–28

Rahbek C, Borregaard M, Colwell R, Dalsgaard B, Holt B, Morueta-Holme N, Nogues-Bravo D, Whittaker R, Fjeldså J (2019a) Humboldt's enigma: what causes global patterns of mountain biodiversity? Science 365(6458):1108–1113

Rahbek C, Borregaard Michael K, Antonelli A, Colwell Robert K, Holt Ben G, Nogues-Bravo D, Rasmussen Christian MØ, Richardson K, Rosing Minik T, Whittaker Robert J, Fjeldså J (2019b) Building mountain biodiversity: geological and evolutionary processes. Science 365(6458):1114–1119

Ramirez-Barahona S, Eguiarte LE (2013) The role of glacial cycles in promoting genetic diversity in the Neotropics: the case of cloud forest during the Last Glacial Maximum. Ecol Evol 3:725–738

Ratnasingham S, Hebert PD (2013) A DNA-based registry for all animal species: the barcode index number (BIN) system. PLoS One 8(7):e66213

Ratnasingham S, Hebert PDN (2007) BOLD: the barcode of life data system (www.barcodinglife.org). Mol Ecol Notes 7(3):355–364

Raven PH, Gereau RE, Phillipson PB, Chatelain C, Jenkins Clinton N, Ulloa Ulloa C (2021) The distribution of biodiversity richness in the tropics. Sci Adv 6(37):eabc6228

Rehm EM, Feeley KJ (2015) The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. Ecography 38(12):1167–1175

Reta-Heredia I, Jurado E, Pando-Moreno M, González-Rodríguez H, Mora-Olivo A, Estrada-Castillón E (2018) Diversidad de arañas en ecosistemas forestales como indicadoras de altitud y disturbio. Rev Mex Cienc Forestales 9:251–273

Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3(2):217–223

Rodriguez J (2009) Integrating molecular, ecological and morphological data to explore the biodiversity of microgastrine parasitoid wasps. University of Illinois at Urbana-Champaign

Rodriguez JJ, Fernandez-Triana JL, Smith MA, Janzen DH, Hallwachs W, Erwin TL, Whitfield JB (2013) Extrapolations from field studies and known faunas converge on dramatically increased estimates of global microgastrine parasitoid wasp species richness (Hymenoptera: Braconidae). Insect Conserv Diver 6(4):530–536

Roeder KA, Roeder DV, Bujan J (2021) Ant thermal tolerance: a review of methods, hypotheses, and sources of variation. Ann Entomol Soc Am 114(4):459–469

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press

Rusek J (1998) Biodiversity of Collembola and their functional role in the ecosystem. Biodivers Conserv 7(9):1207–1219

Sadaka N, Ponge J-F (2003) Soil animal communities in holm oak forests: influence of horizon, altitude and year. Eur J Soil Biol 39(4):197–207

Samson DA, Rickart EA, Gonzales PC (1997) Ant diversity and abundance along an elevational gradient in the Philippines. Biotropica 29(3):349–363

Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: a review of its drivers. Biol Conserv 232:8–27

Sarnat EM, Friedman NR, Fischer G, Lecroq-Bennet B, Economo EP (2017) Rise of the spiny ants: diversification, ecology and function of extreme traits in the hyperdiverse genus Pheidole (Hymenoptera: Formicidae). Biol J Linn Soc 122(3):514–538

Scheffers BR, Joppa LN, Pimm SL, Laurance WF (2012) What we know and don't know about Earth's missing biodiversity. Trends Ecol Evol 27(9):501–510

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH image to ImageJ: 25 years of image analysis. Nat Methods 9(7):671–675

Sfenthourakis S (1992) Altitudinal effect on species richness of Oniscidea (Crustacea; Isopoda) on three mountains in Greece. Glob Ecol Biogeogr Lett 2(5):157–164

Sfenthourakis S, Anastasiou I, Strutenschi T (2005) Altitudinal terrestrial isopod diversity. Eur J Soil Biol 41(3):91–98

Sfenthourakis S, Hornung E (2018) Isopod distribution and climate change. ZooKeys 801:25–61

Shah AA, Dillon ME, Hotaling S, Woods HA (2020) High elevation insect communities face shifting ecological and evolutionary landscapes. Curr Opin Insect Sci 41:1–6

Sheldon K, Huey R, Kaspari M, Sanders N (2018a) Fifty years of mountain passes: a perspective on Dan Janzen's classic article. Am Nat 191(5):553–565

Sheldon KS, Huey RB, Kaspari M, Sanders NJ (2018b) Fifty years of mountain passes: a perspective on Dan Janzen's classic article. Am Nat 191(5):553–565

Siddiky MRK, Schaller J, Caruso T, Rillig MC (2012) Arbuscular mycorrhizal fungi and collembola non-additively increase soil aggregation. Soil Biol Biochem 47:93–99

Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, Slotsbo S, Dong Y, Harley CD, Marshall DJ, Helmuth BS (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecol Lett 19(11):1372–1385

Slabber S, Chown SL (2005) Differential responses of thermal tolerance to acclimation in the sub-Antarctic rove beetle *Halmaeusa atriceps*. Physiol Entomol 30(2):195–204

Smith M, Fernande-Triana J, Roughley R, Hebert PDN (2009) DNA barcode accumulation curves for understudied taxa and areas. Mol Ecol Resour 9:208–216

Smith MA (2012) The encyclopedia of sustainability: Vol. 6 Measurements, indicators, and research methods for sustainability. Daniel Fogel SF, Lisa Harrington, and Ian Spellerberg (ed). Great Barrington, MA: Berkshire Publishing, pp 326–328

Smith MA (2015) Ants, elevation, phylogenetic diversity and community structure. Ecosphere 6(11):1–17

Smith MA (2018) Janzen's mountain passes hypothesis is comprehensively tested in its fifth decade. Proc Natl Acad Sci 115(49):12337–12339

Smith MA, Hallwachs W, Janzen DH (2014) Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. Ecography 37(8):720–731

Smith MA, Hallwachs W, Janzen DH, Longino JT, Branstetter MG (2020) A subterranean ant Acanthostichus Mayr, 1887 is revealed in Costa Rica. Insect Soc 67(2):327–330

Smith MA, Janzen DH, Hallwachs W, Longino JT (2015) Observations of *Adelomyrmex* (Hymenoptera:Formicidae) reproductive biology facilitated by digital field microscopy and DNA barcoding. Can Entomol 147:611–616

Smith MA, Rodriguez JJ, Whitfield JB, Deans AR, Janzen DH, Hallwachs W, Hebert PDN (2008) Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. Proc Natl Acad Sci U S A 105(34):12359–12364

Still CJ, Foster PN, Schneider SH (1999) Simulating the effects of climate change on tropical montane cloud forests. Nature 398(6728):608–610

Stroud JT, Feeley KJ (2017) Neglect of the tropics is widespread in ecology and evolution: a comment on Clarke et al. Trends Ecol Evol 32(9):626–628

Sun X, Marian F, Bluhm C, Maraun M, Scheu S (2020) Response of Collembola to the addition of nutrients along an altitudinal gradient of tropical montane rainforests. Appl Soil Ecol 147:103382

Sunday J, Bennett JM, Calosi P, Clusella-Trullas S, Gravel S, Hargreaves AL, Leiva FP, Verberk WCEP, Olalla-Tárraga MÁ, Morales-Castilla I (2019) Thermal tolerance patterns across latitude and elevation. Philos Trans R Soc B Biol Sci 374(1778):20190036

Swenson NG (2012) DNA barcodes: methods and protocols. Kress WJ, Erickson DL (eds). Humana Press, Totowa, NJ, pp 409–419

Swenson NG (2019) Phylogenetic ecology: a history, critique, and remodeling. University of Chicago Press

Symondson WOC, Sunderland KD, Greenstone MH (2001) Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47:561–594

Team RC (2021) R: a language and environment for statistical computing. Austria

Thayer MK (2005) Handbook of zoology, Vol. IV, Part 38, Coleoptera, Vol. 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Staphyliniformia, Scarabaeiformia, Elateriformia). Beutel RG, RAB L (eds). Berlin: De Gruyter, pp 296–344

Thomas Chris D, Gillingham Phillipa K, Bradbury Richard B, Roy David B, Anderson Barbara J, Baxter John M, Bourn Nigel AD, Crick Humphrey QP, Findon Richard A, Fox R, Hodgson Jenny A, Holt Alison R, Morecroft Mike D, O'hanlon Nina J, Oliver Tom H, Pearce-Higgins James W, Procter Deborah A, Thomas Jeremy A, Walker Kevin J, Walmsley Clive A, Wilson Robert J, Hill Jane K (2012) Protected areas facilitate species' range expansions. Proc Natl Acad Sci 109(35):14063–14068

Townes H (1962) Design for a Malaise trap. Proc Entomol Soc Wash 64(4):253–262

Townes H (1972) A light-weight Malaise trap. Entomol News 83:239–247

Turnbull AL (1973) Ecology of the true spiders (Araneomorphae). Annu Rev Entomol 18(1):305–348

Uetz GW (1976) Gradient analysis of spider communities in a streamside forest. Oecologia 22:373–385

Uhler J, Redlich S, Zhang J, Hothorn T, Tobisch C, Ewald J, Thorn S, Seibold S, Mitesser O, Morinière J, Bozicevic V, Benjamin CS, Englmeier J, Fricke U, Ganuza C, Haensel M, Riebl R, Rojas-Botero S, Rummler T, Uphus L, Schmidt S, Steffan-Dewenter I, Müller J (2021) Relationship of insect biomass and richness with land use along a climate gradient. Nat Commun 12(1):5946

Urban Mark C (2018) Escalator to extinction. Proc Natl Acad Sci 115(47):11871–11873

Van Der Hammen T, Ward PS (2005) Ants from the Ecoandes expeditions: diversity and distribution (Hormigas de las expediciones de Ecoandes: diversidad y distribucion). Stud Trop Andean Ecosyst 6:239–248

Veijalainen A, Sääksjärvi IE, Tuomisto H, Broad GR, Bordera S, Jussila R (2014) Altitudinal trends in species richness and diversity of Mesoamerican parasitoid wasps (Hymenoptera: Ichneumonidae). Insect Conserv Diver 7(6):496–507

Waagner D, Bayley M, Holmstrup M (2011) Recovery of reproduction after drought in the soil living Folsomia candida (Collembola). Soil Biol Biochem 43(3):690–692

Wagner David L, Grames Eliza M, Forister Matthew L, Berenbaum May R, Stopak D (2021) Insect decline in the Anthropocene: death by a thousand cuts. Proc Natl Acad Sci 118(2):e2023989118

Wagner DL (2020) Insect declines in the anthropocene. Annu Rev Entomol 65(1):457–480

Ward PS (2006) Ants. Curr Biol 16(5):R152–R155

Warne CPK, Hallwachs W, Janzen DH, Smith MA (2020) Functional and genetic diversity changes through time in a cloud forest ant assemblage. Biotropica 52:1084–1091

Warren RJ, Chick LD, Demarco B, Mcmillan A, De Stefano V, Gibson R, Pinzone P (2016) Climate-driven range shift prompts species replacement. Insect Soc 63(4):593–601

Weber NA (1938) The biology of the fungus-growing ants. Part IV. Additional new forms. Part V. The Attini of Bolivia. Rev Entomol 9(1–2):154–206

Westgate MJ, Barton PS, Lane PW, Lindenmayer DB (2014) Global meta-analysis reveals low consistency of biodiversity congruence relationships. Nat Commun 5(1):3899

Whalen JK, Sampedro L (2010) Soil ecology and management. CABI

Whitfield JB, Austin AD, Fernandez-Triana JL (2018) Systematics, biology, and evolution of microgastrine parasitoid wasps. Annu Rev Entomol 63(1):389–406

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York

Williams JJ, Bates AE, Newbold T (2020) Human-dominated land uses favour species affiliated with more extreme climates, especially in the tropics. Ecography 43(3):391–405

Wilson RJ, Fox R (2021) Insect responses to global change offer signposts for biodiversity and conservation. Ecol Entomol 46(4):699–717

Wolda H (1987) Altitude, habitat and tropical insect diversity. Biol J Linn Soc 30:313–323

Xie Z, Sun X, Lux J, Chen T-W, Potapov M, Wu D, Scheu S (2022) Drivers of Collembola assemblages along an altitudinal gradient in Northeast China. Ecol Evol 12(2):e8559

Xu G-L, Kuster TM, Günthardt-Goerg MS, Dobbertin M, Li M-H (2012) Seasonal exposure to drought and air warming affects soil Collembola and mites. PLoS One 7(8):e43102

Yanoviak SP, Kragh G, Nadkarni NM (2003) Spider assemblages in Costa Rican cloud forests: effects of forest level and forest age. Stud Neotropical Fauna Environ 38(2):145–154

Yoshimura M, Fisher BL (2012) A revision of male ants of the Malagasy Amblyoponinae (Hymenoptera: Formicidae) with resurrections of the genera *Stigmatomma* and *Xymmer*. PLoS One 7(3)

Zou Y, Sang W, Zhou H, Huang L, Axmacher JC (2014) Altitudinal diversity patterns of ground beetles (Coleoptera: Carabidae) in the forests of Changbai Mountain, Northeast China. Insect Conserv Diver 7(2):161–171

Chapter 11
Neotropical Gradients of Insect Groups in Brazilian Mountains

Lucas Neves Perillo, Frederico de Siqueira Neves, Flávio Siqueira de Castro, and Ricardo Ribeiro de Castro Solar

11.1 Introduction

11.1.1 Mountainous Environments as Natural Laboratories for Insect Studies

Amidst countless challenges, such as the need to see the real importance of mechanisms for maintaining species diversity (Chesson 2000), we must invest strong efforts to collect biological data on Neotropical gradients. Despite the large number of variables and mechanisms deriving from these gradients, the theory of ecological communities can be used to understand the processes responsible for generating and maintaining diversity in biological communities (Graham et al. 2014; Vellend 2010). With the current biodiversity crisis, especially caused by anthropic actions, we must explore the evolution of analyses and the growth (in quality and quantity) of databases to allow us to use a range of explanatory variables to calculate complex properties of biological communities (Baselga and Orme 2012) and reduce sampling problems, such as temporal pseudo-replication (Crawley 2013).

Mountainous environments are natural laboratories for biodiversity studies, with elevation as the most important environmental driver (Perillo et al. 2021) that promotes different environmental conditions (such as climate and soil) in a reduced

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geographical area (Wolda 1987; McCain and Grytnes 2010; Fernandes et al. 2016; Tito et al. 2020). Its elevational variations represent one of the great biogeographic frontiers to be studied and allow studies on the environmental variations of organisms to be proposed (Knapp 2005). Changes in elevation can impose barriers to species dispersal (Moura et al. 2016; Qian et al. 2013), favoring a large number of endemic species, due to a combination of environmental filtering, isolation effect (Körner 2007), ecological and evolutionary processes (Lomolino 2001; Rahbek 1995), and allopatric speciation (Baselga et al. 2012). An indirect effect of area (i.e., reduced compiled area in higher elevations) can also influence the number of species (Romdal and Grytnes 2007) through the reduction of the regional species pool (Cornell and Harrison 2014).

The complexity of montane systems imposes several challenges for biodiversity studies, such as how environmental variability in space and time affect the community structure and what is the role of its environmental gradients in the patterns and mechanisms that determine biodiversity. In this scenario, there are many advantages of studying invertebrates: in addition to being easily sampled, they normally have short generation times and respond rapidly to environmental changes (Kremen et al. 1993). Arthropod populations are sensitive to short and long-term changes in ecosystems (Basset et al. 2001; Missa et al. 2009). Insects stand out for representing a large part of animal biodiversity in mountainous environments, with some taxa especially sensitive to natural environmental filters and to habitat disturbances.

Most species communities are negatively influenced by high elevations (Peters et al. 2016) and high latitudes (Willig et al. 2003), even when latitudinal and elevational patterns are acting together (Kraft et al. 2011). Explanations range from ecological and evolutionary to geographic (Lamanna et al. 2014), involving environmental heterogeneity and stability, effective evolutionary time, mean temperature and productivity, interspecific interactions and abundance–adaptation hypotheses (Longino and Branstetter 2019; Schluter and Pennell 2017). Elevation, through its influence on climatic and environmental variations, can exert selective pressure on physiological, morphological, and behavioral characteristics, inducing adaptive responses of insects (Slatyer and Schoville 2016; Ouisse et al. 2020). Changes in body size (Kubota et al. 2007), life cycle (Sota 1996), in addition to wings loss (Mani 1968), dormancy period increase, sex ratio, and body color changes, can be caused by elevation in several taxonomic groups (Mani 1962; Hodkinson 2005). But defining which variable affected by elevation is responsible for changes at community level can be challenging (Hagen et al. 2008).

There is still a considerable gap in species surveys in the Neotropics, and the knowledge of Brazilian terrestrial biodiversity go through a strong influence of collection bias (Oliveira et al. 2016). Despite the alarming decline in insect species predicted worldwide over the next few decades (Sánchez-Bayo and Wyckhuys 2019; Cardoso et al. 2020), invertebrates are often neglected in biodiversity conservation policies (Cardoso et al. 2011; Samways et al. 2020), especially in mountainous environments (Pryke and Samways 2010). Several reasons lead to this scenario, such as the huge diversity (Basset et al. 2012), poor taxonomy (Ely et al. 2017), and a gap remains unfilled to understand ecological dynamics, since the majority of tropical taxa has been the focus of conservation studies (Lewis and Basset 2007).

11.1.2 Neotropical Mountain Insects

Since Alexander von Humboldt's expedition to Latin America in 1799, the scientific community is fascinated with neotropical mountains. In his forays into the Ecuador mountains, he documented several discoveries about biogeography, botany, and zoology. During the Chimborazo expedition, Humboldt idealized his wonderful *Naturgemälde* (nature painting – Fig. 11.1), a meticulous diagram that depicts the relationship between elevation and vegetation zones. Inspired by this work, Humboldt began to formulate possible hypothesis to explain the global patterns for the vegetation distribution.

Humboldt also collected insects, which were described by multiple European taxonomists (Papavero 1971). But most of the effort and concern (even today) are directed to other groups, specially plants (Barthlott et al. 2005). One of the pioneers in high elevation entomology was Mahadeva Subramania Mani (1908–2003), a researcher that led the first entomological expeditions to the North West Himalaya, collecting a considerable insect number (Ananthakrishnan 2007). Mani described several characteristics of highland insects for the first time, publishing several books (Mani 1962; Mani 1968; Mani 1973).

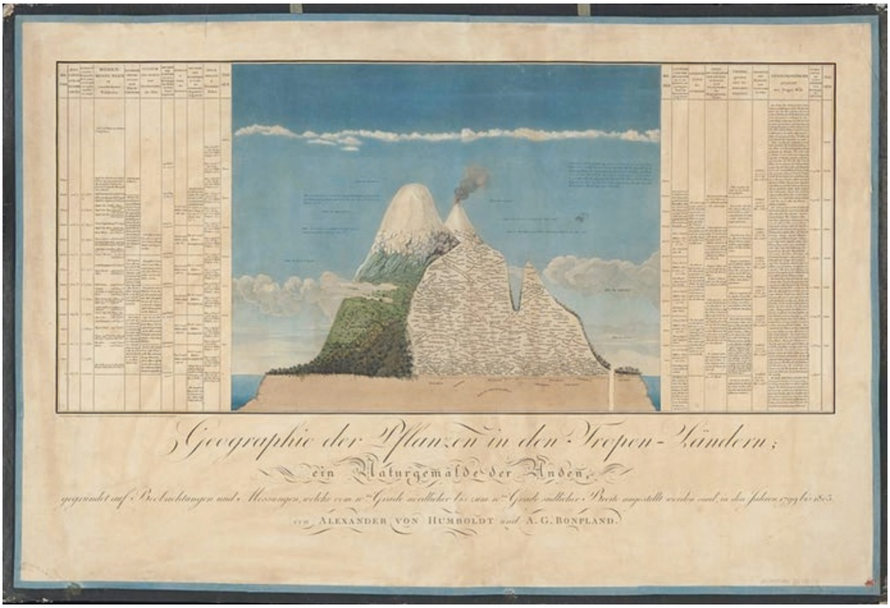

Fig. 11.1 Humboldt's *Naturgemälde* (View of nature). Wikipedia Commons

11.1.3 Brazilian Mountains

Brazil hosts a set of mountains, but the elevations rarely exceed 2000 m.a.s.l. The highest Brazilian Mountain is *Pico da Neblina*, reaching 2995 m in the Amazon region. In the southeast region, the Serra do Caparaó, which hosts the *Pico da Bandeira* (2891 m), Serra da Mantiqueira, with *Pico das Agulhas Negras* (2791 m) and Serra do Espinhaço, with *Pico do Sol* (2072 m) are some examples. They are not high, especially compared to the Andes, which reaches 6961 m at Aconcágua peak, but its elevational gradient is enough to generate variations in diversity. Despite having narrow elevational ranges, Brazilian mountains underpin modifications in intensity and displacement of synoptic systems due to its orography (Seluchi et al. 2011) and the biogeographical effects provided by the mountain chains drive high diversity (Perillo et al. 2021).

The knowledge about Brazilian mountains' biodiversity began to intensify after the arrival of the European naturalists. With the Brazilian ports opening and the arrival of the Portuguese royal family to Brazil in 1808 due to the Napoleonic Wars, the expedition of naturalists to study its natural resources was encouraged (Padoan 2015). Several kingdoms sent their best researchers to explore the new Neotropical world. Important naturalists and biologists made expeditions in Brazilian territory. Some legendary names that passed through the Brazilian mountains were Maximilian de Wied von Neuwied (1815–17), Auguste de Saint Hilaire (1816–1822), George Heirinch von Langsdorff (1816–17 and 1824), Karl Friedrich Philip von Martius and Johann Baptist von Spix (1818–1824), Johann Baptist Emmanuel Pohl (1820), Ludwig Riedel (1824), Ernst Ule (1892), Auguste François Marie Glaziou (1858), Peter Claussen (1843), Frederik Christian Raben (1836), George Gardner (1840), and Edvard Wainio (1885) (Zico 1979; Padoan 2015; Bolle 2017). Charles Darwin, despite not having traveled in the Brazilian mountains, mentions in his passage through the Atlantic Forest that: "… the insects make such a noise that they can be heard from the ship…" (Darwin 2006).

Despite this constant presence of naturalists in the mountains of southeastern Brazil since the beginning of the nineteenth century, few had the insects as their main focus of study. Some are worth mentioning, such as the French naturalist entomologist Pierre Emile Gounelle in 1885, Edouard Ménétries, renowned naturalist and entomologist (creator of the Russian Entomological Society) and Frederich Sellow (1819 and 1830) which, despite being a botanist, collected more than 110,000 species of insects in Brazil. An interesting compilation of the naturalists that collected invertebrates in Brazil during the XIX century can be found in Papavero (1971). But it was only from the first half of the twentieth century that the first great Brazilian entomologists and taxonomists emerged, such as Ângelo Moreira da Costa Lima (Rio de Janeiro, author of "Insetos do Brasil" in 1938), Cândido F. de Mello-Leitão (Arachnida, Museu Nacional do Rio de Janeiro), the couple Benedito A.M. Soares and Hélia H.M. Soares (Arachnida), Cincinnato R. Gonçalves (Rio de Janeiro, Formicidae) and Priest Jesús S. Moure (Apoidea) (Drummond 2009).

Although there has been a constant effort to survey biodiversity in the tropics, insects are poorly explored in mountainous environments (Pryke and Samways 2010), especially considering studies on biogeography, elevational, latitudinal, and environmental variations. In the mountaintops, the lack of data is even greater (Perillo et al. 2021). Ancient tropical mountains are megadiverse, yet little is known about the distribution of their species. This is especially true when we consider insects, a megadiverse group that hosts more than one million described species (Purvis and Hector 2000). In the last years, there have been important studies with insects in Brazilian mountains, considering elevational and vegetational effects on species diversity (Henriques et al. 2022) and exploring mountain environmental filter (Lasmar et al. 2020). For instance, in these mountainous environments, we may be losing species, phytophysiognomies, and habitats at rates never seen before (Fernandes et al. 2016).

11.1.4 The Espinhaço Range and **Campo Rupestre**

Among the mountainous areas found in Brazil, the Espinhaço Range stands out as the largest mountainous formation that extends for more than 1200 km north–south between the Brazilian states of Bahia and Minas Gerais (Fig. 11.2). Espinhaço acts as an important barrier to moisture that comes from the Atlantic Ocean and is responsible for dividing the Cerrado to the west (countryside formation) and the Atlantic Forest to the east (forest formation).

In Brazil, the Espinhaço Mountain Range hosts the majority of the *Campo Rupestre* (CR) ecosystem (rupestrian grassland), the hottest Brazilian biodiversity hotspot. It is a herbaceous-shrub ecosystem located on the rocky outcrops of Brazilian mountaintops (Silveira et al. 2016; Fernandes et al. 2020), and that is predominant at the highest elevations of the Espinhaço Mountain Range. The Espinhaço is the most ancient and extensive mountain range in eastern South America (Vasconcelos et al. 2020), and is located in a region between two biodiversity hotspots, the Cerrado to the west and the Atlantic Forest to the east, with the Caatinga biome to the northeast (Fernandes 2016; Silveira et al. 2016). The *Campo Rupestre* (CR) has great strategic importance for the conservation of unique natural environments, with a great diversity of species and natural resources. Several species are highly restricted to certain elevations or latitudinal ranges, and endemic species are relatively common in the CR, e.g., amphibians (Leite et al. 2008; Oswald et al. 2022), birds (Chaves et al. 2014), ants (Costa et al. 2015) and plants (Mota et al. 2018). In this ecosystem, there are advances in flora knowledge (Fernandes 2016), but little is known about the insects distribution patterns and mechanisms, which have most of the work in montane environments in Brazil restricted to punctual sampling (Perillo et al. 2017). This accumulated knowledge highlights the key importance of studying such an ecosystem and its biogeographical patterns, especially considering the threats imposed by current drivers of global change (Fernandes et al. 2018). Therefore, all these characteristics make the CR a valuable source for

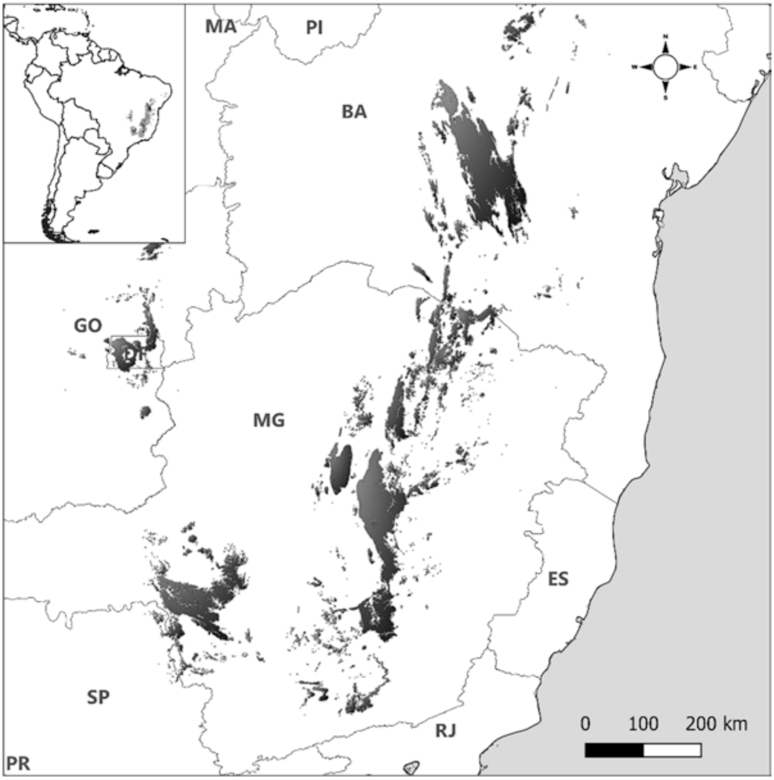

Fig. 11.2 Map with the original distribution of the Campo Rupestre ecosystem and the Espinhaço Mountain Range, Brazil

studies of evolutionary patterns and geographic distribution of species (Silveira et al. 2019).

CR is predominantly an open ecosystem, but it is also very heterogeneous in phytophysiognomies. Many factors contribute to the great biological diversity of these grassland formations, such as the variation in elevation (Alves et al. 2014), which causes populations' isolation between and within mountains, the ancestral age of their geological formations, the variety of microclimates (Barbosa et al. 2015), and the presence of a vegetational mosaic with grassland matrix and forest physiognomies (Rapini et al. 2008).

Associated with the opened matrix of CR, we can find forested formations, such as gallery forests and *capões de mata* (Coelho et al. 2017). The *capões de mata* are forest islands with arboreal vegetation immersed on mountaintops. These forest islands have a floristic composition similar to the Seasonal Semideciduous Forests of Southeastern Brazil, associated with the Atlantic Forest domain, and their establishment and development is especially dependent on climate and soil (Coelho et al. 2016) (Fig. 11.3).

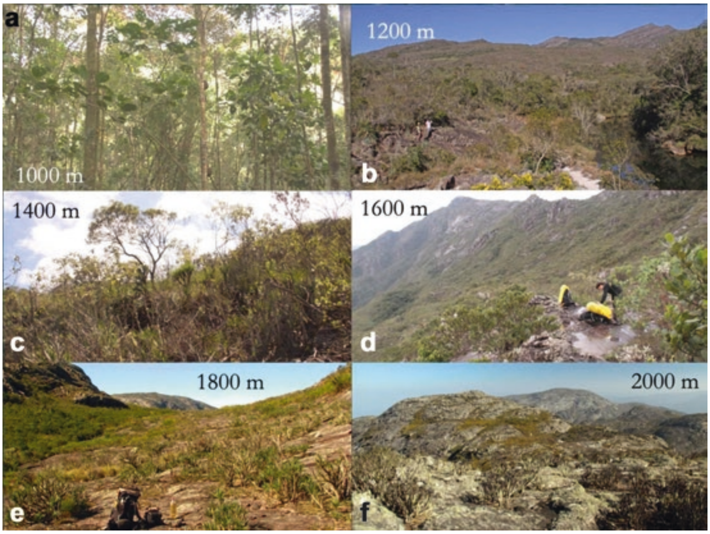

Fig. 11.3 The *Campo Rupestre* ecosystem in Espinhaço Mountain Range, Brazil in different elevations at RPPN Santuário do Caraça, Minas Gerais, Brazil. (**a**) 1000 m above sea level, (**b**) 1200 m, (**c**) 1400 m, (**d**) 1600 m, (**e**) 1800 m, and (**f**) 2000 m. (Photos: Lucas Perillo)

Our goal with this chapter is to integrate information about mountain insects in Brazilian CR ecosystem considering multiple gradients that can be studied on mountains.

11.2 Quantifying Insect Diversity

In the Brazilian mountains, especially in the CR, insects are protagonists in fauna studies considering gradients, especially with elevation patterns. Most of the available insect data was produced in a Long-term Ecological Research (PELD CRSC/CNPq Project) in which seven sampling sites are distributed along an 800–1400 m elevational gradient at Serra do Cipó, Minas Gerais state (Silveira et al. 2019). In the project, the study of some taxonomic groups was prioritized, such as plants (Mota et al. 2018), fungi (Coutinho et al. 2015) and insects (Pereira et al. 2017; da Silva et al. 2019; Castro et al. 2019; Castro et al. 2020; Nunes et al. 2020; Perillo et al. 2020; Brant et al. 2021). The project is still in progress and there are multiple researcher teams collecting insects with different methods.

11.2.1 *Sampling Methods*

To access mountain insect diversity, each taxonomic group has a specific method for collecting data. The active collecting method depends on human performance that immediately collect the specimens from the environment (Ferro and Summerlin 2019). In contrast, the passive methods can allow high sampling effort and avoid the biases associated with collectors' skills (Moreira et al. 2016). Using a range of sampling methods is always indicated and can access a greater species diversity (Missa et al. 2009). As an example, for CR environment, the methods used to capture bees and wasps were complementary, with Malaise trap collecting the majority of morphospecies, followed by pan trap and pitfall trap (Fig. 11.4) (see Perillo et al. 2021).

11.2.1.1 Entomological Nets

The entomological net (Fig. 11.5a) is an active collecting method. It can be made more efficient with the application of attractive solutions (composed of water, honey, sugar, and salt) (Noll and Gomes 2009) or focusing directly on floral resources (Gostinski et al. 2016). In ecological gradients studies, their use should be chosen wisely. For the comparison among different locations, the sampling effort must be standardized temporally (seasonally or during specific hours of the day) and spatially, defining a transect size and a collector walking speed. Yet, the collector must have some experience in collecting actively and a knowledge of when and where a specimen can be collected.

11.2.1.2 Pan Traps

The pan trap is a passive method originally conceived as a 25 cm diameter aluminum container painted yellow (Moericke 1951) with a killing solution comprised of salt, water, and detergent (Fig. 11.5b). Nowadays even disposable plastic pans are

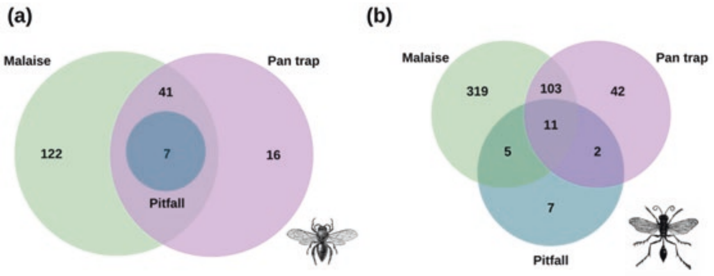

Fig. 11.4 Venn diagram showing bees (**a**) and wasps (**b**) morphospecies collected in Malaise, Moericke and pitfall traps. (Data from Perillo et al. 2021). The authors used only ants collected with pitfall traps

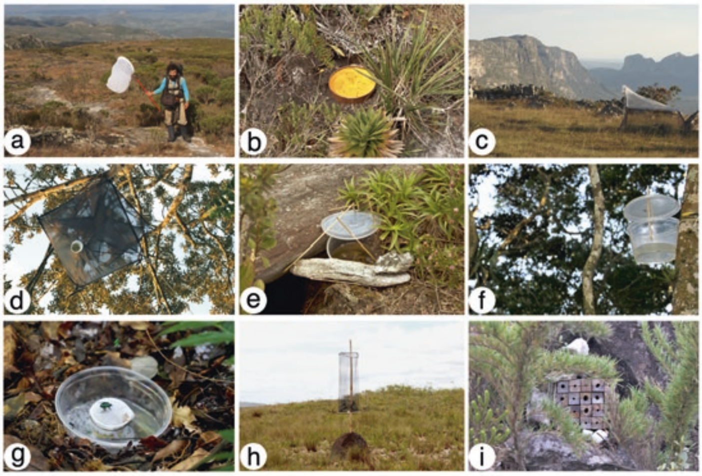

Fig. 11.5 Multiple methods used to capture mountain insects in Brazil. They were used to sample different groups in projects at Espinhaço Mountain Range, in Minas Gerais and Bahia states, Brazil. (**a**) Entomological Net (**b**) Pan trap (**c**) Malaise trap (**d**) Malaise Window trap (**e**) Soil Pitfall (**f**) Arboreal Pitfall (**g**) Pitfall traps baited with human feces (**h**) Van Someren-Rydon (**i**) Trap nest. (Photos: Lucas Perillo)

used. Other colors, such as blue and white, are also frequently used and present different capture successes depending on the sampled group (Moreira et al. 2016) and can be used together to complement the sample. In essence, it simulates a floral resource and can be especially used for sampling bees and wasps (Perillo et al. 2017). Normally they are used for 48 hours and are placed directly on the ground.

11.2.1.3 Malaise Traps

Malaise traps have been used for decades (Malaise 1937; Townes 1972) to capture flying insects. It is a wide flight intercept trap made of cloth (Fig. 11.5c). Malaise traps have excellent autonomy, as the insects are directed through a sloping roof to a collection container with a substance that already conserves the sampled specimens (typically alcohol). With little maintenance, the traps can be on the field for multiple days and can be set up on mountaintops (Perillo et al. 2021). The Malaise Window is a version that can access the canopy insect diversity. Despite the canopy of CR being predominantly reduced, it is an interesting method to collect insects in the forest patches associated with the grassland matrix, such as free-living herbivorous (Kuchenbecker et al. 2021) and bees and wasps (Perillo et al. 2020) (Fig. 11.5d). The use of malaise traps can achieve extensive species coverage if the samplings are continued and well spatially distributed, with a high potential for monitoring the effects of environmental change on biodiversity (Fraser et al. 2008).

11.2.1.4 Pitfall Traps

This method is used for sampling insects that forage on different surfaces. In litter (soil surface), epigeal pitfalls are used (Fig. 11.5e). Pitfall traps are considered the most effective method of collecting ground-dwelling ants in grassland ecosystems (Bestelmeyer et al. 2000; Montgomery et al. 2021). To capture insects that forage in trees, the Arboreal Pitfall (Fig. 11.5f) is used. It usually is used as supplementary survey and can be installed 1.5 m above the ground in the nearest tree from the soil trap (see Brant et al. 2021). Both are made with plastic recipient with 11 cm in height and 19 cm in diameter (internal volume: 1 liter) containing a killing solution (salt, water, and detergent). Each trap is usually on field for 48 hours. The pitfall can also be increased with different baits. For collecting dung beetles, for example, pig or human feces are the best way to attract the beetles (see Marsh et al. 2013) (Fig. 11.5g).

11.2.1.5 Van Someren-Rydon

Used to capture fruit-feeding butterflies (DeVries 1987), these traps have a bait, normally produced with the fermentation of banana and sugarcane juice (Freitas et al. 2014). Consisting of a closed cylinder at the upper side with a platform at the base, on which a 50 ml plastic cup containing the bait is placed. Attracted by the odor, the butterflies enter through the lower entrance and get caught when they try to leave through the upward movement. It can be installed approximately 1 m above the ground tied directly on shrubby vegetation or on an artificial pole in open areas (Fig. 11.5h). It can be installed on field for days, but the bait must be replaced between 24 to 48 hours to keep equivalent attractiveness throughout sampling days (Freitas et al. 2014).

11.2.1.6 Trap Nests

Trap nests are used to capture insect species (mainly bees and wasps) that nest or use pre-existing cavities above ground (in dead wood or stems) (Krombein 1967). They are important tools for understanding the life cycle of the colonizers, its preys, and can be used for environmental assessment and conservation (Tscharntke et al. 1998). The nests can be made of resistant wood, bamboo, paperboard or plastic and must be installed in groups of nests with different diameters (Morato and Martins 2006). Trap nests have low colonization rates (rarely exceeds 10%) and need to be monitored at least every 15 days. The colonized trap nests are collected and monitored in the laboratory until the emergence of adults. Yet, trap nests were found to be relatively unsuitable for altitudinal surveys, mainly due to well-known method selectivity and to the small capture rates for Aculeata species at higher elevations (Perillo et al. 2017) (Fig. 11.5i).

11.2.1.7 Other Methods

Several other methods can be used to capture insects, especially with greater specificity with the group of interest. To attract Euglossini bees, for example, the use of odoriferous baits (scents analogous to flower substances) is constantly used on gradient projects (Antonini et al. 2017). Beating sheets is also a great method for sampling non-flying insects that live on tree and shrubs since it is cheap, easy to build, and straightforward to use (Monteiro et al. 2020a; Montgomery et al. 2021). Novel methods are also being developed to, for instance, collect aquatic macroinvertebrates (Martins et al. 2018; Castro et al. 2019), plant-inhabiting arthropods at high height (Viana-Junior et al. 2021) or different substances to attract insects (Souza et al. 2015), emphasizing the complementarity of survey methods and reducing negative aspects in using a simple trap model (Häuser and Riede 2015).

11.3 Explanatory Variables and Analysis

11.3.1 Measures of Diversity

To study neotropical gradients, there are multiple possibilities that can be explored to explain patterns of diversity at different spatial and temporal scales.

There are multi-dimensional components of biodiversity, in which we can consider both species diversity (i.e., taxonomic diversity – TD), functional diversity (FD), and phylogenetic diversity (PD) to capture different aspects of ecological contents (Devictor et al. 2010). Understanding the link between them can help us to identify the mechanisms that shapes local communities (Pavoine and Bonsall 2011). Functional diversity (FD) considers morphological, ecological, and behavioral differences between species, but also between groups or individuals (Devictor et al. 2010). FD is an important measure to assess the influence of species on ecological processes and ecosystem functioning (Díaz et al. 2007) Still, phylogenetic diversity (PD) considers the measurement of the branch lengths in a phylogenetic tree (Faith 1992), and can provide comparable evolutionary measures of biodiversity surpassing taxonomic surveys (Miller et al. 2018). PD used to explore biogeographical gradients, making it a very useful tool for monitoring changes in biodiversity (Chao et al. 2016).

A useful tool to understand biological dynamics at multiple scales is to explore the relationship between local (α-alpha) and regional (γ-gamma) diversities, which can be obtained through beta diversity (β), which indicates what makes assemblages of species more or less similar to each other at different places and times (Anderson et al. 2011; Baselga 2010a; Legendre et al. 2005; Whittaker 1972) and quantify the overall heterogeneity in species composition among any number of sites (Baselga 2013; Tuomisto 2010a, b). β-diversity is an important property of these communities and is influenced by different spatial scales (Barton et al. 2013), time (Legendre

2019), and by species–area relationship (Horner-Devine et al. 2004). Likewise, β-diversity can be decomposed into species replacement (turnover) and species gain/loss (nestedness) (Baselga 2010b), an approach that can provide useful information to understand biogeographic, ecological, and conservation issues, and also how those community patterns are related to the main processes that underlie species distribution. β-diversity can also be useful to understand variation across temporal, environmental, and geographical gradients, with a common pattern of increase of dissimilarity with geographic and environmental distances, species replacement being the main process behind species differences (Antão et al. 2019; Nekola and White 1999). Using more current metrics, it is possible to verify patterns of colonization and extinction, with components of beta diversity (Tatsumi et al. 2021), thus, through temporal studies, it will be possible to verify losses and gains of species in gradients or even on mountaintops. Therefore, the local scale species composition is influenced by the diversity amount at the regional scale along tropical elevational gradients (Arellano et al. 2014), which are determined by processes such as speciation and dispersion (Leibold et al. 2004).

11.3.2 Climatic Variables

Spatial gradients can be underpinned by environmental variables, of which climate exerts constant influence on variation in diversity (Moura et al. 2016). Temperature is one of the most important drivers for plants and animals (Peters et al. 2016) as well as precipitation (Andersen et al. 2015). Those two climatic variables can shape community's composition through the evolutionary time (Brown 2014) and are directly related with elevational and latitudinal constraints (Moya-Laraño 2010). Both variables can vary significantly in elevational and latitudinal gradients. Increases in wind speed, light intensity, and variations in humidity are also common in high-mountain environments and can restrict species that are capable of exploiting these environments (Mani 1962; Körner 2007).

Climate effects can also vary in different scales. On local scale, distinct microclimate can be stimulated by spatial heterogeneity, in which canopy cover, elevation, and soil humidity can underpin its variation (Ramos and Santos 2006; Deák et al. 2021). To access this information, climatic variables can be measured locally (in each sample site) with portable climatic stations. In a larger scale, one of the available datasets to access climatic variables is the WorldClim (https://www.worldclim.org/), a set of global climate layers (climate grids) extrapolated to all regions of the planet (WorldClim version 2; 1970–2000). The data is compiled with a spatial resolution of about 1 kmr2. Then, its values can be used to explain diversity locally or globally. At WorldClim platform, we can obtain specific values of mean annual temperature (˚C), precipitation (mm), solar radiation (kJ m^{-2} day^{-1}), wind speed (m s^{-1}), and water vapor pressure (kPa).

11.3.3 Habitat Structural Measurements

Another explanatory variable that is possible to quantify to explore gradients is the habitat structural measures. In nature, there are countless possibilities to choose explanatory variables and the researcher must find which ones are best for explaining patterns of your study group. For instance, the same chosen variable can exert different relevance to species when we compare the responses at different spatial scales. On the local scale, we can, for example, quantify variables such as heterogeneity/complexity of vegetation, canopy and understory cover, presence/distance of water, distance from forests (see Fig. 11.6). Those variables can be sampled on field and be associated with each sample point during the analysis. At the regional scale (also in landscape scale), variables such as percentage of conserved area, connectivity, or distance from urban environments can be considered. These metrics can be provided in open online databases and can be extracted from open maps and satellite images.

To explore climate or habitat structure as explanatory variables in statistical models, a correlation analysis must be performed to detect possible relationships between them. Different variables can be correlated and the inclusion of redundant variables in the model can lead to misinterpretation and decrease the analysis accuracy. The best way to deal with correlated variables is group them into a single

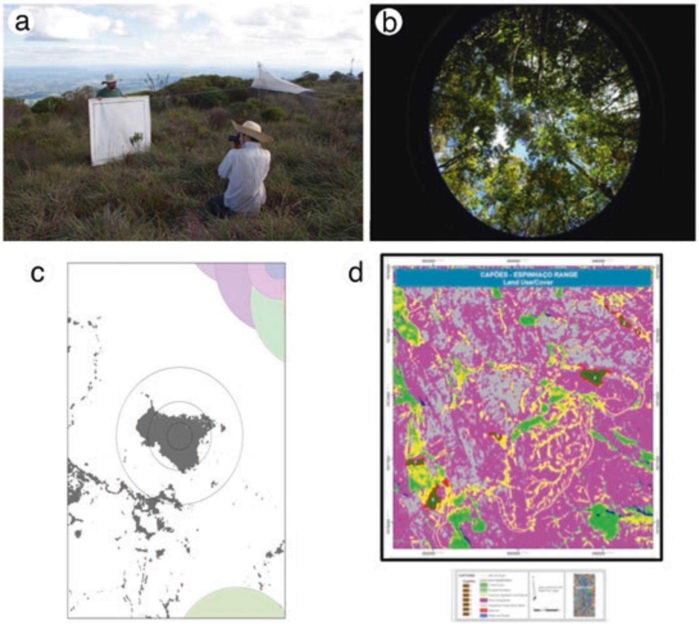

Fig. 11.6 Examples of some explanatory variables that can be measured to explore insect variation in elevational gradients. (**a**) understory cover (**b**) canopy cover (**c**) concentric circular sectors used to select landscape variables for each sample (**d**) satellite image with land use classification

variable. The choice for the most relevant variable among the correlated should be carried out considering the biological explanation of each variable. In literature, there is a suggestion to group explanatory variables with high correlation values, such as those with Pearson's correlation coefficient (r) greater than 0.7 (see Graham 2003; Dormann et al. 2013). Then, non-correlated variables can be included in statistical models to test their relative importance.

11.4 Elevational Gradient of *Campo Rupestre* (CR) Insects

Elevation interferes in a series of variables, such as temperature, humidity, and wind speed, and these characteristics influence the spatial distribution of species in different elevational ranges (Wolda 1987). The common pattern is a decrease in species richness with increasing elevation for different groups (Wolda 1987; Kraft et al. 2011; Peters et al. 2016). But we can focus in multiple other diversity metrics to evaluate the effects of elevation in biodiversity. When we explore other diversity metrics, such as spatial and temporal variation of species composition using beta diversity metrics (Nunes et al. 2020; Perillo et al. 2021), or approaches, such as functional diversity (Castro et al. 2020), the results can be different.

We accessed multiple published articles that focused on the study of elevational gradients patterns of CR insects of Espinhaço Mountain Range. There are many other studies that explore insects in CR, but without questioning the elevational patterns (see recent examples in Brant et al. 2021 for ants, Perillo et al. 2020 for bees and wasps, and Pereira et al. 2017 for butterflies). The springer book "Ecology and Conservation of Mountaintop grasslands in Brazil", organized by Fernandes (2016) gathers valuable information on CR researches, including results of invertebrate groups. One of the chapters is dedicated to patterns of species distribution and the forces shaping them along an elevational gradient (Fernandes et al. 2016). An important particularity should be mentioned when we work on elevational gradients in CR: this ecosystem is mainly distributed above 900 m (a.s.l) and elevational diversity patterns can be altered if we consider the global insect distribution (i.e., since sea level).

11.4.1 Hymenoptera

The importance of this order for humans is indisputable. Most angiosperm plants depend on biotic pollinators for reproduction (Ollerton et al. 2011; Novais et al. 2016), with Hymenoptera containing the largest representatives (Potts et al. 2010). Hymenoptera richness and abundance decline at higher elevations (Fig. 11.7). There is probably a decrease in the importance of these groups as pollinators of high mountains, being replaced by Diptera and Lepidoptera (Müller 1880; Pyrcz et al.

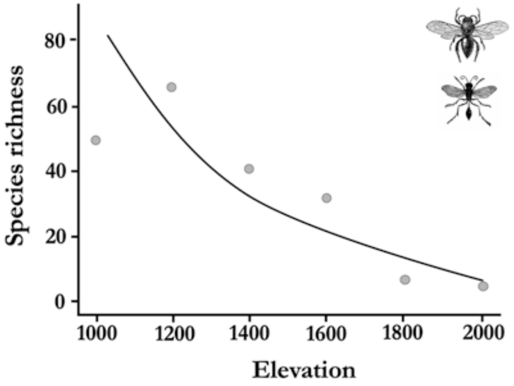

Fig. 11.7 Representation of the effect of elevation on bees and wasps' richness collected with pan traps in *Campo Rupestre* of RPPN Santuário do Caraça, Minas Gerais, Brazil. (Adapted from the article Perillo et al. 2017)

2009). This ecological disadvantage may be related to the reduction of floral resources, high wind intensities, and low temperatures (Neff and Simpson 1993).

CR bees and wasps received a considerable effort in studies (for example, see Silveira and Cure 1993; Azevedo et al. 2008). But they have not explored the effects of mountain elevation gradients. The first article, using pan traps and trap nests, found a decrease in species richness with elevation increase (Perillo et al. 2017) (Fig. 11.7). The same pattern for species richness (alpha diversity) in an elevational gradient was found in a larger scale for bees, wasps, and ants separately, in which the difference in species composition increased with mountain elevation range, and with the geographical and environmental distances (Perillo et al. 2021). The beta diversity pattern was not that clear. Beta diversity increased with increasing elevation for bees, but for wasps and ants this relationship was not significant (Perillo et al. 2021). However, an article that considered only euglossine bee community, abundance decreased with elevation, while it was not statistically related to bee species richness (Santos et al. 2020).

Considering ants, the first article that we found exploring elevational patterns of CR was performed in Serra do Cipó, Minas Gerais state (Araújo and Fernandes 2003). A few years later, a checklist for the CR ants was performed through a compilation of information from empirical studies and literature records (Costa et al. 2015). A total of 288 species was recorded in CR, accrediting this ecosystem to be a hotspot for ant diversity. This survey also diagnosed a decrease of ant species richness with elevation (Fig. 11.8).

When we consider ant functional diversity, turnover was very low and the elevation does not underpin this component of spatial and temporal beta diversity (Castro et al. 2020; Nunes et al. 2020), with few changes of spatiotemporal functional diversity along the elevation gradient.

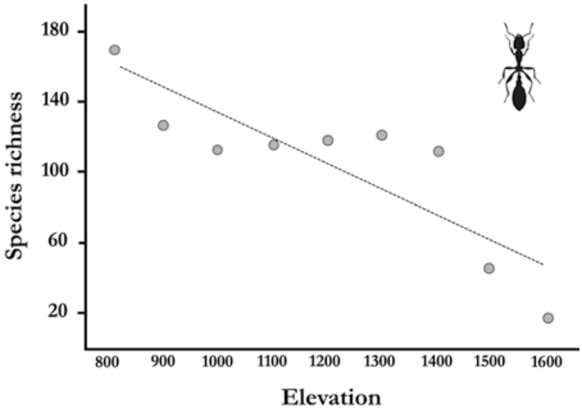

Fig. 11.8 Representation of the effect of elevation on ants' richness in *Campo Rupestre* ecosystem in Brazil. Generated from compiled data of eight articles about the elevational range distribution of ant species, available in Costa et al. 2015

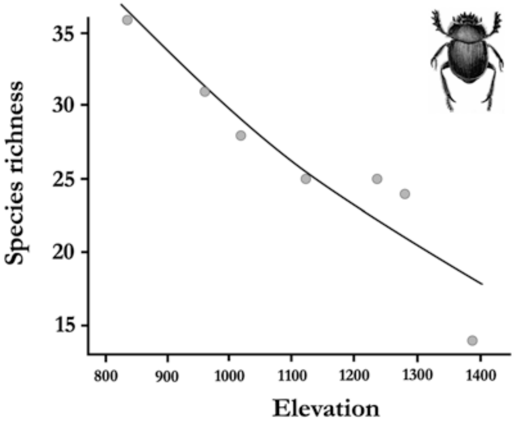

Fig. 11.9 Representation of the effect of elevation on dung beetles' species richness in *Campo Rupestre* of Serra do Cipó, Minas Gerais, Brazil ($F = 24.311$, $p = 0.0043$, $R^2 = 0.82$). (Adapted from Nunes et al. 2016)

11.4.2 Scarabeinae (Dung Beetles)

A published article with dung beetle of CR described a species richness decline with increasing elevation (Nunes et al. 2016) (Fig. 11.9). This common pattern was contrasted with other findings. The dung beetle functional alpha diversity (expressed by alpha Rao FD) was not influenced by elevation. Also, the gamma FD is mainly explained by the Alpha1 component (94.7%), which indicates that there is little difference in the FDs among the communities of different elevations (Nunes et al. 2016). Nevertheless, dung beetle ecological functions (such as dung removal, soil

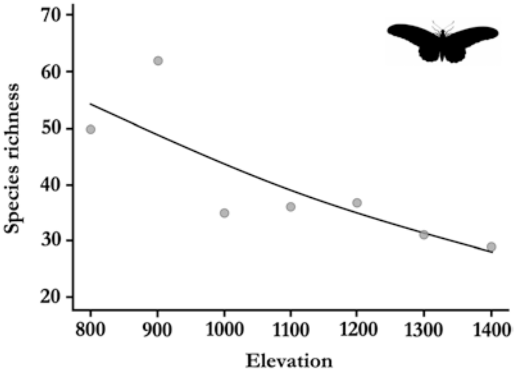

Fig. 11.10 Representation of the effect of elevation on butterfly richness in Serra do Cipó mountain in Brazil. (Adapted from the results found in Pires et al. 2020)

excavation, and seed dispersal) declined with elevation and the FD itself is not enough to explain functions performance (Nunes et al. 2018).

11.4.3 Lepidoptera (Butterflies)

Butterflies have been well studied in Espinhaço mountain range, with many published articles focused on species description (see Razowski and Becker 2002; Rosa et al. 2019). The thermal tolerance of fruit-feeding butterflies in a locality of Espinhaço mountain range was explored comparing the specimens collected in open areas (*Campo Rupestre stricto* sensu) and forest islands (Silva et al. 2020). The authors found that species from opened areas had a higher mean maximum critical temperature than the species of forest islands, but that difference was not correlated phylogenetically.

The effects of the Espinhaço elevational gradient on fruit-feeding butterflies species' richness was also linearly negative (i.e., the highest places host less species richness) (Pires et al. 2020; Beirão et al. 2021) (Fig. 11.10). Also, beta diversity varies throughout the mountain elevational gradient with species replacement (turnover) being more important (Beirão et al. 2021).

11.4.4 Blattodea (Termites)

For termite, climatic and vegetational variables underpin a decline in species richness with increasing elevation (Nunes et al. 2016) (Fig. 11.11). On the other hand, when the functional diversity is considered, there was little difference of functional groups among different elevations, although represented by distinct species.

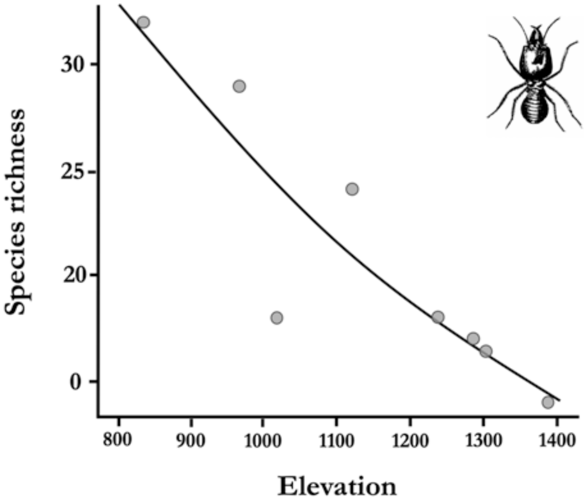

Fig. 11.11 Representation of the effect of elevation on termites richness in Serra do Cipó mountain in Brazil ($F = 24.311$, $p = 0.0043$, $R^2 = 0.826$). (Adapted from the results found in Nunes et al. 2016)

The termitaria interactions were also investigated in an elevational gradient in CR (Viana-Junior et al. 2021). The authors found a positive relationship between species richness and abundance of termitaria cohabitants, indicating that the nests may offer shelter to termitophile specimens to surpass the effects of environmental harshness on mountaintops, such as already documented for wildfires areas (Monteiro et al. 2017).

11.4.5 Insect Galls

Probably that's the most studied group of insects in CR ecosystem due to decades of researches performed by the Laboratory of Evolutionary Ecology and Biodiversity of the Institute of Biological Sciences (ICB-UFMG), led by the professor Geraldo Wilson Fernandes (see a list of researches on insect galls in Brazil in Araújo 2018). The seminal article about biogeographical gradients in galling species richness was performed in CR (Fernandes and Price 1988). Cerrado is probably the richest fauna of galling insects worldwide (Lara and Fernandes 1996) and most of the researches show that species richness of gall-forming insects reduces with elevation (Fernandes and Price 1988, 1992; Lara et al. 2002; Carneiro et al. 2014; Fernandes and Santos 2014) (Fig. 11.12).

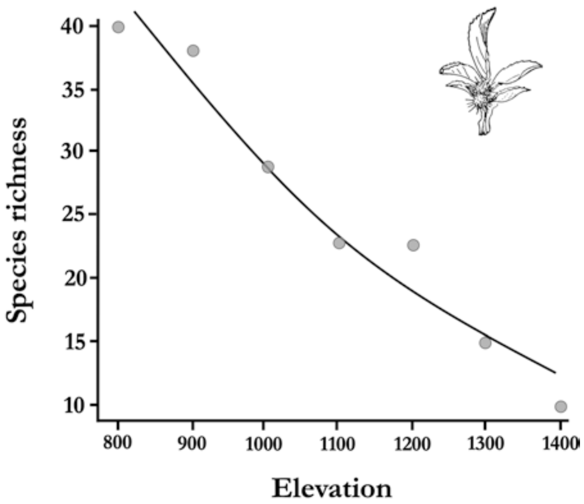

Fig. 11.12 Representation of the effect of elevation on galling species' richness in *Campo Rupestre* of Serra do Cipó, Minas Gerais, Brazil ($R^2 = 0.94$). (Adapted from Nunes et al. 2016)

11.4.6 Free-Feeding Herbivorous Insects

There are some published articles considering free-feeding insect herbivores in Serra do Espinhaço (Telhado et al. 2010; Terra et al. 2017; Kuchenbecker et al. 2021), but there are few that explored the elevational gradient effects on diversity. In Serra do Cipó, there was no consistent relationship between species richness and elevation (Ribeiro et al. 1998). But when the species richness of free-feeding insects is divided into different habitat types and seasons, the results can be different (see Fig. 11.15). In an article that considered ecological interactions among insect herbivores, ants, and a specific host plant *Baccharis dracunculifolia,* the composition of herbivorous insect species differed among elevations and the richness and abundance were highest at the intermediate elevation only for sap-sucking insect group (Monteiro et al. 2020b).

11.4.7 Aquatic Insects

The aquatic macroinvertebrates group also deserves attention in CR, since they are bioindicators of water quality. They provide ecological functions on freshwater ecosystems, connecting the energy flow from terrestrial to aquatic strata. There is a decrease on aquatic insects' richness with increasing elevation (Fig. 11.13) (Castro et al. 2019). Furthermore, beta diversity increased with increasing elevation (also found for bees; Perillo et al. 2021). Therefore, more species are added to the regional

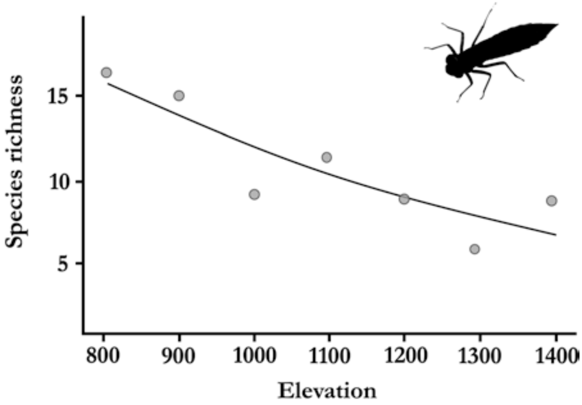

Fig. 11.13 Representation of the effect of elevation on aquatic macroinvertebrate species richness in *Campo Rupestre* of Serra do Cipó, Minas Gerais, Brazil. (Adapted from Castro et al. 2019)

community, generating differences in composition between elevational sites (Castro et al. 2019).

11.5 Other Gradients in *Campos Rupestres*

There are other gradients that deserve in-depth study for insect groups in CR in the mountains of eastern Brazil. We opt to focus only on elevational gradients, since they are the ones that host the majority of the published articles. But there are articles that consider other gradients.

11.5.1 Latitudinal Gradients

The prevalent effect of latitude on biological communities is a higher species diversity in lower latitudes (Pianka 1966; Kraft et al. 2011; Cancello et al. 2014). Studies that explore latitudinal gradients are scarce in the Espinhaço Mountain Range. Since databases on most invertebrate groups are insufficient to explore latitudinal relations with species diversity, primary data collection must be carried out in different locations, increasing the cost of the projects and a larger team of researchers is needed. Considering CR invertebrates, we found only the article published by our group (Perillo et al. 2021).

In this study, a unique dataset was built from sampling species of bees, wasps, and ants (Aculeata: Hymenoptera). Twenty-four study sites were sampled across 12 mountains, installing 120 trap sets. It covered more than 1000 km from south to north and an elevational range of 1000–2000 m (Fig. 11.14). Each trap set

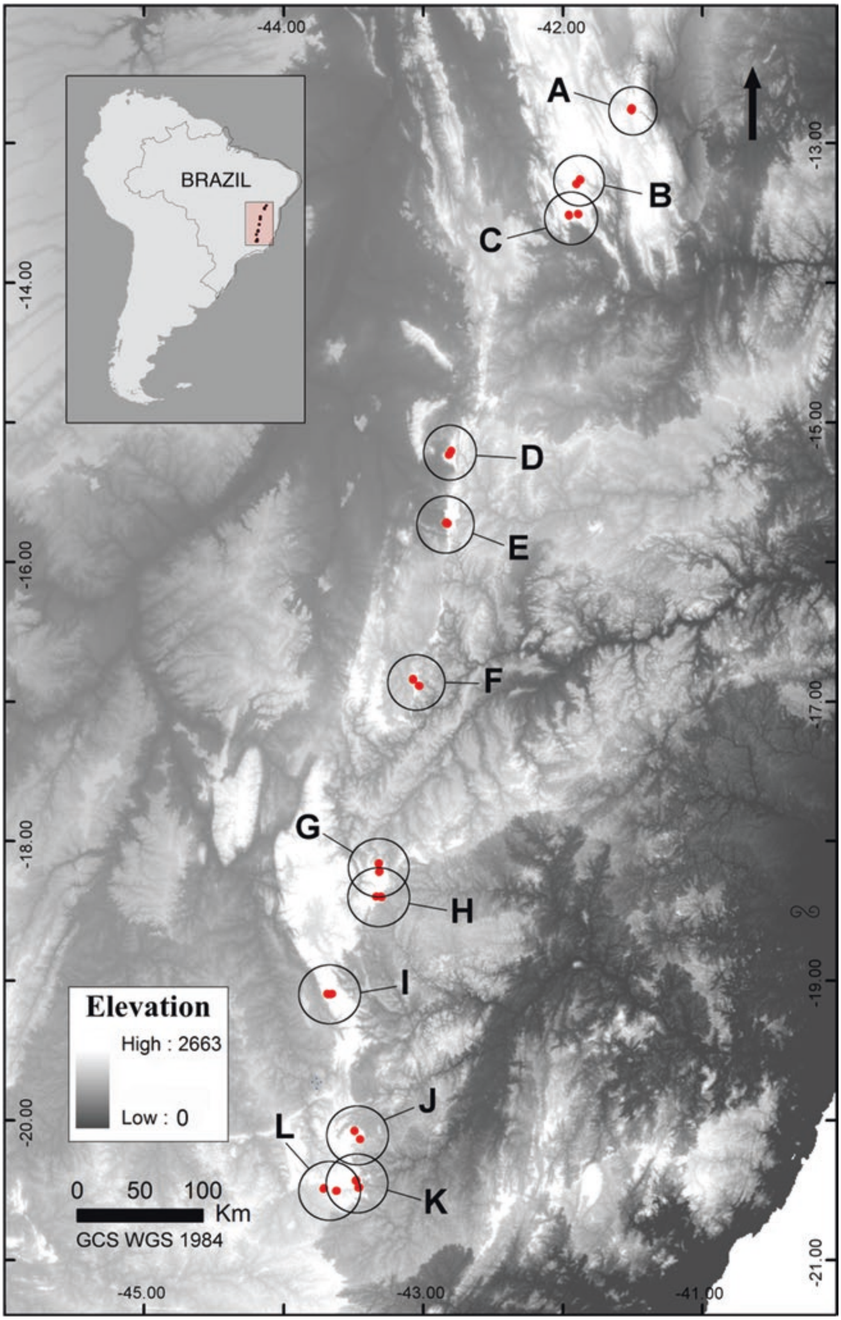

Fig. 11.14 Latitudinal and elevational gradient with 12 *Campo Rupestre* sample localities through the Espinhaço Mountain Range. A: PN Chapada Diamantina; B: Pico do Barbado; C: Pico das Almas; D: Pico da Formosa; E: PE Serra Nova; F: Serra de Botumirim; G: PE do Rio Preto; H: PE Pico do Itambé; I: Pico do Breu; J: RPPN Santuário do Caraça; K: PE Pico do Itacolomi; L: PE Serra do Ouro Branco

comprised one malaise trap, four Moericke traps (or yellow pan traps), and four pitfall traps. The main objective was disentangling the effects of latitudinal and elevational gradients on the distribution of Aculeata and to understand the effects of climatic variables in CR ecosystem.

Latitude had no effect on diversity. In Espinhaço Mountain Range, variation in species richness and composition across mountains is strongly associated with elevational gradient, which showed stronger climatic variation than the latitudinal gradient. Temperature, wind, and precipitation, which were important drivers of diversity, varies more within a single mountain than across mountains at different latitudes.

11.5.2 Longitudinal Gradients

The longitudinal gradient is difficult to be explored in CR, especially in Espinhaço Mountain Range, since, although it extends for more than 1200 km North–South (see Fig. 11.2), it rarely has its east–west width exceeding 100 km (Harley 1995).

11.5.3 Xeric-to-Mesic Gradients

Gradients can be found between habitats with different characteristics. Xeric (i.e., places with arid conditions) and mesic (i.e., habitat neither extremely dry nor extremely wet) gradients can be studied in *Campos Rupestres*. Due to its heterogeneous landscapes, in small distances, we can change from environments near waterfalls, canyons, and rivers to habitats with restricted access to water sources.

The most common pattern found in CR xeric-to-mesic gradient is that mesic habitats are generally richer in herbivorous species than xeric habitats (Carneiro et al. 1995). But other diversity patterns, such as found for elevational gradient, can be influenced by xeric-to-mesic gradients. For free-feeding insect herbivores in a CR mountain, despite the lack of a consistent relationship between species richness and elevation, when only xeric habitats are considered, the species richness decreased with increasing elevation in the wet season. And the opposite result was found for mesic habitats during dry season, with higher species richness with increasing elevation (Ribeiro et al. 1998; Fernandes et al. 2016) (Fig. 11.15). However, ant's species richness increased with decreasing elevation for both mesic and xeric habitats (Araújo and Fernandes 2003). The use of the generalist and specialist concept can also be used to understand the processes occurring in forest (mesic) and *Campo Rupestre stricto* sensu (xeric) habitats (see Neves et al. 2021).

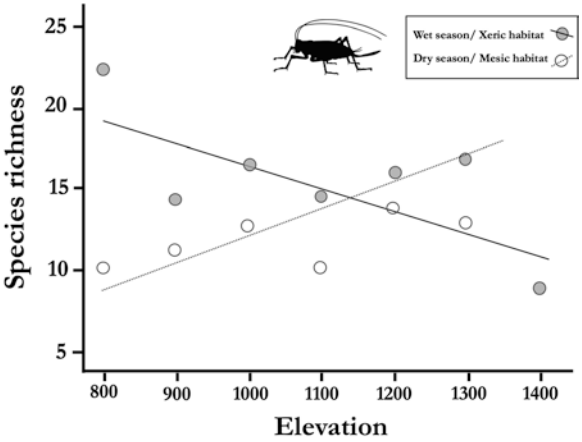

Fig. 11.15 Significant regression of the relation between free feeding herbivore species and elevation for xeric habitats in wet season (solid line, closed circles) and mesic habitats in dry season (dotted line, open circles). (Adapted from Fernandes et al. 2016)

11.5.4 Seasonal and Temporal Variation

Seasonal variations are also common in tropical environments, especially when considering changes in species composition (Tylianakis et al. 2005). Temporal variations (Rosenzweig 1995) are important aspects that must be considered in order to find possible patterns of diversity in biological communities. Insect seasonality in seasonal tropical systems is determined mostly by variation in rain and humidity (Wolda 1987; Abrahamczyk et al. 2011). There is much information about seasonal and temporal variation for CR insects (see Pereira et al. 2017; da Silva et al. 2019; Nunes et al. 2020; Perillo et al. 2020; Brant et al. 2021). Most of them follow a recurring pattern for the tropics, in which we find higher species richness and abundance in the summer season due to differences in resource availability and vegetation structure over time, and to changes in weather conditions (Tylianakis et al. 2005).

To understand the temporal dynamics of communities, we can also consider the temporal beta diversity, in which the change in species composition can be measured and compared among surveys (Legendre 2019). In CR, species composition differs over time, influencing temporal beta diversity for forest-dependent species of dung beetles (da Silva et al. 2019), bees and wasps (Perillo et al. 2020), ants (Nunes et al. 2020), butterflies (Beirão et al. 2021) manly due to beta diversity species replacement (turnover). For instance, the winter communities did not represent subsets of summer communities for bees and wasps, since there is an elevated temporal turnover among seasons (88%) with low contribution of nestedness between seasons (Perillo et al. 2020). But for ants within CR forest islands, there was an increase in the contribution of the nestedness-resultant component of temporal β-diversity for both forest-dependent and especially habitat generalist species (Brant et al. 2021). Although habitat generalist species can contribute to nestedness more than habitat specialists (Neves et al. 2021), Nunes et al. (2020) found a high temporal replacement of ant species in the CR.

Due to a considerable daily fluctuation of abiotic factors at CR, the daily dynamics also deserves attention. Calazans et al. (2020) found that the daily temperature oscillation leads to high heterogeneity in ant species thermal responses, causing a stratification in ants foraging during the day.

11.6 Problems and Solutions for *Campos Rupestres* Insect Communities

We currently face numerous challenges for the conservation of biological diversity. Global climate change, exotic species, extensive landscapes interventions, and extinction of natural environments are occurring at ever-accelerating rates, including in tropical mountainous areas (Catalan et al. 2017). Worldwide, the main sources of threat to insects are also global environmental change, especially habitat loss and contamination with harmful pesticides (Cardoso et al. 2020; Samways et al. 2020). To make matters worse, consistent data on ecological mechanisms and even basic data on species distribution and diversity are lacking in Brazil (Oliveira et al. 2016), hindering the elaboration of conservation and management goals that should be applied in the scenario of estimated changes for the near future (Tylianakis et al. 2008). The lack of investment in taxonomy, management, and data sharing also generates knowledge gaps, especially in megadiverse environments (Ely et al. 2017). We also could only find one study on butterflies (Silva et al. 2020) that considered a phylogenetic diversity approach. This is a great opportunity to understand how evolutionary processes underpinned the insect's biogeographical gradients.

In mountainous tropical regions, climate change can cause even greater harm, as species restricted to high environments, conditioned to the mountaintop extreme environments, will have nowhere to migrate (Hoffmann et al. 2015). The colder mountain environments at highest spots will disappear, excluding the endemic species. Greater impacts will also be observed in these areas in relation to precipitation, frosts incidence, and humidity, directly affecting the regional climate and further maximizing the effects of global warming (Fernandes et al. 2016; Tito et al. 2020). These changes will modify ecological and evolutionary responses (Parmesan 2006), directly affecting the functioning of these ecosystems (Hughes 2000; McCarty 2001). Therefore, despite having narrow elevational ranges, the biogeographical effects of tropical mountains drive high diversity. Facing global climate changes, this limited elevational gradient may limit species range shifts, leading to severe biodiversity losses.

Despite the already documented importance of CR for the maintenance of interactions between plants and animals and the persistence of biodiversity, in addition to their potential for the provision of ecosystem services, information compared to other ecosystems is still scarce (Fernandes 2016). Due to its habitat heterogeneity, there are the presence of several associated ecosystems, such as fragments of *Cerrado*, gallery forests, and relictual hilltop forests (Silveira et al. 2016; Caminha-Paiva et al. 2022). Some of them are associated with water sources that are tributaries of two important rivers in Brazil, the São Francisco and Doce rivers (Callisto et al. 2016). Rivers are used in various activities such as agriculture, fishing, human consumption of water, and recreation. Recent studies point to ecological connections between forest formations and the CR, mainly with regard to the supply of resources to pollinators (Guerra et al. 2016; Perillo et al. 2020). These natural landscapes continue to be drastically altered through a combination of land use changes (causing habitat loss and fragmentation) and chronic disturbances such as overgrazing by extensively cattle farming and frequent and intense fire episodes (Fernandes et al. 2018; Silveira 2021), elements that make an intensification of their studies even more urgent. The Espinhaço also faces a historic mining pressure. Since the gold and diamond cycle, especially in the eighteenth and nineteenth centuries, countless mountains have been exploited without control and much of the biodiversity has been lost. Among the biggest current threats of CR, especially the ferruginous, is the expansion of iron ore mining. The large-scale mining generates irreversible losses of mountainous areas (Kamino et al. 2020) and promotes countless socio-environmental risks and environmental liability that is very difficult to resolve (Le Stradic et al. 2014; Carmo et al. 2020). The published Action Plan for the CR (Fernandes et al. 2020), which aims to reconcile the socio-economic and environmental values of this megadiverse ecosystem, must be implemented by public policies.

The solution for maintaining insect populations in the CR is not different from fighting against the main causes of loss of biodiversity worldwide. Habitat loss, climate changes, contamination, and exotic invasive species are also within the main problems to maintain insect diversity (Samways et al. 2020). An integrated pest management must be implemented, especially in Brazil, which is breaking records for pesticide imports and plans to jeopardize the current law with a new agrochemical bill (Brown 2022). Furthermore, a pro-insect legislation will never be implemented if their ecological services are still unknown to the general public (Cardoso et al. 2011; Montgomery et al. 2020).

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References

Abrahamczyk S, Kluge J, Gareca Y, Reichle S, Kessler M (2011) The influence of climatic seasonality on the diversity of different tropical pollinator groups. PLoS One 6:e27115. https://doi.org/10.1371/journal.pone.0027115

Alves RJV, Silva NG, Oliveira JA, Medeiros D (2014) Circumscribing *campo rupestre* – megadiverse Brazilian rocky montane savanas. Braz J Biol 74:355–362

Ananthakrishnan TN (2007) Professor M. S. Mani the man, scientist, and philosopher. Orient Insects 41(1):5–7. https://doi.org/10.1080/00305316.2007.10417495

Andersen AN, Del Toro I, Parr CL (2015) Savanna ant species richness is maintained along a bioclimatic gradient of increasing latitude and decreasing rainfall in northern Australia. J Biogeogr 42(12):2313–2322. https://doi.org/10.1111/jbi.12599

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol Lett 14(1):19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Antão LH, McGill B, Magurran AE, Soares AMVM, Dornelas M (2019) β-diversity scaling patterns are consistent across metrics and taxa. Ecography 42(5):1012–1023. https://doi.org/10.1111/ecog.04117

Antonini Y, Machado CB, Galetti Júnior PM, Oliveira ML, Dirzo R, Fernandes GW (2017) Patterns of orchid bee species diversity and turnover among forested plateaus of Central Amazonia. PLoS One 12:e0175884

Araújo WS (2018) 30 years of research on insect galls in Brazil: a scientometric review. Papéis Avulsos de Zoologia 58:e20185834. https://doi.org/10.11606/1807-0205/2018.58.34

Araújo LM, Fernandes GW (2003) Altitudinal patterns in a tropical ant assemblage and variation in species richness between habitats. Lundiana 4:103–109

Arellano G, Cayola L, Loza I, Torrez V, Macía MJ (2014) Commonness patterns and the size of the species pool along a tropical elevational gradient: insights using a new quantitative tool. Ecography 37(6):536–543. https://doi.org/10.1111/j.1600-0587.2013.00546.x

Azevedo A, Silveira F, Aguiar C, Pereira V (2008) Fauna de abelhas (Hymenoptera, Apoidea) nos campos rupestres da Cadeia do Espinhaço (Minas Gerais e Bahia, Brasil): riqueza de espécies, padrões. Megadiversidade 4:154–181

Barbosa NPU, Fernandes GW, Sanchez-Azofeifa A (2015) A relict species restricted to a quartzitic mountain in tropical America: an example of microrefugium? Acta Bot Bras 29(3):299–309

Barthlott W, Mutke J, Rafiqpoor D, Kier G, Kreft H (2005) Global centers of vascular plant diversity. Nova Acta Leopoldina 342:61–83

Barton PS, Cunningham SA, Manning AD, Gibb H, Lindenmayer DB, Didham RK (2013) The spatial scaling of beta diversity. Glob Ecol Biogeogr 22:639–647

Baselga A (2010a) Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. Ecology 91:1974–1981

Baselga A (2010b) Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19:134–143

Baselga A (2013) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. Ecography 36:124–128

Baselga A, Orme CDL (2012) Betapart: an R package for the study of beta diversity. Methods Ecol Evol 3:808–812

Baselga A, Lobo JM, Svenning JC, Araújo MB (2012) Global patterns in the shape of species geographical ranges reveal range determinants. J Biogeogr 39:760–771

Basset Y, Charles E, Hammond DS, Brown VK (2001) Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. J Appl Ecol 38:1045–1058

Basset Y, Cizek L, Cuénoud P, Didham RK, Guilhaumon F, Missa O, Novotny V, Ødegaard F, Roslin T, Schmidl J, Tishechkin AK, Winchester NN, Roubik DW, Aberlenc H, Bail J, Barrios H, Bridle JR, Castaño-Meneses G, Corbara B, Curletti G, Rocha WD, Bakker DD, Delabie

JHC, Dejean A, Fagan LL, Floren A, Kitching RL, Medianero E, Miller SE, Oliveira EG, Orivel J, Pollet M, Rapp M, Ribeiro SP, Roisin Y, Schmidt JB, Sørensen L, Leponce M (2012) Arthropod diversity in a tropical forest. Science 338(6113):1481–1484

Beirão MV, Neves FS, Fernandes GW (2021) Climate and plant structure determine the spatio-temporal butterfly distribution on a tropical mountain. Biotropica 53(1):191–200. https://doi.org/10.1111/btp.12860

Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WL, Delabie JHC, Silvestre R (2000) Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC, pp 122–144

Bolle W (2017) De Ouro Preto a Diamantina: refazendo a viagem de Spix e Martius de 1818. Pandaemonium Germanicum 21(33):16–35. Available at: https://www.revistas.usp.br/pg/article/view/140879

Brant HSC, da Silva PG, de Castro FS, Perillo LN, Neves FS (2021) Spatiotemporal patterns of ant metacommunity in a montane forest archipelago. Neotrop Entomol 50:886–898. https://doi.org/10.1007/s13744-021-00901-2

Brown JH (2014) Why are there so many species in the tropics? J Biogeogr 1670(41):8–22

Brown S (2022) Brazil agrochemical bill nears passage in Bolsonaro's 'agenda of death'. Mongabay, 18 February 2022. In: https://news.mongabay.com/2022/02/brazil-agrochemical-bill-nears-passage-in-bolsonaros-agenda-of-death/. Accessed in 6 Mar 2022

Calazans EG, Costa FV, Cristiano MP, Cardoso DC (2020) Daily dynamics of an ant community in a mountaintop ecosystem. Environ Entomol 49(2):383–390. https://doi.org/10.1093/ee/nvaa011

Callisto M, Gonçalves JF, Ligeiro R (2016) Water resources in the rupestrian grasslands of the Espinhaço mountains. In: Fernandes GW (ed) Ecology and conservation of mountaintop grasslands in Brazil. Springer, Cham, pp 87–99

Caminha-Paiva D, Gomes VM, Cunha-Blum J, Santiago JC, Negreiros D, Fernandes GW (2022) Floristic mosaics of the threatened Brazilian *campo rupestre*. Nat Conserv Res 7(1):10–18. https://doi.org/10.24189/ncr.2022.004

Cancello EM, Silva RR, Vasconcellos A, Reis YT, Oliveira LM (2014) Latitudinal variation in termite species richness and abundance along the Brazilian Atlantic Forest hotspot. Biotropica:1–10. https://doi.org/10.1111/btp.12120

Cardoso P, Erwin TL, Borges PAV, New TR (2011) The seven impediments in invertebrate conservation and how to overcome them. Biol Conserv 144:2647–2655

Cardoso P, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima CS, Gaigher R, Habel JC, Hallmann CA, Hill MJ, Hochkirchi A, Kwak ML, Mammola S, Noriega JA, Orfinger AB, Pedraza F, Pryke JS, Roque FO, Settele J, Simaika JP, Stork NE, Suhling F, Vorster C, Samways MJ (2020) Scientists' warning to humanity on insect extinctions. Biol Conserv 242:108426. https://doi.org/10.1016/j.biocon.2020.108426

Carmo FF, Lanchotti AO, Kamino LHY (2020) Mining waste challenges: environmental risks of gigatons of mud, dust and sediment in megadiverse regions in Brazil. Sustainability 12:8466. https://doi.org/10.3390/su12208466

Carneiro MAA, Ribeiro SP, Femandes GW (1995) Artrópodos de um Gradiente Altitudinal na Serra do Cipó, Minas Gerais. Bras Rev Bras Entomol 39(3):597–604

Carneiro MAA, Coelho MS, Fernandes GW (2014) Chapter 16: Galls in Brazilian mountains: new reports and perspectives. In: Fernandes GW, Santos JC (eds) Neotropical insect galls, vol 550. Springer, Dordrecht, 550 p

Castro DMP, Callisto M, Solar RRC, Macedo DR, Fernandes GW (2019) Beta diversity of aquatic invertebrates increases along an altitudinal gradient in a neotropical mountain. Biotropica 51(3):399–411. https://doi.org/10.1111/btp.12660

Castro FS, Da Silva PG, Solar R, Fernandes GW, Neves FS (2020) Environmental drivers of taxonomic and functional diversity of ant communities in a tropical mountain. Insect Conserv Diver 13(4):393–403. https://doi.org/10.1111/icad.12415

Catalan J, Ninot JM, Aniz MM (eds) (2017) High mountain conservation in a changing world, Advances in global change research, vol 62. Springer, Cham, 413 p. https://doi.org/10.1007/978-3-319-55982-7

Chao A, Chiu CH, Jost L (2016) Phylogenetic diversity measures and their decomposition: a framework based on Hill numbers. In: Pellens R, Grandcolas P (eds) Biodiversity conservation and phylogenetic systematics, Topics in biodiversity and conservation, vol 14. Springer, Cham. https://doi.org/10.1007/978-3-319-22461-9_8

Chaves AV, Freitas GHS, Vasconcelos MF, Santos F (2014) Biogeographic patterns, origin and speciation of the endemic birds from eastern Brazilian mountaintops: a review. Syst Biodivers 13:1–16

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Coelho MS, Neves FS, Perillo LN, Morellato P, Fernandes GW (2017) Forest archipelagos: a natural model of metacommunity under the threat of fire. Flora 238:244–249. https://doi.org/10.1016/j.flora.2017.03.013

Coelho MS, Fernandes GW, Pacheco P, Diniz V, Meireles A, Santos RM, Carvalho FA, Negreiros D (2016) Archipelago of montane forests surrounded by rupestrian grasslands: new insights and perspectives. In: Fernandes GW (ed) Ecology and Conservation of mountain-top grasslands in Brazil, Springer, New York, pp 129–146

Cornell HV, Harrison SP (2014) What are species pools and when are they important? Annu Rev Ecol Evol Syst 45:45–67. https://doi.org/10.1146/annurev-ecolsys-120213-091759

Costa FV, Mello R, Lana TC, Neves FDS (2015) Ant fauna in megadiverse mountains: a checklist for the rocky grasslands. Sociobiology 62:228–245. https://doi.org/10.13102/sociobiology.v62i2.228-245

Coutinho ES, Fernandes GW, Berbara RLL, Valério HM, Goto BT (2015) Variation of arbuscular mycorrhizal fungal communities along an altitudinal gradient in rupestrian grasslands in Brazil. Mycorrhiza 25:627–638. https://doi.org/10.1007/s00572-015-0636-5

Crawley MJ (2013) The R book, 2nd edn. Wiley, Chichester, p 1080

da Silva PG, Nunes CA, Ferreira LF, Braga RF, Beiroz W, Perillo LN, Solar RRC, de Siqueira Neves F (2019) Patch and landscape effects on forest-dependent dung beetles are masked by matrix-tolerant dung beetles in a mountaintop rainforest archipelago. Sci Total Environ 651:1321–1331. https://doi.org/10.1016/j.scitotenv.2018.09.195

Darwin C (2006) O diário do Beagle. UFPR Press, Curitiba, 528 p

Deák B, Kovács B, Rádai Z, Apostolova I, Kelemen A, Kiss R, Lukács K, Palpurina S, Sopotlieva D, Báthori F, Valkó O (2021) Linking environmental heterogeneity and plant diversity: the ecological role of small natural features in homogeneous landscapes. Sci Total Environ 763:144199. https://doi.org/10.1016/j.scitotenv.2020.144199

Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol Lett 13:1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x. PMID: 20545736

DeVries PJ (1987) The butterflies of Costa Rica and their natural history. I: Papilionidae, Pieridae and Nymphalidae. Princeton University Press, Princeton

Díaz S, Lavorel S, de Bello F, Quétier F, Grigulis K, Robson TM (2007) Incorporating plant functional diversity effects in ecosystem service assessments. Proc Natl Acad Sci U S A 104:20684–20689. https://doi.org/10.1073/pnas.0704716104

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Drummond GM, (Org.) (2009) Biota Minas: diagnóstico do conhecimento sobre a biodiversidade no Estado de Minas Gerais subsídio ao programa Biota Minas. Fundação Biodiversitas, Belo Horizonte, pp 96–159

Ely CV, Bordignon SAL, Trevisan R, Boldrini II (2017) Implications of poor taxonomy in conservation. J Nat Conserv 36:10–13

Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biol Conserv 61:1–10

Fernandes GW (2016) Ecology and conservation of mountaintop grasslands in Brazil. Springer, New York

Fernandes GW, Price PW (1988) Biogeographical gradients in galling species richness: tests of hypotheses. Oecologia 76(2):161–167. https://doi.org/10.1007/BF00379948

Fernandes GW, Price PW (1992) The adaptive significance of insect gall distribution: survivorship of species in mesic and xeric habitats. Oecologia 90:14–20

Fernandes GW, Santos JC (eds) (2014) Neotropical insect galls, vol 550. Springer, Dordrecht, 550 p

Fernandes GW, Almeida HA, Nunes CA, Xavier JHA, Cobb NS, Carneiro MAA, Cornelissen T, Neves FS, Ribeiro SP, Nunes YRF, Pires ACV, Beirão MV (2016) Cerrado to rupestrian grasslands: patterns of species distribution and the forces shaping them along an altitudinal gradient. In: Fernandes G (ed) Ecology and conservation of mountaintop grasslands in Brazil. Springer, Cham. https://doi.org/10.1007/978-3-319-29808-5_15

Fernandes GW, Barbosa NPU, Alberton B, Barbieri A, Dirzo R, Goulart F, Guerra TJ, Morellato LPC, Solar R (2018) The deadly route to collapse and the uncertain fate of the rupestrian grasslands. Biodivers Conserv 27:2587–2603

Fernandes GW, Arantes-Garcia L, Barbosa M, Barbosa NPU, Batista EKL, Beiroz W, Resende FM, Abrahão A, Almada ED, Alves E, Alves NJ, Angrisano P, Arista M, Arroyo J, Arruda AJ, Bahia TO, Braga L, Brito L, Callisto M, Caminha-Paiva D, Carvalho M, Conceição AA, Costa LN, Cruz A, Cunha-Blum J, Dagevos J, Braulio Dias BFS, Pinto VD, Dirzo R, Domingos DQ, Echternacht L, Fernandes S, Figueira JEC, Fiorini CF, Giulietti AM, Gomes A, Gomes VM, Gontijo B, Goulart F, Guerra TJ, Junqueira PA, Lima-Santos D, Marques J, Meira-Neto J, Miola DTB, Morellato LPC, Negreiros D, Neire E, Neves AC, Neves FS, Novais S, Oki Y, Oliveira E, Oliveira RS, Pivari MO, Junior EP, Ranieri BD, Ribas RP, Scariot A, Schaefer CE, Sena L, da Silva PG, Siqueira PR, Soares NC, Soares-Filho B, Solar R, Tabarelli M, Vasconcellos R, Vilela E, Silveira FAO (2020) Biodiversity and ecosystem services in the *Campo Rupestre*: a road map for the sustainability of the hottest Brazilian biodiversity hotspot. Perspect Ecol Conserv 18:213–222

Ferro ML, Summerlin M (2019) Developing a standardized list of entomological collection methods for use in databases. ZooKeys 861:145–156. https://doi.org/10.3897/zookeys.861.32347

Fraser SEM, Dytham C, Mayhew PJ (2008) The effectiveness and optimal use of Malaise traps for monitoring parasitoid wasps. Insect Conserv Diver 1:22–31. https://doi.org/10.1111/j.1752-4598.2007.00003.x

Freitas AVL, Iserhard CA, Santos JP, Carreira JYO, Ribeiro DB, Melo DHA, Rosa AHB, Marini-Filho OJ, Accacio GM, Uehara-Prado M (2014) Studies with butterfly bait traps: an overview. Rev Colomb Entomol 40:203–212

Gostinski LF, Carvalho GCA, Rêgo MMC, Albuquerque PMC de (2016) Species richness and activity pattern of bees (Hymenoptera, Apidae) in the restinga area of Lençóis Maranhenses National Park, Barreirinhas, Maranhão, Brazil. Revista Brasileira de Entomologia 60:319–327. https://doi.org/10.1016/j.rbe.2016.08.004

Guerra TJ, Carstensen DW, Morellato LPC, Silveira FAO, Costa FV (2016) Mutualistic interactions among free-living species in Rupestrian grasslands. In: Fernandes GW (eds) Ecology and Conservation of mountain-top grasslands in Brazil. Springer, New York. pp 291–310

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815. https://doi.org/10.1890/02-3114

Graham CH, Carnaval AC, Cadena CD, Zamudio KR, Roberts TE, Parra JL, McCain CM, Bowie RCK, Moritz C, Baines SB, Schneider CJ, Vanderwal J, Rahbek C, Kozak KH, Sanders NJ

(2014) The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. Ecography 37:711–719. https://doi.org/10.1111/ecog.00578

Hagen SB, Jepsen JU, Yoccoz NG, Ims RA (2008) Anisotropic patterned population synchrony in climatic gradients indicates nonlinear climatic forcing. Proc R Soc Biol 275:1509–1515

Harley RM (1995) Introduction. In: Stannard BL, Harvey YB, Harley RM (eds) Flora of the Pico das Almas, Chapada Diamantina – Bahia. Royal Botanic Garden, Kew

Häuser CL, Riede K (2015) Field methods for inventorying insects. In: Watson MF, Lyal CHC, Pendry CA (eds) For more descriptive taxonomy: the foundation of biodiversity research. Chapter 16. Part IV – the influence of technology on data gathering in the field. Cambridge University Press, pp 190–213. https://doi.org/10.1017/CBO9781139028004.021

Henriques NR, Lourenço GM, Diniz ÉS, Cornelissen T (2022) Is elevation a strong environmental filter? Combining taxonomy, functional traits and phylogeny of butterflies in a tropical mountain. Ecol Entomol 47:1–13. https://doi.org/10.1111/een.13145

Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. Biol Rev 80:489–513. https://doi.org/10.1017/S1464793105006767

Hoffmann D, Vasconcelos MF, Martins RP (2015) How climate change can affect the distribution range and conservation status of an endemic bird from the highlands of eastern Brazil: the case of the gray-backed Tachuri, *Polystictus superciliaris* (Aves, Tyrannidae). Biota Neotropica 15:1–12

Horner-Devine MC, Lage M, Hughes JB, Bohannan BJM (2004) A taxa–area relationship for bacteria. Nature 432:750–753. https://doi.org/10.1038/nature03073

Hughes L (2000) Biological consequences of global warming: is the signal already. Trends Ecol Evol 15:56–61

Kamino LHY, Pereira EO, Carmo FF (2020) Conservation paradox: large-scale mining waste in protected areas in two global hotspots, southeastern Brazil. Ambio 49:1629–1638. https://doi.org/10.1007/s13280-020-01326-8

Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA (1993) Terrestrial arthropod assemblages: Their use in conservation planning. Conserv Biol 7:796–808. https://doi.org/10.1046/j.1523-1739.1993.740796.x

Knapp S (2005) Biogeography: space, form and time. J Biogeogr 32:3–4

Körner C (2007) The use of “altitude” in ecological research. Trends Ecol Evol 22:569–574. https://doi.org/10.1016/j.tree.2007.09.006

Kraft NJB, Comita LS, Chase JM, Sanders NJ, Swenson NG, Crist TO, Stegen JC, Vellend M, Boyle B, Anderson MJ, Cornell HV, Davies KF, Freestone AL, Inouye BD, Harrison SP, Myers JA (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. Science 333:1755–1758

Krombein KV (1967) Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Press, Washington, DC, 570 p

Kubota U, Loyola RD, Almeida AM, Carvalho DA, Lewinsohn TM (2007) Body size and host range co-determine the altitudinal distribution of Neotropical tephritid flies. Glob Ecol Biogeogr 16:632–639

Kuchenbecker J, Macedo-Reis LE, Fagundes M, Neves FS (2021) Spatiotemporal distribution of herbivorous insects along always-green mountaintop Forest Islands. Front For Glob Change 4:709403. https://doi.org/10.3389/ffgc.2021.709403

Lamanna C, Blonder B, Violle C, Kraft NJB, Sandel B, Šímová I, Donoghue JC 2nd, Svenning J, McGill BJ, Boyle B, Buzzard V, Dolins S, Jørgensen PM, Marcuse-Kubitza A, Morueta-Holme N, Peet RK, Piel WH, Regetz J, Schildhauer M, Spencer N, Barbara Thiers B, Wiser SK, Enquist BJ (2014) Functional trait space and the latitudinal diversity gradient. Proc Natl Acad Sci 111:13745–13750. https://doi.org/10.1073/pnas.1317722111

Lara ACF, Fernandes GW (1996) The highest diversity of galling insects: Serra do cipó, Brazil. Biodivers Lett 3:111–114

Lara ACF, Fernandes GW, Gonçalves-Alvim SJ (2002) Tests of hypotheses on patterns of gall distribution along an altitudinal gradient. Trop Zool 15:219–232

Lasmar CJ, Ribas CR, Louzada J, Queiroz ACM, Feitosa RM, Imata MMG, Alves GP, Nascimento GB, Neves FS, Domingos DQ (2020) Disentangling elevational and vegetational effects on ant diversity patterns. Acta Oecol 102:103489. https://doi.org/10.1016/j.actao.2019.103489

Le Stradic S, Buisson E, Fernandes GW (2014) Restoration of Neotropical grasslands degraded by quarrying using hay transfer. Appl Veg Sci 17:482–492. https://doi.org/10.1111/avsc.12074

Legendre P (2019) A temporal beta-diversity index to identify sites that have changed in exceptional ways in space–time surveys. Ecol Evol 9(6):3500–3514. https://doi.org/10.1002/ece3.4984

Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecol Monogr 75:435–450

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology: the metacommunity concept. Ecol Lett 7:601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Leite FSF, Eterovick PC, Juncá FA (2008) Status do conheci- mento, endemismo e conservação de anfíbios anuros da Cadeia do Espinhaço. Brasil Megadiverisdade 4(1–2):158–176

Lewis OT, Basset Y (2007) Insect conservation in tropical forests. In: Stewart AJA, New TR, Lewis OT (eds) Insect conservation biology. CABI Publishing, Wallingford, pp 34–56

Lomolino M (2001) Elevation gradients of species-density: historical and prospective views. Glob Ecol Biogeogr 10:3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

Longino JT, Branstetter MG (2019) The truncated bell: an enigmatic but pervasive elevational diversity pattern in middle American ants. Ecography 42:272–283. https://doi.org/10.1111/ecog.03871

Malaise R (1937) A new insect-trap. Entomologisk Tidskrift, Stockholm 58:148–160

Mani MS (1962) Introduction to high altitude entomology. Methuen and Co. Ltd, London, p 302

Mani MS (1968) Ecology and biogeography of high altitude insects. Dr. W. Junk N. V. Publishers, The Hague

Mani MS (1973) Fundamental of high altitude biology. Oxford and IBH, New Delhi. 196 pp

Marsh CJ, Louzada J, Beiroz W, Ewers RM (2013) Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: Scarabaeinae). PLoS One 8:e73147. https://doi.org/10.1371/journal.pone.0073147

Martins I, Ligeiro R, Hughes RM, Macedo DR, Callisto M (2018) Regionalization is key to establish reference conditions for neotropical savanna streams. Mar Freshw Res 69:82–94. https://doi.org/10.1071/MF16381

McCain CM, Grytnes JA (2010) Elevational gradients in species richness. Enc Life Sci 15:1–10. https://doi.org/10.1002/9780470015902.a0022548

McCarty JP (2001) Ecological consequences of recent climate change. Conserv Biol 15(2):320–331

Miller JT, Jolley-Rogers G, Mishler BD, Thornhill AH (2018) Phylogenetic diversity is a better measure of biodiversity than taxon counting. J Syst Evol 56:663–667. https://doi.org/10.1111/jse.12436

Missa O, Basset Y, Alonso A, Miller SE, Curletti G, Meyer MD, Eardley C, Mansell MW, Wagner T (2009) Monitoring arthropods in a tropical landscape: relative effects of sampling methods and habitat types on trap catches. J Insect Conserv 13:103–118

Moericke V (1951) Eine Farbfalle zur Kontrolle des Fluges von Blattlausen, insbesondere der Pfisichblattlaus *M. ersicae* (Sulz). Nachrbl Dtsch Pflzschutzd 3:23–24

Monteiro I, Viana-Junior AB, de Castro Solar RR, Neves FS, Souza O (2017) Disturbance-modulated symbioses in termitophily. Ecol Evol 7:10829–10838. https://doi.org/10.1002/ece3.3601

Monteiro GF, Novais S, Barbosa M, Antonini Y, Passos MFO, Fernandes GW (2020a) The mistletoe *Struthanthus flexicaulis* reduces dominance and increases diversity of plants in *campo rupestre*. Flora 271:151690. https://doi.org/10.1016/j.flora.2020.151690

Monteiro GF, Macedo-Reis LE, Dáttilo W, Fernandes GW, Castro FS, Neves FS (2020b) Ecological interactions among insect herbivores, ants and the host plant *Baccharis dracunculifolia* in a Brazilian mountain ecosystem. Austral Ecol 45:158–167. https://doi.org/10.1111/aec.12839

Montgomery GA, Dunn RR, Fox R, Jongejans E, Leather SR, Saunders ME, Shortall CR, Tingley MW, Wagner DL (2020) Is the insect apocalypse upon us? How to find out. Biol Conserv 241:108327. https://doi.org/10.1016/j.biocon.2019.108327

Montgomery GA, Belitz MW, Guralnick RP, Tingley MW (2021) Standards and best practices for monitoring and benchmarking in- sects. Front Ecol Evol 8:579193. https://doi.org/10.3389/fevo.2020.579193

Morato EF, Martins RP (2006) An overview of proximate factors affecting the nesting behavior of solitary wasps and bees (hymenoptera: Aculeata) in preexisting cavities in wood. Neotrop Entomol 35(3):285–298

Moreira EF, Santos RL, Penna UL, Angel-Coca C, Oliveira FF, Viana BF (2016) Are pan traps colors complementary to sample community of potential pollinator insects? J Insect Conserv 20:583–596. https://doi.org/10.1007/s10841-016-9890-x

Mota GS, Luz GR, Mota NM, Coutinho ES, Veloso MDM, Fernandes GW, Nunes YRF (2018) Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in South-Eastern Brazil. Flora 238:32–42. https://doi.org/10.1016/j.flora.2017.03.010

Moura MR, Villalobos F, Costa GC, Garcia PCA (2016) Disentangling the role of climate, topography and vegetation in species richness gradients. PLoS One 11(3):e0152468. https://doi.org/10.1371/journal.pone.0152468

Moya-Laraño J (2010) Can temperature and water availability contribute to the maintenance of latitudinal diversity by increasing the rate of biotic interactions? Open Ecol J 3:1–13

Müller H (1880) The fertilisers of alpine flowers. Nature 21(534):275. https://doi.org/10.1038/021275d0

Neff JL, Simpson BB (1993) Bees, pollination systems and plant diversity. In: LaSalle J, Gauld ID (eds) Hymenoptera and Biodiversity. Wallingford, USA, CAB International. pp 143–168

Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. J Biogeogr 26(4):867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x

Neves FS, da Silva PG, Solar R, Nunes CA, Beirão MV, Brant H, Castro FS, Dáttilo W, Guevara R, Fernandes GW (2021) Habitat generalists drive nestedness in a tropical mountaintop insect metacommunity. Biol J Linn Soc 133:577–586

Noll FB, Gomes B (2009) An improved bait method for collecting hymenoptera, especially social wasps (Vespidae: Polistinae). Neotrop Entomol 38(4):477–481

Novais SMA, Nunes CA, Santos NB, D'Amico AR, Fernandes GW, Quesada M, Braga RF, Neves ACO (2016) Effects of a possible pollinator crisis on food crop production in Brazil. PLoS One 11(11):e0167292

Nunes CA, Braga RF, Resende FM, Figueira JEC, Neves FS, Fernandes GW (2016) Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. PLoS One 11(6):e0157442. https://doi.org/10.1371/journal.pone.0157442

Nunes CA, Braga RF, Resende FM, Neves FS, Figueira JEC, Fernandes GW (2018) Linking biodiversity, the environment and ecosystem functioning: ecological functions of dung beetles along a tropical elevational gradient. Ecosystems 21:1244–1254. https://doi.org/10.1007/s10021-017-0216-y

Nunes CA, Castro FS, Brant HSC, Powell S, Solar R, Fernandes GW, Neves FS (2020) High temporal Beta diversity in an ant metacommunity, with increasing temporal functional replacement along the elevational gradient. Front Ecol Evol 8:571439. https://doi.org/10.3389/fevo.2020.571439

Oliveira U, Paglia AP, Brescovit AD, Carvalho CJB, Silva DP, Rezende DT, Leite FSF, Batista JAN, Barbosa JPPP, Stehmann JR, Ascher JS, Vasconcelos MF, Marco P Jr, Löwenberg-Neto P, Dias PG, Ferro VG, Santos AJ (2016) The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. Diversity Distrib 22:1232–1244. https://doi.org/10.1111/ddi.12489

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321–326

Oswald CB, Lemes P, Thomé MTC, Pezzuti TL, Santos FR, Garcia PCA, Leite FSF, Magalhães RF (2022) Colonization rather than fragmentation explains the geographical distribution and diversification of treefrogs endemic to Brazilian shield sky islands. J Biogeogr 00:1–19

Ouisse T, Day E, Laville L, Hendrickx F, Convey P, Renault D (2020) Effects of elevational range shift on the morphology and physiology of a carabid beetle invading the sub-Antarctic Kerguelen Islands. Sci Rep 10:1234. https://doi.org/10.1038/s41598-020-57868-0

Padoan LLF (2015) Exploring the unknown: the contributions of naturalists travelers to the natural sciences in Brazil of XVIII/XIX century. Revista Eletrônica em Gestão, Educação e Tecnologia Ambiental 19(1):194–201. https://doi.org/10.5902/2236117015794

Papavero N (1971) Essays on the history of Neotropical Dipterology with special reference to collectors. Museu de Zoologia, Universidade de São Paulo, São Paulo, p 446

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–639

Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: a unified approach. Biol Rev 86:792–812. https://doi.org/10.1111/j.1469-185X.2010.00171.x

Pereira GCN, Coelho MS, Beirão MV, Braga RF, Fernandes GW (2017) Diversity of fruit-feeding butterflies in a mountain archipelago of rainforest. PLoS One 12:e0180007

Perillo LN, Neves FS, Antonini Y, Martins RP (2017) Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient. PLoS One 12(7):e0182054

Perillo LN, Barbosa NPU, Solar RRC, Neves FS (2020) Patterns of diversity in a metacommunity of bees and wasps of relictual mountainous forest fragments. J Insect Conserv 24:17–34. https://doi.org/10.1007/s10841-019-00194-2

Perillo LN, Castro FS, Solar R, Neves F (2021) Disentangling the effects of latitudinal and elevational gradients on bee, wasp, and ant diversity in an ancient neotropical mountain range. J Biogeogr 00:1–15

Peters MK, Hemp A, Appelhans T, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Haas M, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Mwangomo E, Ngereza C, Otte I, Röder J, Rutten G, Costa DS, Tardanico J, Zancolli G, Deckert J, Eardley CD, Peters RS, Rödel M, Schleuning M, Ssymank A, Kakengi V, Zhang J, Böhning-Gaese K, Brandl R, Kalko EKV, Kleyer M, Nauss T, Tschapka M, Fischer M, Steffan-Dewenter I (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nat Commun 7:13736. https://doi.org/10.1038/ncomms13736

Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. Am Nat 100(910):33–46

Pires ACV, Barbosa M, Beiroz W, Beirão MV, Marini-Filho OJ, Duarte M, Mielke OHH, Ladeira FA, Nunes YRF, Negreiros D, Fernandes GW (2020) Altitudinal variation in butterfly community associated with climate and vegetation. An Acad Bras Cienc 92(suppl 2):e20190058. https://doi.org/10.1590/0001-3765202020190058

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25(6):345–353. https://doi.org/10.1016/j.tree.2010.01.007

Pryke JS, Samways MJ (2010) Significant variables for the conservation of mountain invertebrates. J Insect Conserv 14:247–256. https://doi.org/10.1007/s10841-009-9253-y

Purvis A, Hector A (2000) Getting the measure of biodiversity. Nature 405:212–219

Pyrcz TW, Wojtusiak J, Garlacz R (2009) Diversity and distribution patterns of Pronophilina butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an altitudinal transect in north-western Ecuador. Neotrop entomol 38:716–726. https://doi.org/10.1590/S1519-566X2009000600003

Qian H, Lingfeng C, Mao L, Ouyang Z (2013) Drivers of β-diversity along latitudinal gradients revisited. Glob Ecol Biogeogr 22(6):659–670. https://doi.org/10.1111/geb.12020

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Ecography 18:200–205. https://doi.org/10.1111/j.1600-0587.1995.tb00341.x

Ramos FN, Santos FAM (2006) Microclimate of Atlantic forest fragments: regional and local scale heterogeneity. Braz Biol Technol 49:935–944. https://doi.org/10.1590/S1516-89132006000700011

Rapini A, Ribeiro PL, Lambert S, Pirani JR (2008) A flora dos campos rupestres da Cadeia do Espinhaço. Megadiversidade 4:15–23

Razowski J, Becker VO (2002) Systematic and faunistic data on Neotropical Cochylini (Lepidoptera: Tortricidae), with description of new species. Part 1. Acta Zool Cracov 45:287–316

Ribeiro SP, Carneiro MAA, Fernandes GW (1998) Free-feeding herbivores along environmental gradients in Serra do Cipó: basis for a management plant. J Insect Conserv 2:107–118

Romdal TS, Grytnes J-A (2007) An indirect area effect on elevational species richness patterns. Ecography 30:440–448. https://doi.org/10.1111/j.0906-7590.2007.04954.x

Rosa AHB, Perillo LN, Neves FS, Ribeiro DB, Freitas AVL (2019) Butterflies collected using malaise traps as useful bycatches for ecology and conservation. J Threated Taxa 11:14235–14237. https://doi.org/10.11609/jott.4919.11.9.14235-14237

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge.

Samways MJ, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima CS, Gaigher R, Habel JC, Hallmann CA, Hill MJ, Hochkirch A, Kaila L, Kwak ML, Maes D, Mammola S, Noriega JA, Orfinger AB, Pedraza F, Pryke JS, Roquet FO, Settelev J, Simaika JP, Stork NE, Suhling F, Vorster C, Cardoso P (2020) Solutions for humanity on how to conserve insects. Biol Conserv 242:108427. https://doi.org/10.1016/j.biocon.2020.108427

Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: a review of its drivers. Biol Conserv 232:8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Santos FM, Beiroz W, Antonini Y, Martén-Rodríguez S, Quesada M, Fernandes GW (2020) Structure and composition of the euglossine bee community along an elevational gradient of rupestrian grassland vegetation. Apidologie 51:675–687. https://doi.org/10.1007/s13592-020-00752-7

Schluter D, Pennell MW (2017) Speciation gradients and the distribution of biodiversity. Nature 546:48–55

Seluchi ME, Chou SC, Gramani M (2011) A case study of a winter heavy rainfall event over the Serra do Mar in Brazil. Geofis Int 50:41–56

Silva VD, Beirão MV, Cardoso DC (2020) Thermal tolerance of fruit-feeding butterflies (Lepidoptera: Nymphalidae) in contrasting mountaintop environments. Insects 11:278. https://doi.org/10.3390/insects11050278

Silveira FAO (2021) Where to graze? An edaphic grassland perspective of grazing management in grassy ecosystems. Trop Conserv Sci 14:194008292110422. https://doi.org/10.1177/19400829211042255

Silveira FA, Cure JR (1993) High altitude bee fauna of southeastern Brazil: implications for biogeographic patterns (Hymenoptera: Apoidea). Stud Neotropical Fauna Environ 28:47–55

Silveira FAO, Negreiro D, Barbosa NPU, Buisson E, Carmo FF, Carstensen DW, Conceição AA, Cornelissen TG, Echternacht L, Fernandes GW, Garcia QS, Guerra TJ, Jacobi CM, Lemos-Filho JP, Le Stradic S, Morellato LPC, Neves FS, Oliveira RS, Schaefer CE, Viana PL, Lambers H (2016) Ecology and evolution of plant diversity in the endangered *campo rupestre*: a neglected conservation priority. Plant Soil 403(129–152):2637–2638

Silveira FAO, Barbosa M, Beiroz W, Callisto M, Macedo DR, Morellato LPC, Neves FS, Nunes YRF, Solar RR, Fernandes GW (2019) Tropical mountains as natural laboratories to study global changes: a long-term ecological research project in a megadiverse biodiversity hotspot. Perspect Plant Ecol Evol Syst 38:64–73. https://doi.org/10.1016/j.ppees.2019.04.001

Slatyer RA, Schoville SD (2016) Physiological limits along an elevational gradient in a radiation of montane ground beetles. PLoS One 11(4):e0151959. https://doi.org/10.1371/journal.pone.0151959

Sota T (1996) Altitudinal variation in life cycles of carabid beetles: life-cycle strategy and colonization in alpine zones. Arct Alp Res 28:441–447

Souza MM, Perillo LN, Barbosa BC, Prezoto F (2015) Use of flight interception traps of Malaise type and attractive traps for social wasps record (Vespidae: Polistinae). Sociobiology 62(3):450–456

Tatsumi S, Iritani R, Cadotte MW (2021) Temporal changes in spatial variation: partitioning the extinction and colonisation components of beta diversity. Ecol Lett 24(5):1063–1072. https://doi.org/10.1111/ele.13720

Telhado C, Esteves D, Cornelissen T, Fernandes GW, Carneiro MAA (2010) Insect herbivores of *Coccoloba cereifera* do not select asymmetric plants. Environ Entomol 39(3):849–855. https://doi.org/10.1603/EN09179

Terra BR, Gatti FD, Carneiro MAA, Costa MKM (2017) The grasshoppers (Orthoptera: Caelifera) of the grasslands in the southern portion of the Espinhaço Range, Minas Gerais, Brazil. Check List 13:2052. https://doi.org/10.15560/13.1.2052

Tito R, Vasconcelos HL, Feeley KJ (2020) Mountain ecosystems as natural laboratories for climate change experiments. Front For Glob Change 3:38. https://doi.org/10.3389/ffgc.2020.00038

Townes H (1972) A light-weight Malaise trap. Entomol News 83:239–247

Tscharntke T, Gathmann A, Steffan-Dewenter I (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. J Appl Ecol 35:708–719

Tuomisto H (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33:2–22

Tuomisto H (2010b) A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33:23–45

Tylianakis JM, Klein AM, Tscharntke T (2005) Spatiotemporal variation in the effects of a tropical habitat gradient on Hymenoptera diversity. Ecology 86:3296–3302. https://doi.org/10.1890/05-0371

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Vasconcelos TNC, Alcantara S, Andrino CO, Forest F, Reginato M, Simon MF, Pirani JR (2020) Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient neotropical mountains. Proc Biol Sci 287(1923):20192933. https://doi.org/10.1098/rspb.2019.2933

Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol 85(2):183–206

Viana-Junior AB, Quijano-Cuervo LJ, Ferreira JC, Reis RRN, Santos IA, Martins MB (2021) Collecting arboreal arthropods: a technique for sampling plant-inhabiting arthropod communities in a tropical forest understory. Entomol Exp Appl 169:312–321. https://doi.org/10.1111/eea.13012

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

Wolda H (1987) Altitude, habitat and tropical insect diversity. Biol J Linn Soc 30:313–323

Zico JT (1979) Caraça, ex-alunos e visitantes. Ed. São Vicente, Belo Horizonte

Chapter 12
Altitudinal Pattern of Soil Organic Carbon and Nutrients in a Tropical Forest in Puerto Rico

Dingfang Chen, Mei Yu, Grizelle González, and Qiong Gao

12.1 Introduction

Tropical forests have the highest net primary productivity (Chapin et al. 2012) and soil carbon flux (Silver 1998); thus, they play an important role in global C dynamics and changes in climate. Soil physical and chemical properties are essential in influencing soil respiration and plant nutrient status (Valentina et al. 2019), and they vary significantly in tropical forests (Cox et al. 2002; Diekmann et al. 2007; Hutchings et al. 2003; de Souza et al. 2018). Soil age, parent material, disturbance history, vegetation type, and climatic conditions cause considerable temporal and spatial variations in soil physicochemical properties (Augusto et al. 2017; Jackson and Caldwell 1993; Tsui et al. 2004). Such variations in soil properties, especially soil clay content (Müller and Höper 2004), soil organic carbon (SOC), and temperature-moisture conditions (Wan et al. 2007), have been well reported to have significant effects on soil respiration (Chen et al. 2017; Griffiths et al. 2009; Raich and Tufekciogul 2000). Soil texture can affect soil organic matter (SOM) decomposition rate, that is, soil heterotrophic respiration rate, by altering soil water availability, nutrient availability, and surface area (Scott et al. 1996). Using soil laboratory incubations, Scott et al. (1996) concluded that the effects of soil texture combined with soil water pressure influenced decomposition rates significantly. Soil retention characteristics were found to impact the soil microbe respiration (Ghezzehei et al. 2019). From an extensive literature review, Müller and Höper (2004) studied the relationship between soil clay content and SOM turnover rate and concluded that

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soil clay content strongly related to soil respiration rate through soil microbial biomass (Müller and Höper 2004).

Climate change affects SOC (Davidson and Janssens 2006; Kirschbaum 2006), especially in the tropics, although it is still on debate whether tropical soils respond as a carbon sink or source to the increased atmospheric carbon dioxide (CO_2) and global warming (Malhi et al. 2004; Trumbore and Czimczik 2008). Forest soil is also one of the most important sources of nutrients, such as N, P, S, K, Na, Ca, and Mg, for vegetation (Tsui et al. 2004). Therefore, it is ecologically significant to study the patterns of tropical soil properties in the context of global climate change, especially considering that tropics accounts for about 11% of the world's soil C, and contributes 46% of the world's living terrestrial C (Silver 1998).

The Luquillo Experimental Forest (LEF) is a tropical wet montane forest. With the changes in temperature and moisture conditions along the altitudinal gradient, the vegetation displays a distinct distribution pattern from lower altitude to the summit. The altitudinal range in the LEF provides a natural gradient to understand the patterns of soil properties driven by long-term changes in tropical forest ecosystems. In this study, we collected soil samples at a tropical elevation gradient and measured soil physical properties, including soil particle size distribution, bulk density, and moisture content, and soil C, macro- and micronutrients along the elevation gradient. We hypothesized that most of these properties depend significantly on both elevation and vegetation type. We analyzed soil physicochemical characteristics along the altitudinal gradient and then discussed the impacts of climate change on tropical soils, particularly on soil carbon processes.

12.2 Methods and Materials

12.2.1 Field Sites

All the experiment plots were in the Luquillo Experimental Forest (LEF) (18°20′N, 65°49′W), northeastern Puerto Rico (Fig. 12.1). The mean monthly temperature ranges from 23.5 °C in January to 27 °C in September at low elevation, while it ranges from 17 to 20 °C at high elevation (Garcia-Martinó et al. 1996). Rainfall increases with altitude, ranging from an average of 3537 mm per year at low altitude to 4849 mm per year at high altitude (Garcia-Martinó et al. 1996). With the abundant annual rainfalls, moisture is generally not a limiting factor for vegetation growth. The soils in the LEF are mainly derived from volcaniclastic sediments, except for one high-altitude area where the soils are from quartz diorite (Barone et al. 2008). From low to high elevation, four typical forests with distinct dominant species and structures are distributed in LEF: tabonuco forest, palm forest, palo colorado forest, and elfin woodland (Gould et al. 2006; Weaver 2000) (Table 12.1).

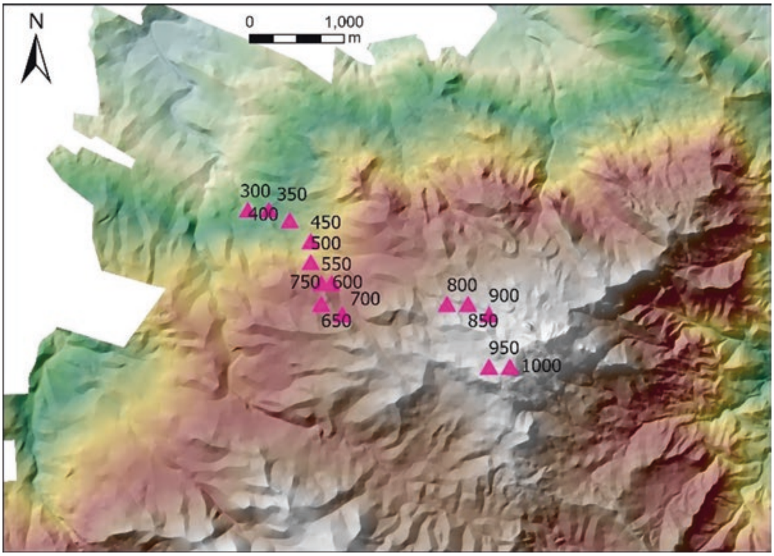

Fig. 12.1 Distribution of the 15 experiment plots along an altitudinal gradient, 300–1000 m, within the Luquillo Experimental Forest in northeast Puerto Rico

12.2.2 Soil Sampling and Lab Analysis

12.2.2.1 Soil Sampling

We collected the soil samples from 15 plots evenly distributed along the altitudinal gradient, that is, 300–1000 m a.s.l., of the LEF in July 2009, and each plot is 20 m by 50 m (Table 12.1). Before collecting soil samples, we removed all the coarse litter debris and organic matters from the surface. For soil extractable nutrients and SOC analyses, we collected for each plot five soil samples, each of which composed of three soil cores of 5 cm in diameter and 15 cm in depth, using a cylindrical soil corer. For soil texture analysis, we collected three soil samples, each separated into two depths of 0–15 cm and 15–30 cm, with a stainless corer (diameter of 1.68 cm) from each plot.

12.2.2.2 Soil Bulk Density (Db) and Soil Water Content (WC)

All the soil samples were oven-drying at 105 °C for 48 h to constant weight. We recorded the weights of both fresh soil samples and oven-drying samples. Soil bulk density (Db, g cm^{-3}) was calculated as the oven-drying soil weight in g divided by the bulk volume of soil solid in cm^3, and soil water content (WC, %) was calculated

Table 12.1 Geographic coordinates of the 15 experiment plots distributed along the altitudinal gradient (from 300 to 1000 m) with three vegetation types in the Luquillo Experimental Forest, Puerto Rico

Plot	Altitude (m)	Latitude	Longitude	Forest type
1	300	18.323	−65.820	Tabonuco
2	350	18.323	−65.818	Tabonuco
3	400	18.322	−65.816	Tabonuco
4	450	18.320	−65.814	Tabonuco
5	500	18.318	−65.814	Tabonuco
6	550	18.316	−65.813	Tabonuco
7	600	18.316	−65.813	Tabonuco/Palo Colorado
8	650	18.314	−65.813	Palo Colorado
9	700	18.313	−65.811	Palo Colorado
10	750	18.316	−65.812	Palo Colorado
11	800	18.314	−65.801	Palo Colorado
12	850	18.314	−65.799	Palo Colorado
13	900	18.313	−65.797	Palo Colorado
14	950	18.308	−65.797	Elfin
15	1000	18.308	−65.795	Elfin

as the difference between fresh weight and oven-drying weight divided by the oven-drying weight.

12.2.2.3 Soil pH and Particle Size

After oven-drying at 105 °C for 24 h to nearly constant weight, the dry soil samples were crushed and sieved with a 10 mesh sieve to remove coarse organic materials and gravels. Then, we measured pH values with an advanced thermo pH meter (Orion 350 PerHect benchtop pH meter with ROSS Micro pH electrode and ATC probe, Thermo Scientific®, Waltham, MA, U.S.A) through a standard procedure (Mclean 1982). We measured the pH values in both water solution and 1 mol L^{-1} potassium chloride solution. The sample preparation for particle size analysis was the same as that for soil pH analysis. The concentration of soil particles with different sizes was measured with a buoyancy soil hydrometer (ASTM 152H, Thermo Scientific ERTCO®, Waltham, MA, U.S.A) through a standard method used by Soil Science Society of America (Dane and Topp 2002). This method is based on the principle that the sedimentation speed in a soil-water suspension varies with different soil particle size and their concentrations (Stokes' law) (Dane and Topp 2002). By calculating the relative solution density at a certain time, the relative proportion of various soil particles can be extrapolated. The proportions of sand, clay, and silt (%) are determined by the following equations:

$$\mathbf{sand} = 100 - \left(R_{40\mathrm{s}} - R_{\mathrm{L1}}\right) \times \left(\frac{100}{\text{Sample weight}}\right) \tag{12.1}$$

$$\mathbf{clay} = \left(R_{7\mathrm{h}} - R_{\mathrm{L2}}\right) \times \left(\frac{100}{\text{Sample weight}}\right) \tag{12.2}$$

$$\mathbf{silt} = 100 - \left(\text{sand} + \text{clay}\right) \tag{12.3}$$

where $R_{40\mathrm{s}}$ is hydrometer reading in soil suspension at 40 s in g L^{-1}; $R_{\mathrm{L1,2}}$ is hydrometer reading of blank solution at the measurement time in g L^{-1}; $R_{7\mathrm{h}}$ is hydrometer reading in soil suspension at 7 h in g L^{-1}; and the unit of sample weight is g.

The buoyancy hydrometer was calibrated at 20 °C. While calculating soil particle proportions, the hydrometer readings were adjusted by adding 0.2 g L^{-1} per degree of the difference in temperature.

12.2.2.4 SOM and Soil Extractable Nutrients

After air-drying for 1 week, the soil samples were oven-drying to constant mass at 50 °C, and then ground and passed through a 20 mesh sieve. We removed stones, coarse root detritus, and other organic materials before further analyses. All the soil physicochemical properties including total organic carbon (*TC*), total nitrogen (*TN*), loss on ignition (*LOI*), and extractable nutrient elements such as aluminum (Al), calcium (Ca), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), and phosphorus (P) were measured at International Institute of Tropical Forestry (IITF), USDA Forest Service, in Río Piedras, Puerto Rico. All the extractable nutrient elements were detected using ICP-Spectro Ciros CCD (Spectro®, SPECTRO Analytical Instruments GmbH, Kleve, Germany). Soil samples to test Ca, Mg, Na, and Al contents were prepared with a standard 1N KCl extraction method of ICP-Spectro Ciros CCD, whereas the samples to test Fe, Mn, K, and P contents were prepared using Olsen-EDTA (NH4-EDTA-NaHCO3) procedure (Anderson and Ingram 1993). Total organic carbon, TN, and LOI were determined using CNS LECO-2000 Analyzer (LECO®, LECO Corporation, Michigan, U.S.A) following the protocol given in a standard procedure.

12.2.3 Statistical Analyses

We first calculated the correlations between all possible pairs of soil properties in the 15 experiment plots. Because the soil properties tend to be highly correlated, we then divided the soil properties into three groups in addition to soil organic carbon, macronutrients that include N, P, K, Ca, and Mg, micronutrients that include Al, Mn, Na, and Fe, and soil physical properties including clay, bulk density, and water content. To explore essential roles of elevation and vegetation in the distribution of soil properties, we regressed the soil physical and chemical properties on the elevation and vegetation types and all variables of soil properties were multiplied by 10 and then log-transformed before regressions. We applied multiple regression to soil C and C:N ratio and multivariate multiple regression to each of the three groups. We then applied multivariate analysis of variance to get a glimpse of the overall response of each group to elevation and vegetation type. We ran all the statistical analyses in R (R Core Team 2020).

12.3 Results

12.3.1 Soil Physical Properties

We plotted soil physical properties including soil texture, bulk density, and soil moisture content against the elevation (Fig. 12.2). Clay contents in both top- and sub-layers decrease, but soil moisture content in the top-layer increases, with the

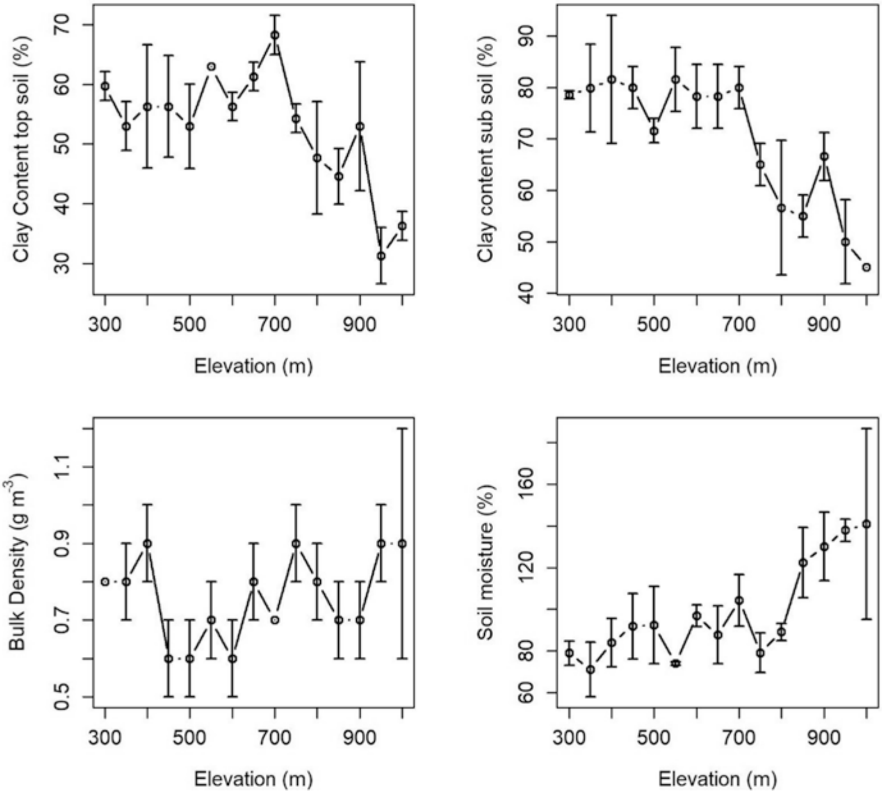

Fig. 12.2 Clay content in both top and sub-soil layers (top panels), and bulk density and soil water content in the top layer (bottom panels) in the 15 plots along the elevation gradient of 300–1000 m

Table 12.2 Multivariate multiple regression of soil physical properties on elevation

	Intercept	Elev	Elev^2	R^2
Clay_T	5.67^a	2.74^a	-2.57^a	0.70
Db	2.35^a	−1.31	1.07	0.17
WC	6.89^a	−1.10	1.47^b	0.75
Clay_S	6.48^a	1.20	-1.54^a	0.83

Clay_T, Db, and WC are soil clay content, bulk density, and moisture content in top-soil layer, respectively. Clay_S is soil clay in sublayer. Elev is the elevation. We did not find significant relationship between soil physical properties and the vegetation

[a] and [b], significant at 0.05 and 0.1, respectively

elevation. However, there is no obvious pattern in soil bulk density at the top-layer along the elevation gradient. The top layer and sublayer have mean clay contents of 53% and 70%, respectively, and t-test indicated that the clay content in sublayer was significantly higher than that in the top layer ($p < 0.01$, one-tailed). For the top layer, soil clay content is significantly correlated with soil water content (Pearson's correlation coefficient of −0.69). However, the soil texture and soil water content are not significantly correlated with the bulk density.

The multivariate regression showed that the soil clay content and water content significantly depend on elevation (Table 12.2). The multivariate ANOVA showed that the p-value of the Pillai statistics for elevation is 0.0003, and that of the squared elevation is 0.05. Thus, as a whole, the soil physical properties significantly depend on elevation.

12.3.2 Soil Carbon and Macronutrients

Soil carbon and macronutrients in top layer (Fig. 12.3) also showed apparent patterns with respect to elevation gradient. Carbon, nitrogen, and phosphorus tend to increase with the elevation. In contrast, potassium, calcium, and magnesium decrease with the elevation. The Pearson's correlation among the macronutrients showed that carbon was significantly correlated with nitrogen ($r = 0.94$, $p < 0.0001$) and phosphorus ($r = 0.45$, $p = 0.1$), that nitrogen was significantly correlated with phosphorus ($r = 0.54$, $p = 0.04$), and that calcium was correlated with magnesium ($r = 0.44$, $p = 0.1$).

Carbon content is an important indicator of soil carbon storage and the regressions of soil carbon content (C) and C:N ratio resulted in the following equations:

$$C = 1.52 + 1.23N + 1.10\ \text{Elev} + 0.30\ \text{Colorado} + 0.35\ \text{Tabonuco} \qquad R^2 = 0.98 \tag{12.4}$$

$$\frac{C}{N} = 4.40 + 0.99\ \text{Elev} + 0.19\ \text{Colorado} + 0.16\ \text{Tabonuco} \qquad R^2 = 0.84 \tag{12.5}$$

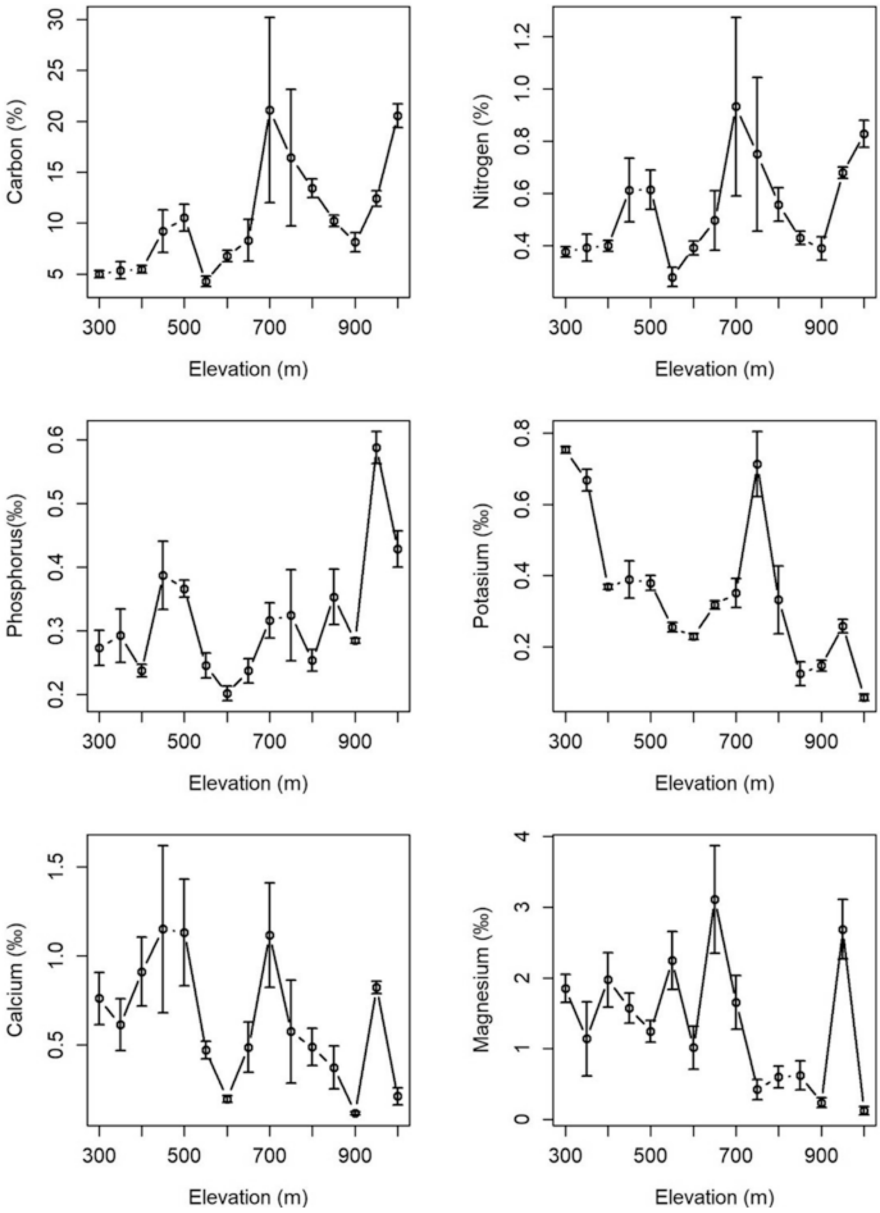

Fig. 12.3 Distribution of soil carbon and macronutrients in top-soil layer along the elevation gradient of 300–1000 m

Table 12.3 Mean and standard deviation of carbon, macronutrient, and micronutrient among different vegetation types

	Tabonuco	Palo Colorado	Elfin
C (%)	6.6 ± 2.4	12.9 ± 5.1	16.5 ± 5.8
N (%)	0.44 ± 0.13	0.59 ± 0.21	0.75 ± 0.10
P (mg g^{-1})	0.29 ± 0.07	0.29 ± 0.04	0.51 ± 0.11
K (mg g^{-1})	0.43 ± 0.20	0.33 ± 0.21	0.16 ± 0.14
Ca (mg g^{-1})	0.75 ± 0.35	0.52 ± 0.33	0.52 ± 0.43
Mg (mg g^{-1})	1.58 ± 0.46	1.11 ± 1.1	1.41 ± 1.81
Al (mg g^{-1})	30.9 ± 2.9	40.7 ± 5.4	50.8 ± 8.8
Fe (mg g^{-1})	64.0 ± 6.7	73.5 ± 21.4	47.9 ± 22.8
Mn (mg g^{-1})	0.41 ± 0.41	0.22 ± 0.19	0.13 ± 0.14
Na (mg g^{-1})	0.094 ± 0.022	0.089 ± 0.035	0.085 ± 0.035

All the coefficients except the one for Tabonuco in C:N ratio (Eq. 12.5) are statistically significant. By including nitrogen as an independent variable, carbon content is significantly dependent on elevation and vegetation types. Hence, both soil carbon content and C:N ratio significantly increase with the elevation.

ANOVA test of soil properties on vegetation showed that only C, N, P, and K differed significantly among the vegetation types. Elfin forest has higher C, N, and P than the palo colorado forest, and palo colorado forest has greater C and N than the tabonuco forest (Table 12.3).

The multivariate regression of macronutrients involving N, P, K, Ca, and Mg showed their great dependence on the vegetation types (Table 12.4). The multivariate ANOVA of the model showed the pillai's statistics had p-values of 0.008, 0.1, and 0.085 for elevation, elevation squared, and vegetation type, respectively.

12.3.3 Soil Micronutrients

The top-layer micronutrients (Fig. 12.4) do not show apparent patterns with respect to the elevation due to the large variations. However, when including vegetation types in the regression, the ANOVA of the model (Table 12.4) still showed significant dependence on elevation and the Pillai statistics had p-value of 0.00005, 0.04, and 0.097 for first- and second-order of elevation and the forest types, respectively. Thus, the micronutrients as a whole significantly responded to both elevation and the forest type.

Table 12.4 Multivariate multiple regressions of macronutrients and micronutrients on elevation and vegetation types

	Intercept	Elev	Elev^2	Colorado	Tabonuco	R^2
Macronutrients						
N	2.20[a]	3.34	−3.61	−0.86[a]	−1.49[a]	0.52
P	1.87[a]	−0.54	0.28	−0.56[b]	−0.66	0.53
K	3.88[a]	−0.53	−3.33	−0.42	−1.56[b]	0.70
Ca	4.27[a]	5.73	−8.86[b]	−1.86[a]	−3.09[a]	0.60
Mg	3.33	13.24[b]	−15.23[a]	−2.30[a]	−3.33[a]	0.63
Micronutrients						
Al	5.73[a]	2.64[a]	−2.18[a]	−0.44[a]	−0.72[a]	0.83
Na	0.33	5.57[b]	−6.28[a]	−1.03[a]	−1.58[a]	0.51
Mn	5.16[b]	−16.03[b]	10.92	1.11	0.80	0.41
Fe	6.11[a]	−0.52	0.54	0.53	0.47	0.27

Significance is based on one-tailed *p*-value

[a] and [b], significant at 0.05 and 0.1, respectively

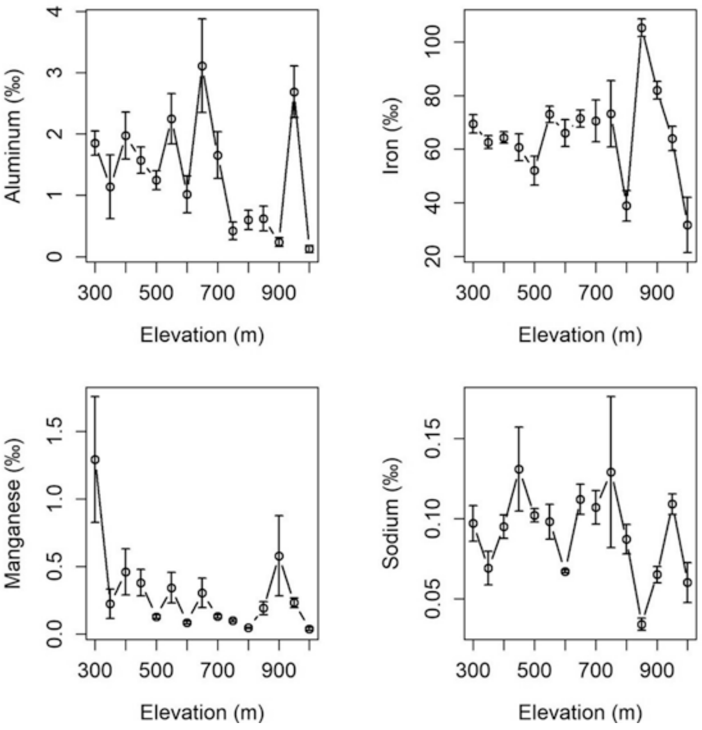

Fig. 12.4 Soil Al, Fe, Mn, and Na in the top layer along the elevation gradient of 300–1000 m

12.4 Discussion

In this study, we characterized soil physicochemical properties along an altitudinal gradient in LEF, which helps understand the interactions among soil patterns, vegetation distribution, and climate changes. Vegetation type and altitude were related to each other, and vegetation type varied significantly with altitude in the tropics (Barone et al. 2008; Gould et al. 2006; Lieberman et al. 1996; Lovett 1996; Weaver 1991; Weaver 2000). Our results on soil physicochemical characteristics were consistent with existing studies in this area. The range of clay content at the depth of 0–15 cm (31.3–68.3%), which is one important factor influencing soil respiration, fell closely within the ranges (22.35–68.25%) reported from long-term soil chemical and physical analyses by IITF, USDA, in Río Piedras, Puerto Rico (Sánchez et al. 1997). Other soil properties (e.g., bulk density and the contents of some extractable nutrient elements such as Al, Ca, Fe, P, Mg, and Na) in this study also had ranges aligned to those reported in existing studies (Sánchez et al. 1997; Soil Survey Staff 1995).

The elevation profile of soil physiochemical properties is the result of long-term balance of interaction with the vegetation, physical and chemical weathering (Bétard 2012), external input, and rainfall-driven leaching gravity. These processes depend on climate, forest type (Zimmermann and Bird 2012), and properties of parent materials (Augusto et al. 2017). According to the recent update, the mean annual rainfall in Luquillo mountain areas was quantified as a quadratic function of elevation so that precipitation increases nonlinearly to about 2000–4000 mm $yr.^{-1}$ (Murphy et al. 2017). The mean annual temperature on the other hand is found to be a linearly decreasing with elevation from 26.9 to 19.4 °C (Waide et al. 2013). The excessive rainfall in the high altitude often saturates the soil, together with the low temperature, suppresses the microbial activities (Cantrell et al. 2013), and brings down the decomposition and ecosystem productivity (Chen et al. 2017). The higher C, N, and P at high elevation found in this study may be a result of long-term accumulation in the soil due to the low decomposition rate.

Leaching driven by rainfall is another strong shaping force of the altitudinal profile of clay and cation in the macronutrients. Leaching contributes to the accumulation of fine particles especially clay in the low altitude. Leaching also tends to reduce K, Ca, and Mg in high altitude but tends to enhance these cations in the low altitude. This trend can also be strengthened by the temperature gradient (White et al. 1999). P, K, and other extractable nutrients such as Ca, Na, and Mg are usually reported as the main limitations to productivity at mountains due to their strong leaching at the high altitude (Diekmann et al. 2007; Tanner et al. 1998; Tsui et al. 2004).

The distribution of forest type along the altitudinal gradient is not only a result of the climate and soil, but also contributes to the formation of the gradient of soil physiochemical properties. Plant growth and productivity decrease at the tops of mountains in the tropics, which are probably caused by lower decomposition rate at higher altitude limited by the lower temperature and more saturated soil (Tanner et al.

1998). The forest in low altitude has thinner leaf with short lifespan and greater nutrient concentration than those growing in higher altitudes (Harris and Medina 2013). On the other hand, the sclerophyllous-leaved species in elfin dwarf forest makes it difficult to decompose. The litter of the tabonuco forest in the low altitude thus is easier to decompose and the nutrient cycling is faster than the elfin dwarf cloud forest in the high altitude, so that the means of the total C, N, P, and *C*:*N* have the following order in our plots: Elfin > Palo Colorado > Tabonuco. Soil *C*:*N* ratio is primarily affected by vegetation type and the *C:N* balance of soil microbes (Cox et al. 2002; Gifford 1994; Rastetter et al. 1991; Schlesinger and Andrews 2000; Silver et al. 1994). Typically, the *C*:*N* ratio in soils is in the range of 8–20 (Gifford 1994), and the maximum can extend to 30 in the acidic and humus-rich soils found in the tropics (Rastetter et al. 1991). Soil *C*:*N* ratio in the LEF increased with altitude from low to top in our study, ranging from 11.9 to 24.9.

Previous experiments at a large scale showed that there were no fixed distribution patterns for most nutrient elements (Appel et al. 2003; Burghouts et al. 1998; Tanner et al. 1998). However, when including both elevation and vegetation types in the regression, we found most nutrients showed significant dependence on elevation and/or vegetation types (Table 12.4).

Spatial heterogeneity of dry and wet depositions might also contribute to the altitudinal gradient of soil chemistry (McClintock 2014). Puerto Rico received great amount of African dust each year (Pett-Ridge 2009). On the other hand, the analysis of rainfall and cloud water chemistry showed that Cl, Na, and Mg with marine origin dominated the deposition. Ca is primarily from the dust, and N is primarily from the anthropogenic activities. McClintock et al. (2019) found that the dry deposition of dust differed by more than two folds in two sites of about 10 km apart, with the east site having higher dry deposition. Our study sites extend from the northwest (low altitude) to the southeast (high altitude) with a horizontal distance of ~3 km. Therefore, the high altitude in the east might receive more dust when compared to the low altitude in the west.

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References

Anderson JM, Ingram JSI (1993) Tropical soil biology and fertility: a handbook of methods, 2nd edn. C. A. B. International, Wallingford

Appel C, Ma LQ, Rhue RD, Reve W (2003) Selectivities of potassium-calcium and potassium-lead exchange in two tropical soils approved for publication as Florida agricultural experiment station journal series No. R-07373. Soil Sci Soc Am J 67(6):1707–1714. https://doi.org/10.2136/sssaj2003.1707

Augusto L, Achat DL, Jonard M, Vidal D, Ringeval B (2017) Soil parent material—a major driver of plant nutrient limitations in terrestrial ecosystems. Glob Chang Biol 23(9):3808–3824. https://doi.org/10.1111/gcb.13691

Barone JA, Thomlinson J, Cordero PA, Zimmerman JK (2008) Metacommunity structure of tropical forest along an elevation gradient in Puerto Rico. J Trop Ecol 24:525–534. https://doi.org/10.1017/s0266467408005208

Bétard F (2012) Spatial variations of soil weathering processes in a tropical mountain environment: the Baturité massif and its piedmont (Ceará, NE Brazil). Catena 93:18–28. https://doi.org/10.1016/j.catena.2012.01.013

Burghouts TBA, Straalen NMV, Bruijnzeel LA (1998) Spatial heterogeneity of element and litter turnover in a Bornean rain forest. J Trop Ecol 14(4):477–506. https://doi.org/10.1017/S0266467498000352

Cantrell S, Lodge D, Cruz C, García L, Perez-Jimenez JR, Molina M (2013) Differential abundance of microbial functional groups along the elevation gradient from the coast to the Luquillo Mountains. Ecol Bull 54:87–100

Chapin FS, Matson PA, Vitousek PM (2012) Principles of terrestrial ecosystem ecology, 2nd edn. Springer, New York

Chen D, Yu M, González G, Zou X, Gao Q (2017) Climate impacts on soil carbon processes along an elevation gradient in the tropical Luquillo experimental forest. Forests 8(3):90

Cox SB, Willig MR, Scatena FN (2002) Variation in nutrient characteristics of surface soils from the Luquillo experimental forest of puerto rico: a multivariate perspective. Plant Soil 247(2):189–198

Dane JH, Topp CG (2002) Methods of soil analysis: part 4 physical methods. Soil Science Society of America, Madison

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440(7081):165–173. https://doi.org/10.1038/nature04514

de Souza JJLL, Fontes MPF, Gilkes R, Costa LMD, Oliveira TSD (2018) Geochemical signature of amazon tropical rainforest soils. Rev Bras Ciênc Solo 42:e0170192

Diekmann LO, Lawrence D, Okin GS (2007) Changes in the spatial variation of soil properties following shifting cultivation in a Mexican tropical dry forest. Biogeochemistry 84(1):99–113. https://doi.org/10.1007/s10533-007-9107-1

Garcia-Martinó AG, Warner GS, Scatena FN, Civco DL (1996) Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. Caribb J Sci 32(4):413–424

Ghezzehei TA, Sulman B, Arnold CL, Bogie NA, Berhe AA (2019) On the role of soil water retention characteristic on aerobic microbial respiration. Biogeosciences 16:1187–1209

Gifford R (1994) The global carbon cycle: a viewpoint on the missing sink. Funct Plant Biol 21(1):1–15. https://doi.org/10.1071/PP9940001

Gould WA, González G, Carrero RG (2006) Structure and composition of vegetation along an elevational gradient in Puerto Rico. J Veg Sci 17(5):653–664

Griffiths RP, Madritch MD, Swanson AK (2009) The effects of topography on forest soil characteristics in the Oregon Cascade Mountains (USA): Implications for the effects of climate change on soil properties. For Ecol Manag 257(1):1–7. https://doi.org/10.1016/j.foreco.2008.08.010

Harris HL, Medina E (2013) Changes in leaf properties across an elevation gradient in the Luquillo Mountains, Puerto Rico. Ecol Bull 54:169–179

Hutchings MJ, John EA, Wijesinghe DK (2003) Towards understanding the consequences of soil heterogeneity for plant populations and communities. Ecology 84(9):2322–2334. https://doi.org/10.1890/02-0290

Jackson RB, Caldwell MM (1993) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74(2):612–614. https://doi.org/10.2307/1939320

Kirschbaum MUF (2006) The temperature dependence of organic-matter decomposition—still a topic of debate. Soil Biol Biochem 38(9):2510–2518. https://doi.org/10.1016/j.soilbio.2006.01.030

Lieberman D, Lieberman M, Peralta R, Hartshorn GS (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J Ecol 84:137–152

Lovett JC (1996) Altitudeal and latitudinal changes in tree association and diversity in the Eastern Arc mountains of Tanzania. J Trop Ecol 12:629–650

Malhi Y, Phillips OL, Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. Philos Trans R Soc Lond B Biol Sci 359(1443):477–491. https://doi.org/10.1098/rstb.2003.1426

McClintock MA (2014) Spatial variability of dust deposition in the Luquillo Mountains, Puerto Rico. Master of Science, Oregon State University

McClintock MA, McDowell W, González G, Schulz M, Pett-Ridge J (2019) African dust deposition in Puerto Rico: analysis of a 20-year rainfall chemistry record and comparison with models. Atmos Environ:116907. https://doi.org/10.1016/j.atmosenv.2019.116907

Mclean EO (1982) Soil pH and lime requirement. In: Page AL (ed) Methods of soil analysis. Part 2. Chemical and microbiological properties. American Society of Agronomy, Soil Science Society of America, Madison, pp 199–224

Müller T, Höper H (2004) Soil organic matter turnover as a function of the soil clay content: consequences for model applications. Soil Biol Biochem 36(6):877–888. https://doi.org/10.1016/j.soilbio.2003.12.015

Murphy SF, Stallard RF, Scholl MA, González G, Torres-Sánchez AJ (2017) Reassessing rainfall in the Luquillo Mountains, Puerto Rico: local and global ecohydrological implications. PLoS One 12(7):e0180987–e0180987. https://doi.org/10.1371/journal.pone.0180987

Pett-Ridge J (2009) Contributions of dust to phosphorus cycling in tropical forests of the Luquillo Mountains, Puerto Rico. Biogeochemistry 94:63–80. https://doi.org/10.1007/s10533-009-9308-x

R Core Team (2020) R: a language and environment for statistical computing. Vienna, Austria. Retrieved from http://www.R-project.org/

Raich JW, Tufekciogul A (2000) Vegetation and soil respiration: Correlations and controls. Biogeochemistry 48(1):71–90. https://doi.org/10.1023/a:1006112000616

Rastetter EB, Ryan MG, Shaver GR, Melillo JM, Nadelhoffer KJ, Hobbie JE, Aber JD (1991) A general biogeochemical model describing the responses of the C-cycle and N-cycle in terrestrial ecosystems to changes in Co2, climate, and N-deposition. Tree Physiol 9(1–2):101–126

Sánchez MJ, Lopez E, Lugo AE (1997) Chemical and physical analyses of selected plants and soils from Puerto Rico (1981–1990). Research Note IITF-RN-1. Retrieved from Rio Piedras, Puerto Rico

Schlesinger WH, Andrews JA (2000) Soil respiration and the global carbon cycle. Biogeochemistry 48(1):7–20. https://doi.org/10.1023/a:1006247623877

Scott NA, Cole CV, Elliott ET, Huffman SA (1996) Soil textural control on decomposition and soil organic matter dynamics. Soil Sci Soc Am J 60(4):1102–1109. https://doi.org/10.2136/sssaj1996.03615995006000040020x

Silver WL (1998) The potential effects of elevated Co2 and climate change on tropical forest soils and biogeochemical cycling. Clim Chang 39(2):337–361. https://doi.org/10.1023/a:1005396714941

Silver WL, Scatena FN, Johnson AH, Siccama TG, Sanchez MJ (1994) Nutrient availability in a montane wet tropical forest: Spatial patterns and methodological considerations. Plant Soil 164(1):129–145. https://doi.org/10.1007/bf00010118

Soil Survey Staff (1995) Order 1 soil survey of the Luquillo long-term ecological research grid, Puerto Rico. Retrieved from

Tanner EVJ, Vitousek PM, Cuevas E (1998) Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. Ecology 79(1):10–22. https://doi.org/10.2307/176860

Trumbore SE, Czimczik CI (2008) An uncertain future for soil carbon. Science 321(5895):1455–1456. https://doi.org/10.1126/science.1160232

Tsui C-C, Chen Z-S, Hsieh C-F (2004) Relationships between soil properties and slope position in a lowland rain forest of southern Taiwan. Geoderma 123(1):131–142. https://doi.org/10.1016/j.geoderma.2004.01.031

Valentina C, Martinez-Garza C, Jiménez Hernández HE, Márquez-Torres J, Campo J (2019) Effects of initial soil properties on three-year performance of six tree species in tropical dry forest restoration plantings. Forests 10:428. https://doi.org/10.3390/f10050428

Waide RB, Comarazamy DE, Conzales JE, Hall CAS, Lugo AE, Luvall JC, Murphy DJ, Ortiz-Zayas JR, Ramirez-Beltran ND, Scatena FN, Silver WL (2013) Climate variability at multiple spatial and temporal scales in the Luquillo Mountains, Puerto Rico. Ecol Bull 54:21–41

Wan S, Norby RJ, Ledford J, Weltzin JF (2007) Responses of soil respiration to elevated CO2, air warming, and changing soil water availability in a model old-field grassland. Glob Chang Biol 13(11):2411–2424. https://doi.org/10.1111/j.1365-2486.2007.01433.x

Weaver PL (1991) Environmental gradient affect forest composition in the Luquillo Mountains of Puerto Rico. Interciencia 16:142–151

Weaver PL (2000) Environmental gradients affect forest structure in Puerto Rico's Luquillo Mountains. Interciencia 25(5):254–259

White AF, Blum AE, Bullen TD, Vivit DV, Schulz M, Fitzpatrick J (1999) The effect of temperature on experimental and natural chemical weathering rates of granitoid rocks. Geochim Cosmochim Acta 63(19–20):3277–3291. https://doi.org/10.1016/s0016-7037(99)00250-1

Zimmermann M, Bird MI (2012) Temperature sensitivity of tropical forest soil respiration increase along an altitudinal gradient with ongoing decomposition. Geoderma 187–188:8–15. https://doi.org/10.1016/j.geoderma.2012.04.015

Chapter 13
Elevational and Latitudinal Species Richness Patterns of Dung Beetles in North and South America and the Role Played by Historical Factors

Jorge M. Lobo

13.1 Introduction

Latitudinal and elevational gradients in the diversity and composition of plant and animal species are among the first foundational patterns that intrigued ecologists and biogeographers (von Humboldt 1858), and their study has given rise to many ideas and hypotheses about the factors fostering diversity and composition differences in natural assemblages (Rahbek et al. 2019). The comparable variation in environmental conditions along latitudinal and elevational gradients and the functional similarity of the assemblages that can be found along these two gradients has led to their analogy, fueling the suspicion that there is a common cause to explain both gradients (Halbritter et al. 2013). Many different factors have been proposed to explain latitudinal gradients, highlighting those related with the contingent Earth history and plate tectonics events (Ricklefs and Schluter 1993), the stability of climatic conditions (Fine 2015), the environmental heterogeneity (Yang et al. 2015), or the variation in the available energy (Currie et al. 2004). In the case of elevation gradients, mountain building processes (Antonelli et al. 2018), the orientation and isolation of the mountain ranges (Lobo and Halffter 2000), the history of the region harboring the elevation gradient (Hagen et al. 2021), and, therefore, the composition of the regional pool (Lessard et al. 2012) are factors frequently mentioned apart from the pervasive influence of temperature, energy, and environmental heterogeneity (Hodkinson 2005). The effects of latitude and elevation on biodiversity may

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interact positively or negatively so that a similar increase in altitude could have a different influence depending on latitude (Leithead and Anand 2013). The nonlinear character of the relationships between environmental variables, ecosystem changes and biodiversity, and mainly the idiosyncratic evolutionary history of the considered regions (Scheffer et al. 2001; Newbold et al. 2020, hereafter historical factors) are factors prompting the role of the interaction between latitude and elevation.

In the case of America these historical factors are evident in the differential geological and evolutionary history of North and South America, which probably affected the elevational and latitudinal patterns of variation in biodiversity. North America has a long history of connections with Asia and Europe as consequence of the contact of North American, Eurasian, and Caribbean plates (Sanmartín et al. 2001). Briefly, the division of Laurasia in Euroamerica and Asiamerica during the Cretaceous (≈100 mya; Noonan 1988) was maintained until the Paleocene (≈60 mya) although the connection of North America with Europe could have continued to the Late Eocene (≈40 mya) (Sanmartín et al. 2001). Similarly, the connection between North America and the Eastern Palearctic was maintained intermittently until the Pleistocene glaciations (Sanmartín et al. 2001). In contrast with North America, the geological history of South America is recognized as less complex because this continent remained isolated since its separation from Gondwana around 100 mya, until the connection of North and South America (Great American Biotic Interchange) due to the volcanic emergence of the Isthmus of Panama around 2.8 mya (O'Dea et al. 2016).

Scarabaeinae dung beetles constitutes the main invertebrate group specialized in the consumption of mammal feces, which are used both for feeding and breeding (Halffter and Matthews 1966). As a consequence, dung beetles constitute the main group responsible for recycling the nutrients provided by this decay material (Milotić et al. 2019). The origin of Scarabaeinae species is dated from the Upper Cretaceous (from 92 to 84 mya; see Ahrens et al. 2014) in Gondwanaland under warmer and humid climatic conditions (Davis et al. 2002; Scholtz et al. 2009), and the conservatism of this general thermal preference (Wiens and Donoghue 2004) would still condition the current geographic distribution of these species in the western Palaearctic (Hortal et al. 2011). Thus, a low number of Scarabaeinae species are able to inhabit under cold temperate conditions (Hanski and Cambefort 1991; Lobo et al. 2002). According to Cambefort (1991) and Davis and Scholtz (2001), around 1163 species and 68 genera are recognized as inhabiting the Neotropical region, and 88 species and 11 genera in the Nearctic. More recent data (Vaz-De-Mello et al. 2011; Schoolmeesters 2022) also corroborate this difference: 83 and 6 Scarabaeinae genera would be present in the Neotropical (94% endemic) and Nearctic regions (none of them endemic), respectively. Furthermore, dung beetle assemblages below and above the 35° parallel in North America are clearly different both in species richness and in composition (Lobo 2000), so that southern North America can be considered as a transition area between Nearctic and Neotropical faunas (Halffter 1976).

Compiling a comprehensive database of local studies in the Americas, this study aims to determine and compare the rate of decline of local Scarabaeinae species richness along elevational and latitudinal gradients in North and South America, attempting to estimate the effect of the interaction between elevation and latitude that could be attributed to geological and environmental differences between the two land masses. Furthermore, as these geographic gradients imply a change in the average environmental temperature, we will also examine how species richness varies with this variable. Additionally, the predictive capacity of different types of predictors on the variation in species richness is assessed. While the isolated character and the long-term climatic stability of South America might have promoted the accumulation of species over time (Antonelli and Sanmartín 2011), the Pliocene connection of North and South America would have stimulated the extinction of those native species with a larger body size as a consequence of the disappearance of mammalian megafauna (Schweiger and Svenning 2018) and the arrival of more generalist northern species (Carrillo et al. 2020). Thus, we would expect that the presence of taxa adapted to a cold-temperate climate in North America could make it possible to colonize mid- and high-mountain ecosystems, thus decreasing the rate of species richness decline with elevation, compared to South America. On the other hand, in South America with a larger regional pool of species, there may have been colonization of northern elements ("horizontal colonization" sensu Lobo and Halffter 2000) but also an evolution of native elements toward mountain conditions ("vertical colonization"). These processes would facilitate the establishment of species adapted to mountain conditions in South America, thus decreasing the slope of the relationships between species richness and elevation. Keeping all these arguments in mind, this study will estimate the likelihood of three types of relationships between species richness and elevation in the Americas (Fig. 13.1), always considering that the intercepts should be statistically different in both land masses (i.e., mean species richness at sea level must be always higher in South America). (i) If the differential geological history of both land masses barely affects the elevational gradient and/or the conservation of the thermal niche is strongly manifested in Scarabaeinae, then slopes will hardly differ and the mountain colonization of species would be similar and infrequent in both North and South America (Fig. 13.1a).

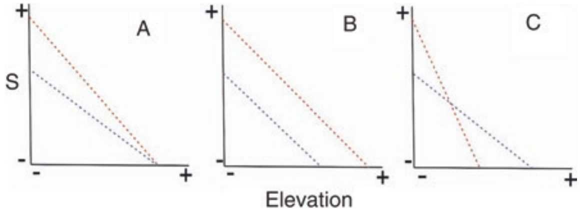

Fig. 13.1 Three potential relationships between species richness (S) and elevation for south (red broken line) and north (blue broken line) local assemblages, assuming that the number of species at sea level is always higher in the south (higher intercept). (**a**) The slopes of the relationship between species richness and elevation may differ, but the number of species that colonise the high mountains is similar in North and South America. (**b**) Slopes may be similar, but mountain South America assemblages are more species-rich. (**c**) Steeper slope in the relationship between species richness and elevation in South America because some cold-adapted species have been able to colonise North American mountains but not those of South America

(ii) If the high basal diversity and geological history South America have promoted the colonization of mountainous environments by overcoming thermal constraints, we should expect that South American dung beetle assemblages would be able to reach higher elevations, although the slopes of the linear regression between species richness and elevation may or may not differ between North and South America (Fig. 13.1b). Finally, (iii) if the presence of some species adapted to cold-temperate climatic conditions has facilitated the colonization of mountains in North America but not those in South America, one would expect a steeper slope in the relationship between species richness and elevation in South America (Fig. 13.1c).

13.2 Methods

13.2.1 Data Origin

Web of Science and Google Scholar were used to search for American faunistic or ecological studies on dung beetles. The found studies were complemented by some publications belonging to the author's library. In total, the so generated exhaustive database compiles the data of 260 published studies, PhD theses, and different grey literature mentioning species richness information on local American Scarabaeinae dung beetle assemblages (see Appendix 13.1). Only those studies that provide Scarabaeinae local data on areas of 10 hectares or less have been considered in order to minimize the effect of area differences on species richness values. All these documents have made it possible to obtain data from 1192 different localities heterogeneously distributed over the whole American continent (Fig. 13.2). The exhaustive nature of this compilation is evident when one considers that a recent study gathering dung beetle data for the Neotropical region retrieve 170 studies and 290 local sampling sites (Pessôa et al. 2020, 2021). In our case, a total of 440 localities are placed at latitudes above the Isthmus of Panama, and 752 localities at latitudes below this isthmus.

The Isthmus of Panama (≈9°) was used as the boundary of the two land masses (hereafter, North and South America) considered here, because they have their own geological history, and the purpose of this study is to examine the influence of these historical differences on the elevational variation of Scarabaeinae species richness. North America includes here both the North American and Caribbean plates, thus covering part of the Nearctic (excluding Greenland) and Neotropical biogeographic realms (from central Mexico to Panama) delimited using biological information (Holt et al. 2013). South America is considered here to consist of all the territories below the Isthmus of Panama, although the history of the Caribbean Plate and Central America shows the existence of intermittent connections between North and South America from the Cretaceous (Iturralde-Vinent 2005). Before the definitive Pliocene connection between South and North America, the geological history of

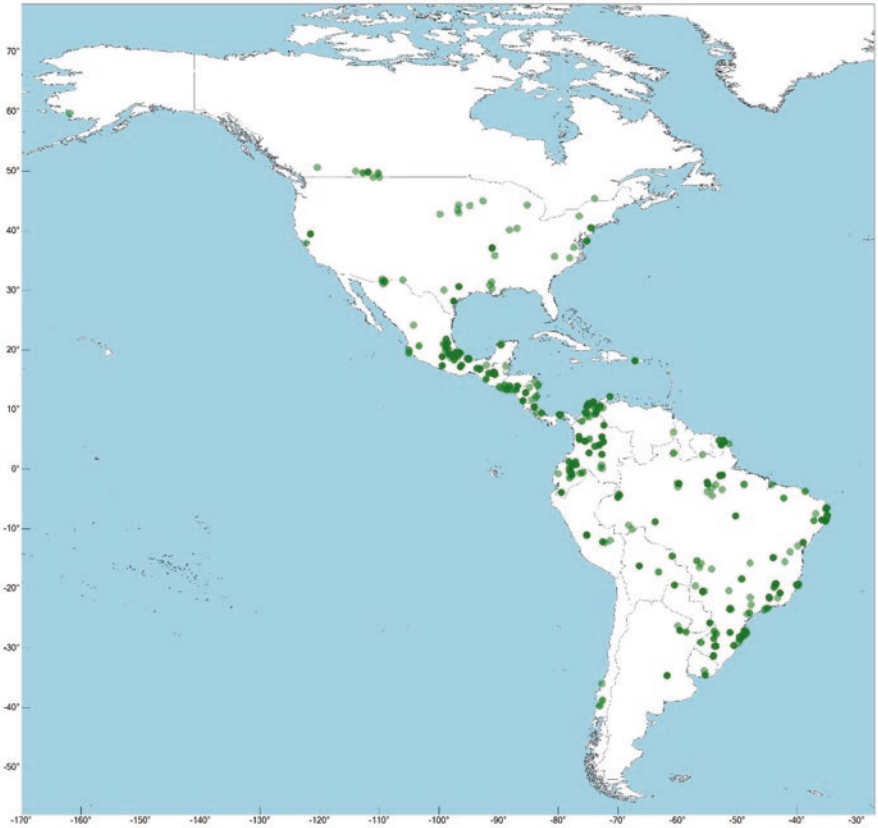

Fig. 13.2 Geographical location of all the used studies

Central America would have allowed a more effective connection of these lands with the northern continent (Mann et al. 2007).

Compiled data belong to 21 countries corresponding 81.6% of total localities to Brazil (35%), Mexico (25%), Colombia (17%) and USA (5%). The database gathers information on the authors, the locality and country of collection, its longitude and latitude, the year of sampling, elevation, the number of collected species, the general habitat sampled, the average temperature and precipitation of the locality, the approximate surveyed area of each study, the number of sampled months, and the number of used pitfall-traps. These three last variables are used as surrogates of the survey effort carried out by each study. Temperature and precipitation values come from the WorldClim 2.1 database (Fick and Hijmans 2017; average data for 1970–2000) at a resolution of 2.5 minutes (4.6 × 4.6 km at the equator). The habitat of each locality is coded as Open (e.g., grasslands), Half-Closed (e.g., scrubs), and Closed (natural and secondary forest). These variables are dummy-coded using only two of these variable states. The location of the studies in North or South America was also coded as a dummy variable.

13.2.2 Data Treatment

Generalized linear models (McCullagh and Nelder 1997) have been used to summarize the relationship between Scarabaeinae dung beetle species number and the above-mentioned explanatory variables in order simply to compare their explanatory capacity. A Poisson error distribution for the number of dung beetle species was assumed, which are linked to the set of predictor variables via a logarithmic link function. Environmental variables were standardized to eliminate the effect of differences in measurement scale, and each variable or variable groups were firstly related separately to species richness. The explanatory capacity was measured by the deviance statistics, comparing the reduction in deviance of a predictor with a full model in which the number of parameters was equal to the total number of observations (Dobson 1990). All the two-way interactions among predictors were also examined but their effects considered only if the explanatory capacity of the interaction is higher than those of the two predictors when included at the same time (i.e., the additive main effects were obviated when the interaction is far more explanatory). A complete model including all the considered predictors at the same time was also performed, measuring the statistical significance of the obtained regression coefficients with the Wald statistic based on maximum likelihood estimates. Type III sums of squares were used in this case to estimate the partial effect of each explanatory predictor once the effects of the other predictors were controlled for.

The relationships among species richness, latitude, elevation, and temperature are typically triangular or "factor ceiling" due to the existence of an upper limit generated by one or several variables that, however, are not able to precisely determine the variability of the response variable (Thomson et al. 1996). In this study we have chosen to divide the data set into classes and conducting regressions using only the highest value within each class (see Blackburn et al. 1992). Observations were thus grouped into a number of equal classes representing equal increments of the predictor variables (latitude, elevation or temperature) and the maximum species richness value within each class is calculated. In the case of latitude 26 classes were delimited each two degrees in latitude in North America (from 8° to 60°), and 25 classes in South America (from −40° to 10°). An equal number of classes were delimited in the two regions in the case of elevation and temperature: 16 classes each 250 meters for elevation (from 0 to 4000 meters) and 15 classes each 1°C in the case of mean temperature (from 0 °C to 29 °C). The number of selected classes would be adequate according to Blackburn et al. (1992). Subsequently, the so attained maximum values were submitted as response variables to a linear regression model against the corresponding predictor variable to estimate the slope of the upper bounds and their statistical significances. All these statistics were carried out using StatSoft's STATISTICA v 10.0 (StatSoft Inc. Tulsa, Oklahoma, USA).

13.3 Results

All the considered explanatory variables allow explaining more than 54% of total variability in species richness, highlighting the role played by the three predictors aiming to represent survey effort and area differences (Table 13.1a). The explanatory capacity of climatic predictors (≈22%) is higher than those of elevation (≈16%) or latitude (≈7%) mainly due to the relevance of air temperature (≈21%). In the complete model, all the considered predictors are statistically significant except the number of sampled months (Table 13.1b), underlining the positive effects of temperature, area, closed habitats and the negative effects of latitude and elevation (Table 13.1b). None of the interactions between any pair of predictors is able to better explain the variation in species richness than the sum of the individual effects (not showed). Thus, the interaction between latitude and elevation hardly accounted for 3% of total variability. Highest species richness values are located at lowlands below 20° in latitude and the rule is that no species have been observed above 2000–2500 meters at latitudes below −20° in South America (Fig. 13.3).

The latitudinal variation in species richness shows a clear triangular pattern in which the maximum species richness value is attained at the equator (Fig. 13.4). The slopes of the relationship between the maximum species richness and latitude

Table 13.1 (a) Deviance and explanatory capacity (% Dev) of the considered predictors on the variability in local species richness of Scarabaeinae in America calculated as the reduction in deviance on a full model without predictors. Sampling effort predictors are sampled area + number of traps + number of sampled months, climatic predictors are mean annual mean temperature and mean annual precipitation, habitat is a qualitative variable with three states (closed, half-closed, and open), and South/North is a qualitative variable representing the location of the study in South or North America. (b) Coefficients and standard errors (se) of the complete model including all the considered predictors, values of the Wald statistic measuring the statistical significance of the regression coefficients and associated probability of each predictor in accounting for the variation in American Scarabaeinae species richness

(a)				(b)				
	Deviance	d.f.	% Dev		Coefficient	se	Wald stat.	*p*
Null	9895.9			Latitude	−0.28	0.02	298.88	<0.0001
Complete model	4537.9	1000	54.1	Annual mean Temperature	0.29	0.02	256.82	<0.0001
Sampling effort predictors	6720.7	1023	32.1	Sampled area	0.13	0.01	256.38	<0.0001
Climatic predictors	7739.1	1189	21.8	Annual Precipitation	0.09	0.01	121.42	<0.0001
Elevation	8340.4	1190	15.7	Closed habitat	0.21	0.02	80.28	<0.0001
Habitat	8663.4	1172	12.5	Number of traps	0.05	0.01	73.91	<0.0001
South/North	9054.1	1190	8.5	South/North	−0.23	0.03	54.02	<0.0001
Latitude	9219.8	1190	6.8	Elevation	−0.09	0.02	32.67	<0.0001
				Number of sampled months	0.02	0.02	1.98	0.16

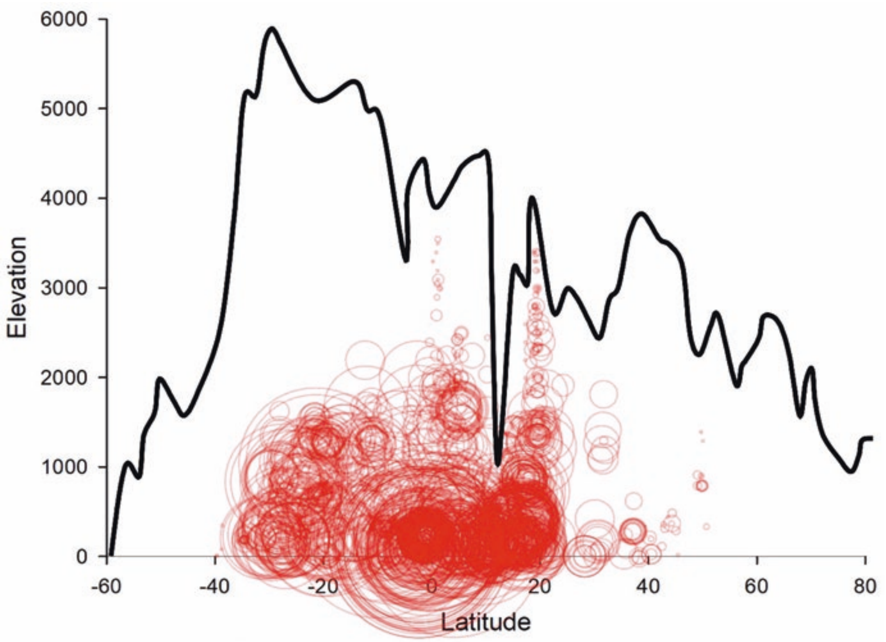

Fig. 13.3 Variation in the species richness of local Scarabaeinae assemblages represented by the size of the circles across latitudinal and elevational gradients in America. The upper line illustrates the latitudinal variation in the maximum elevation throughout the continent

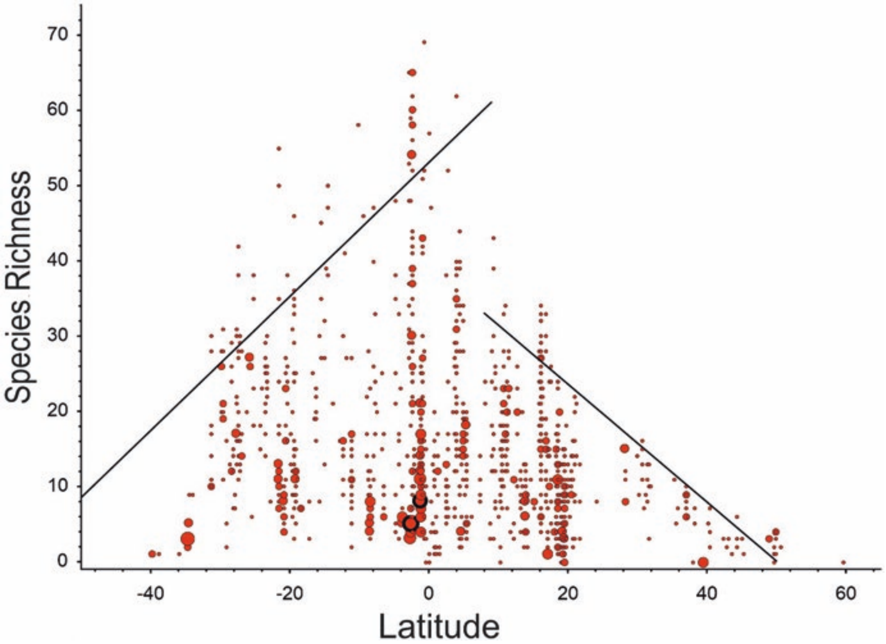

Fig. 13.4 Relationship between the species richness of American Scarabaeinae species in local studies and the latitudinal position of these studies. The maximum species richness values in two degrees bins of latitude are calculated and the linear regression of these values against latitude is estimated for the data above and below the Isthmus of Panama (9°; continuous line). The size of the points is proportional to the frequency of values

(in absolute values) are relatively similar in the north (−0.78 ± 0.17; ± 95% CI; $t = 10.1$, $p < 0.001$) and south (0.89 ± 0.43; $t = 4.26$, $p < 0.001$) of the Isthmus of Panama as manifested by the overlap in the values of the confidence limits of these slopes (Fig. 13.4).

North-South differences are more evident when the number of species in local studies is related with the mean annual temperature of the cells in which these studies are located (Fig. 13.5). An increase in environmental temperature implies an increase in the maximum species richness both above and below the Isthmus of Panama, but the difference between the two slopes is close to be statistically significant ($F_{1,22} = 3.97$; $p = 0.06$); the slope of maximum values per bin in southern studies is 2.58 ± 1.34 ($t = 4.29$, $p = 0.001$), while the slope in northern ones is 1.45 ± 0.43 ($t = 7.33$, $p < 0.001$). The difference in the rate of species increase with the environmental temperature is evident at temperatures above 15 °C (see Fig. 13.5c) in which the species richness of South America is almost twice that of North America.

A decrease in species richness with the increase in elevation is the rule both in the north and south of the Isthmus of Panama (Fig. 13.6), although the slope in South America (−0.016 ± 0.0047; $t = 9.43$, $p < 0.001$) is clearly higher than those of North America (−0.009 ± 0.002; $t = 12.02$, $p < 0.001$) ($F_{1,36} = 14.82$; $p < 0.001$). In average, around 33 species would be present at sea level in the north of the Isthmus of Panama (intercept = 33.08 ± 4.18) and almost 58 in the south (57.81 ± 9.60). However, a similar low number of species inhabit elevations above 2500 meters (Fig. 13.6c).

13.4 Discussion

All the considered explanatory variables show a statistically significant relationship with species richness. Thus, despite the great variety of conditions in the studies, it is possible to explain more than 50% of the total variability in the species richness data about American dung beetles. The large number of considered and unconsidered variables (quantity and variety of dung resources, soil conditions, cattle management, degree of anthropization, etc.) determine the triangular character of the relationships (Thomson et al. 1996). Minimum species richness remains constant across the complete range of latitude or elevation values, but the ceiling of the relationship does show a pattern.

Assuming that the maximum species richness attained at different latitude or altitude values reflects the limit in the number of species capable of inhabiting under optimal conditions, this number decreases with absolute latitude and elevation values. A change in one degree north or south from the Isthmus of Panamá means a similar decrease of around 0.8/0.9 species. However, if one takes into account the temperature below which the development stops in Coleoptera (Lower Developmental Threshold; ≈15 °C; see Stejskal et al. 2019) and the studies with a mean temperature below this threshold are obviated, a change of one degree in latitude means a decrease of 1.1 ± 0.1 species in North America but only 0.6 ± 0.2

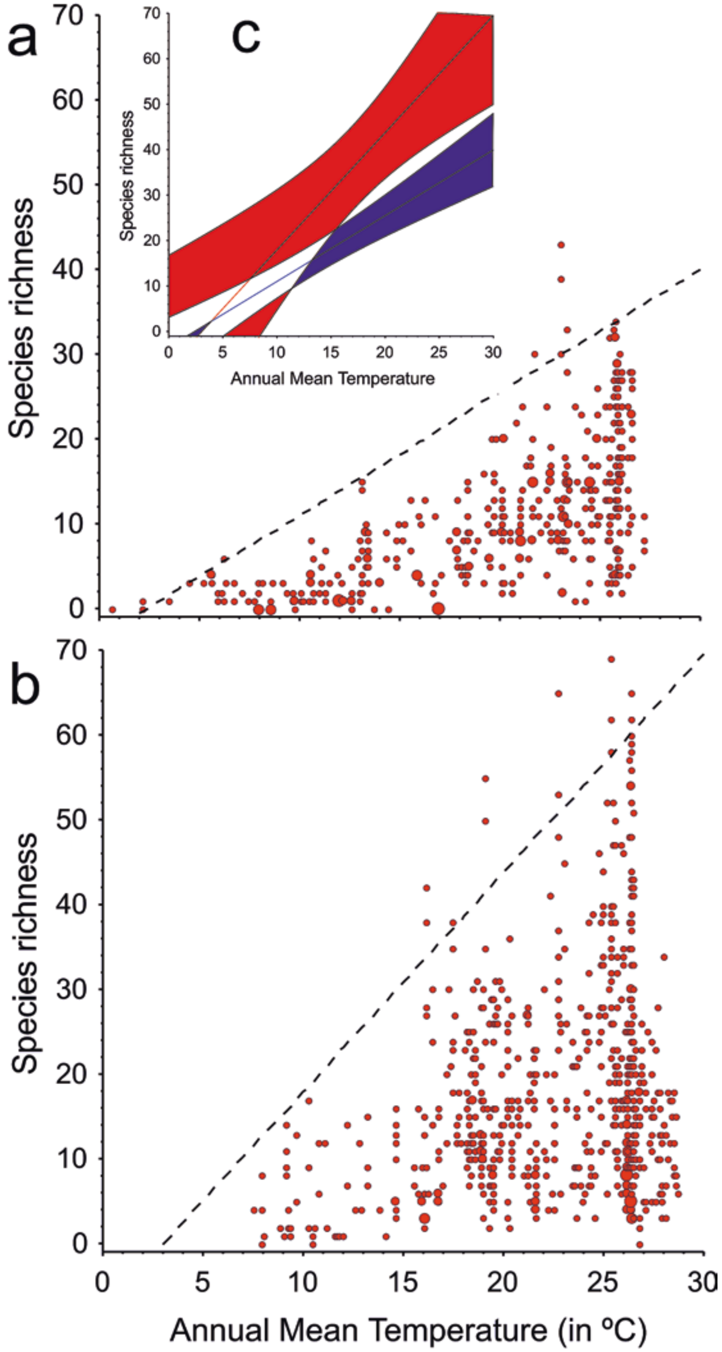

Fig. 13.5 Relationships between the species richness of American Scarabaeinae species in local studies and the annual mean temperature of the 2.5 minutes cells in which these studies are located above (**a**) and below (**b**) the Isthmus of Panama. Broken lines represent the linear regressions of the values of maximum species richness in bins of one Celsius degree. The top fig. (**c**) represents both regressions with their 95% confidence intervals showing in red and blue the nonoverlapped ranges The size of the points is proportional to the frequency of values

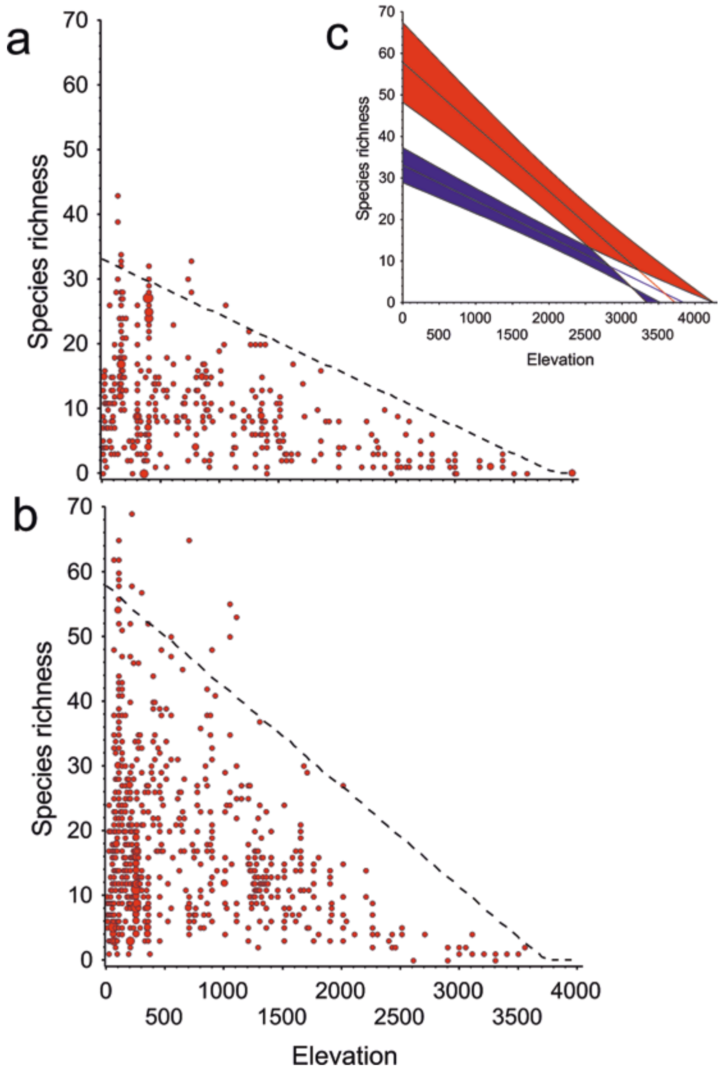

Fig. 13.6 Relationships between the species richness of American Scarabaeinae species in local studies and the elevation of these studies above (**a**) and below (**b**) the Isthmus of Panama. Broken lines represent the linear regressions of the values of maximum species richness in bins of one hundred meters. The top fig. (**c**) represents both regressions with their 95% confidence intervals showing in red and blue the nonoverlapped ranges The size of the points is proportional to the frequency of values

species in South America. This happens because a one degree change in latitude represents 0.71 °C in North America, but 0.33 °C in South America, and there is a greater change in species richness in South America per degree of temperature (2.6 species per degree) than in North America (1.5 species per degree). Even when only those cells with a mean temperature higher than 15 °C (16% in North America and 83% in South America) are considered, one degree in latitude represents a change of 0.38 °C in North America, but 0.22 °C in South America. Thus, the temperature changes more slowly per unit of latitude in South America and this effect is not only due to the greater extension of cold and cold-temperate areas in North America, but also to the higher average temperature (20.3 °C in areas with more 15 °C in the north and 23.5 °C in the south) and the geographical homogeneity of South America temperature values. If temperature is a fundamental factor in explaining the latitudinal and altitudinal gradient of variation in species richness, as these and others results suggest (Uvarov 1931; Halsch et al. 2021), the latitudinal gradient in species richness would be proportionally inflated in North America simply because one degree in latitude represents a higher variation in temperature.

In the case of elevation, species richness declines around 0.9 species each 100 meters in North America and 1.6 species in South America. The decline in the number of Scarabaeinae species is more dramatic in the southern continent, because the average number of species at the sea level is almost twice that those of North America. However, the species richness above 2000–2500 meters is similar in both land masses. Around 1.9 species are collected on average in the 44 studies carried out above 2500 meters in North America, while 1.8 species are collected on average in the 18 South American studies accomplished above this elevation. Interestingly, the highest elevations of North American dung beetles are reached around the 19th parallel in the Trans-Mexican Volcanic Belt of the so-called Mexican Transition Zone (Halffter and Morrone 2017). The highest elevations reached by dung beetles in South America would be near the equator, being the southernmost mountain peaks barely colonized. These results suggest that the discrepancy in the geological history of the two land masses would have had little influence in their rates of colonization of high altitude environments, although it would have done so in determining the higher basal richness of South America. The incapacity of Scarabaeinae to colonize high mountain environments may be attributed to the relatively recent appearance of the Andes. The Andean mountain range is the consequence of the plate contact between the South American continent and the subducting oceanic Nazca plate. Although the final uplift of the Andes occurred during the Pliocene, the initial uplift can be traced back to the Cretaceous (Milnes 1987). The role of Miocene and Pliocene Andean uplifts on diversification processes is well established in plants (Luebert and Weigend 2014; Lagomarsino et al. 2016), but less so in insects (Polato et al. 2018). Alpine insect lineages in South America are considered as relatively young (less than 10 mya; see Hoorn et al. 2010) although highly diversified and endemic in some groups (Larsen et al. 2011). In general, the low number of Scarabaeinae species in these high altitude environments constitutes a recognized pattern in all the continents (Jay-Robert et al. 1997; Şenyüz et al. 2019; Escobar et al. 2006; Da Silva et al. 2018; Davis et al. 1999 or Monteith 1985).

Lobo and Halffter (2000) differentiate a "horizontal colonization" process by elements originated from lineages inhabiting cold-temperate latitudes, and a "vertical colonization" of mountains by lowland lineages inhabiting at the same latitude. Horizontal colonization would be severely hampered in South America by historical and dispersal limitation factors, so that northern lineages would have contributed little to the diversity of South American mountain assemblages. For its part, vertical colonization would have required to surpass the conservation of the ancestral thermal niche of a Scarabaeinae clade originated in Gondwanaland under warm and humid conditions (Davis et al. 2002; Hortal et al. 2011). It has long been known that the thermal niche breadths of tropical insect species are narrow and with a limited capacity of evolution (Janzen 1967; Polato et al. 2018), and that Neotropical lineages show a limited adaptation capacity to surpass cold-temperate conditions (Smith et al. 2012). The idiosyncratic nature of the history of North and South America would indeed have influenced the compositional difference of high altitude dung beetle assemblage. Alpine Scarabaeinae dung beetle assemblages are dominated by *Onthophagus* species in North America; 12 out of the 20 species reported in localities above 2500 meters belong to this genus (see, e.g., Arriaga-Jiménez et al. 2018; Lobo and Halffter 2000 or Moctezuma et al. 2016). *Onthophagus* is a hyperdiverse genera with more than 2200 species (Schoolmeesters 2022) widely distributed across biogeographic regions of the world: Afrotropical (45% of total species), Oriental (20%), Australian (16%), Palaearctic (12%), Neotropical (5%) and Nearctic (2%) (Cambefort 1991). New World species of *Onthophagus* are monophyletic, probably originated from an Asian-Palaearctic lineage (Zunino 1979; Breeschoten et al. 2016), and their evolutionary success is linked to a wider environmental tolerance able to colonize high altitude biomes. However, South American localities above 2500 meters are colonized by a high diversity of genera endemic of the Neotropical region such as *Cryptocanthon*, *Uroxys*, *Scybalocanthon*, *Homocopris,* or *Ontherus,* or distributed in the Nearctic and Neotropical regions such as *Dichotomius* (see Escobar et al. 2007; Martínez-Revelo and Lopera-Toro 2014; Alvarado-Roberto and Arias-Butirica 2015 or Noriega and Realpe 2018). Thus, although historical factors may be responsible for the compositional and species richness differences between North and South America, the conservation of the thermal niche in Scarabaeinae would be the most likely factor constraining similarly the colonization of alpine environments in both continents.

Appendix 13.1 – List of Included Publications

Aguilar-Amuchastegui N, Henebry GM (2007) Assessing sustainability indicators for tropical forests: spatiotemporal heterogeneity, logging intensity, and dung beetle communities. For Ecol Manag 253:56–67 da SP de Almeida S, Louzada JNC (2009) Estrutura da comunidade de Scarabaeinae (Scarabaeidae: Coleoptera) em fitofisionomias do Cerrado e sua importância para a conservação. Neotrop Entomol 38:32–43

Almeida S, Louzada J, Sperber C, Barlow J (2011) Subtle land-use change and tropical biodiversity: dung beetle communities in Cerrado grasslands and exotic pastures. Biotropica 43:704–710

Alvarado F, Escobar F, Montero-Muñoz J (2014) Diversity and biogeographical makeup of the dung beetle communities inhabiting two mountains in the Mexican transition zone. Org Divers Evol 14:105–114

Amato KR, Estrada A (2010) Seed dispersal patterns in two closely related howler monkey species (Alouatta palliata and A. pigra): a preliminary report of differences in fruit consumption, traveling behavior, and associated dung beetle assemblages. Neotrop Primates 17:59–66

Amell-Caez Y, DeCastro-Arrazola I, García H, Monroy-G JD, Noriega JA (2019) Spatial diversity of dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) in five ecoregions from Sucre, Colombian Caribbean coast. Revista Colombiana de Entomología 45:e7963

Amézquita S, Favila ME (2010) Removal rates of native and exotic dung by dung beetles (Scarabaeidae: Scarabaeinae) in a fragmented tropical rain forest. Environ Entomol 39:328–336

Amézquita SJ, Forsyth A, Lopera AT, Camacho A (1999) Comparación de la composición y riqueza de especies de escarabajos coprófagos (Coleoptera: Scarabaeidae) en remanentes de bosque de la Orinoquía Colombiana. Acta Zool Mex 76:113–126

Andresen E (1999) Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. Biotropica 31:145–158

Andresen E (2000) The role of dung beetles in the regeneration of rainforest plants in Central Amazonia. Ph.D. thesis, University of Florida, Gainesville, Florida

Andresen E (2005) Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. Biotropica 37:291–300

Andresen E (2008) Short-term temporal variability in the abundance of tropical dung beetles. Insect Conserv Diver 1:120–124

Andresen E, Laurance SGW (2007) Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica 9:41–146

Anduaga S (2004) Impact of the activity of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) inhabiting pasture land in Durango, Mexico. Environ Entomol 33:1306–1312

Aragón-García A, Morón MA, Damián-Huato MA, López-Olguín JF, Pinson-Rincón EP, Pérez-Quintanilla JN (2012) Fauna de Coleoptera Lamellicornia de la zona cañera del ingenio de Atencingo, Puebla, México. Acta Zoológica Mexicana 28:161–171

Arellano L, Castillo-Guevara C (2014) Efecto de los incendios forestales no controlados en el ensamble de escarabajos coprófagos (Coleoptera: Scarabaeidae) en un bosque templado del centro de México. Revista Mexicana de Biodiversidad 85:854–865

Arellano L, León-Cortés JL, Halffter G (2008) Response of dung beetle assemblages to landscape structure in remnant natural and modified habitats in southern Mexico. Insect Conserv Diver 1:253–262

Arellano L, León-Cortés JL, Halffter G, Montero J (2013) Acacia woodlots, cattle and dung beetles (Coleoptera: Scarabaeinae) in a Mexican silvopastoral landscape. Revista Mexicana de Biodiversidad 85:650–660

Arnaudin ME (2012) Benefits of dung beetles (Coleoptera: Scarabaeidae) on nutrient cycling and forage growth in alpaca pastures. Master of Science Thesis, Virginia Polytechnic Institute, EEUU

Arriaga-Jiménez A, Rös M, Halffter G (2018b) High variability of dung beetle diversity patterns at four mountains of the Transmexican Volcanic Belt. PeerJ 6:e4468

Audino LD, da Silva PG, Nogueira JM, Moraes LP, Vaz-de-Mello FZ (2011) Scarabaeinae (Coleoptera, Scarabaeidae) de um bosque de eucalipto introduzido em uma região originalmente campestre. Iheringia Série Zoologia 101:121–126

Avendano-Mendoza C, Morón-Ríos A, Cano EB, León-Cortés J (2005) Dung beetle community (Coleoptera: Scarabaeidae: Scarabaeinae) in a tropical landscape at the Lachua region, Guatemala. Biodivers Conserv 14:801–822

Barragán F, Moreno CE, Escobar F, Bueno-Villegas J, Halffter G (2014) The impact of grazing on dung beetle diversity depends on both biogeographical and ecological context. J Biogeogr 41:1991–2002

Barraza JM, Montes JF, Martínez NH, Deloya C (2010) Ensamblaje de escarabajos coprófagos (Scarabaeidae; Scarabaeinae) del bosque tropical seco, Bahía Concha, Santa Marta (Colombia). Revista Colombiana de Entomología 36:285–291

Bertone M, Green J, Washburn S, Poore M, Sorenson C, Watson DW (2005) Seasonal activity and species composition of dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) inhabiting cattle pastures in North Carolina. Ann Entomol Soc Am 98:309–321

Bett JZ, Farias PM (2014) Escarabeíneos copro-necrófagos associados a sistemas pecuários no municipio de Lauro Müller (SC). In Anais do XXV Congresso Brasileiro de Entomologia, CEB

Bezanson GA (2019) Assessing the effect of habitat, location and bait treatment on dung beetle (Coleoptera: Scarabaeidae) diversity in southern Alberta, Canada. Thesis, Trent University

Bitencourt BS, da Silva PG (2016) Forest regeneration affects dung beetle assemblages (Coleoptera: Scarabaeinae) in the southern Brazilian Atlantic Forest. J Insect Conserv 20:855–866

Bitencourt BS, da Silva PG, Morato EF, Gomes de Lima Y (2019) Dung beetle responses to successional stages in the Amazon rainforest. Biodivers Conserv 28:2745–2761

Bitencourt BS, Dimas TM, Da Silva PG, Morato EF (2020) Forest complexity drives dung beetle assemblages along an edge-interior gradient in the Southwest Amazon rainforest. Ecol Entomol 45:259–268

Blume RR (1970) Insects associated with bovine droppings in Kerr and Bexar counties, Texas. J Econ Entomol 63:1023–1024

Blume RR (1972) Additional insects associated with bovine droppings in Kerr and Bexar counties, Texas. J Econ Entomol 65:621

Bogoni JA, Hernández MIM (2014) Attractiveness of native mammal's feces of different trophic guilds to dung beetles (Coleoptera: Scarabaeinae). J Insect Sci 14:299

Bogoni JA, Graipel ME, de Castilho PV, Fantacini FM, Khnen VV, Luiz MR, Maccarini TB, Marcon CB, Teixeira C, Tortato MA, Vaz-de-Mello FZ, Hernández MIM (2016) Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodivers Conserv 25:1661–1675

Braga RF, Korasaki V, Andresen E, Louzada J (2013) Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. PLoS One 8:e57786

Bustamante-Sánchez M, Grez A, Simonetti J (2004) Dung decomposition and associated beetles in a fragmented temperate forest. Rev Chil Hist Nat 77:107–120

Bustos-Gómez Lira F, Lopera Toro A (2003) Preferencia por cebo de los escarabajos coprofagos (Coleoptera: Scabaeidae: Scarabaeinae) de un remanente de bosque seco tropical al norte del Tolima (Colombia). In: Onore G, Reyes-Castllo P, Zunino M (eds) Escarabeidos de Latinoamérica: Estado del conocimiento, Monografías Tercer Milenio, vol 3. SEA, Zaragoza, pp 59–65

Cajaiba RL, Périco E, Barreto da Silva W, Leote P, Santos M (2018) Are small dung beetles (Aphodiinae) useful for monitoring neotropical forests' ecological status? Lessons from a preliminary case study in the Brazilian Amazon. For Ecol Manag 429:115–123

Camero E (2019) Diversidad de escarabajos coprófagos (Coleoptera: Scarabaeidae) de la zona norte de la Serrania de La Lindosa, Guaviare-Colombia. Acta Biologica Colombiana 24:311–321

Campos RC, Hernández MIM (2015a) Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. Ecol Indic 49:216–227

Campos RC, Hernández MIM (2015b) The Importance of maize management on dung beetle communities in Atlantic forest fragments. PLoS One 10:e0145000

Cancino-López RJ, Chamé-Vázquez ER, Gómez BG (2014) Escarabajos necrófilos (Coleoptera: Scarabaeinae) en tres hábitats del Volcán Tacaná, Chiapas, México. Dugesiana 21:135–142

Carpio C, Donoso DA, Ramón G, Dangles O (2009) Short term response of dung beetle communities to disturbance by road construction in the Ecuadorian Amazon. Annales de la Société entomologique de France (NS) 45:455–469

Cervenka VJ, Moon RD (1991) Arthropods associated with fresh cattle dung pats in Minnesota. J Kansas Entomol Soc 64:131–145

Cheli GH, Corley JC, Bruzzone O, Brío M, Martínez F, Roman NM, Ríos I (2010) The ground-dwelling arthropod community of Península Valdés in Patagonia, Argentina. J Insect Sci 10:50

Concha CM, Gallego MC, Pardo-Locarno LC (2010) Fragmentación de ecosistemas montanos e impactos estructurales y poblacionales sobre la comunidad de escarabajos coprófagos (Col.: Scarabaeinae) en el alto Río Cauca, Popayán, Colombia. Boletín Científico Museo de Historia Natural 14:43–55

Correa CMA, Puker A, Korasaki V, de Oliveira NG (2013) Dung beetles (Coleoptera, Scarabaeinae) attracted to sheep dung in exotic pastures. Revista Brasileira de Entomologia 57:113–116

Correa CMA, Puker A, Korasaki V, Ferreira KR, Abot AR (2016) Attractiveness of baits to dung beetles in Brazilian savanna and exotic pasturelands. Entomol Sci 19:112–123

Costa-Silva V, Cipolatto RP, Abegg AD, Rosa CM, Silva PG, Di Mare RA (2014) Escarabeídeos (Coleoptera: Scarabaeidae) de campo e floresta da Reserva Biológica de São Donato, Rio Grande do Sul, Brasil. Biotemas 27:63–71

Culot L, Bovy E, Vaz-de-Mello FZ, Guevara R, Galetti M (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biol Conserv 163:79–89

Cultid CA (2015) Evaluación multiescalar de la diversidad de escarabajos coprófagos en un paisaje agrícola dominado por cultivos de cafe de sol, Andes Occidentales de Colombia. Tesis Doctoral, Universidad del Valle, Colombia

da Costa CMQ, Silva FAB, Farias ÂI, Moura R (2009) Diversidade de Scarabaeinae (Coleoptera, Scarabaeidae) coletados com armadilha de interceptação de vôo no Refúgio Ecológico Charles Darwin, Igarassu-PE, Brasil. Revista Brasileira de Entomologia 53:88–94

da Silva PG (2011) Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) of two non-native habitats in Bagé, Rio Grande do Sul, Brazil. Zool Stud 50:546–559

da Silva PG, Audino LD (2011) Escarabeíneos (Coleoptera: Scarabaeidae) atraídos a diferentes iscas em campo nativo de Bagé, Rio Grande do Sul, Brasil. Revista Brasileira de Zoociências 13:241–247

da Silva PG, Di Mare RA (2012) Escarabeíneos copro-necrófagos (Coleoptera, Scarabaeidae, Scarabaeinae) de fragmentos de Mata Atlântica em Silveira Martins, Rio Grande do Sul, Brasil. Iheringia Série Zoologia 102:197–205

Da Silva PG, Hernández MIM (2016) Spatial variation of dung beetle assemblages associated with forest structure in remnants of southern Brazilian Atlantic Forest. Revista Brasileira de Entomologia 60:73–81

da Silva PG, Rosa-García AM, Vidal MB (2008a) Espécies de besouros copro-necrófagos (Coleoptera: Scarabaeidae) da Região da Campanha do Rio Grande do Sul. Revista de Ciências Agroveterinárias 7:143–149

da Silva PG, Garcia MAR, Vidal MB (2008b) Besouros copro-necrófagos (Coleoptera: Scarabaeidae stricto sensu) coletados em ecótono natural de campo e mata em Bagé, RS. Ciência e Natura 30:71–91

da Silva PG, Garcia MAR, Vidal MB (2009) Besouros copro-necrófagos (Coleoptera: Scarabaeidae sensu stricto) do município de Bagé, RS (Bioma Campos Sulinos). Biociencias 17:33–43

da Silva PG, Audino LD, Nogueira JM, Moraes LP, Vaz-de-Mello FZ (2012) Escarabeíneos (Coleoptera: Scarabaeidae: Scarabaeinae) de uma área de campo nativo no bioma Pampa, Rio Grande do Sul, Brasil. Biota Neotropica 12:246–253

da Silva PG, Vaz-de-Mello FZ, Di Mare RA (2013) Diversity and seasonality of Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in Santa Maria, Rio Grande do Sul, Brazil. An Acad Bras Cienc 85:679–697 da Silva PG, Lobo JM, Carpintero Hensen M, Vaz-de-Mello FZ, Hernández MIM (2018b) Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. Divers Distrib 24:1277–1290

da Silva PG, Lobo JM, Hernández MIM (2019a) The role of habitat and daily activity patterns in explaining the diversity of mountain Neotropical dung beetle assemblages. Austral Ecol 44:300–312

da Silva PG, Nunes CA, Ferreira LF, Braga RF, Beiroz W, Perillo LN, Solar RRC, de Siqueira NF (2019b) Patch and landscape effects on forest-dependent dung beetles are masked by matrix-tolerant dung beetles in a mountaintop rainforest archipelago. Sci Total Environ 651:1321–1331

Dajoz R (1994) Les Coléopteres coprophages du sud-est de L' Arizona (États-Unis). Composition spécifique, biogéographie et structure des peuplements. Annales de la Sociéte Entomologique de France 30:159–167

Damborsky MP, Bar ME, Alvarez Bohle MC, Oscherov EB (2008) Comunidad de escarabajos copronecrófagos (Coleoptera: Scarabaeidae) en dos bosques del Chaco Oriental Húmedo, Argentina. Revista de la Sociedad Entomológica Argentina 67:145–153

Damborsky MP, Alvarez Bohe MC, Ibarra Polesel MG, Porcel EA, Fontana JL (2015) Spatial and temporal variation of dung beetle assemblages in a fragmented landscape at eastern humid Chaco. Neotrop Entomol 44:30–39

Daniel GM, Nunes LGOA, Vaz-de-Mello FZ (2014) Species composition and functional guilds of dung beetles (Insecta: Coleoptera: Scarabaeidae: Scarabaeinae) in different vegetational types in the Brazilian Shield–Chacoan depression border. Annales de la Société Entomologique de France (N.S.) 50:183–190

De Alburquerque Correa CM, Puker A, Korasaki V, de Oliveira NG (2013) Dung beetles (Coleoptera, Scarabaeinae) attracted to sheep dung in exotic pastures. Revista Brasileira de Entomologia 57:113–116

Delgado-Gómez P, Lopera A, Rangel JO (2012) Variación espacial del ensamblaje de escarabajos coprófagos (Scarabaeidae: Scarabaeinae) en remanentes de bosque seco en Chimichagua (Cesar, Colombia). In: Rangel JO (ed) Colombia diversidad biótica xii: la región Caribe de Colombia. Universidad Nacional de Colombia, Bogotá, pp 833–849

Delgado JM, Castro-Ramírez AE, Morón MA, Ruiz-Montoya L (2012) Diversidad de Scarabaeoidea (Coleoptera) en las principales condiciones de hábitat de Montebello, Chiapas, México. Acta Zoológica Mexicana 28:185–210

Deloya C, Madora MA, Covarrubias DM (2013) Scarabaeidae y Trogidae (Coleoptera) necrófilos de Acahuizotla, Guerrero, México. Revista Colombiana de Entomología 39:88–94

Díaz A, Galante E, Favila ME (2010) The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest. J Insect Sci 10:1–16

Domínguez D, Marín-Armuos D, Ruz C (2015) Structure of dung beetle communities in an altitudinal gradient of Neotropical dry Forest. Neotrop Entomol 44:40–46

Durães R, Martins WP, Vaz-de-Mello FZ (2005) Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brazil. Neotrop Entomol 34:721–731

Endres AA, Creão-Duarte AJ, Hernández MIM (2007) Diversidade de Scarabaeidae s. str. (Coleoptera) da Reserva Biológica Guaribas, Mamanguape, Paraíba, Brasil: uma comparação entre Mata Atlântica e Tabuleiro Nordestino. Revista Brasileira de Entomologia 51:67–71

Escobar F, Chacón de Ulloa P (2000) Distribución espacial y temporal en un gradiente de sucesión de la fauna de coleópteros coprófagos (Scarabaeinae, Aphodiinae) en un bosque tropical montano, Nariño – Colombia. Rev Biol Trop 48:961–975

Escobar F, Halffter G, Arellano L (2007b) From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of dung beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. Ecography 30:293–208

Escobar F, Lobo JM, Halffter G (2005) Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in Colombian Andes. Glob Ecol Biogeogr 14:327–337

Espinoza VR, Noriega JA (2018) Diversity of the dung beetles (Coleoptera: Scarabaeinae) in an altitudinal gradient in the east slope of los Andes, Napo province, Ecuador. Neotrop Biodivers 4:144–150

Favero S, Souza HA, Oliveira AKM (2011) Coleoptera (Insecta) as forest fragmentation indicators in the Rio Negro sub-region of the Pantanal, Mato Grosso do Sul, Brazil. Braz J Biol 71:291–295

Feer F (2013) Variations in dung beetles assemblages (Coleoptera: Scarabaeidae) within two rain forest habitats in French Guiana. Rev Biol Trop 61:753–758

Feer F, Boissier O (2015) Variations in dung beetle assemblages across a gradient of hunting in a tropical forest. Ecol Indic 57:164–170

Feer F, Hingrat Y (2005) Effects of forest fragmentation on a dung beetle community in French Guiana. Conserv Biol 19:1103–1112

Feer F, Pincebourde S (2005) Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles. J Trop Ecol 21:21–30

Ferreira SC (2018) Variabilidade espaço-temporal de Scarabaeinae (Coleoptera: Scarabaeidae) em quatro localidades com diferentes níveis de alteração no Rio Grande do Sul, Brasil. Universidade Federal de Santa Maria, Santa Maria

Ferreira SC, da Silva PG, Paladini A, Di Mare RA (2018) Climatic variables drive temporal patterns of α and β diversities of dung beetles. Bull Entomol Res 109:290–397

Fiene JG, Connior MB, Androw R, Baldwin B (2011) Surveys of Arkansas dung beetles (Coleoptera: Scarabaeidae and Geotrupidae): phenologies, mass occurrences, state and distributional records. Am Midl Nat 165:319–337

Filgueiras BKC, Liberal CN, Aguiar CDM, Hernández MIM, Iannuzzi L (2009) Attractivity of omnivore, carnivore and herbivore mammalian dung to Scarabaeinae (Coleoptera, Scarabaeidae) in a tropical Atlantic rainforest remnant. Revista Brasileira de Entomologia 53:422–427

Filgueiras BKC, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biol Conserv 144:362–369

Fincher GT, Blume RR, Hunter JS, Beerwinkle KR (1986) Seasonal distribution and diel flight activity of dung-feeding scarabs in open and wooded pasture in east-central Texas. Southwest Entomol 10:1–35

Flechtmann CAH, Tabet VG, Quintero I (2009) Influence of carrion smell and rebaiting time on the efficiency of pitfall traps to dung beetle sampling. Entomol Exp Appl 132:211–217

Flechtmann CAH, Rodrigues SR, Gaspareto CL (1995) Controle biológico da mosca-dos-chifres (Haematobia irritans irritans) em Selvíria, Mato Grosso do Sul. 5. Seleção de besouros coprófagos. Revista Brasileira de Entomologia 39:277–286

Floate KD, Gill BD (1998) Seasonal activity of dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung in southern Alberta and their geographic distribution in Canada. Can Entomol 130:131–151

Floate KD, Kadiri N (2013) Dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung on native grasslands of southern Alberta, Canada. Can Entomol 145:647–654

Forbes V, Sikes D (2018) A survey of beetles (Coleoptera) from the tundra surrounding the Nunalleq archaeological site, Quinhagak, southwestern Alaska. Biodivers Data J 6:e22788

França FM, Korasaki V, Louzada J, Vaz-de-Mello FZ (2016a) First report on dung beetles in intra-Amazonian savannahs in Roraima, Brazil. Biota Neotropica 16:e0034

França F, Louzada J, Korasaki V, Griffiths H, Silveira JM, Barlow J (2016b) Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. J Appl Ecol 53:1098–1105

Frizzas MR, Batista JLFL, Rocha MVC, Oliveira CM (2020) Diversity of Scarabaeinae (Coleoptera: Scarabaeidae) in an urban fragment of Cerrado in central Brazil. Eur J Entomol 117:273–281

Ganho NG, Marinoni RC (2005) A diversidade inventarial de Coleoptera (Insecta) em uma paisagem antropizada do Bioma Araucária. Revista Brasileira de Entomologia 49:535–543

García-Ramirez JC, Pardo-Locarno LC (2004) Escarabajos Scarabaeinae saprófagos (Coleóptera: Scarabaeidae) en un bosque húmedo premontano de los Andes occidentales colombianos. Ecología Aplicada 3:59–63

Gardner TA, Hernández MI, Barlow J, Peres CA (2008) Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for Neotropical dung beetles. J Appl Ecol 45:883–893

González Chang MA (2010) Presencia otoñal de escarabajos estercoleros nativos paracópridos (Scarabaeidae: Scarabaeinae) en renovales de bosque nativo y praderas naturales asociadas. Tesis de grado, Facultad de Ciencias Agrarias, Universidad Austral de Chile, Valdivia, Chile. 82p

González-Hernández AL, Navarrete-Heredia JL, Quiroz-Rocha GA, Deloya C (2015) Coleópteros necrócolos (Scarabaeidae: Scarabaeinae, Silphidae y Trogidae) del Bosque Los Colomos, Guadalajara, Jalisco, México. Revista Mexicana de Biodiversidad 86:764–770

González-Maya JF, Mata-Lorenzen J (2008) Dung-beetles (Coleoptera: Scarabeidae) from the zona Protectora Las Tablas, Talamanca, Costa Rica. Check List 4:458

González-Vainer P, Morelli E (2008) Relevamiento de los coleópteros coprófilos y necrófilos de Sierra de Minas, Uruguay (Insecta: Coleoptera). Boletín de La Sociedad Zoológica Del Uruguay 17:20–33

Gries R, Louzada J, Almeida S, Macedo R, Barlow J (2012) Evaluating the impacts and conservation value of exotic and native tree afforestation in Cerrado grasslands using dung beetles. Insect Conserv Diver 5:175–185

Guzman-Miranda AV (2018) Efecto del manejo del ganadero en la diversidad de escarabajos (Scarabaeidae) de la Huasteca potosina. Tesis de maestría, IPICYT Available at https://repositorio.ipicyt.edu.mx/handle/11627/4673

Halffter G, Arellano L (2002) Response of dung beetle diversity to human-induced changes in a tropical landscape. Biotropica 34:144–154

Halffter G, Favila ME, Halffter V (1992) A comparative study of the structure of the scarab guild in Mexican tropical rain forest and derived ecosystems. Folia Entomológica Mexicana 84:131–156

Halffter G, Favila ME, Arellano L (1995) Spatial distribution of three groups of Coleoptera along an altitudinal transect in the Mexican transition zone and its biogeographical implications. Elytron 9:151–185

Halffter G, Pineda E, Arellano L, Escobar F (2007) Instability of copronecrophagous beetle assemblages (Coleoptera: Scarabaeinae) in a mountainous tropical landscape of Mexico. Environ Entomol 36:1397–1407

Halffter G, Verdú JR, Moreno CE, Halffter V (2012) Historical and ecological determinants of dung beetle assemblages in two arid zones of central Mexico. J Arid Environ 76:54–60

Hamel-Leigue AC, Herzog SK, Mann DJ (2008) Composición y riqueza de una comunidad de escarabajos peloteros (Coleoptera: scarabaeinae) en los Yungas bajos de la Cordillera Mosetenes, Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 23:39–49

Harada LM, Araújo IS, Overal WL, Silva FAB (2020) Comparison of dung beetle communities (Coleoptera: Scarabaeidae: Scarabaeinae) in oil palm plantations and native forest in the eastern Amazon, Brazil. Revista Brasileira de Entomologia 64:e2019102

Harvey CA, González J, Somarriba E (2006) Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. Biodivers Conserv 15:555–585

Hernández MIM (2007) Besouros Escarabeíneos (Coleoptera: Scarabaeidae) da Caatinga Paraibana, Brasil. Oecologia Brasileira 11:356–364

Hernández MIM, Vaz-de-Mello F (2009) Seasonal and spatial species richness variation of dung beetle (Coleoptera, Scarabaeidae s. str.) in the Atlantic Forest of southeastern Brazil. Revista Brasileira de Entomologia 53:607–613

Hernández B, Maes JM, Harvey CA, Vílchez S, Medina A, Sánchez D (2003) Abundancia y diversidad de escarabajos coprófagos y mariposas diurnas en un paisaje ganadero en el departamento de Rivas, Nicaragua. Agroforestería en las Americas 10:93–102

Hernández MIM, Barreto PSCS, Costa VH, Creão-Duarte AJ, Favila ME (2014) Response of a dung beetle assemblage along a reforestation gradient in Restinga forest. J Insect Conserv 18:539–546

Horgan FG (2001) Burial of bovine dung by coprophagous beetles (Coleoptera: Scarabaeidae) from horse and cow grazing sites in El Salvador. Eur J Soil Biol 37:103–111

Horgan FG (2002) Shady field boundaries and the colonisation of dung by coprophagous beetles in central American pastures. Agric Ecosyst Environ 91:25–36

Horgan FG (2005) Aggregated distribution of resources creates competition refuges for rainforest dung beetles. Ecography 28:603–618

Horgan FG (2007) Dung beetles in pasture landscapes of Central America: proliferation of synanthropogenic species and decline of forest specialists. Biodivers Conserv 16:2149–2165

Horgan FG (2008) Dung beetle assemblages in forests and pastures of El Salvador: a functional comparison. Biodivers Conserv 17:2961–2978

Horgan FG (2009) Invasion and retreat: shifting assemblages of dung beetles amidst changing agricultural landscapes in central Peru. Biodivers Conserv 18:3519–3541

Howden HF, Scholtz CH (1986) Changes in a Texas dung beetle community between 1975 and 1985 (Coleoptera: Scarabaeidae, Scarabaeinae). Coleopt Bull 40:313–316

Ibarra-Polesel MG, Damborsky MP, Porcel E (2015) Escarabajos copronecrófagos (Scarabaeidae: Scarabaeinae) de la Reserva Natural Educativa Colonia Benítez, Chaco, Argentina. Revista Mexicana de Biodiversidad 86:744–753

Ix-Balam A, Deloya C, Ballina-Gómez H, Sauri-Duch E, Cuevas-Glory L (2011) Diversidad de escarabajos necrófagos (Coleoptera: Scarabaeidae y Trogidae) de la selva baja caducifolia de Conkal, Yucatan, México. Entomología Mexicana 10:177–181

Jiménez-Ferbans L, Mendieta-Otálora W, García H, Amat-García G (2008) Notas sobre los escarabajos coprófagos (Coleoptera: Scarabaeinae) en ambientes secos de la región de Santa Marta, Colombia. Acta Biológica Colombiana 13:203–208

Kadiri N, Lumaret JP, Floate KD (2014) Functional diversity and seasonal activity of dung beetles (Coleoptera; Scarabaeoidea) on native grasslands in southern Alberta, Canada. Can Entomol 146:291–305

Kessler H, Balsbaugh EU (1972) Succession of adult Coleoptera in bovine manure in East Central South Dakota. Ann Entomol Soc Am 65:1333–1336

Kessler H, Balsbaugh EU, McDaniel B (1974) Faunistic comparison of adult Coleoptera recovered from cattle and sheep manure in East-Central South Dakota. Entomol News 84:67–71

Kirk AA (1992) Dung beetles (Coleoptera: Scarabaeidae) active in patchy forest and pasture habitats in Santa Cruz Province, Bolivia, during spring. Folia Entomológica Mexicana 84:45–54

Klein B (1989) Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. Ecology 70:1715–1725

Kohlmann B (1991) Dung beetles in subtropical North America. In: Hanski I, Cambefort Y (eds) Dung beetle ecology, pp 116–132

Kohlmann B, Sánchez C (1984) Structure of a Scarabaeinae community: a numerical-behavioural study (Coleoptera: Scarabaeinae). Acta Zool Mex 2:1–27

Koller WW, Gomes A, Rodrigues SR, Alves RGO (1999) Besouros coprófagos (Coleoptera: Scarabaeidae) coletados em Campo Grande, MS, Brasil. Anais da Sociedade Entomológica do Brasil 28:403–412

Korasaki V, Vaz-de-Mello FZ, Braga RF, Zanetti R, Louzada J (2012) Taxocenose de Scarabaeinae (Coleoptera: Scarabaeidae) em Benjamin Constant, AM. Acta Amazon 42:423–432

Korasaki V, Lopes J, Brown GG, Louzada J (2013) Using dung beetles to evaluate the effects of urbanization on Atlantic forest biodiversity. Insect Sci 20:393–406

Larsen TH (2004) Dung beetles/escarabajos peloteros. In: Vriesendorp C, Rivera-Chavez L, Moskovits D, Shopland J (eds) Peru: Megantoni. Rapid biological inventories report 15. The Field Museum, Chicago, pp 77–84

Larsen TH (2013) Dung beetles of the upper Palumeu river watershed (Grensgebergte and Kasikasima) of Southeastern Suriname (Coleoptera: Scarabaeidae: Scarabaeinae). In: Alonso

LE, Larsen TH (eds) A rapid biological assessment of the upper Palumeu river watershed (Grensgebergte and Kasikasima) of Southeastern Suriname, RAP bulletin of biological assessment 67. Conservation International, Arlington, pp 90–101

Latha T, Huang PY, Perez GA, Paquiul IO (2016) Dung beetle assemblage in a protected area of Belize: a study on the consequence of forest fragmentation and isolation. J Entomol Zool Stud 4:457–463

Lima MGA, Silva RPDA, Sousa MDF, Costa EM (2013) Diversidade de Scarabaeinae (Coleoptera: Scarabaeidae) no Parque Botânico do Ceará, Caucaia – CE, Brasil. Revista Ago@mbiente 7:89–94

Liberal CN, de Farias ÂMI, Meiado MV, Filgueiras BKC, Iannuzzi L (2011) How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. J Insect Sci 11:1–114

Lima JDN, Costa Silva V, Bianchi V, da Silva PG, Di Mare RA (2015) Estrutura e organização de assembleias de Scarabaeinae (Coleoptera, Scarabaeidae) em diferentes fitofisionomias no sul do Brasil. Iheringia Serie Zoologia 105:393–402

Lobo JM, Halffter G (2000b) Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera, Scarabaeoidea): a comparative study. Ann Entomol Soc Am 93:115–126

Lopes PP, Louzada JNC, Vaz-de-Mello FZ (2006) Organization of dung beetle communities (Coleoptera: Scarabaeidae) in areas of vegetation re-establishment in Feira de Santana, Bahia, Brazil. Sitientibus Série Ciências Biológicas 6:261–266

Lopes J, Korasaki V, Catelli LL, Marçal VVM, Nunes MPBP (2011) A comparison of dung beetle assemblage structure (Coleoptera: Scarabaeidae: Scarabaeinae) between an Atlantic Forest fragment and adjacent abandoned pasture in Paraná, Brazil. Fortschr Zool 28:72–79

Louzada JNC, Silva PRCE (2009) Utilisation of introduced Brazilian pastures ecosystems by native dung beetles: diversity patterns and resource use. Insect Conserv Diver 2:45–52

Louzada J, Lima AP, Matavelli R, Zambaldi L, Barlow J (2010) Community structure of dung beetles in Amazonian savannas: role of fire disturbance, vegetation and landscape structure. Landsc Ecol 25:631–641

Louzada JNC, Lopes FS, Vaz-de-Mello FZ (2007) Structure and composition of a dung beetle community (Coleoptera: Scarabaeinae) in a small forest patch from Brazilian Pantanal. Revista Brasileira de Zoociências 9:199–203

Luzuriaga Quichimbo CX (2013) Escarabajos coprófagos (Coleoptera: Scarabaeidae: Scarabaeinae) como indicadores de diversidad biológica en la Estación Biológica Pindo Mirador. In: Pastaza-Ecuador. Trabajo fin de titulación. Centro Universitario Puyo, Puyo

Macqueen A, Beirne BP (1974) Lnsects and mites associated with fresh cattle dung in the southern interior of British Columbia. J Entomol Soc Br Columbia 71:5–9

Marchiori CH (2000) Espécies de Scarabaeidae (Insecta: Coleoptera) coletadas em fezes bovinas e carcaça de suínos em Itumbiara, Goiás, Brasil. Pesquisa Agropecuária Tropical 30:1–4

Marchiori CH (2003) Insects (Arthropoda: Insecta) collected on bovine feces after different times of field exposure in Itumbiara, Goias, Brazil. Arquivos do Instituto Biológico São Paulo 70:377–380

Marchiori CH, Caldas ER, Almeida KGS (2003) Succession of Scarabaeidae on bovine dung in Itumbiara, Goiás, Brazil. Neotrop Entomol 32:172–176

Martínez NJ, Franz NM, Acosta JA (2009a) Structure of the scarab beetle fauna (Coleoptera: Scarabaeoidea) in forest remnants of western Puerto Rico. Entomotropica 24:1–9

Martínez NJ, García H, Pulido LA, Ospino D, Narváez JC (2009b) Escarabajos coprófagos (Coleoptera: Scarabaeinae) de la vertiente noroccidental, Sierra Nevada de Santa Marta, Colombia. Neotrop Entomol 38:708–715

Martínez NJ, Cañas LM, Rangel JL, Barraza JM, Montes JM, Blanco OR (2010a) Coleópteros coprófagos (Scarabaeidae: Scarabaeinae) en un fragmento de bosque seco tropical en el departamento del Atlántico, Colombia. Boletín del Museo de Entomología de la Universidad del Valle 11:21–30

Martínez NJ, Cañas LM, Rangel JL, Blanco O, Mendoza JD, Cohen S (2010b) Coleópteros coprófagos (Scarabaeidae: Scarabaeinae) en la Reserva Natural Las Delicias (RND), Sierra Nevada de Santa Marta (SNSM). Colombia Boletín Científico Centro de Museos Museo de Historia Natural 14:187–200

Martínez-Falcón AP, Zurita GA, Ortega-Martínez IJ, Moreno CE (2018) Populations and assemblages living on the edge: dung beetles responses to forests-pasture ecotones. PeerJ 6:e6148

Martínez-Hernández N, Salcedo Muñoz G, Sierra Quintero K, Berraza Méndez J (2012) Escarabajos coprófagos (Coleoptera: Scarabaeinae) asociados a excrementos de mamíferos en un fragmento de bosque seco tropical en el Departamento del Atlántico, Colombia. Ecol Austral 22:203–210

Martín-Piera F, Fernández-Torres A (1996) Coleópteros de la Sierra de Chiribiquete (Dpto. del Caquetá, Colombia). Elytron 10:23–50

Martín-Piera F, Lobo JM (1993) Altitudinal distribution patterns of copro-necrophague Scarabaeoidea (Coleoptera) in Veracruz, Mexico. The Coleopterist Bulletin 47:321–334

Martínez-Revelo DE, Lopera-Toro A (2014b) Escarabajos coprófagos (Coleoptera: scarabaeidae: scarabaeinae) de los páramos del departamento de Nariño, Colombia. Biota Colombiana 15:62–72

Masís A, Marquis RL (2009) Effects of even-aged and uneven-aged timber management on dung beetle community attributes in a Missouri Ozark forest. For Ecol Manag 257:536–545

Matheson MM (1987) Insects associated with cattle dung in southern Quebec. M.Sc, McGill University, Montreal, Québec, Canada. Available from https://escholarship.mcgill.ca/

McDaniel B, Boddicker ML, Balsbaugh EU (1971) Coleoptera inhabiting bovine manure in a pasture on the Big Sioux river flood plain in South Dakota. Proc South Dakota Acad Sci 50:220–237

Medina AM, Lopes PP (2014) Resource utilization and temporal segregation of Scarabaeinae (Coleoptera: Scarabaeidae) community in a Caatinga fragment. Neotrop Entomol 43:127–133

Medina CA, Escobar F, Kattan GH (2002) Diversity and habitat use of dung beetles in a restored Andean landscape. Biotropica 34:181–187

Medina CA, González-Alvarado A, Neita JC (2018) Caracterización preliminar de escarabajos coprófagos y fitófagos (Coleoptera: Scarabaeidae, Melolonthidae) del bosque seco de la serranía de la Macuira, Alta Guajira, Colombia. Cuadernos de Biodiversidad 54:28–40

Medri IM, Lopes J (2001) Scarabaeidae (Coleoptera) do Parque Estadual Mata dos Godoy e de área de pastagem, no norte do Paraná, Brasil. Revista Brasileira de Zoologia 18:135–141

Mendes J, Linhares AX (2006) Coleoptera associated with undisturbed cow pats in pastures in Southeastern Brazil. Neotrop Entomol 35:715–723

Mendoza SJV (2009) Efecto de la composición y estructura del paisaje y del hábitat sobre distintos grupos taxonómicos en un agropaisaje en Matiguás, Nicaragua. Tesis de Postgrado, CATIE, Costa Rica

Merritt RW, Anderson JR (1977) The effects of different pasture and rangeland ecosystems on the annual dynamics of insects in cattle droppings. Hilgardia 45:31–71

Minor P, Morón MA (2016) Coleópteros coprófagos (Coleoptera: Scarabaeoidea) de la Barranca de Huehuetitla, Tlaxcala, México. Acta Zoológica Mexicana 32:310–322

Moctezuma V, Halffter G, Escobar F (2016b) Response of copronecrophagous beetle communities to habitat disturbance in two mountains of the Mexican transition zone: influence of historical and ecological factors. J Insect Conserv 20:945–956

Mohr CO (1943) Cattle droppings as ecological units. Ecol Monogr 13:275–298

Montoya-Molina S, Giraldo-Echeverri C, Montoya-Lerma J, Chará J, Escobar F, Calle Z (2016) Land sharing vs. land sparing in the dry Caribbean lowlands: a dung beetles' perspective. Appl Soil Ecol 98:204–212

Morelli E (2005) Diversidad, distribución temporal y trófica, y patrones de nidificación de un agregado de especies de Escarabeidos coprófagos (Coleoptera) en un campo natural pastoreado (Cerro Colorado, dpto.. de Florida, Uruguay). Tesis de Doctorado, Universidad de la Republica, Uruguay

Morón MA, Terrón R (1984) Distribución altitudinal y estacional de insectos necrófilos en la sierra norte de Hidalgo, México. Acta Zoológica Mexicana 3:1–47

Mourglia Pons V (2010) Selección de macrohábitat y variación estacional de coleópteros coprófagos en Sierra de Minas, Uruguay. Tesina de Pasaje de Curso, available at https://www.colibri.udelar.edu.uy/jspui/bitstream/20.500.12008/1635/1/uy24-13953.pdf

Muñoz-Hernández A, Morón MA, Aragón A (2008) Coleoptera Scarabaeoidea de la región de Teziutlán, Puebla, México. Acta Zoológica Mexicana 24:55–78

Murillo-Ramos L, Ayazo R, Medina CA (2016) Diversidad de escarabajos coprófagos (Coleoptera: Scarabaeinae) en un remanente ribereño y un fragmento de bosque húmedo tropical en Córdoba, Colombia. Ecol Austral 26:17–26

Navarrete D, Halffter G (2008) Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. Biodivers Conserv 17:2869–2898

Navarro Iriarte LE, Román KM (2009) Comparación de la comunidad de escarabajos coprófagos (Coleoptera: Scarabaeidae: Scarabaeinae) en una zona de uso ganadero y en un relicto de bosque seco tropical del departamento de Sucre. Tesis de Pregrado, Departamento de Biología, Facultad de Educación y Ciencias. Universidad de Sucre, Sincelejo, 87 p

Nealis VG (1977) Habitat associations and community analysis of South Texas dung beetles (Coleoptera: Scarabaeinae). Can J Zool 55:138–147

Neita JC, Escobar F (2012) The potential value of agroforestry to dung beetle diversity in the wet tropical forests of the Pacific lowlands of Colombia. Agrofor Syst 85:121–131

Neves FS, Fonseca Oliveira VH, do Espírito-Santo MM, Vaz-de-Mello FZ, Louzada J, Sanchez-Azofeifa A, Fernandes GW (2010) Successional and seasonal changes in a community of dung beetles (Coleoptera: Scarabaeinae) in a Brazilian tropical dry forest. Natureza Conservação 8:160–164

Noriega JA, Barranco W, Hernández J, Hernández E, Castillo S, Monroy D, García H (2016) Estructura estacional del ensamblaje de escarabajos coprófagos (Coleoptera: Scarabaeinae) en una parcela permanente de bosque seco tropical. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 40:75–83

Noriega JA, Cubillos AM, Castañeda C, Sánchez AM (2008) Actividad diaria de colonización del recurso alimenticio en un emsamblaje de escarabajos coprófagos (Coleoptera: Scarabaeidae) en la Amazonía Colombiana. Acta Biologica Colombiana 13:75–86

Noriega JA, Realpe E (2018b) Altitudinal turnover of species in a Neotropical peripheral mountain system: a case study with dung beetles (Coleoptera: Aphodiinae and Scarabaeinae). Environ Entomol 47:1376–1387

Noriega JA, Realpe E, Fagua G (2007) Diversidad de escarabajos coprófagos (Coleoptera: Scarabaeidae) en un bosque de galería con tres estados de alteración. Univ Sci 12:51–63

Novais SMA, Evangelista LA, Reis-Júnior R, Neves FS (2016) How does dung beetle (Coleoptera: Scarabaeidae) diversity vary along a rainy season in a tropical dry forest? J Insect Sci 16:1–6

Nunes RV, Frizzas MR, Vaz-de-Mello FZ (2012) Scarabaeinae (Coleoptera: Scarabaeidae) of a rupestrian field at Caatinga, Distrito Federal, Brazil: commented list of species. Biota Neotropical 12:125–129

Nunes CA, Braga RF, Figuera JEC, Neves FS, Fernandes GW (2016) Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. PLoS One 11:e0157442

Oliveira-Monteiro CM, Koller WW, dos Reis ES (2006) Besouros coprófagos (Coleoptera; Scarabaeoidea) presentes nas pastagens do campo experimental da Embrapa gado de leite, no município de Coronel Pacheco, Minas Gerais XXIX Semana de Biologia e XII Mostra de Produção Científica-UFJF: 29–33

Pardo-Locarno LC (1997) Muestreo preliminar de los escarabajos Copronecrófilos (Coleoptera Scarabaeidae) de las selvas de la Fragua, Cuenca Baja Río Cajambre (Valle). Cespedesia 22:59–80

Pardo-Locarno LC (2007) Escarabajos Coprófagos (Coleoptera-Scarabaeidae) de Lloró, Departamento del Chocó, Colombia. Boletín Científico-Centro de Museos- Museo de Historia Natural 11:377–388

Pardo-Locarno LC, Delgado L (2002a) Contribución al estudio de los escarabajos copronecrófilos (Coleoptera Scarabaeidae) de la Quebrada Río Azul, Calima, Chocó Biogeográfico, Colombia. Boletín Científico Museo Historia Natural Universidad de Caldas 6:161–176

Pardo-Locarno LC, Delgado L (2002b) Muestreo preliminar de los escarabajos copronecrófilos (Coleoptera Sacarabaeidae) de las Selvas de Chancos, Chocó Biogeográfico, Valle. Boletín Científico Museo Historia Natural Universidad de Caldas 6:11–27

Pardo-Locarno LC, Camero RE (2014) Escarabajos coprófagos (Coleoptera-Scarabaeinae) en siete microcuencas del río Dagua. Chocó biogeográfico de Colombia Bol SEA 54:207–224

Peck SB, Forsyth A (1982) Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae). Can J Zool 600:1624–1634

Peitzmeier BA, Campbell JB, Thomas GD (1992) Lnsect fauna of bovine dung in Northeastern Nebraska and their possible effect on the face fly Musca autumnalis (Diptera: Muscidae). J Kansas Entomol Soc 65:267–274

Pereira CCA, Chaves DP, Koller WW, Conceição WLF, Rodrigues SR, Gomes A, Costa-Júnior LM (2003) Ocorrência de coleópteros Scarabaeidae (coprófagos e necrófagos), Aphodiidae, Histeridae e Hydrophilidae em fezes bovinas na Ilha de São Luís, Maranhão, Brasil – resultados preliminares. Revista Universidade Rural 23:327–328

Pessôa MB, Izzo TJ, Vaz-de-Mello FZ (2017) Assemblage and functional categorization of dung beetles (Coleoptera: Scarabaeinae) from the Pantanal. PeerJ 5:e3978

Peyras M, Vespa NI, Bellocq MI, Zurita GA (2013) Quantifying edge effects: the role of habitat contrast and species specialization. J Insect Conserv 17:807–820

Pineda E, Moreno C, Escobar F, Halffter G (2005) Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. Conserv Biol 19:400–410

Poorbaugh JH, Anderson JR, Burger JF (1968) The insect inhabitants of undisturbed cattle droppings in northern California. California Vector Views 15:17–36

Price DL, Feer F (2012) Are pitfall to pitfalls? Dung beetle sampling in French Guiana. Org Divers Evol 123:325–331

Price DL (2004) Species diversity and seasonal abundance of Scarabaeoid dung beetles (Coleoptera: Scarabaeidae, Geotrupidae and Trogidae) attracted to cow dung in Central New Jersey. J New York Entomol Soc 112:334–347

Puker A, Correa CMA, Korasaki V, Ferreira KR, Oliveira NG (2013) Dung beetles (Coleoptera: Scarabaeidae) attracted to dung of the largest herbivorous rodent on Earth: a comparison with human feces. Environ Entomol 42:1218–1225

Puker A, da Silva KKG, dos Santos DC, Correa CMA, Vaz-de-Mello FZ (2020) Dung beetles collected using flight intercept traps in an Amazon rainforest fragment and adjacent agroecosystems. Int J Trop Insect Sci 40:1085–1092

Pulido LA, Riveros R, Gast F, Von Hildebrand P (2003) Escarabajos coprófagos (Coleoptera: Scarabaeidae: Scarabaeinae) del Parque Nacional Natural “Serranía de Chiribiquete”, Caquetá, Colombia (Parte 1). Monografías Tercer milenio (S.E.A.) 3:51–58

Quintero I, Roslin T (2005) Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. Ecology 86:3303–3311

Quintero I, Halffter G (2009) Temporal changes in a community of dung beetles (Insecta: Coleoptera: Scarabaeinae) resulting from the modification and fragmentation of tropical rain forest. Acta Zoológica Mexicana 25:625–649

Radtke MG, Fonseca DRV, Williamson GB (2007) The old and young Amazon: dung beetle biomass, abundance, and species diversity. Biotropica 39:725–730

Radtke MG, Carlton CE, Williamson GB (2008) A dung beetle assemblage in an urban park in Louisiana. Southeast Nat 7:101–110

Radtke MG, Fonseca DRV, Williamson GB (2010) Dung beetle communities: a neotropical-North temperate comparison. Neotrop Entomol 39:19–27

Ramirez Gutierrez JM (2018) Distribución altitudinal y tolerancia térmica de los escarabajos coprófagos en la Orinoquía colombiana. Ph D (unpublished), available at https://repositorio.unillanos.edu.co/handle/001/1476

Rangel-Acosta JL, Blanco-Rodríguez OR, Gutiérrez-Rapalino BP, Martínez-Hernández NJ (2012) Coleópteros coprófagos (Scarabaeidae: Scarabaeinae) asociados a excrementos de mamíferos de la Reserva Natural Luriza (RNL), Departamento del Atlántico, Colombia. Boletín de la Sociedad Entomológica Aragonesa 50:409–419

Rangel-Acosta JL, Martínez-Hernández NJ, Gutiérrez-Rapalino BP, Gutiérrez-Moreno LC, Borja-Acuña RA (2016a) Efecto del tamaño de la ronda hidráulica sobre las comunidades de escarabajos coprófagos (Scarabaeidae: Scarabaeinae) en la cuenca media y baja del rio Cesar, Colombia. Entomotropica 31:109–130

Rangel-Acosta JL, Blanco-Rodríguez OR, Martínez-Hernández NJ (2016b) Escarabajos copronecrófagos (Scarabaeidae: Scarabaeinae) en diferentes usos del suelo en la Reserva Campesina la Montaña (RCM) en el departamento del Atlántico, Colombia. Boletín Científico Centro de Museos Museo de Historia Natural 20:78–97

Rangel-Acosta JL, Solano-Torres JA, Martínez-Hernández NJ (2018) Variación temporal y vertical de los escarabajos coprófagos (Scarabaeidae: Scarabaeinae) en dos fragmentos de bosque seco tropical en el departamento del Atlántico-Colombia. Boletín Científico Centro de Museos Museo de Historia Natural de la Universidad de Caldas 22:179–198

Rangel-Acosta JL, Martínez-Hernández NJ, Yonoff-Zapata R (2020) Respuesta de los escarabajos coprófagos (Scarabaeidae: Scarabaeinae) a la modificación del hábitat causada por un incendio forestal en la Reserva Bijibana, Atlántico-Colombia. Revista Mexicana de Biodiversidad 91:e912879

Rebolledo R, Gonzalez Jiménez R, Elgueta Donoso M, Palma Millanao R, Medel Meza V, Reyes Schencke M (2017) Dung beetles of Chile, with emphasis in La Araucania region. In: Shields VDC (ed) Insect physiology and ecology. InTech, pp 25–36

Rentz E, Price DL (2016) Species diversity and succession of dung beetles (Coleoptera: Geotrupidae and Scarabaeidae) attracted to horse dung on Assateague Island. Coleopt Bull 70:95–104

Reyes-Novelo E, Delfín-González H, Morón MA (2007) Copro-necrophagous beetle (Coleoptera: Scarabaeidae) diversity in an agroecosystem in Yucatan, Mexico. Rev Biol Trop 55:83–99

Rivera JD, Cantarero KJ (2011) Comunidad de escarabajos coprófagos (Coleoptera: Scarabaeidae: Scarabaeinae) en hábitats bajo distinta intensidad de uso en Yuscarán, Honduras. Ceiba 52:212–229

Rodrigues SR, Marchini LC (1998) Besouros coprófagos (Coleoptera; Scarabaeidae) coletados em Piracicaba, SP. Sci Agric 55:53–58

Rodrigues SR, Puker A (2013) Species of Geotrupidae (Coleoptera: Scarabaeoidea) in Aquidauana, Mato Grosso do Sul, Brazil. Biota Neotropical 13(1):349. https://doi.org/10.1590/S1676-06032013000100034

Rodrigues SR, de Barros ATM, Puker A, Taira TL (2010) Diversidade de besouros coprófagos (Coleoptera, Scarabaeidae) coletados com armadilha de interceptaτπo de voo no Pantanal Sul-Mato-Grossense, Brasil. Biota Neotropical 10:123–127

Ronqui DC, Lopes J (2006) Composição e diversidade de Scarabaeoidea (Coleoptera) atraídos por armadilha de luz em área rural no norte do Paraná, Brasil. Iheringia 96:103–108

Rounds RJ, Floate KD (2012) Diversity and seasonal phenology of coprophagous beetles at Lake City, Michigan, USA, with a new state record for Onthophagus taurus (Schreber) (Coleoptera: Scarabaeidae). Coleopt Bull 66:169–172

Salomão RP, Lira AFA, Iannuzzi L (2014) Dominant dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) species exhibit wider trophic niches on fruits, excrement, and carrion in Atlantic forest, Brazil. Coleopt Bull 68:686–688

Salomão RP, Iannuzzi L (2015) Dung beetle (Coleoptera, Scarabaeidae) assemblage of a highly fragmented landscape of Atlantic forest: from small to the largest fragments of northeastern Brazilian region. Revista Brasileira de Entomologia 59:126–131

Salomão RP, Gonçalves LKS, de Morais RF, Costa Lima LR (2019) Dung beetles (Coleoptera: Scarabaeinae) in a mosaic habitat at the ecotone between two savanna ecosystems in the Neotropical region. Int J Trop Insect Sci 39:249–256

Salomão RP, Favila ME, González-Tokman D (2020) Spatial and temporal changes in the dung beetle diversity of a protected, but fragmented, landscape of the northernmost Neotropical rainforest. Ecol Indic 1111:105968

Sánchez-de-Jesús HA, Arroyo-Rodríguez V, Andresen E, Escobar F (2016) Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. Landsc Ecol 31:843–854

Sánchez-Hernández G, Gómez B, Delgado L, Rodríguez-López ME, Chamé-Vázquez ER (2018) Diversidad de escarabajos copronecrófagos (Coleoptera: Scarabaeidae: Scarabaeinae) en la Reserva de la Biosfera Selva El Ocote, Chiapas, México. Caldasia 40:144–160

Sanders DP, Dobson RC (1966) The insect complex associated with bovine manure in Indiana. Ann Entomol Soc Am 59:955–959

Sanmartín I, Enghoff H, Ronquist F (2001b) Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biol J Linn Soc 73:345–390

Santos EB, Da Silva PG, Favretto MA, Müller GA (2017) Occurrence of beetles (Insecta: Coleoptera) in mosquito ovitraps (Diptera: Culicidae, Culicinae) in an Atlantic Forest fragment. Revista Brasileira de Zoociencias 18:41–46

Scheffler P (2005) Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. J Trop Ecol 21:9–19

Schiffler G, Vaz-de-Mello FZ, Azevedo CO (2003) Scarabaeidae s.str. (Coleoptera) do Delta do Rio Doce e Vale do Suruaca no Município de Linhares, Estado do Espírito Santo, Brasil. Revista Brasileira de Zoociências 5:205–211

Schoenly K (1983) Arthropods associated with bovine and equine dung in an ungrazed Chihuahuan desert ecosystem. Ann Entomol Soc Am 76:790–796

Silva FAB, Hernández MIM, Ide S, Moura RC (2007) Comunidade de escarabeíneos (Coleoptera, Scarabaeidae) copro-necrófagos da região de Brejo Novo, Caruaru, Pernambuco, Brasil. Revista Brasileira de Entomologia 51:228–233

Silva FAB, Costa CMQ, Moura RC, Farias AI (2010) Study of the dung beetle (Coleoptera: Scarabaeidae) community at two sites: Atlantic forest and clear-cut, Pernambuco, Brazil. Environ Entomol 39:359–367

Solís C, Noriega JA, Herrera G (2011) Escarabajos coprófagos (Coleoptera: Scarabaeinae) en tres bosques secos del departamento del Atlántico-Colombia. Boletín del Museo de Entomología de la Universidad del Valle 12:33–41

Spector S, Ayzama S (2003) Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian neotropical forest-savanna ecotone. Biotropica 35:394–404

Trevilla-Rebollar A, Deloya C, Padilla-Ramírez J (2010) Coleópteros necrófilos (Scarabaeidae, Silphidae y Trogidae) de Malinalco, Estado de México, México. Neotrop Entomol 39:486–495

Trujillo-Miranda A, Carrillo RH, Rivas-Arancibia SP, Andrés-Hernández AR (2016) Estructura y composición de la comunidad de escarabajos (Coleoptera: Scarabaeoidea) en el cerro Chacateca, Zapotitlán, Puebla, México. Revista Mexicana de Biodiversidad 87:109–122

Valiela I (1969) The arthropod fauna of bovine dung in Central New York and sources on its natural history. J New York Entomol Soc 77:210–220

Verdú JR, Moreno CE, Sánchez-Rojas G, Numa C, Galante E, Halffter G (2007) Grazing promotes dung beetle diversity in the xeric landscape of a Mexican biosphere reserve. Biol Conserv 140:308–317

Vidaurre T, Gonzales L, Ledeza JM (2008) Escarabajos coprófagos (Scarabaeidae: Scarabaeinae) del Palmar de las Islas, Santa Cruz, Bolivia. Kempffiana 4:3–20

Viegas G, Stenert C, Schulz UH, Maltchik L (2014) Dung beetle communities as biological indicators of riparian forest widths in southern Brazil. Ecol Indic 36:703–710

Vieira L, Silva FAB (2012) List dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) of the Floresta Nacional Contendas do Sincorá, Bahia, Brazil. Check List 8:733–739

Vulinec K, Lima AP, Carvalho EAR, Mellow DJ (2008) Dung beetles and long-term habitat fragmentation in Alter do Chão, Amazônia, Brazil. Trop Conserv Sci 1:111–121

Yanes-Gómez G, Morón MA (2010) Fauna de coleópteros Scarabaeoidea de Santo Domingo Huehuetlán, Puebla, México. Su potencial como indicadores ecológicos. Acta Zoológica Mexicana 26:123–145

Yanes-Gómez G, Pérez-Méndez M, Ramírez-González OI, Morón MA, Carrillo-Ruiz H, Romero-López AA (2015) Diversidad de coleópteros copro-necrófagos en el “Rancho Canaletas”, Paso del Macho, Veracruz, México. Acta Zoológica Mexicana 31:283–290

References

Ahrens D, Schwarzer J, Vogler AP (2014) The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. Proc R Soc B 281:1471–2954

Alvarado-Roberto F, Arias-Butirica J (2015) Highest elevation for a nesting dung beetle (Coleopa: Scarabaeidae: Scarabaeinae) in the Americas. Coleopt Bull 69:789–792

Antonelli A, Sanmartín I (2011) Why are there so many plant species in the Neotropics? Taxon 60:403–414

Antonelli A, Kissling WD, Flantua SGA, Bermúdez MA, Mulch A (2018) Geological and climatic influences on mountain biodiversity. Nat Geosci 11:718–725

Arriaga-Jiménez A, Rös M, Halffter G (2018) High variability of dung beetle diversity patterns at four mountains of the Transmexican Volcanic Belt. PeerJ 6:e4468

Blackburn TM, Lawton JH, Perry JN (1992) A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. Oikos 65:107–112

Breeschoten T, Doorenweerd C, Tarasov S, Vogler AP (2016) Phylogenetics and biogeography of the dung beetle genus *Onthophagus* inferred from mitochondrial genomes. Mol Phylogenet Evol 105:86–95

Cambefort Y (1991) Biogeography and evolution. In: Hanski I, Cambefort Y (eds) Dung beetle ecology. Princeton University Press, Princeton, pp 51–67

Carrillo JD, Faurby S, Silvestro D, Zizka A, Jaramillo C (2020) Disproportionate extinction of South American mammals drove the asymmetry of the Great American Biotic Interchange. Proc Natl Acad Sci USA 117:26281–26287

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guegan J (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol Lett 7:1121–1134

Da Silva PG, Lobo JM, Carpintero Hensen M, Vaz-de-Mello FZ, Hernández MIM (2018) Altitudinal gradient driving spatial and temporal β-diversity components: turnover and nestedness in subtropical dung beetle assemblages. Divers Distrib 24:1277–1290

Davis ALV, Scholtz CH (2001) Historical vs. ecological factors influencing global patterns of scarabaeine dung beetle diversity. Divers Distrib 7:161–174

Davis ALV, Scholtz CH, Chown SL (1999) Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. J Biogeogr 26:1039–1055

Davis ALV, Scholtz CH, Philips TK (2002) Historical biogeography of scarabaeine dung beetles. J Biogeogr 29:1217–1256

Dobson AJ (1990) An introduction to generalized linear models. Chapman & Hall, London

Escobar F, Lobo JM, Halffter G (2006) Assessing the origin of Neotropical mountain dung beetle assemblages (Scarabaeidae: Scarabaeinae): the comparative influence of vertical and horizontal colonization. J Biogeogr 33:1793–1803

Escobar F, Halffter G, Arellano L (2007) From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of dung beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. Ecography 30:293–208

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315

Fine PVA (2015) Ecological and evolutionary drivers of geographic variation in species diversity. Annu Rev Ecol Evol Syst 46:369–392

Hagen O, Skeels A, Onstein RE, Jetz W, Pellissier L (2021) Earth history events shaped the evolution of uneven biodiversity across tropical moist forests. Proc Natl Acad Sci USA 118:e2026347118

Halbritter AH, Alexander JM, Edwards PJ, Billeter R (2013) Elevational and latitudinal climate limits. Glob Ecol Biogeogr 22:1228–1237

Halffter G (1976) Distribución de los insectos en la Zona de Transición Americana. Relaciones con la entomofauna de Norteamérica. Folia Entomol Mex 35:1–64

Halffter G, Matthews EG (1966) The natural history of dung beetles of the subfamily. Scarabaeinae (Coleoptera: Scarabaeidae). Folia Entomol Mex 12–14:1–312

Halffter G, Morrone JJ (2017) An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. Zootaxa 4226:1–46

Halsch CA, Shapiro AM, Fordyce JA, Nice CC, Thorne JH (2021) Insects and recent climate change. Proc Natl Acad Sci USA 118:e2002543117

Hanski I, Cambefort Y (1991) Dung beetle ecology. Princeton University Press, Princeton

Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. Biol Rev 80:489–513

Holt B, Lessard JP, Borregaard MK, Fritz SA, Araujo MB (2013) An update of Wallace's zoogeographic regions of the world. Science 339:74–78

Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A (2010) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330:927–931

Hortal J, Diniz-Filho JAF, Bini LM, Rodríguez MÁ, Baselga A (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles: ice age determines European scarab diversity. Ecol Lett 14:741–748

Iturralde-Vinent MA (2005) La Paleografía del Caribe y sus implicaciones para la biogeografía histórica. Revista del Jardín Botánico Nacional 15–26:49–78

Janzen DH (1967) Why mountain passes are higher in the tropics. Am Nat 101:233–249

Jay-Robert P, Lobo JM, Lumaret JP (1997) Elevational turnover and species richness variation in European mountain dung beetle assemblages. Arct Antarct Alp Res 29:196–205

Lagomarsino LP, Condamine FL, Antonelli A, Mulch A, Davis CC (2016) The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). New Phytol 210:1430–1442

Larsen TH, Escobar F, Armbrecht I (2011) Insects of the Tropical Andes: diversity patterns, processes and global change. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen H (eds) Climate change and biodiversity in the Tropical Andes, Inter-American Institute for Global Change Research and Scientific Committee on Problems of the Environment, pp 228–244

Leithead M, Anand M (2013) Latitude, elevation, richness and hotspots of change across the Americas: a test of Orlóci's plant compositional transition hypotheses throughout the Holocene. Community Ecol 14:231–242

Lessard JP, Borregaard MK, Fordyce JA, Rahbek C, Weiser MD (2012) Strong influence of regional species pools on continent-wide structuring of local communities. Proc R Soc B 279:266–274

Lobo JM (2000) Species diversity and composition of dung beetle (Coleoptera: Scarabaeoidea) assemblages in North America. Can Entomol 132:307–321

Lobo JM, Halffter G (2000) Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera, Scarabaeoidea): a comparative study. Ann Entomol Soc Am 93:115–126

Lobo JM, Lumaret JP, Jay-Robert P (2002) Modelling the species richness of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. Glob Ecol Biogeogr 11:265–277

Luebert F, Weigend M (2014) Phylogenetic insights into Andean plant diversification. Front Ecol Evol 2:27

Mann P, Rogers RD, Gahagan L (2007) Overview of plate tectonic history and its unresolved tectonic problems. In: Bundschuh J, Alvarado GE (eds) Central America: geology, resources and hazards. Taylor & Francis, London, pp 201–237

Martínez-Revelo DE, Lopera-Toro A (2014) Escarabajos coprófagos (Coleoptera: scarabaeidae: scarabaeinae) de los páramos del departamento de Nariño, Colombia. Biota Colombiana 15:62–72

McCullagh P, Nelder JA (1997) Generalized linear models: monographs on statistics and applied probability. Chapman & Hall, London

Milnes AG (1987) Tectonic evolution of the southern Andes, Tierra del Fuego: a summary. In: Schaer JP, Rodgers J (eds) The anatomy of mountain ranges. Princeton University Press, Princenton, pp 173–177

Milotić T, Baltzinger C, Eichberg C, Eycott AE, Heurich M (2019) Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. J Biogeogr 46:70–82

Moctezuma V, Halffter G, Escobar F (2016) Response of copronecrophagous beetle communities to habitat disturbance in two mountains of the Mexican transition zone: influence of historical and ecological factors. J Insect Conserv 20:945–956

Monteith GB (1985) Altitudinal transect studies at Cape Tribulation, North Queensland VII. Coleoptera and Hemiptera (Insecta). Queensland Nat 26:70–80

Newbold T, Tittensor DP, Harfoot MBJ, Scharlemann JPW, Purves DW (2020) Non-linear changes in modelled terrestrial ecosystems subjected to perturbations. Sci Rep 10:14051

Noonan GR (1988) Faunal relationships between eastern North American and Europe, as shown by insects. Mem Entomol Soc Can 144:39–53

Noriega JA, Realpe E (2018) Altitudinal turnover of species in a Neotropical peripheral mountain system: a case study with dung beetles (Coleoptera: Aphodiinae and Scarabaeinae). Environ Entomol 47:1376–1387

O'Dea A, Lessios HA, Coates AG, Eytan RI, Restrepo-Moreno SA (2016) Formation of the Isthmus of Panama. Sci Adv 2:e1600883

Pessôa MB, Alves-Martins F, De Marco Júnior P, Hortal J (2020) A database of Neotropical dung beetle local richness from standardized inventories. DIGITAL.CSIC. https://doi.org/10.20350/digitalCSIC/12635

Pessôa MB, Alves-Martins F, De Marco JP, Hortal J (2021) Unveiling the drivers of local dung beetle species richness in the Neotropics. J Biogeogr 48:861–871

Polato NR, Gill BA, Shah AA, Gray MM, Casner KL (2018) Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. Proc Natl Acad Sci USA 115:12471–12476

Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG (2019) Humboldt's enigma: what causes global patterns of mountain biodiversity? Science 365:1108–1113

Ricklefs RE, Schluter D (1993) Species diversity in ecological communities. University of Chicago Press, Chicago

Sanmartín I, Enghoff H, Ronquist F (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biol J Linn Soc 73:345–390

Scheffer M, Carpenter S, Foley J, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Scholtz CH, Davis ALV, Kryger U (2009) Evolutionary biology and conservation of dung beetles. Pensoft Publishers, Sofia and Moscow

Schoolmeesters P (2022) World Scarabaeidae database. In: Bánki O, Roskov Y, Döring M, Ower G, Vandepitte L, Hobern D, Remsen D, Schalk P, RE DW, Keping M, Miller J, Orrell T, Aalbu R, Adlard R, Adriaenssens E, Aedo C, Aescht E, Akkari N, Alonso-Zarazaga MA (eds) Catalogue of life checklist (version 2022-01-10). https://doi.org/10.48580/d4tn-38g

Schweiger AH, Svenning JC (2018) Down-sizing of dung beetle assemblages over the last 53 000 years is consistent with a dominant effect of herbivore losses. Oikos 127:1243–1250

Şenyüz Y, Lobo JM, Dindar K (2019) Altitudinal gradient in species richness and composition of dung beetles (Coleoptera: Scarabaeidae) in an eastern Euro-Mediterranean locality: functional, seasonal and habitat influences. Eur J Entomol 116:309–319

Smith BT, Bryson RW, Houston DD, Klicka J (2012) An asymmetry in niche conservatism contributes to the latitudinal species diversity gradient in New World vertebrates. Ecol Lett 15:1318–1325

Stejskal V, Vendl T, Li Z, Aulicky R (2019) Minimal thermal requirements for development and activity of stored product and food industry pests (Acari, Coleoptera, Lepidoptera, Psocoptera, Diptera and Blattodea): a review. Insects 10:149

Thomson JD, Weiblen G, Thomson BA, Alfaro S, Legendre P (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. Ecology 77:1698–1715

Uvarov BP (1931) Insects and climate. Ecol Entomol 79:1–232

Vaz-de-Mello FZ, Edmonds WD, Ocampo FC, Schoolmeesters P (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). Zootaxa 2854:1–73

Von Humboldt A (1858) Cosmos: a sketch of a physical description of the universe. Harper & Brothers, New York

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends Ecol Evol 19:639–644

Yang Z, Liu X, Zhou M, Ai D, Wang G (2015) The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. Sci Rep 5:15723

Zunino M (1979) Gruppi artificiali e gruppi naturali negli *Onthophagus* (Coleoptera Scarabaeoidea). Bollettino del Museo di Zoologia dell'Università di Torino 1:1–18

Chapter 14

Diversity Patterns of Vascular Plant Groups Along Gradients of Elevation and Disturbance in Mexico

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14.1 Introduction

Mountains have captured the attention of humans for various reasons, ranging from wonder and curiosity due to the benefits and advantages they offer for our well-being compared to lowlands (Gómez-Díaz and Villalobos 2020). Moreover, mountains are also interesting ecosystems that have fascinated and influenced scientists since the seminal work of Alexander von Humboldt (von Humboldt 1806). Therefore, mountain research still contributes to our understanding of how environmental conditions affect plant distributions (Körner 2004; Malhi et al. 2010; Monge-González 2020). In addition, elevational gradients provide a wide range of opportunities for studying the effects of different ecological and evolutionary factors on plant diversity patterns as they encompass a wide variety of different

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climatic conditions over short distances (McCain and Grytnes 2010; Peters et al. 2019; Guzmán-Jacob 2021). In this sense, mountains in the tropics can be considered natural laboratories due to the confluence of several abiotic factors and hypotheses that can be tested (McCain and Grytnes 2010). Due to their abrupt climatic transformations, mountains are sentinels of change in a rapidly warming world and thus offer unique "natural experiments" to study the mechanisms that drive the origin and maintenance of biodiversity (Körner et al. 2017).

Mountains are important, in particular, for humanity and, in general, for biodiversity, due to different reasons. The world population living in mountainous regions makes up to 10% and more than half of humanity depends on the water that originates from major rivers in mountainous areas (Körner 2007). The importance of these regions lies in the multiple environmental services they provide, which can be of support (dispersion and recycling of nutrients, primary production, habitat of species, etc.), provisioning (food, water, pharmaceuticals, etc.), regulatory (carbon capture and storage, crop pollination, water, and air purification, etc.), and cultural (intellectual and spiritual inspiration, recreational experiences, scientific discovery, etc.) (Williams-Linera et al. 2002; Spehn and Körner 2005; Becker et al. 2007; Gerold et al. 2008; Grau and Aide 2008; Bendix et al. 2013; Homeier et al. 2013; Payne et al. 2017). Also, mountain vegetation provides food, fiber, and fodder; attracts tourists; and often hosts cultural heritage sites and landscapes of exceptional beauty (Körner et al. 2017). Furthermore, half of the 36 biodiversity priority sites on the planet defined by Myers et al. (2000) as areas of high biodiversity, endemism, and habitat loss are found in mountains.

Mountains harbor at least a third of the world's plant species diversity and more than 80% of terrestrial vertebrates (amphibians, birds, and mammals) (Körner 2007; Rahbek et al. 2019). The wide variety of plant species observed in the mountains is particularly important, because the diversity of vegetation helps in the preservation of soils on steep slopes, which contributes to the protection of natural landscapes and human populations against natural hazards and the impact of extreme events (Körner et al. 2017; Williams-Linera et al. 2002). Many of the services provided by montane ecosystems are driven by the intimate links among plants, soils, and associated soil biota (Becker et al. 2007).

Also, mountains can be viewed as climate "hotspots" where change can anticipate or amplify what is occurring elsewhere (Pepin et al. 2022). Mountain ecosystems have provided refuge for organisms and are predicted to also protect flora and fauna from climate change (Colwell et al. 2008; McCain and Colwell 2011). This is another reason why mountain ecosystems represent priority conservation areas (Körner et al. 2017).

Mountain biota will respond to climate change in several ways. There is a consensus in the scientific literature that climate change will push species to higher elevations than they currently are (Colwell et al. 2008; Lenoir et al. 2008; Feeley et al. 2011). For example, Morueta-Holme et al. (2015) documented upward shifts in the distribution of vegetation zones as well as increases in maximum elevation limits of individual plant taxa of >500 m on average. These range shifts are consistent with increased temperatures and glacier retreats on the Chimborazo volcano in

Ecuador since von Humboldt's (1806) study. One of the obvious risks is the loss of species in mountains that are not high enough to offer escape routes in the event of upward movement of less cold-adapted species (Becker et al. 2007).

Plant diversity patterns in tropical mountains report a peak in species richness at mid-elevations, for ferns, epiphytes, and trees (Krömer et al. 2005; Clark et al. 2015; Hernández-Rojas et al. 2018), decreasing with increasing elevation for trees, shrubs, and lianas (Homeier et al. 2010; Bautista-Bello et al. 2019), and low plateau pattern for trees (Monge-González et al. 2020). Proposed hypotheses to explain these patterns are energy availability, water (Wright 1983; Kreft and Jetz 2007), and human disturbances (Peters et al. 2019).

Deforestation and forest fragmentation represent major threats to biodiversity and may modify climatic conditions at local and regional scales, which in turn may affect the response of species (Guzmán-Jacob 2021). Especially, increasing temperatures and changing precipitation patterns may negatively affect mountain biodiversity, causing upward shifts in the treeline (Cazzolla Gatti et al. 2019), and shifting the distribution of plants and animals (McCain et al. 2016). Also, the different levels of disturbance may modify plant diversity patterns and composition (McCain and Grytnes 2010; Peters et al. 2019). For example, if the disturbance is concentrated and high at the low elevations, plant diversity at this elevational site may be lower compared with an old-growth forest (McCain and Grytnes 2010).

Furthermore, land-use change and intensification are occurring at rapid rates and are strongly impacting tropical mountain ecosystems (Payne et al. 2017). Yet, we know little about the impacts of forest-use intensity on plant diversity and composition along environmental gradients, particularly along elevational gradients in tropical forests (Monge-González 2020). In this sense, it is important to quantify and study the effects of forest-use intensity on the distribution of plant species groups, as these can be used as indicators and predictors of what could happen to other taxonomic groups and, because they are the first links in food chains.

Neotropical mountains have been identified as hotspots of biodiversity, centers of endemism, and priority sites for conservation (Jenkins et al. 2013). Especially in Mexico, which is characterized by a high floristic diversity of 23,314 native vascular plant species, with almost 50% having a restricted distribution in the country (Villaseñor 2016). However, Mexico has lost approximately half of its forest cover in the past 50 years (Barsimantov and Kendall 2012; Guzmán-Jacob 2021). According to the Global Mountain Biodiversity Assessment (GMBA), in Mexico, 11 mountainous regions represent 23% of the national territory (Gómez-Díaz and Villalobos 2020). In addition, the most important hydrological basins that provide water to most of Mexico's cities are born in mountainous areas (Gómez-Díaz and Villalobos 2020), which have also served as a refuge not only for biodiversity but also for the different cultures, languages, and worldviews that still exist in the country (Aguirre-Beltrán 1991).

Within Mexico, the state of Veracruz is considered a priority site for the conservation of biodiversity as it hosts a large number of vascular plants (8500 species) of which c. 30% are endemic to the country (Villaseñor 2016; Gómez-Díaz 2017). Yet, Veracruz has one of the highest rates of deforestation with more than 80% of primary vegetation having been converted to pastures, plantations, and secondary vegetation (Ellis et al. 2011; Gómez-Díaz et al. 2018).

In this work, we contribute to the knowledge of how two environmental gradients (elevation and forest-use intensity) interactively affect the tropical plant diversity of six different vascular plant groups (trees, shrubs, lianas, terrestrial herbs, epiphytes, and ferns). The results were obtained in the frame of the interdisciplinary research project "BIOVERA," which aims at documenting and understanding biodiversity patterns along gradients of elevation, climate, soil, and disturbance along an elevational transect at the Cofre de Perote mountain in central Veracruz, Mexico (Carvajal-Hernández et al. 2017; Gómez-Díaz et al. 2017a; Bautista-Bello 2018; Bautista-Bello et al. 2019; Guzmán-Jacob et al. 2020; Monge-González et al. 2020).

14.2 Methodology

14.2.1 Study Area

The study area is located along an elevational gradient (80 km in length) from the sea level close to the Gulf of Mexico to near the tree line at 3545 m a.s.l. on the eastern slopes of the Cofre de Perote mountain, in the central part of the state of Veracruz, Mexico (Fig. 14.1). In this region, the Trans-Mexican volcanic belt and

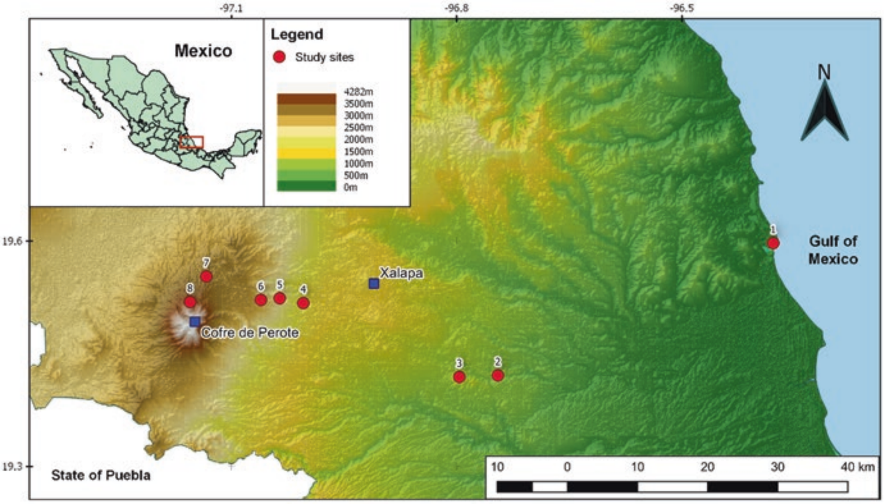


Fig. 14.1 Map of the eastern slopes of the Cofre de Perote mountain in the state of Veracruz, Mexico. Red dots indicate the eight study sites. 1 = 0 m (La Mancha), 2 = 500 m (Palmarejo), 3 = 1000 m (Chavarrillo), 4 = 1500 m (Los Capulines), 5 = 2000 m (El Zapotal), 6 = 2500 m (Encinal), 7 = 3000 m (Los Pescados), 8 = 3500 m (El Conejo). Blue squares indicate the summit of the Cofre de Perote mountain, and the city of Xalapa as reference points. (Taken from Guzmán-Jacob et al. 2020)

the Sierra Madre Oriental converge, creating complex geological conditions and combining floristic elements from the Nearctic and Neotropics (Monge-González 2020). The elevational gradient is characterized by a wide range of different environmental conditions. For instance, the climate varies from tropical-dry at lower elevations, to temperate-humid at mid-elevations, and cold-dry at high elevations (Soto-Esparza and Giddings-Berger 2011). The mean annual temperature ranges from 26 °C near sea level to 9 °C at the highest site. Mean annual precipitation varies between 1222 mm at low elevations, 2952 mm at mid-elevations, and 708 mm at high elevations (Servicio Meteorológico Nacional 2019; Monge-González et al. 2020).

Along the elevational gradient, six main vegetation types are commonly found (Carvajal-Hernandez et al. 2020): (1) semihumid deciduous forest at 0–700 m, (2) tropical oak forest at 700–1300 m, (3) humid montane forest at 1300–2400 m, (4) pine-oak forest at 2400–2800 m, (5) pine forest at 2800–3500 m, and (6) fir forest at 3500–3600 m. However, forest-use change has altered these ecosystems into mostly degraded and secondary forests (Monge-González et al. 2021). The forests in the lowlands (0, 500, 1000 m) have been largely replaced by agricultural systems, for example, sugar cane, corn, mango, and lemon plantations, and grasslands for cattle (Travieso-Bello et al. 2006; Thiébaut and Velázquez Hernández 2017), while the forests at midelevations (1500, 2000, 2500 m) have been transformed by illegal logging for charcoal production and firewood and converted into cattle pastures, coffee plantations, and agricultural fields (Cruz-Angón et al. 2010), and the forests in the highlands (3000, 3500 m) have been altered by timber extraction, agricultural fields for potatoes, and broad beans, as well as pastures for goats and sheep (Pineda-López et al. 2013). Forest-use modifications at every elevational site change with agricultural and livestock activities.

14.2.2 Vegetation Sampling

We selected eight study sites each separated by c. 500 m in altitude along the elevational gradient representing the following elevational ranges (following Guzmán-Jacob et al. 2020): 0–70 m, 610–675 m, 980–1050 m, 1470–1700 m, 2020–2200 m, 2470–2600 m, 3070–3160 m, and 3480–3545 m (hereafter referred to as 0, 500, 1000, 1500, 2000, 2500, 3000, 3500 m). At each study site, we surveyed six groups of vascular plants (trees, shrubs, lianas, terrestrial herbs, epiphytes, and ferns) in five nonpermanent 20 × 20 m plots (Kessler and Bach 1999; Krömer and Gradstein 2016) for each of three forest-use intensity (FUI) levels (Fig. 14.2) yielding a total of 120 plots (120 × 0.04 ha = 4.8 ha). These levels of FUI could consistently be found along the entire gradient (following Gómez-Díaz et al. 2017b): (1) old-growth forests (OFs) encompass mature forests with no or only a few signs of logging and other human impacts, and are classified as the lowest FUI; (2) degraded forests (DFs) are forests with clear signs of past logging, sometimes with ongoing cattle grazing, removal of understory, and/or harvesting of nontimber forest products, and

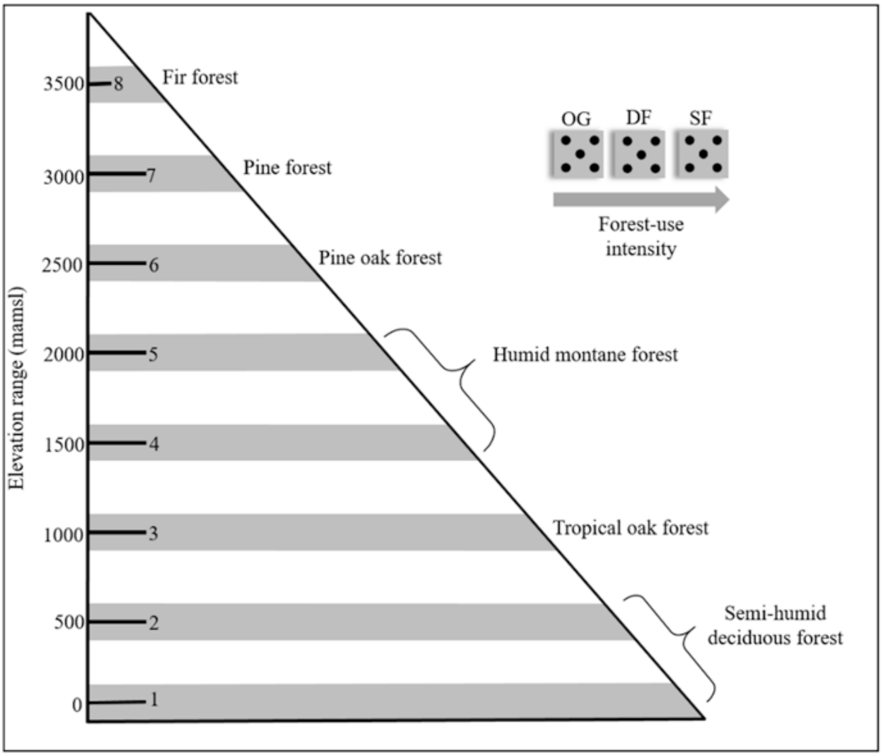


Fig. 14.2 Schematic diagram illustrating the sampling design along the elevational gradient. Eight study sites were placed at every 500 m in elevation (numbered 1–8), and the respective vegetation type is given (following each section of the elevation). Forest-use intensity at each study site is represented by five plots each in the old-growth forest (OF), degraded forest (DF), and secondary forest (SF) (total *n* = 120 plots). (Taken from Guzmán-Jacob et al. 2020)

are classified as intermediate FUI; and (3) secondary forests (SFs) represent forests at an intermediate successional stage 15–25 years after abandonment (based on interviews with local landowners), often with signs of continued human impacts, such as the removal of understory vegetation, nontimber forest products, or partial tree cutting and occasional cattle grazing, and are classified as high FUI.

At each plot, systematic ground-based sampling was performed, which consisted in recording the presence/absence of all terrestrial and saxicolous species (woody and herbaceous), as well as epiphytes in the understory up to a height of about 8 m, using collecting poles and binoculars (Krömer et al. 2007). Additionally, a single mature canopy tree per plot was selected and fully sampled from the base to the outer portion of the tree crown (Krömer and Gradstein 2016), using the single-rope technique (Perry 1978). This technique allows for a nearly complete inventory of epiphyte diversity in the forest canopy (Flores-Palacios and García-Franco 2001). The specimens collected were deposited in the National Herbarium (MEXU) of the Institute of Biology of the UNAM, Mexico City, as well as partially in the herbaria of the University of Veracruz (CIB, CITRO), Xalapa, Autonomous University of Mexico, Iztapalapa (UAMIZ), Mexico City, University of California (UC), Berkeley, USA, and/or the Institute of Ecology, A.C. (XAL), Xalapa. We used a Garmin® GPSMAP 60Cx device (Garmin International, Inc. Kansas, USA) to record geographical coordinates and elevation of all plots.

We placed 42 microclimate data loggers (HOBO PRO v 2; Onset Computer, Bourne, MA, US) to record air temperature and relative humidity, as well as light intensity (HOBO Pendant Temperature/Light Data Logger) for 1 yr. (Jan to Dec 2014) every 30 min at five elevations (500, 1000, 1500, 2500, 3500 m), which represent the five different types of vegetation present along the entire gradient (Carvajal-Hernández et al. 2017). In all three FUI levels, we placed two data loggers that recorded temperature and humidity and one that recorded light intensity (however, at 3500 m, it was not possible to obtain complete data due to a light intensity data logger failure). These were placed on tree trunks 2–3 m above the ground.

14.2.3 Data Analysis

We estimated species diversity as species richness (Hill number $q = 0$) in terms of effective species numbers (Jost 2006). This diversity index gives equal weight to common and rare species (Gómez-Díaz et al. 2023). We estimated species richness with species accumulation curves using sample-based rarefaction and extrapolation (Chao et al. 2014), pooling data by forest-use intensity for each elevation. We used rarefaction and extrapolation because the number of individuals may vary systematically with forest-use intensity, which may bias estimates of species diversity in plots with more individuals. At the plot level, we estimated species diversity using a fixed sample coverage of 95% with the "iNeXT" package (Hsieh et al. 2016) to permit unbiased comparisons of species diversity across forest-use intensities and elevations (Monge-Gónzalez 2020).

For all plant groups (lumped together and apart), we modeled species richness as a dependent variable and elevation and FUI as independent variables. On one hand, in the case of trees and ferns, we fitted linear regression models with the normal distribution; however, since both groups presented heteroskedasticity, we applied a correction with generalized least squares with an unknown form of variance to both groups. On the other hand, since all groups together, shrubs, epiphytes, herbs, and lianas did not follow a normal distribution, we used the function "descdist" of the "fitdistrplus" R-package (Delignette-Muller and Dutang 2015) to evaluate which distribution best fits the previous variables (Alrutz et al. 2022). Therefore, we used a generalized linear model with negative binomial distribution in all cases except for herbs for which we used a Gaussian distribution. Since all plant groups follow a nonlinear trend with elevation, we also considered nonlinear (unimodal) relationships between dependent variables and elevation by adding a quadratic term (elevation^2) to the models. For the selection model, we used the Akaike information criterion (AIC; Akaike 1974). AIC is well suited to situations where the predictive capacity of the model is important. AIC evaluates the likelihood of each model in the set, it considers how well the model fits the data and penalizes for adding additional parameters (Burnham and Anderson 2002). The significance level was set at $\alpha = 0.05$.

We examined changes in community composition of all plant groups among elevational sites and levels of forest-use intensity using nonmetric multidimensional scaling (NMDS) with the incidence-based Ochiai dissimilarity using the function “dist.ldc” of the package “adespatial” (Dray et al. 2018). We then tested for differences in tree community composition across elevations and levels of forest-use intensity with a nested permutational multivariate analysis of variance (PERMANOVA, 999 permutations) using the “adonis2” function in the “vegan” package (Oksanen et al. 2013), followed by pairwise comparisons using the “pairwise.adonis2” function in the “pairwiseAdonis” package (Monge-González 2020). The *p*-values for the pairwise comparisons were Bonferroni-corrected to test differences in species composition among levels of forest-use intensity within elevation.

To assess the role of environmental conditions as drivers of species richness patterns in each plant group, we calculated Pearson correlations between plot-level species richness and environmental gradient values (Jones et al. 2014). All statistical analyses were performed in R 4.1.2 (R Core Team 2022) using the libraries “modEvA” and “lmtest.” For data manipulation and visualization, we used the R packages “dplyr” and “ggplot2,” respectively.

14.3 Results

In general, the accumulation curves for the species richness of all plant groups together showed their highest values at midelevations (2000, 2500 m) of the gradient, while at the highest elevation (3500 m), the species richness was the lowest. There is a clear difference among forest-use intensity levels at 1500 m with OF having the greatest diversity and diminishing with FUI. Also, at 500 and 2000 m, there was an effect of FUI on species richness; however, DF was most diverse at both elevations (Fig. 14.3). Species accumulation curves across forest-use intensities overlapped in the rest of the elevations (0, 1000, 2500, 3000, 3500 m), showing that species pools of degraded and secondary forests were comparable in size to old-growth forests. Species accumulation curves reached the asymptote at 1500 and 3500 m (Fig. 14.3).

We found that alpha diversity for all groups together was mainly affected by elevation ($p < 0.001$), the alpha diversity peaked between 1500 and 2000 m following a hump-shaped pattern, which monotonically declined toward the extremes of the gradient (Fig. 14.4). Along the elevational gradient, SF had the lowest species richness ($p < 0.001$), while there was no difference between OF and DF ($p = 0.145$).

Tree alpha diversity was mainly affected by elevation ($p < 0.001$), with a peak in species richness between 1000 and 1500 m for DF and SF. For most of the

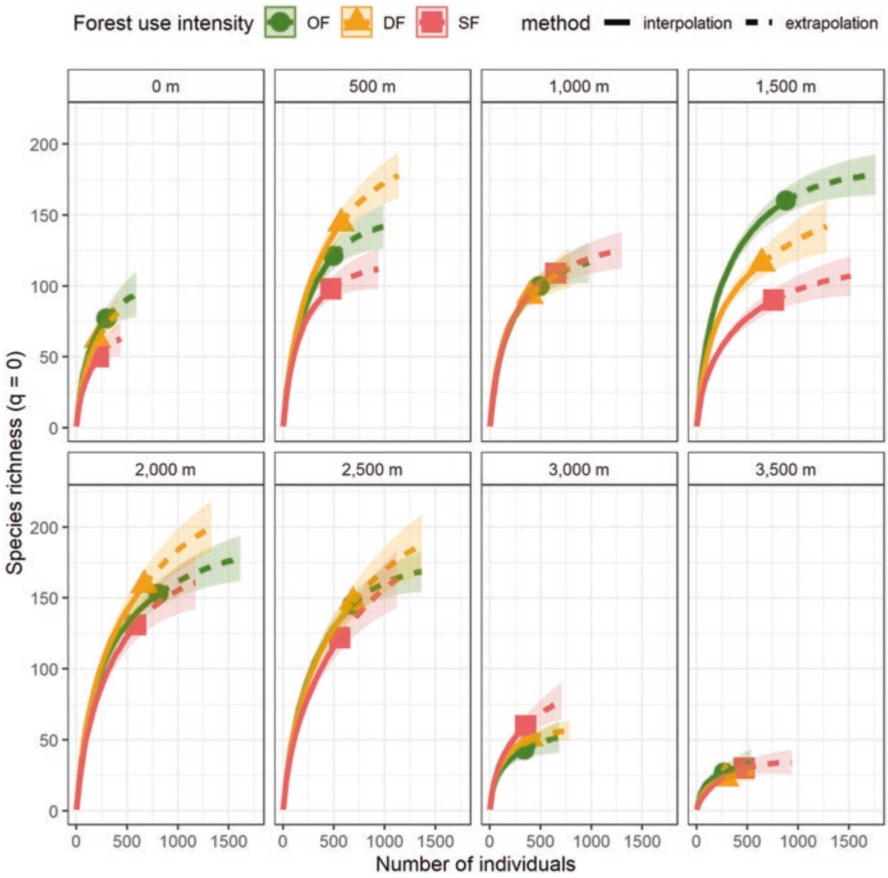


Fig. 14.3 Rarefaction (solid lines) and extrapolated (dashed lines) curves for species richness (Hill number $q = 0$, pooling data by forest-use intensity within each elevation) for all groups together. Shaded areas are the 95% confidence intervals. Forest-use intensity levels are old-growth forest (OF, green), degraded forest (DF, orange), and secondary forest (SF, red)

elevational gradient, SF had lower alpha diversity ($p < 0.001$) than the other FUI levels; however, at higher elevations, this pattern changed by having an increase at 3500 m ($p < 0.001$). In general, there was no difference in species richness of OF and DF except for the lowest part of the gradient where the species richness of DF was similar to SF and lower than OF ($p = 0.022$) (Fig. 14.5a). The alpha diversity of shrubs was only affected by elevation ($p < 0.001$), showing a slight increase with a peak between 1000 and 1500 m and then a decrease toward higher elevations (Fig. 14.5b). The alpha diversity of epiphytes was mainly affected by elevation ($p < 0.001$) with an observed peak in species richness at midelevations, which monotonically decreased from 1500 m towards the upper limit of the elevational gradient (Fig. 14.5c). Nevertheless, a second peak of species richness occurred in

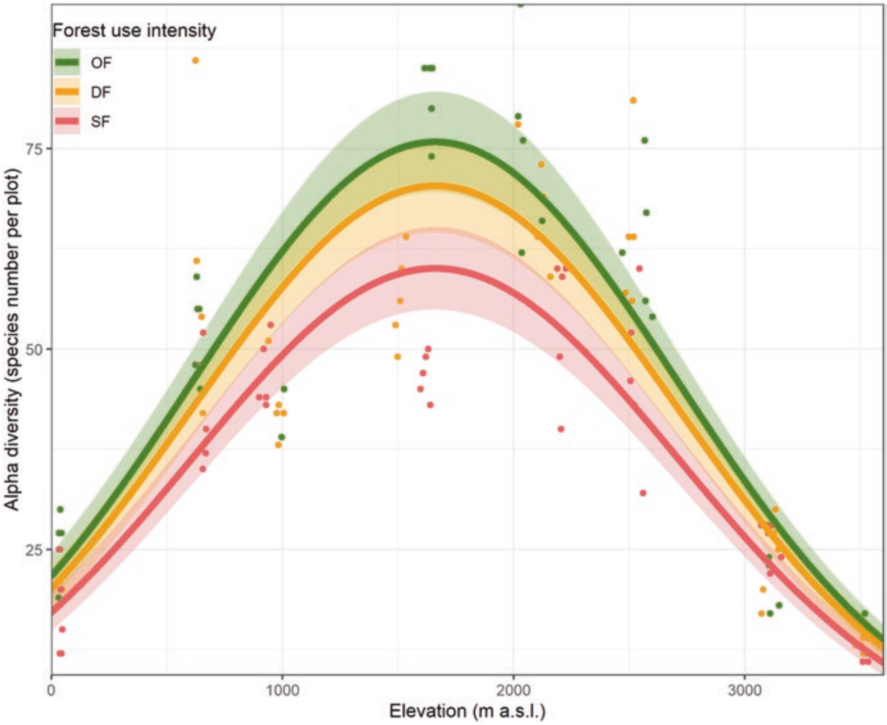


Fig. 14.4 Alpha diversity of all groups together along gradients of elevation and forest-use intensity (old-growth forest in green, degraded forest in orange, and secondary forest in red) at the Cofre de Perote, central Veracruz, Mexico. The shaded area marks confidence intervals (CI = 1.96 times standard error)

tropical oak forests at 500 m. Along the whole elevational gradient SF had the lowest alpha diversity of epiphytes ($p = 0.033$) without any difference between OF and DF ($p = 0.944$; Fig. 14.5c). Regarding the alpha diversity of ferns, these were also mainly affected by elevation ($p < 0.001$), with a higher concentration of species richness observed at intermediate elevations (peak at 2000 m) and a decrease toward the ends of the gradient. Along the elevational gradient, FUI affected alpha diversity of ferns differently, with higher species richness in OF ($p = 0.029$) and lower in SF ($p < 0.001$). However, there was a slight increase in the alpha diversity of SF at 0 m ($p = 0.025$; Fig. 14.5d). The alpha diversity of terrestrial herbs was only influenced by elevation ($p < 0.001$), showing a hump-shaped pattern with a peak of species richness between 2000 and 2500 m (Fig. 14.5e). Finally, the alpha diversity of lianas was only affected by elevation ($p < 0.001$). showing a decrease with elevation (Fig. 14.5f).

Plant communities varied significantly along the elevational gradient ($r^2 = 0.083$, PERMANOVA $F = 10.844$, $p = 0.001$), between FUI levels ($r^2 = 0.022$, PERMANOVA $F = 1.461$, $p = 0.006$), and their interaction ($r^2 = 0.020$, PERMANOVA $F = 1.328$, $p = 0.034$; Fig. 14.6). All elevations were different among them

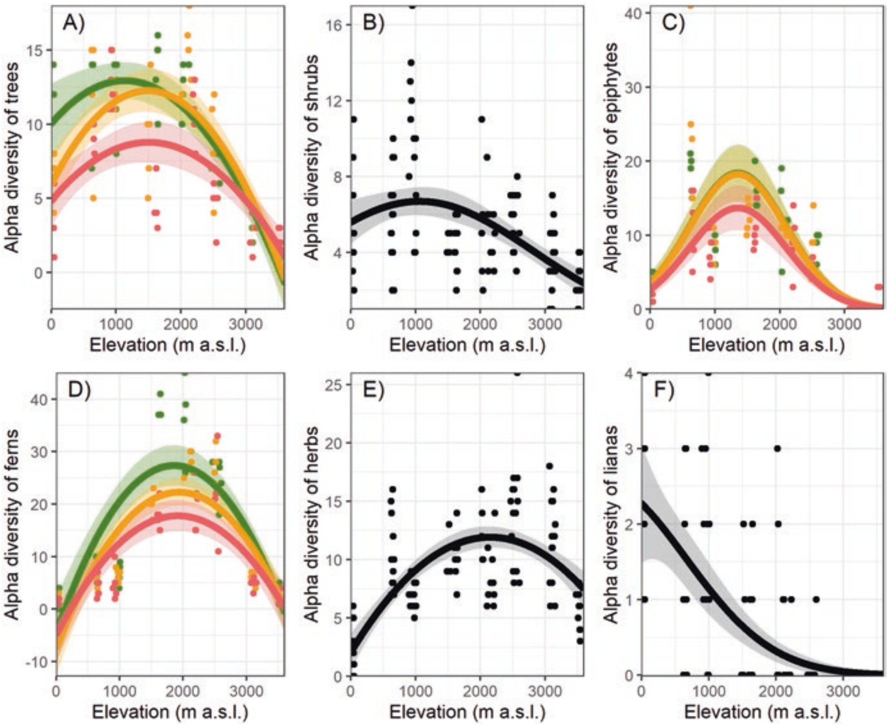


Fig. 14.5 The alpha diversity of trees (**a**), shrubs (**b**), epiphytes (**c**), ferns (**d**), terrestrial herbs (**e**), and lianas (**f**) along gradients of elevation and forest-use intensity (old-growth forest in green, degraded forest in orange, and secondary forest in red) at the Cofre de Perote mountain, central Veracruz, Mexico. Those groups for which there was no significant effect of forest-use intensity are shown in black. The shaded area marks confidence intervals (CI = 1.96 times standard error)

($p < 0.001$) and in some cases, composition was different among FUI levels, mainly between OF and SF ($p = 0.015$).

Plot-level species richness of the plant groups was significantly correlated in most of the cases (Fig. 14.7). The highest correlation was found between all groups together and ferns ($r = 0.838$), all groups and epiphytes ($r = 0.761$), and all groups and trees ($r = 0.698$). The groups with the lowest correlation values were found between ferns and shrubs ($r = 0.004$), lianas and epiphytes ($r = 0.041$), and herbs and shrubs ($r = 0.046$). The only significant negative correlation was found between herbs and lianas ($r = -0.423$). Temperature mainly affected positively the alpha diversity of lianas ($r = 0.69$) and negatively herbs ($r = -0.46$; Fig. 14.7). Humidity mainly affected positively the alpha diversity of trees ($r = 0.64$) and epiphytes ($r = 0.59$).

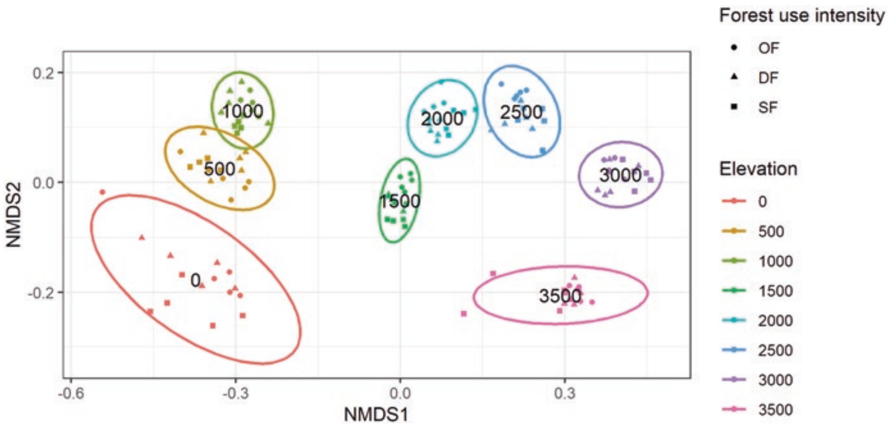
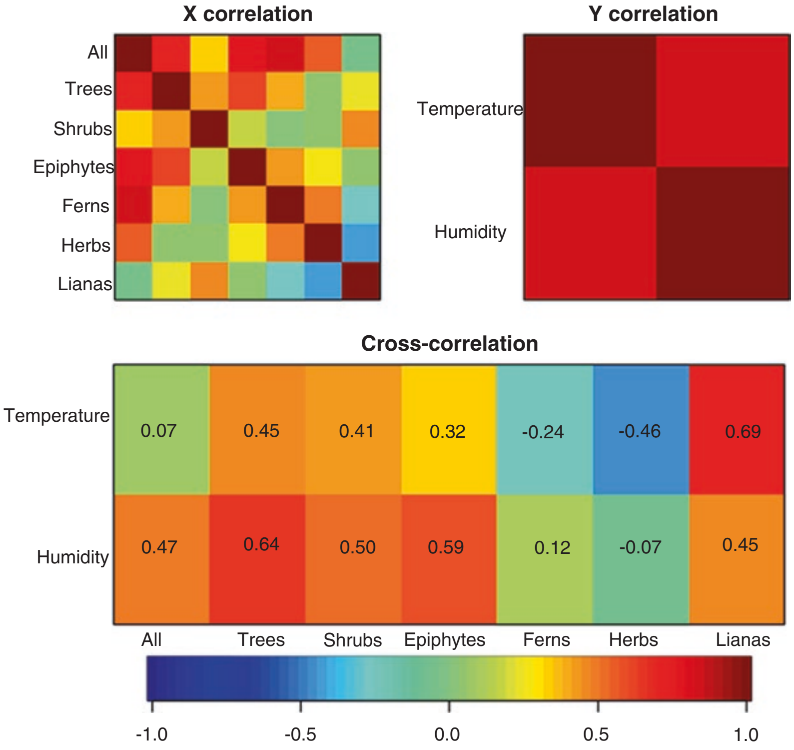


Fig. 14.6 Plant composition of all groups together along eight elevational sites and three different forest-use intensity levels. Nonmetric multidimensional scaling (NMDS) based on Ochiai dissimilarity ($n = 5$ plots per forest-use intensity within elevation), ellipses show the range of each elevation site. Forest-use intensity levels are old-growth forest (OF, circles), degraded forest (DF, triangles), and secondary forest (SF, squares)



	All	Trees	Shrubs	Epiphytes	Ferns	Herbs	Lianas
Temperature	0.07	0.45	0.41	0.32	-0.24	-0.46	0.69
Humidity	0.47	0.64	0.50	0.59	0.12	-0.07	0.45

Fig. 14.7 Correlation matrix within and between two data matrices (abiotic variables and plant richness). Colors represent the level of linear relationship that exists between all of the variables (dark blue $r = -1$ and dark red $r = 1$)

14.4 Discussion

14.4.1 Effects of the Elevational Gradient

In a global meta-analysis, Nogués-Bravo et al. (2008) analyzed 37 elevational species richness gradients in a range from 0 to 6000 m for terrestrial plants, finding that the hump-shaped diversity pattern was the most common (76%), followed by decreasing diversity with elevation (16%). In the case of the hump-shaped pattern, the peak of diversity was on average at 1364 m (SD ± 531 m). Hump-shaped diversity patterns have been reported for different groups of vascular plants (McCain and Grytnes 2010), such as Arecaceae, Acanthaceae, Bromeliaceae, epiphytes, and woody plants along tropical mountain gradients (Krömer et al. 2005; Lovett et al. 2006; Eiserhardt et al. 2011; Salas-Morales and Meave 2012). In this study, we found that the alpha diversity of all six studied plant groups together also followed this general pattern. In the case of plant composition, there is a clear differentiation of each elevational site having its community. In general, there are three groups of elevational ranges: lowland, midelevation, and highland belts (Fig. 14.4).

Generally, tree diversity sharply declined above 3000 m at the high elevations. These results are consistent with previous studies (Jankowski et al. 2013; Huerta-Martínez et al. 2014; Rutten et al. 2015), the high species diversity between 1000 and 2000 m may be related to climatic conditions, e.g. tree diversity increases with temperature and precipitation (Toledo-Garibaldi and Williams-Linera 2014; Monge-González 2020). An explanation for the decline in tree diversity at high elevations may be due to a decrease in temperature and the occurrence of frost in winter (Pereyra et al. 1992): these thermal conditions thus play an important role in the establishment of tropical tree species.

The decrease in shrub species richness above 1500 m, as well as the grouping and restriction of species at higher elevations, is due to the replacement of Neotropical by Nearctic species, since the area from the midelevations (1500 m) toward the upper end (3500 m) of the gradient belongs to the Trans-Mexican Volcanic Belt (Bautista-Bello et al. 2019). Species of Nearctic origin such as *Fuchsia microphylla*, *Acaena elongata*, *Ribes ciliatum*, *Baccharis conferta*, and *Moussonia deppeana* dominate in this area, which are capable of growing in temperate forests with low temperatures, such as the *Pinus* and *Abies* forests, as well as in the humid montane forests with high humidity and precipitation (Whittaker 1956; Palmer and Cowling 1994; Rzedowski 2006; Espinosa et al. 2008). Consequently, the grouping and separation of species at low elevations (0, 500, 1000 m) is due to the fact that more than 50% of the recorded taxa belong to families of neotropical and pantropical origin, which tend to limit their distribution to forests located at low elevations.

Species richness of vascular epiphytes along the elevational gradient peaked in humid montane forests at mid-elevations and monotonically decreased from 1500 m towards the upper limit of the gradient. This observation is consistent with previous studies on elevational patterns in this plant group (Wolf and Flamenco 2003; Krömer et al. 2005; Cardelús et al. 2006). Unexpectedly, species richness showed a second peak occurring in tropical oak forests at 500 m. It is unclear whether this deviation from the expected hump-shaped pattern is related to a high variation of environmental factors that can change substantially in small regions, causing differences in the form of distributional patterns (Rahbek 1995). Nevertheless, it could also be due to an unusually high diversity found at 500 m, which was on average comparable to diversity at 1500 m, or an unusually low diversity of epiphytes at the 1000 m site (Guzmán-Jacob et al. 2020).

Above 2000 m, epiphyte diversity declined with elevation in all forest-use intensities, most likely reflecting changing climatic conditions. A potential explanation for declines of epiphyte diversity at higher elevations are low temperatures and frequent frost events above 3000 m (−3 °C absolute minimum temperature; unpublished data; Bhattarai et al. 2004; Krömer et al. 2005). Besides the effect of harsh climatic conditions, for example, frost at the two uppermost elevations, an alternative factor for the decline of epiphyte diversity at higher elevations might be that conifers of the genera *Pinus* and *Abies* are poor epiphyte hosts (Guzmán-Jacob et al. 2020). Whereas there is no information about the quality of *Abies* as hosts, pine trees have been considered as poor epiphyte hosts, not only because of phenolic and resinous substances (Hietz and Hietz-Seifert 1995; Wolf 2005), but also because of low water-holding capacities of their bark (Callaway et al. 2002).

The highest concentration of fern species richness at intermediate elevations matches the pattern observed in other parts of the Neotropics (Kessler 2001; Kluge and Kessler 2006; Hernández-Rojas et al. 2018). This is due to the climate conditions of high humidity and moderate temperatures characteristic of the mid-mountain ranges that favor the physiological conditions of most fern species. As ferns are faced with the constant loss of water due to the opening of their stomata, they need to be in humid environments to avoid desiccation (Brodribb and McAdam 2011). It is noteworthy that in the lower and upper extremes of the gradient, the richness decreases abruptly, since, in the study area located close to the subtropics, the environmental conditions are strongly contrasting, with prolonged droughts for several months and high temperatures in the lowlands and freezing winter conditions in the highlands.

These harsh climatic conditions represent a limitation for the establishment of many fern species and consequently, in the lower and upper parts of the gradient, there occur mainly species of the genera *Pleopeltis*, *Microgramma*, and *Polypodium*, all belonging to the Polypodiaceae family, which has representatives that can tolerate extreme environmental conditions (Kessler 2010). Besides, in the upper part of the gradient, we found also some species of the genus *Asplenium*, such as *A. castaneum* and related taxa, which coincides with the record of species of this genus at more than 4000 m and particularly *A. castaneum* has been recorded at 5100 m in the Andes (Tryon and Tryon 1982), indicating its adaptability to higher elevations.

In the case of terrestrial herbs, compared to previous findings, our results showed a peak in alpha diversity shifted toward higher elevations, instead of midelevations (Kluge and Kessler 2006). One explanation for this pattern is that herbs are adapted to cold climates and had success in temperate zones due to their annual growth habit and the production of underground structures (e.g., rhizomes and stolons; Hawkins et al. 2011). Also, herbaceous angiosperms are morphologically more flexible in their adaptations to low temperatures and have shorter generation periods than trees, which enables them to diversify more rapidly at higher latitudes (Willinghöfer et al. 2012). Lower elevations in central Veracruz are subject to prolonged dry seasons, which may limit alpha diversity (Gómez-Díaz et al. 2017b).

With increasing elevation, precipitation increases, while temperatures and potential evapotranspiration decrease. In our study, angiosperm herb richness peaked between 2000 and 2500 m, where precipitation and the number of rainy days reached their maximum. Here, the humid montane forests and the pine-oak forests are often subject to fog and environmental humidity, which likely increases the establishment and ground cover of herbs and thus also their diversity (Hawkins et al. 2011). Cicuzza et al. (2013) studied the distributional patterns of tropical herbaceous angiosperms and found that their local difference in species richness is influenced by factors such as temperature, elevation, and actual evapotranspiration. Additionally, they found that higher elevation promotes herbaceous angiosperm richness, although the treeline is the ecological limit of its species richness, which shows a decrease near this zone (Wesche et al. 2008).

Finally, the lianas show a different pattern, since they depend on high temperature and humidity, and thus have greater richness at low altitudes (Bautista-Bello 2018). This elevational distribution follows the global pattern reported by DeWalt et al. (2015), where the diversity of lianas decreases with increasing altitude and latitude, in addition to the influence of other factors such as precipitation and the seasonality of droughts. According to the results of Parthasarathy et al. (2015) reported for the Indian Peninsula, high rainfall (≥3000 mm) is positively related to the increase in the floristic richness of lianas, as long as the temperature remains at high values, as occurs in the humid lowland forests. While long periods of drought (7–8 months) are associated with an increase in the abundance of individuals, but not in the richness of species. This could explain the pattern that we found, since in the sites 0–1000 m, the dry period ranges between 7 and 8 months (Moreno-Casasola et al. 2011) and the average annual precipitation does not exceed 800 mm (Monge-González et al. 2020), coupled with the tropical origin of most of the species that favors their germination and growth in the lowlands.

In contrast, at intermediate elevations, despite the high rainfall (1800 mm), the temperature drives an important and limiting role in the growth of lianas, since it reaches an annual average of 18 °C, descending to 9 ° C at 2500 m. Thus, the low temperatures above 1500 m could explain the presence of few species. According to Leicht-Young and Pavlovic (2015), the species that manage to establish themselves in temperate forests have developed different strategies to avoid freezing embolism. An example is the species of the genus *Vitis* that tend to empty their vessels before the onset of winter, while others produce new vessels each year to replace those that were damaged by the cold (Bautista-Bello 2018). Another characteristic of lianas is to have wide and long vessels that give them growth advantages over other groups in forests with warm climates, but at the same time, it is a limitation for lianas, since this morphology does not allow them to easily recover from low temperatures, limiting their growth in temperate or cold forests (Webb 1968; Ewers et al. 1991; Jiménez-Castillo et al. 2007; Jiménez-Castillo and Lusk 2013; Angyalossy et al. 2015; Ladwig and Meiners 2015).

14.4.2 Effect of the FUI Gradient

There is an effect of FUI on all groups at midelevations. The humid montane forest is currently subject to high forest exploitation and a change in land-use, which has serious consequences for plant diversity (Williams-Linera et al. 2007). Since deforestation rates are higher in tropical countries, large and contiguous primary forests will be rare and isolated in a couple of decades (Köster et al. 2009).

Tree diversity varied among FUI, yet it was not consistent along the elevational gradient, as it showed differences between OF and SF at 0, 1000, and 1500 m, where high FUI affected tree diversity, which supports results from previous studies (Gibson et al. 2011). OF and DF showed similar species diversity at most elevations, suggesting that DF may act as reservoirs of tree diversity (Chazdon et al. 2009). However, tree species diversity may be higher in areas with slight disturbance levels, which is explained by the fact that forest gaps may contribute to the establishment and growth of fast-growing and light-demanding tree species (Denslow 1987). The three forest-use intensity gradients declined strongly toward the tree line, probably due to a decrease in temperature (Pereyra et al. 1992).

In the case of shrubs, the SFs at 500 and 1000 m harbor the highest number of species, while the OFs and DFs show a lower diversity. This indicates that changes in the structure of the forest, caused by human action, can increase the total richness of these forest fragments (Carvajal-Hernández et al. 2020), time modify the floristic composition of shrubs (Bautista-Bello et al. 2019). The alteration of the OF causes the environmental conditions necessary for the arrival and growth of secondary species, mostly heliophilous, which are usually favored by the greater entry of light in anthropized habitats (e.g., *Chileranthemum trifidum*, *Verbesina persicifolia*, *Adelia barbinervis*, *Euphorbia schlechtendalii*).

Epiphyte diversity, richness, and community composition are known to be significantly lower and different in secondary forests than in primary vegetation (Barthlott et al. 2001; Krömer and Gradstein 2003; Köster et al. 2009), and even less if the SF is near an urban area, since people often overexploit epiphytes with commercial or cultural value, for example, many orchid and bromeliad species (Flores-Palacios and Valencia-Díaz 2007; Krömer et al. 2018). In line with previous studies, our results suggest that fragmentation and destruction of the humid montane forests reduce the availability of suitable environments for vascular epiphytes, which explains the low richness of this group in SF. The younger age and reduced structural complexity of host trees in SF could limit the availability of different microhabitats that vascular epiphytes can colonize within a host tree (Hietz and Briones 1998; Krömer and Gradstein 2003; Taylor and Burns 2015). Therefore, the protection of the epiphytes that occur in OF requires the conservation of even small fragments, since they can harbor a high richness and great floristic composition (Krömer et al. 2014, 2021).

In general, a considerable decrease in the richness of ferns is observed as a consequence of anthropogenic disturbance. In a previous study in the region of central Veracruz, a similar pattern was observed, since the environments with the highest degree of disturbance present the lowest richness compared to OF (Carvajal-Hernández et al. 2014). In our study, it is clear that SF had the lowest richness of fern species, especially at intermediate elevations, in the forests with higher humidity. On the other hand, at the extremes of the gradient, besides stressful climatic conditions, some resistant species can establish, in such a way that they can also tolerate the harsher environmental conditions that are characteristic of forests under certain disturbances (Carvajal-Hernández et al. 2017).

Furthermore, with the disturbance not only species but also ecological functions are lost, this situation is accentuated at the elevation with the greatest richness (1500 m). However, at 500 m, despite the significant decrease in richness, the functions are preserved by persisting species that perform similar ecological strategies (Carvajal-Hernández et al. 2018). This shows that the disturbance does not affect all ecosystems along the altitudinal gradient in the same way, since the degree of affectation will depend on the initial richness (Murphy and Romanuk 2014). Therefore, it is highlighted that the species that compose the midelevation ecosystems, which are the richest in terms of the studied plant groups, are also the most vulnerable to anthropogenic disturbance, such is the case of ferns and can be also generalized to epiphytes. This confirms that ferns, as well as some epiphytic groups, are sensitive to the effects of human disturbance, and therefore have been considered good bioindicators for forest quality (Krömer et al. 2014; Carvajal-Hernández et al. 2017).

Surprisingly, the forest-use intensity had no significant effect on the alpha diversity of terrestrial herbs. The lack of a detectable net change in alpha diversity might indicate that herbaceous angiosperms are better adapted to changes in the environment with a profit from better light conditions in degraded or secondary habitats (Gómez-Díaz et al. 2017b). Asteraceae and Poaceae were the families with the greatest increase in species richness concerning FUI; consequently, it has been demonstrated that they are adapted to high light incidence and drought (De Moraes et al. 2016). However, other life forms (e.g., trees, epiphytes, ferns) might show contrasting patterns. It is quite well documented that forest herbs profit from better light conditions in DF or SF. Newbold et al. (2015), for example, found that the richness of vascular plant species can increase by 40% due to the conversion of old-growth forests to secondary vegetation, but more severe habitat conversion, for example, from forest to intensive cropland, decreases species richness.

For lianas there was also no significant effect of forest-use intensity on alpha diversity, although their abundance, diversity, and biomass are usually higher in disturbed areas such as in treefall gaps, than in undisturbed closed-canopy forests (e.g. Putz 1984; Schnitzer et al. 2000; Schnitzer and Carson 2001; Schnitzer and Bongers 2011). However, this depends on the type of vegetation (Bongers and Ewango 2015; Schnitzer et al. 2015) and some liana taxa require specific conditions of moisture, light, and nutrients for their establishment and development, which, thus, are affected by disturbance (DeWalt et al. 2015).

14.4.3 Effect of Climatic Variables

In general, all studied plant groups are more influenced by air humidity. The values of alpha and beta diversity presented along the forest-use intensity gradient are related to conditions in the microclimate.

Our analyses revealed that an increase in tree diversity may be the result of an increase in atmospheric humidity. We found high species diversity of trees from low to mid-elevations that dropped above 2500 m. This pattern coincides with a related study by Carvajal-Hernández et al. (2017), which showed that the highest relative air humidity was found between 500 and 2500 m with a sharp decrease at high elevations (3000–3500 m). A potential explanation of the observed result is that more diverse tree communities are structurally heterogeneous, for example, different stand basal area, density, height, and crows, which can affect microclimatic conditions, for example, temperature and humidity (Kovács et al. 2017; Jucker et al. 2018; Monge-González et al. 2021).

Shrub species richness along the elevational gradient was influenced by humidity; however, this relation was not very strong, which can be due to the ecological strategies that this plant group has to afford. Also, temperature had not a great influence on shrubs, suggesting that other abiotic factors could be influencing their richness along the elevational gradient. Maybe water (precipitation), and not temperature and air humidity, is the most limiting resource for the growth of this group (Damascos and Rapoport 2002; Mesa-Sierra and Laborde 2017).

Environmental conditions, particularly temperature and precipitation, are known to determine species distributions and diversity patterns in vascular epiphytes (Gentry and Dodson 1987; Kreft et al. 2004). In this study, epiphytes showed a high correlation with all groups in general. However, they showed a low correlation with lianas. This might be a sign of the differences in the niche preferences between these two plant groups. For example, epiphyte species with specific habitat requirements, such as shade- and humidity-adapted understory orchids and ferns, might not be able to persist under higher temperatures and lower air humidity (Krömer et al. 2014), whereas many lianas could profit from these conditions. Our results confirm that epiphytes, at least in habitats such as humid montane forests, which are characterized by continuously high moisture input, may indeed be more susceptible than other life forms to changes in precipitation or humidity (Zotz and Bader 2009). In summary, climatic conditions that the tropical montane forests offer may favor plants such as epiphytes that can cope with high cloud cover, high humidity, and lower temperatures, and thus are directly influenced by microclimatic changes (Guzmán-Jacob 2021). This is in contrast to lowland forests with dryer conditions and higher temperatures that might favor species that can survive more extreme environments.

The distribution pattern of the species richness of ferns coincides with the pattern of all groups together. This could be the explanation why, according to the analyses, the ferns are correlated with all groups in general. However, when analyzed separately, ferns do not correlate with shrubs and lianas. This may be since these latter groups present different patterns due to different ecological requirements. Lianas were shown to have a greater preference for ecosystems with a certain degree of disturbance or vegetation in the early stages of ecological succession (Letcher 2015), while there is evidence that shrubs may be favored by the conditions prevailing in environments with disturbance (Bautista-Bello et al. 2019). For these reasons, both lianas and shrubs did not show differences caused by the disturbance. The opposite occurs with ferns, since they require shady and humid conditions that are generally provided by OF (Page 2002; Sharpe and Mehltreter 2010).

Due to the above reasons, it can be noted that ferns occupy environmental niches contrary to those of lianas and shrubs, but coincide with epiphytes and trees. This makes sense if it is noted that around 25% of the ferns in the world are epiphytic (Zotz 2013), while in this study, 42% present this growth habit (Carvajal-Hernández and Krömer 2015). Therefore, epiphytic species require a greater presence of trees that generate adequate microclimatic conditions in the forests and also represent possible hosts. Due to the aforementioned, it is surprising that the analyses do not show a significant correlation of ferns with humidity and temperature, so there may be some indirect influence of these environmental variables on the ferns.

In the case of terrestrial herbs, we have found that they are not directly related to air humidity and are weakly negatively affected by temperature. This confirms that herbs are not that dependent on atmospheric humidity and may be more related to soil parameters, while they are a tolerant group that affords cold climates. Besides, we found that there was no relation with precipitation, which was also shown by Cicuzza et al. (2013), apparently explained by the effect of higher moisture in highlands, as well as evolutionary legacies. In summary, herbs are more directly influenced by microclimatic environments than by macroclimatic limitations (Wang et al. 2009; Gómez-Díaz 2017).

The species richness of lianas is mostly related with temperature, which coincides with the tropical origin of most species and favors their germination and growth in the lowlands, as temperature and the seasonality of droughts play an important and limiting role in their establishment (DeWalt et al. 2015).

14.5 Conclusions

The present study demonstrates that the alpha diversity of different plant groups does not necessarily follow the same patterns along elevational, FUI, and climatic gradients. However, values of beta diversity show that there is a high species turnover due to the elevational gradient and FUI. In terms of diversity along the elevational gradient, we found high values of beta diversity, which indicates a high environmental heterogeneity, when different elevations were compared, even if these are contiguous or they share the same vegetation type. This situation highlights the vulnerability of some plant groups (trees, epiphytes, ferns) adapted to old-growth forests and requires reconsideration of the conservation efforts made in the study area. It is preferable to focus the efforts on preserving heterogeneous systems that include a mosaic of different vegetation types. The high number of species adapted to degraded forests highlights also the importance of this vegetation type as a reservoir of native plants. Therefore, the conservation of fragments of those environments in central Veracruz should be considered in future conservation plans. As the highest species diversity is concentrated in the midelevation ecosystems, the climatic contrast caused by the anthropogenic disturbance is more accentuated, which is an indication that these are the most vulnerable ecosystems for the conservation of native species. Similarly, most of the natural forests present along the studied elevational gradient are at risk of disappearing due to the existing anthropogenic pressures.

The results and findings described in this chapter add new information related to the knowledge on the distribution of plant groups along gradients of elevation and forest-use intensity so far available for Mexico, especially for the state of Veracruz. However, additional studies are needed to understand better how the environmental conditions or territorial dynamics influence the persistence of plant species in the long term. For example, we need to understand which abiotic factors (e.g., microclimate or soil) are influencing the observed diversity patterns, and also how the highly fragmented landscape in central Veracruz is influencing the population dynamics of native species. Therefore, it is necessary to generate more information about the factors that are affecting each of the described patterns. There is information about factors (e.g., paedogenesis, latitude, nutrient availability) that promote alpha diversity in many other taxa (e.g., trees, herbivores, soil microbes), but information about factors promoting alpha or beta diversity of some plant groups is still insufficient. Besides, more research about the concordance of alpha and beta diversity patterns in different taxa would be helpful to understand the potential of using biodiversity surrogates (e.g., endemic plant species).

References

Aguirre-Beltrán G (1991) Regiones de refugio. Fondo de Cultura Económica, México

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–723. https://doi.org/10.1109/TAC.1974.1100705

Alrutz M, Gómez-Díaz J, Schneidewind U, Krömer T, Kreft H (2022) Forest structural parameters and aboveground biomass in old-growth and secondary forests along an elevational gradient in Mexico. Bot Sci 100(1):67-85. https://doi.org/10.17129/botsci.2855

Angyalossy V, Pace MR, Lima AC (2015) Liana anatomy: a broad perspective on structural evolution of the vascular system. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley, Chichester, pp 253–287

Barsimantov J, Kendall J (2012) Community forestry, common property, and deforestation in eight Mexican states. J Environ Dev 21(4):414–437. https://doi.org/10.1177/1070496512447249

Barthlott W, Schmit-Neuerburg V, Nieder J, Engwald S (2001) Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecol 152:145–156

Bautista-Bello, AP (2018) Diversidad de arbustos y lianas leñosas en gradientes de altitud e influencia antrópica en el centro de Veracruz, México. Tesis de maestría. Centro de Investigaciones Tropicales, Universidad Veracruzana. Xalapa, Veracruz, Méxic.

Bautista-Bello AP, López-Acosta JC, Castillo-Campos G, Gómez-Díaz J, Krömer T (2019) Diversidad de arbustos a lo largo de gradientes de elevación y perturbación en el centro de Veracruz, México. Acta Bot Mex 126:1–21. https://doi.org/10.21829/abm126.2019.1369

Becker A, Körner C, Brun J, Guisan A, Tappeiner U (2007) Ecological and land use studies along elevational gradients. Mount Res Dev 27(1):58–65. https://doi.org/10.1659/0276-4741(2007)27[58,EALUSA]2.0.CO;2

Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W (2013) Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of South Ecuador. Springer, Berlin. https://doi.org/10.1007/978-3-642-38137-9

Bhattarai KR, Vetaas OR, Grytnes JA (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. J Bio 31(3):389–400.

Bongers F, Ewango CEN (2015) Dynamics of lianas in DR Congo. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley, Chichester, pp 23–35

Brodribb TJ, McAdam SA (2011) Passive origins of stomatal control in vascular plants. Sci, 331(6017):582–585

Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Callaway RM, Reinhart KO, Moore GW, Moore DJ, Pennings SC (2002). Epiphyte host preferences and host traits: mechanisms for species-specific interactions. Oecologia 132(2):221–230.

Cardelús CL, Colwell RK, Watkins JE (2006) Vascular epiphyte distribution patterns. Explaining the mid-elevation richness peak. J Ecol 94:144–156

Carvajal-Hernández C, Krömer T (2015) Riqueza y distribución de helechos y licófitos en el gradiente altitudinal del Cofre de Perote, centro de Veracruz, México. Bot Sci 93(3):601–614. https://doi.org/10.17129/botsci.165

Carvajal-Hernández C, Vázquez-Torres M, Krömer T (2014) Riqueza y composición florística de pteridobiontes en bosque mesófilo de montaña y ambientes asociados en el centro de Veracruz, México. Rev Mex Biodivers 85:491–501. https://doi.org/10.7550/rmb.41292

Carvajal-Hernández C, Krömer T, López-Acosta JC, Gómez-Díaz J, Kessler M (2017) Conservation value of disturbed and secondary forests for ferns and lycophytes along an elevational gradient in Mexico. Appl Veg Sci 20(4):662–672. https://doi.org/10.1111/avsc.12318

Carvajal-Hernández C, Gómez-Díaz J, Kessler M, Krömer T (2018) Influence of elevation and habitat disturbance on the functional diversity of ferns and lycophytes. Plant Ecol Divers 11(3):335–347. https://doi.org/10.1080/17550874.2018.1484526

Carvajal-Hernandez CI, Gómez-Díaz JA, Bautista-Bello AP, Krömer T (2020) From the sea to the mountains encyclopedia of the World's biomes. In: Goldstein MI, DellaSala DA (eds) Encyclopedia of the World's biomes, vol 3. Elsevier, (pp 79–87). https://doi.org/10.1016/B978-0-12409548-9.11752-X

Cazzolla Gatti R, Callaghan T, Velichevskaya A, Dudko A, Fabbio L, Battipaglia G, Liang J (2019) Accelerating upward treeline shift in the Altai Mountains under last-century climate change. Sci Rep 9(1):7678. https://doi.org/10.1038/s41598-019-44188-1

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45–67. https://doi.org/10.1890/13-0133.1

Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, Stork NE, Miller SE (2009) The potential for species conservation in tropical secondary forests. Conserv Biol 23:1406–1417

Cicuzza D, Krömer T, Poulsen AD, Abrahamczyk S, Delhotal T, Piedra HM, Kessler M (2013) A transcontinental comparison of the diversity and composition of tropical forest understory herb assemblages. Biodivers Conserv 22:755–772

Clark DB, Hurtado J, Saatchi SS (2015) Tropical rain forest structure, tree growth and dynamics along a 2700-m Elevational Transect in Costa Rica. PLoS One 10(4):e0122905. https://doi.org/10.1371/journal.pone.0122905

Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT (2008) Global Warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322(5899):258–261. https://doi.org/10.1126/science.1162547

Cruz-Angón A, Escobar-Sarria F, Gerez-Fernández P, Muñiz-Castro M, Ramírez-Ramírez F, Williams-Linera G (2010) Centro de Veracruz. In: Toledo-Aceves T, Galindo-Leal C (eds) El Bosque Mesófilo de Montaña en México: Amenazas y Oportunidades para su Conservación y Manejo Sostenible. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, pp 80–87

Damascos MA, Rapoport EH (2002) Diferencias en la flora herbácea y arbustiva entre claros y áreas bajo dosel en un bosque de *Nothofagus pumilio* en Argentina. Rev Chil Hist Nat 75:465–472

De Moraes MG, De Carvalho MAM, Franco AC, Pollock CJ, Figueiredo-Ribeiro RDCL (2016) Fire and drought: soluble carbohydrate storage and survival mechanisms in herbaceous plants from the Cerrado. Bioscience 66:107–117. https://doi.org/10.1093/biosci/biv178

Delignette-Muller ML, Dutang C (2015) Fitdistrplus: an R package for fitting distributions. J Stat Softw 64:1–34

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Syst 18:431–451

DeWalt SJ, Schnitzer SA, Alves LF, Bongers F, Burnham RJ, Cai Z et al (2015) Biogeographical patterns of liana abundance and diversity. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley, Chichester, pp 131–146

Dray S, Blanchet G, Borcard D, Guenard G, Jombart T, Larocque G et al (2018) Package 'adespatial'. R Package 2018:3–8

Eiserhardt WL, Svenning JC, Kissling WD, Balslev H (2011) Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. Ann Bot 108(8):391–1416.

Ellis EA, Martínez-Bello M, Monroy-Ibarra R (2011) Focos rojos para la conservación de la biodiversidad. In: Cruz-Angón A (ed) La biodiversidad en Veracruz: Estudio de estado, vol I. CONABIO, México, pp 351–367

Espinosa D, Ocegueda S, Aguilar-Zuñiga CS, Flores-Villela C, Llorente-Bousquets O, Ocegueda-Cruz J, Vázquez Benítez S, Espinosa B, Challenger O, González Medrano FA, Morrone-Lupi JJ (2008) El conocimiento biogeográfico de las especies y su regionalización natural. In: Capital natural de México, Conocimiento actual de la biodiversidad, vol I. CONABIO, México, pp 33–65

Ewers FW, Fisher JB, Fichtner K (1991) Vine physiology and development. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 127–160

Feeley KJ, Silman MR, Bush MB, Farfan W, Cabrera KG, Malhi Y et al (2011) Upslope migration of Andean trees. J Biogeogr 38(4):783–791

Flores-Palacios A, García-Franco JG (2001) Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. Selbyana 2:181–191

Flores-Palacios A, Valencia-Díaz S (2007) Local illegal trade reveals unknown diversity and involves a high species richness of wild vascular epiphytes. Biol Conserv 136:372–387

Gentry AH, Dodson CH (1987) Diversity and biogeography of Neotropical vascular epiphytes. Ann Mo Bot Gard 74:205–233. https://doi.org/10.2307/2399395

Gerold G, Schawe M, Bach K (2008) Hydrometeorologic, pedologic and vegetation patterns along an elevational transect in the montane forest of the Bolivian Yungas. Erde 139(1–2):141–168

Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378–381

Gómez-Díaz, JA (2017) Diversity patterns of herbaceous angiosperms along gradients of elevation and forest use intensity in Central Veracruz, Mexico (Doctoral dissertation, Dissertation, Göttingen, Georg-August Universität). 149 p

Gómez-Díaz JA, Villalobos F (2020) Montañas: cómo se definen y su importancia para la biodiversidad y la humanidad. CIENCIA ergo-sum 27(2):1. https://doi.org/10.30878/ces.v27n2a9

Gómez-Díaz JA (2017) Diversity patterns of herbaceous angiosperms along gradients of elevation and forest use intensity in Central Veracruz, Mexico (Doctoral dissertation, Dissertation, Göttingen, Georg-August Universität). 149 p

Gómez-Díaz J, Krömer T, Carvajal-Hernández C, Gerold G, Heitkamp F (2017a) Richness and distribution of herbaceous angiosperms along gradients of elevation and forest disturbance in Central Veracruz, Mexico. Bot Sci 95(2):307–328. https://doi.org/10.17129/botsci.859

Gómez-Díaz JA, Krömer T, Kreft H, Gerold G, Carvajal-Hernández CI, Heitkamp F (2017b) Diversity and composition of herbaceous angiosperms along gradients of elevation and forest-use intensity. PLoS One 12(8):e0182893. https://doi.org/10.1371/journal.pone.0182893

Gómez-Díaz JA, Brast K, Degener J, Krömer T, Ellis E, Heitkamp F, Gerold G (2018) Long-term changes in forest cover in Central Veracruz, Mexico (1993–2014). Trop Conserv Sci 11:1–12. https://doi.org/10.1177/1940082918771089

Gómez-Díaz JA, Carvajal-Hernández CI, Bautista-Bello AP, Monge ML, Guzmán-Jacob V, Kreft H, Krömer T, Villalobos F (2023) Humboldt's legacy: explaining the influence of environmental factors on the taxonomic and phylogenetic diversity of angiosperms along a Neotropical elevational gradient. AoB PLANTS 15(1):plac056. https://doi.org/10.1093/aobpla/plac056

Grau HR, Aide M (2008) Globalization and land use transitions in Latin America. Ecol Soc 13(2):16. https://doi.org/10.1057/9780230603554

Guzmán-Jacob V, Zotz G, Craven D, Taylor A, Krömer T, Monge-González ML, Kreft H (2020) Effects of forest-use intensity on vascular epiphyte diversity along an elevational gradient. Divers Distrib 26(1):4–15. https://doi.org/10.1111/ddi.12992

Guzmán-Jacob V (2021) Diversity and Leaf Functional Traits of Vascular Epiphytes Along Gradients of Elevation and Forest-use Intensity (Doctoral dissertation, Georg-August-Universität Göttingen). 126 p

Hawkins BA, Rodríguez MÁ, Weller SG (2011) Global angiosperm family richness revisited: linking ecology and evolution to climate. J Biogeogr 38:1253–1266

Hernández-Rojas A, Krömer T, Carvajal-Hernández C, Kessler M, Weigand A, Kluge J (2018) Richness patterns of ferns along an elevational gradient in Sierra de Juarez, Oaxaca, Mexico: a comparison with Central and South American. Am Fern J 108(3):76–94. https://doi.org/10.1640/0002-8444-108.3.76

Hietz P, Hietz-Seifert U (1995) Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. J Veg Sci 6(4):487–498.

Hietz P, Briones O (1998) Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. Oecologia 114:305–316. https://doi.org/10.1007/s004420050452

Homeier J, Breckle S-W, Günter S, Rollenbeck RT, Leuschner C (2010) Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. Biotropica 42(2):140–148. https://doi.org/10.1111/j.1744-7429.2009.00547.x

Homeier J, Werner FA, Gawlik J, Peters T, Diertl K-HJ, Richter M (2013) Plant diversity and its relevance for the provision of ecosystem services. In: Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W (eds) Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of South Ecuador. Springer, Berlin, pp 93–106. https://doi.org/10.1007/978-3-642-38137-9

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451–1456

Huerta-Martínez FM, Briones-Tirado JE, Neri-Luna C, Muñoz-Urías A, Rosas-Espinoza VC (2014) Relaciones entre comunidades arbóreas, suelo y el gradiente altitudinal en el volcán de Tequila, Jalisco. Rev Mex Cienc Forestales 5:202–215

Jankowski JE, Merkord CL, Rios WF, Cabrera KG, Revilla NS, Silman MR (2013) The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. J Biogeogr 40:950–962

Jenkins CN, Pimm SL, Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and conservation. Proc Natl Acad Sci 110(28):E2602–E2610

Jiménez-Castillo M, Lusk CH (2013) Vascular performance of woody plants in a temperate rain forest: lianas suffer higher levels of freeze–thaw embolism than associated trees. Funct Ecol 27(2):403–412

Jiménez-Castillo M, Wiser SK, Lusk CH (2007) Elevational parallels of latitudinal variation in the proportion of lianas in woody floras. J Biogeogr 34:163–168

Jost L (2006) Entropy and diversity. Oikos 113:363–375

Jones MM, Cicuzza D, van Straaten O, Veldkamp E, Kessler M (2014)Determinants of fern and angiosperm herb community structure in lower montane rainforest in Indonesia. J Veg Sci 25(5):1216–1224.

Jucker T, Hardwick SR, Both S, Elias DMO, Ewers RM, Milodowski DT, Swinfield T, Coomes DA (2018) Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. Glob Chang Biol 24(11):5243–5258. https://doi.org/10.1111/gcb.14415

Kessler M (2001) Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. Biodivers Conserv 10:1897–1920

Kessler M (2010) Biogeography of ferns. In: Mehltreter K, Walker LR, Sharpe JM (eds) Fern ecology. Cambridge University Press, Cambridge, pp 22–60

Kessler M, Bach K (1999) Using indicator groups for vegetation classification in species-rich Neotropical forests. Phytocoenologia 29:485–502

Kluge J, Kessler M (2006) Fern endemism and its correlates: contribution from an elevational transect in Costa Rica. Divers Distrib 12:535–545

Körner C (2004) Mountain biodiversity, its causes and function. Ambio 13:11–17. https://doi.org/10.1007/0044-7447-33.sp13.11

Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22(11):569–574. https://doi.org/10.1016/j.tree.2007.09.006

Körner C, Jetz W, Paulsen J, Payne D, Rudmann-Maurer K, Spehn EM (2017) A global inventory of mountains for bio-geographical applications. Alp Bot 127(1):1–15. https://doi.org/10.1007/s00035-016-0182-6

Köster N, Friedrich K, Nieder J, Barthlott W (2009) Conservation of epiphyte diversity in an Andean landscape transformed by human land use. Conserv Biol 23(3):911–919. https://doi.org/10.1111/j.1523-1739.2008.01164.x

Kovács B, Tinya F, Ódor P (2017) Stand structural drivers of microclimate in mature temperate mixed forests. Agric For Meteorol 234-235:11–21. https://doi.org/10.1016/j.agrformet.2016.11.268

Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. Proc Natl Acad Sci 104(14):5925–5930. https://doi.org/10.1073/pnas.0608361104

Kreft H, Köster N, Küper W, Nieder J, Barthlott W (2004) Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador. J Biogeogr 31:1463–1476. https://doi.org/10.1111/j.1365-2699.2004.01083.x

Krömer T, Gradstein SR (2003) Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. Selbyana 24:190–195

Krömer T, Gradstein SR (2016) Vascular epiphytes. In: Larsen T (ed) Core standardized methods for rapid biological field assessment. Conservation International, Arlington, pp 25–36

Krömer T, Kessler M, Gradstein SR, Acebey AR (2005) Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. J Biogeogr 32(10):1799–1809. https://doi.org/10.1111/j.1365-2699.2005.01318.x

Krömer T, Kessler M, Gradstein SR (2007) Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol 189:261–278. https://doi.org/10.1007/s11258-006-9182-8

Krömer T, García-Franco JG, Toledo-Aceves T (2014) Epífitas vasculares como bioindicadores de la calidad forestal: impacto antrópico sobre su diversidad y composición. In: González-Zuarth CA, Vallarino A, Pérez-Jiménez JC, Low-Pfeng AM (eds) Bioindicadores: guardianes de nuestro futuro ambiental. Instituto Nacional de Ecología y Cambio Climático (INECC) – El Colegio de la Frontera Sur (ECOSUR), D. F. y Campeche, pp 605–623

Krömer T, Acebey AR, Toledo-Aceves T (2018) Aprovechamiento de plantas epífitas: implicaciones para su conservación y manejo sustentable. In: Silva-Rivera E, Martínez-Valdéz V, Lascurain M, Rodríguez-Luna E (eds) De la recolección a los agroecosistemas: soberanía alimentaria y conservación de la biodiversidad, perteneciente a la serie: Hacia la sustentabilidad. Editorial de la Universidad Veracruzana, Xalapa, pp 175–196

Krömer T, Viccon-Esquivel J, Gómez-Díaz JA (2021) Efectos antrópicos sobre la diversidad de epífitas vasculares y orquídeas en el centro de Veracruz. In: Viccon Esquivel J, Castañeda Zárate M, Castro Cortés R, Cetzal Ix W (Coords) Las orquídeas de Veracruz. Editorial de la Universidad Veracruzana, Xalapa, pp 235–252

Ladwig LM, Meiners SJ (2015) The role of lianas in temperate tree communities. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley, Chichester, pp 188–202

Leicht-Young SA, Pavlovic NB (2015) Lianas as invasive species in North America. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley, Chichester, pp 427–442

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320(5884):1768–1771

Letcher S (2015) Patterns of liana succession in tropical forest. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley, Chichester, pp 116–130

Lovett JC, Marshall AR, Carr J (2006) Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. Afr J Ecol 44:478–490

Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S (2010) Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Glob Chang Biol 16(12):3171–3175. https://doi.org/10.1111/j.1365-2486.2010.02323.x

McCain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecol Lett 14(12):1236–1245. https://doi.org/10.1111/j.1461-0248.2011.01695.x

McCain CM, Grytnes J-A (2010) Elevational gradients in species richness. In: Encyclopedia of Life Sciences (ELS). Wiley, Chichester. https://doi.org/10.1002/9780470015902.a0022548

McCain CM, Szewczyk T, Bracy Knight K (2016) Population variability complicates the accurate detection of climate change responses. Glob Chang Biol 22(6):2081–2093. https://doi.org/10.1111/gcb.13211

Mesa-Sierra M, Laborde J (2017) Insights for the conservation of native tree species gleaned from the advanced regeneration community in a seasonally dry tropical landscape. Trop Conserv Sci 10:1–15

Monge-González LM (2020) Interactive Effects of Elevation and Forest-use Intensity on Tropical Tree Diversity in Veracruz, Mexico (Doctoral dissertation, Niedersächsische Staats-und Universitätsbibliothek Göttingen). 136 p

Monge-González ML, Craven D, Krömer T, Castillo-Campos G, Hernández-Sánchez A, Guzmán-Jacob V, Guerrero-Ramírez N, Kreft H (2020) Response of tree diversity and community composition to forest use intensity along a tropical elevational gradient. Appl Veg Sci 23(1):69–79. https://doi.org/10.1111/avsc.12465

Monge-González ML, Guerrero-Ramírez N, Krömer T, Kreft H, Craven D (2021) Functional diversity and redundancy of tropical forests shift with elevation and forest-use intensity. J Appl Ecol 58(9):1827–1837. https://doi.org/10.1111/1365-2664.13955

Monge González ML, Weigelt P, Guerrero-Ramírez N, Craven D, Castillo-Campos G, Krömer T, Kreft H (2021) BIOVERA-Tree: tree diversity, community composition, forest structure and functional traits along gradients of forest-use intensity and elevation in Veracruz, Mexico. Biodiversity Data Journal 9: e69560. https://doi.org/10.3897/BDJ.9.e69560

Moreno-Casasola P, Infante M, Madero-Vega C (2011) Germinación y supervivencia de dos especies de acahuales de selva baja importantes para restaurar dunas costeras. Rev Mex Cienc Forestales 2(6):19–36

Morueta-Holme N, Engemann K, Sandoval-Acuña P, Jonas JD, Segnitz RM, Svenning JC (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. Proc Nat Acad Sci 112(41):12741–12745

Murphy GEP, Romanuk TN (2014) A meta-analysis of declines in local species richness from human disturbances. Ecol Evol 4(1):91–103

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858. https://doi.org/10.1038/35002501

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA et al (2015) Global effects of land use on local terrestrial biodiversity. Nature 520:45–50

Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C (2008) Scale effects and human impact on the elevational species richness gradients. Nature 453:216–219

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB et al (2013) Package 'vegan'. Community Ecol Packag Version 2(9):1–295

Page CN (2002) Ecological strategies in fern evolution: a neopteridological overview. Rev Paleobot Palynol 119:1–33

Palmer AR, Cowling RM (1994) An investigation of topo-moisture gradients in the eastern Karoo, South Africa, and the identification of factors responsible for species turnover. J Arid Environ 26:135–147

Parthasarathy N, Muthuramkumar S, Muthumperumal C, Vivek P, Ayyappan N, Sridhar-Reddy M (2015) Liana composition and diversity among tropical forest types of peninsular India. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley, Chichester, pp 36–49

Payne D, Spehn EM, Snethlage M, Fischer M (2017) Opportunities for research on mountain biodiversity under global change. Curr Opin Environ Sustain 29:40–47. https://doi.org/10.1016/j.cosust.2017.11.001

Pepin NC, Arnone E, Gobiet A, Haslinger K, Kotlarski S, Notarnicola C et al (2022) Climate changes and their elevational patterns in the mountains of the world. Rev Geophys 60:e2020RG000730. https://doi.org/10.1029/2020RG000730

Perry D (1978) A method of access into the crowns of emergent and canopy trees. Biotropica 10:155–157. https://doi.org/10.2307/2388019

Pereyra D, Palma G, & G., Zitacuaro CI (1992) Correlation between northers of Gulf of Mexico and frosts at Las Vigas, Veracruz, Mexico. Atmósfera 5:109–118.

Peters M, Hemp A, Appelhans T, Becker J, Behler C, Classen A et al (2019) Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568(7750):88–92. https://doi.org/10.1038/s41586-019-1048-z

Pineda-López MR, Velasquez LS, Dominguez GV, Alboreca AR (2013) The effects of land use change on carbon content in aerobial biomass of an Abies religiosa (Kunth Schltdl. et Cham.) forest in central Veracruz, Mexico. For Sys 22(1):82–93

Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–1724

R Core Team (2022) R: a language and environment for statistical computing. R Found Stat Comput, Vienna

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Ecography 18:200–205

Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, Morueta-Holme N, Nogues-Bravo D, Whittaker RJ, Fjeldså J (2019) Humboldt's enigma: what causes global patterns of mountain biodiversity? Science 365:1108–1113

Rutten G, Ensslin A, Hemp A, Fischer M (2015) Vertical and horizontal vegetation structure across natural and modified habitat types at Mount Kilimanjaro. PLoS One 10:e0138822

Rzedowski J (2006) Vegetación de México. Editorial LIMUSA, versión digital, México

Salas-Morales SH, Meave JA (2012) Elevational patterns in the vascular flora of a highly diverse region in southern Mexico. Plant Ecol 213:1209–1220

Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82:913–919

Schnitzer SA, Dalling JW, Carson WP (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. J Ecol 88:655–666

Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecol Lett 14(4):397–406

Schnitzer SA, Bongers F, Burnham RJ, Putz FE (2015) Ecology of lianas. Wiley, Chichester, p 461

Servicio Meteorológico Nacional (2019) Servicio Meteorológico Nacional. Data from 1951–2010. URL: https://smn.cna.gob.mx/es/informacion-climatologica-por-estado?estado=ver

Sharpe JM, Mehltreter K (2010) Ecological insights from fern population dynamics. In: Mehltreter K, Walker LR, Sharpe JM (eds) Fern ecology. Cambridge University Press, Cambridge, pp 61–110

Soto-Esparza M, Giddings-Berger LE (2011) Clima. In: Cruz-Angón A (ed) La biodiversidad en Veracruz: Estudio de estado, vol I. CONABIO, México, pp 35–52

Spehn EM, Körner C (2005) Global Mountain biodiversity assessment, vol 7. Routledge

Taylor A, Burns K (2015) Epiphyte community development throughout tree ontogeny: an island ontogeny framework. J Veg Sci 26:902–910. https://doi.org/10.1111/jvs.12289

Thiébaut V, Velázquez Hernández E (2017) Entre la agricultura y el trabajo urbano: dos estudios de caso en la periferia de Xalapa, una ciudad media del estado de Veracruz (México). LiminaR 15(1):142–162. https://doi.org/10.2536/liminar.v15i1.500

Toledo-Garibaldi M, Williams-Linera G (2014) Tree diversity patterns in successive vegetation types along an elevation gradient in the Mountains of Eastern Mexico. Ecol Res 29:1097–1104

Travieso-Bello A, Gómez R, Moreno-Casasola P (2006) Los cultivos, los pastizales y los acahuales. In: Moreno-Casasola P (ed) Entornos veracruzanos: la costa de La Mancha. Instituto de Ecología, AC, Xalapa, México, pp 261–272

Tryon RM, Tryon AF (1982) Ferns and allied plants with special reference to tropical America. Springer, New York

Villaseñor JL (2016) Checklist of the native vascular plants of Mexico. Rev Mex Biodivers 87(3):559–902. https://doi.org/10.1016/j.rmb.2016.06.017

von Humboldt A (1806) Essai sur la geographie des plantes; accompagné d'un tableau physique des régions équinoxales, accompagné d'un tableau physique des régions équinoctiales. Schoel & Co., Paris

Wang X, Fang J, Sanders NJ, White PS, Tang Z (2009) Relative importance of climate vs local factors in shaping the regional patterns of forest plant richness across Northeast China. Ecography 32:133–142. https://doi.org/10.1111/j.1600-0587.2008.05507.x

Webb LJ (1968) Environmental relationships of the structural types of Australian rain forest vegetation. Ecology 49:296–311

Wesche K, Cierjacks A, Assefa Y, Wagner S, Fetene M, Hensen I (2008) Recruitment of trees at tropical alpine treelines: *Erica* in Africa versus *Polylepis* in South America. Plant Ecol Divers 1:35–46. https://doi.org/10.1080/17550870802262166

Whittaker RH (1956) Vegetation of the great smoky mountains. Ecol Monogr 26(1):1–80

Williams-Linera G, Manson RH, Isunza-Vera E (2002) La fragmentación del bosque mesófilo de montaña y patrones de uso del suelo en la región oeste de Xalapa, Veracruz, México. Madera y Bosques 8(1):73–89

Williams-Linera G, Guillén-Servent A, Gómez-García O, Lorea-Hernández F (2007) Conservación en el centro de Veracruz, México. El bosque de niebla: ¿reserva archipiélago o corredor biológico? In: Halffter G, Guevara S, Melic A (eds) Hacia una cultura de conservación de la diversidad biológica. Sociedad Entomológica Aragonesa Comisión Nacional para el Conocimiento y Uso de la Biodiversidad Comisión Nacional de Áreas Naturales Protegidas Consejo Nacional de Ciencia y Tecnología Instituto de Ecología, A. C. Organización de las Naciones Unidas para, Spain, pp 303–310

Willinghöfer S, Cicuzza D, Kessler M (2012) Elevational diversity of terrestrial rainforest herbs: when the whole is less than the sum of its parts. Plant Ecol 213:407–418

Wolf JHD, Flamenco SA (2003) Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. J Biogeogr 30:1689–1707

Wolf JH (2005) The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. For Eco Manage 212(1–3):376–393.

Wright DH (1983) Species-energy theory: an extension of species-area theory. Oikos, 496–506.

Zotz G (2013) The systematic distribution of vascular epiphytes – a critical update. Bot J Linn Soc 171:453–481

Zotz G, Bader MY (2009) Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. Progress Bot 70:147–170

Chapter 15
Gradients and the Structure of Neotropical Metacommunities: Effects of Disturbance, Elevation, Landscape Structure, and Biogeography

Steven J. Presley and Michael R. Willig

15.1 Introduction

The metacommunity concept explicitly recognizes that the composition of local communities, as well as spatial variation in composition among communities, are influenced by local (e.g., biotic interactions, environmental tolerances, habitat preferences) and regional (e.g., dispersal, habitat fragmentation, landscape structure) processes (Leibold et al. 2004). In contrast, research that focuses on local communities typically ignores aspects of spatial variation, making it difficult to detect mechanisms that mold patterns of local coexistence and that operate at larger spatial scales (Ricklefs 2008). Consequently, examining species distributions along salient environmental gradients represents a complementary approach to the perspective that focuses on arbitrarily circumscribed “local communities” (Ricklefs 2006). This focus on the distributions of species, rather than the coexistence of species, has formed the basis for an evolving framework to evaluate community and metacommunity structure. Moreover, understanding the contributions of regional factors to local community assembly (i.e., how species from a regional species pool are filtered at local spatial scales) has changed perceptions of the community concept to expand it beyond the simple definition of a localized group of interacting species to one in which environmental or spatial distributions of species have become a greater focus for understanding patterns of co-occurrence and local biodiversity (Ricklefs 2008).

Even though the term “metacommunity” had not been coined at the time, early metacommunity work was conducted in the Neotropics to understand patterns of biodiversity (Terborgh 1977) and distribution (Terborgh 1971; Terborgh 1985) of birds along extensive elevational gradients in the Andes. High biodiversity, a

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complex biogeographical history, and a heterogeneous topography associated with orogenic events combine to make the Neotropics an ideal test bed for theories related to ecological gradients and the assembly of communities. In this chapter, we define and use the term "metacommunity structure" to mean an emergent pattern defined by relationships among the distributions of species along a latent environmental gradient (sensu Leibold and Mikkelson 2002; Presley et al. 2010).

Our goals are fourfold: (1) to introduce the conceptual underpinnings of metacommunity ecology, especially as they relate to latent environmental gradients; (2) to outline the methods used to detect metacommunity structures (sensu Leibold and Mikkelson 2002) as well as complementary approaches for identifying the processes that give rise to them; (3) to provide a selective summary of research along gradients in the Neotropics, with a focus on those related to disturbance, elevation, landscape structure and fragmentation, and biogeographical history; and (4) to make recommendations for advancing ecological understanding derived from research on Neotropical metacommunities.

15.2 Metacommunity Ecology

A metacommunity perspective provides ecological insight into spatiotemporal dynamics, because it explicitly considers the structure and organization of communities along environmental gradients, and seeks to understand the local and regional processes that generate these larger-scale patterns (Leibold and Chase 2018). More specifically, a metacommunity is a network of communities that are potentially connected to each other via dispersal of individuals among constituent communities (Leibold and Mikkelson 2002). Local emigration and immigration, when coupled with other spatially explicit ecological processes such as species sorting, habitat filtering, priority effects, or interspecific competition, imbue the network with an emergent structure that corresponds to underlying environmental gradients (Leibold et al. 2004; Leibold 2011).

Since its inception, the domain, theories, and hypotheses associated with metacommunity ecology have received increasing attention, amplification, and refinement (Leibold and Chase 2018). In general, two complementary approaches exist for studying metacommunities: one focuses on processes and the other focuses on patterns. The framework of the process-based approach is built on four archetypical mechanistic models (i.e., neutral theory, patch dynamics, species sorting, mass effects). These models differ in their assumptions about the role of particular processes (e.g., competition, dispersal) and sources of variation (e.g., habitat heterogeneity, species-specific capacity) to make predictions about community composition (Leibold and Chase 2018). The pattern-based approach focuses on patterns of species distributions (e.g., nestedness, Clementsian, Gleasonian) along environmental gradients (Leibold and Mikkelson 2002; Presley et al. 2010). It is predicated on the idea that it is generally useful to identify emergent patterns before hypothesizing the relative importance of mechanisms that give rise to those patterns.

The four archetypical models forming the basis for a mechanistic framework evaluate the contributions of patch heterogeneity (i.e., local processes) and community connectivity (i.e., regional processes) to variation in the composition of communities (Leibold 2011). Species sorting models assume that species are highly responsive to among-site variation in environmental characteristics, and that dispersal is insufficient to support persistence in habitats with negative population growth (Tilman 1982; Chase and Leibold 2003), resulting in species composition being determined exclusively by local environmental factors. Mass effects models also assume that species respond to environmental variation among sites, but that dispersal allows species to persist in less suitable habitats via source-sink dynamics (Holt 1993), resulting in species composition being determined by a combination of local environmental characteristics and their spatial structure. The neutral model (Hubbell 2001) makes predictions about community composition based on the premise that all species are "ecologically equivalent" and do not differ greatly in rates important to metacommunity dynamics (e.g., dispersal, competitive ability, birth rates, death rates). Consequently, species should not exhibit strong associations with local environmental factors and spatial variation among sites should be determined only by spatial processes. Like the neutral model, patch dynamics recognizes the importance of spatial processes in determining the composition of local communities, but patch dynamics incorporates tradeoffs between dispersal and competitive abilities, resulting in temporally dynamic species composition in local communities (Yu et al. 2001). In general, processes and mechanisms associated with multiple archetypical models combine to determine the composition of local communities and variation in composition among local communities (Leibold and Chase 2018).

Metacommunity structure is an emergent property that reflects ecological processes operating at different spatiotemporal scales to mold species distributions along a geographical or environmental gradient (Leibold and Mikkelson 2002; Presley et al. 2010). Throughout the history of ecology, several conceptual models of spatial structure have been identified that describe patterns of species distribution along spatial or environmental gradients. Clements (1916) described an idealized metacommunity structure based on shared evolutionary history and inter-dependent ecological relationships, resulting in coincident range boundaries for groups of species along different portions of an environmental gradient. Each set of communities that harbor a distinct group of species represents a compartment (Lewinsohn et al. 2006), with compartments replacing one another along an environmental gradient. In contrast, Gleason (1926) described a structure arising from species-specific responses to the environment, with local coexistence being a byproduct of similarities in ecological requirements or abiotic tolerances and with species range boundaries occurring idiosyncratically along an environmental gradient. In situations where interspecific competition exists, trade-offs in competitive ability may result in distributions that are more evenly spaced along environmental gradients than are expected by chance (Tilman 1982). Finally, species-poor communities may form nested subsets of increasingly species-rich communities (Patterson and Atmar 1986), with predictable patterns of species gain associated with variation in species-specific characteristics (e.g., dispersal ability, habitat specialization, abiotic tolerance). These idealized structures form the framework representing a continuum of possible structures, from those with high species turnover (e.g., as described by Clements or Gleason) to those with low species turnover (e.g., nested subsets), and from those structures characterized by coincident range boundaries (i.e., as described by Clements) to those characterized by hyperdispersed range boundaries (i.e., as described by Tilman).

As metacommunity ecology endeavors to evaluate how local and regional processes combine to structure local communities and generate variation among them, analytical approaches that use communities as replicates to understand variation in characteristics of communities (e.g., species presences, species abundances, biodiversity) in response to environmental variation (e.g., temperature, precipitation, seasonality, vegetative structure, soil nutrient concentration) or spatial structure (e.g., Moran's eigen vector maps, pairwise distances between sites, elevation) are useful for exploring metacommunity dynamics. These include methods such as canonical correspondence analysis (CCA) (Ter Braak 1986; Ter Braak and Prentice 1988), variation partitioning (Cottenie 2005; Peres-Neto et al. 2006; Peres-Neto et al. 2012), hierarchical partitioning of biodiversity (Jost 2007), and elements of metacommunity structure (Leibold and Mikkelson 2002; Presley et al. 2010, Presley et al. 2019b; Presley 2020). We focus on elements of metacommunity structure (EMS) as a means of exploring how a single approach can elucidate different patterns and structuring mechanisms associated with various gradients and can do so at multiple spatiotemporal scales. Nonetheless, EMS represents a point of departure for understanding spatial structure. Supporting (e.g., canonical correspondence analysis, hierarchical partitioning of biodiversity, general linear models) and complementary (e.g., variation partitioning) analyses are required to determine the nature of environmental gradients along which the metacommunity is structured, the number and locations of compartments, or the relative influence of potential structuring mechanisms. Therefore, we first outline the EMS approach, and then highlight approaches that are commonly used to understand metacommunity structures in empirical examples selected from the Neotropics.

15.3 Elements of Metacommunity Structure

The common conceptual aspect to all nonrandom metacommunity structures is that the ranges of species in these metacommunities are molded by a common environmental gradient, with sites reflecting environmental variation along this gradient. Similarly, a fundamental principle in ecology is that species occurrences along an environmental gradient represent underlying continuous distributions. More specifically, species should occupy sites that represent a coherent range of the underlying environmental gradient (i.e., a species that occurs at temperatures of 10 and 20 °C should also occur at all temperatures between those values). For an entire metacommunity to exhibit coherence, the distributions of a preponderance of species must be associated with the same environmental gradient (Presley et al. 2010). However, the extent and location of species distributions along the gradient may differ (i.e., although responding to the same gradient, responses to the gradient are not the same), such that coherent metacommunities may evince many different discernible structures. In contrast, if the distributions of a preponderance of species do not respond to the same environmental gradient, coherence is not achieved, and structure is considered to be random (Leibold and Mikkelson 2002).

The Elements of Metacommunity Structure comprise three attributes of species distributions (i.e., coherence, species range turnover, and range boundary clumping) that combine to discriminate among many nonrandom metacommunity structures (Fig. 15.1: Leibold and Mikkelson 2002; Presley et al. 2010). EMS is based on an indirect gradient analysis (Ter Braak and Prentice 1988) that uses reciprocal averaging (also called correspondence analysis) to determine the gradient along which sites and species are organized. These gradients are generally called "latent" environmental gradients, because they are not directly measured or explicitly incorporated in the ordination, but are defined by the responses of species to environmental

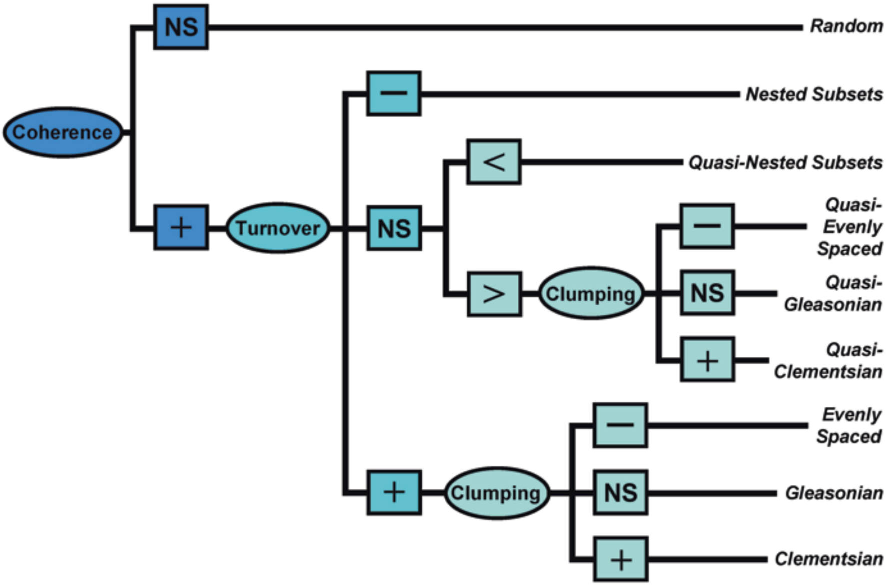

Fig. 15.1 A diagrammatic representation (after Presley et al. 2010) of combinations of the three elements of metacommunity structure (ovals) that differentiate among five idealized metacommunity structures and four quasistructures. Possible results for tests for each element appear in squares: a positive sign (+) indicates results consistent with greater coherence, range turnover, or range boundary clumping than expected by chance, a negative sign (−) indicates results that are consistent with less range turnover or range boundary clumping than expected by chance, and NS indicates results that are indistinguishable from chance expectations. Quasistructures arise when the range turnover is less than (<) or greater than (>) the mean from the simulations, but not significantly so. (Note: there is no ecological or conceptual basis to expect metacommunities to exhibit less coherence than expected by chance; therefore, this analysis is conducted as a one-tailed test (Presley et al. 2019b))

variation. These latent gradients represent variation in biotic and abiotic environmental factors that are important for defining the distributions of species. Typically, subsequent analyses (e.g., canonical correspondence analysis, variation partitioning, or general linear models) are used to determine the relationship of the latent gradient to variation in important environmental factors that determine the distributions of species (e.g., Presley and Willig 2010; Presley et al. 2009; Presley et al. 2011; Presley et al. 2012; López-González et al. 2012; Dallas and Presley 2014; de la Sancha et al. 2014; Cisneros et al. 2015; Willig et al. 2011; Willig et al. 2021). Importantly, coherence, range turnover, and range boundary clumping are evaluated with respect to particular latent gradients (Presley et al. 2009; Presley et al. 2019b) and are based on incidence (presence versus absence) rather than abundance. This aspect of analysis explicitly recognizes that multiple gradients can structure the same metacommunity and that a different structure can manifest along different gradients (e.g., Presley et al. 2009; López-González et al. 2012). The explicit identification of a gradient along which species are distributed distinguishes the EMS approach from other popular and superficially similar approaches, such as co-occurrence analyses (Stone and Roberts 1990; Presley 2020), which ignore any potential underlying gradient.

Reciprocal averaging is an ordination method that simultaneously optimizes the proximity of species that have similar distributions and the proximity of communities that have similar species compositions (Gauch et al. 1977). Effectively, this ordination allows the entire suite of species distributions (i.e., occurrences at sites in the metacommunity) to define the response gradient (Presley et al. 2009) and is considered to be the best indirect ordination procedure for this purpose. If a preponderance of species in a metacommunity does not respond to the same environmental gradient, the metacommunity is noncoherent and has random structure (Fig. 15.1). Importantly, random structure does not indicate that species occur in communities at random, only that they occur at random with respect to each other (i.e., that their distributions are not defined by the same environmental gradient). In contrast, coherent structures are characterized by species distributions that are molded by a common environmental gradient, with the locations and extents of the distributions of species along the gradient, and the relationships among these distributions defining the structure of the metacommunity (Fig. 15.1). Nested structures are defined by negative range turnover (i.e., less turnover than expected by chance) along the environmental gradient. In these structures, the distributions of species with narrow environmental tolerances or habitat preferences are contained within those of species with wider environmental tolerances or habitat preferences. In contrast, Clementsian, Gleasonian, and evenly spaced structures are defined by positive range turnover (i.e., more range turnover than expected by chance) along the gradient. Quasi-structures have range turnover that is indistinguishable from that expected by chance, but have structures that are otherwise consistent with the conceptual underpinning of Clementsian, evenly spaced, Gleasonian, or nested distributions (Presley et al. 2010). Range boundary clumping is used to distinguish among three types of nestedness as well as among structures with positive range turnover (Leibold and Mikkelson 2002; Presley et al. 2010). In the case of significantly nested metacommunities, clumped range boundaries suggest that species are lost (or added) in groups along a gradient (i.e., not randomly with respect to each other). For metacommunities with significant range turnover, positive range boundary clumping corresponds to the existence of compartments (Clementsian structure), negative range boundary clumping corresponds to evenly spaced structures, and range boundary clumping that does not differ from chance is consistent with Gleasonian structure (idiosyncratic range boundary locations along the gradient).

This framework originally contained the concept of a "checkerboard metacommunity structure" associated with the idea of negative coherence (i.e., a metacommunity that is less coherent than expected by chance). Checkerboards originally described geographically interspersed patterns of mutual exclusion by pairs of ecologically similar species (MacArthur et al. 1972; Diamond 1975). Subsequently, this concept was expanded to entire metacommunities by adding the criterion that distributions of each mutually exclusive pair should be independent from other such pairs (Leibold and Mikkelson 2002). Critically, this definition is nearly identical to that of random metacommunity structure (i.e., noncoherence). The only difference between random and checkerboard metacommunity structures is that each species has one mutually exclusive association in a checkerboard, with all other interspecific associations being random. The dominant mechanism for both of these structures is randomness, and the developed methodology cannot effectively distinguish between random and checkerboard structures (Presley et al. 2019b). Consequently, the idea that checkerboard structures can be detected via analyses of coherence should be abandoned, and analyses of coherence should be implemented as one-tailed tests (Schmera et al. 2018; Presley 2020).

15.4 Useful Methods for Understanding Metacommunity Structure and Structuring Mechanisms

Although EMS can identify particular emergent structures based on the distributions of species, complementary or supplementary analyses are required to (1) identify the gradient that structures the metacommunity, (2) determine the number and location of compartments in compartmentalized structures, and (3) evaluate the relative importance of structuring mechanisms. The underlying gradient along which a metacommunity is structured can be identified via relatively simple approaches such as linear or rank correlation analyses, or by more comprehensive approaches such as canonical correspondence analysis (Ter Braak 1986; Ter Braak and Prentice 1988) or generalized linear mixed-effects models (Bates et al. 2015). The number of compartments, as well as the species or sites that comprise each compartment, can be identified via hierarchical partitioning of biodiversity (Jost 2007) and cluster analysis (Legendre and Legendre 2012), respectively. Finally, variation partitioning can discern the relative contributions of local environmental factors and spatial processes to variation among communities in their composition (Cottenie 2005; Peres-Neto et al. 2006; Peres-Neto et al. 2012).

15.4.1 Canonical Correspondence Analysis

Canonical correspondence analysis (CCA) is a multivariate technique (Ter Braak 1986) and an extension of correspondence analysis (reciprocal averaging) that uses environmental variation among sites to understand variation in community composition. CCA uses linear combinations of the environmental variables to identify ordination axes, such that variation in community composition is directly related to environmental variation. Consequently, the meaning of ordination axes is easy to uncover. Importantly, CCA is an efficient ordination technique when species have bell-shaped response curves to environmental gradients (e.g., Gaussian distributions), making it more appropriate for analyzing data on community composition and environmental variables than is canonical correlation analysis (Ter Braak 1986). The significance of relationships between species composition and environmental factors is determined via Monte Carlo simulations (Ter Braak and Prentice 1988). Because CCA is a marriage of reciprocal averaging and multiple regression, the axes are defined by the same ordination as used in analyses for EMS, resulting in a powerful method for determining associations of environmental factors with metacommunity structure (López-González et al. 2012).

15.4.2 Hierarchical Partitioning of Biodiversity

Understanding the spatial organization of biodiversity is necessary for determining the scales at which mechanisms operate to generate variation in the composition of communities and the abundances of species. More specifically, β-diversity has emerged as an important concept because of its relationships with multifunctionality of ecosystems and the manners in which the hierarchical configuration of biodiversity varies with respect to environmental or geographical gradients (Wilsey et al. 2005; Higgins 2010; Mori et al. 2018; Willig and Presley 2019). Patterns of biodiversity are often scale dependent, highlighting the role of spatial compartmentalization in heterogeneous landscapes (e.g., Scheiner et al. 2000; Jackson and Fahrig 2014). In general, biodiversity may be partitioned into three spatial components: alpha (α), beta (β), and gamma (γ) partitions. α estimates mean biodiversity of local sites, β estimates the degree of compositional differentiation among sites, and γ represents the biodiversity for a region regardless of its constituent spatial units. Biodiversity at larger spatial scales (γ components) can be driven by local biodiversity (α components), if little compositional variation characterizes communities (Gering and Crist 2002), or can be driven by among-site variation (β components), which signals the importance of spatial heterogeneity at landscape or regional scales (Belmaker et al. 2008; Willig and Presley 2019). The contributions of α- or β-partitions to γ-partitions are largely dependent on the nature of environmental variation within a domain of interest (Freestone and Inouye 2006) and the ways in which different species respond to spatial variation in the environment.

Biodiversity can be partitioned using an additive ($\gamma = \alpha + \beta$) or a multiplicative model ($\gamma = \alpha \times \beta$). Only β differs between these models; α and γ are the same (Jost 2007). In the additive model, β represents the average number of species in the metacommunity that do not occur at a site ($\beta = \gamma - \alpha$), whereas in the multiplicative model, β represents the number of distinct communities or compartments in the metacommunity ($\beta = \gamma/\alpha$). An advantage of the additive model is that all partitions represent effective numbers of species. This facilitates comparisons of the proportion of regional diversity (γ) that is a consequence of the diversity of local communities (α) versus a consequence of variation among local communities (β). However, within the context of metacommunity structure, multiplicative β estimates the effective number of distinct communities (i.e., compartments in Clementsian structures) that exist along an environmental gradient, with particular metacommunity structures indicating the form of transition (pattern of species turnover) between compartments (de la Sancha et al. 2014). In addition, cluster analysis can be used to identify which groups of sites or species represent compartments (multiplicative β estimates only the number of compartments, not the number or identity of the sites that compose them).

15.4.3 Variation Partitioning

Variation partitioning (also called variance decomposition) can be used to determine the relative importance of sets of environmental factors as well as spatial characteristics in structuring communities (Borcard et al. 1992; Cottenie 2005; Legendre 2007; Legendre et al. 2012). Variation partitioning can be used to evaluate variation among populations (e.g., species abundance) or among communities (e.g., relative abundances of each species in a metacommunity). In addition, partitions can represent single explanatory variables (e.g., temperature, canopy height) or entire suites of variables (e.g., abiotic factors, soil characteristics, percent cover of vegetation types). Variation partitioning identifies unique variation explained by each set of explanatory variables, as well as shared variation explained by combinations of sets of explanatory variables. This method provides considerable flexibility depending on data structure, facilitating the partitioning of explained variation based on two, three, four, or more sets of explanatory variables.

The classical use of variation partitioning to understand relative contributions of mechanisms that structure metacommunities involves use of a set of environmental factors and a set of spatial factors to calculate four components of variation: (1) total variation in species composition accounted for by both environmental and spatial variables, (2) proportion of variation in species composition accounted for by the environmental variables after accounting for effects of spatial variables (unique environment partition), (3) proportion of variation in species composition accounted for by spatial variables after accounting for effects of environmental variables (unique spatial structure), and (4) proportion of variation in species composition shared by both environmental and spatial variables (i.e., spatial structure in environmental variation). These partitions can be used to evaluate the relative contributions of mechanisms associated with each of four dispersal-mediated mechanistic models (i.e., neutral theory, patch dynamics, species sorting, mass effects) thought to contribute to the structure of metacommunities (Stevens et al. 2007; López-González et al. 2015; Cisneros et al. 2016; Leibold and Chase 2018).

15.5 Empirical Gradients

We summarize metacommunity structures as determined by EMS and the mechanisms or processes that structure these metacommunities along a variety of empirical gradients that commonly occur in Neotropical settings, including gradients associated with elevation, landscape structure, and historical biogeography, and do so for gradients representing a broad range of spatial extents (from less than 1 km to more than 2000 km). In addition, we explore the utility of a wide range of complementary methods (e.g., partitioning of biodiversity, variation partitioning, canonical correspondence analysis, cluster analysis, simple correlations or regressions) used to understand how spatial environmental variation structures these Neotropical metacommunities. We do not endeavor to present a comprehensive review of all Neotropical metacommunity research. Rather, we provide an overview of the current understanding of metacommunity structure in the Neotropics associated with a variety of ecological gradients, taxonomic groups, structuring mechanisms, and spatial scales.

15.5.1 Elevation

Environmental gradients in montane settings are useful for evaluating processes that mold spatial patterns of species composition (e.g., Terborgh 1971; Terborgh 1985; Presley et al. 2011; Presley et al. 2012; Willig et al. 2011; López-González et al. 2012; Willig and Presley 2016). Along elevational gradients, dramatic variation in environmental characteristics (e.g., solar insolation, temperature, humidity, precipitation, habitat type) occurs over short geographical extents, such that ecological mechanisms, rather than biogeographical or historical mechanisms, mold biological responses. This contrasts greatly with latitudinal gradients, for which considerably greater geographical distances are necessary to produce comparable variation in environmental drivers, making it difficult to disentangle effects associated with ecological mechanisms from those associated with biogeographical processes (Willig and Presley 2013; Willig and Presley 2018). Elevational gradients in biodiversity and species composition continue to be of interest, because effects of climate change are expected to manifest soonest and most strongly at high elevations, especially in tropical environs (Colwell et al. 2008; Malhi et al. 2010). This may be particularly true to the extent that tropical species have evolved in environments with less intra-annual variability in climatic conditions, leading to narrower niche breadths compared to their extratropical counterparts (Janzen 1967).

Changes in abiotic characteristics (e.g., temperature, precipitation) and floral associations (physiognomy and species composition) are predictable along elevational gradients; however, these changes differ in form. Abiotic characteristics change gradually, but not necessarily linearly, with elevation (Barry 2008), whereas variation in vegetation often exhibits more-or-less discrete boundaries recognized as habitat types or life zones (Martin et al. 2007; Barone et al. 2008). Because habitat specialization and responses to abiotic characteristics are important in defining faunal ranges, the structure of metacommunities along elevational gradients is contingent on which of these mechanisms predominantly determines the distributions of species. If habitat boundaries along an elevational gradient are more-or-less discrete, and many species in a metacommunity have distributions determined by habitat preferences or specializations, multiple species with range boundaries that are coincident with ecotones should result in the clumped range boundaries characteristic of Clementsian structure. Alternatively, if species distributions are primarily determined by responses to abiotic characteristics that change gradually with elevation, species-specific responses to abiotic variation should result in randomly associated range boundaries that are characteristic of Gleasonian structure. Finally, elevational variation in temperature combined with resource abundance and diversity may create physiological constraints associated with energy budgets (Speakman and Thomas 2003), resulting in nested elevational distributions. More specifically, species that are highly constrained by environmental conditions will have distributions that are nested within those of species that can maintain populations along larger portions of the gradient (Presley et al. 2012).

In addition to responses to elevational variation in abiotic factors, resource abundance, and habitat types, interspecific interactions (e.g., competition, predation) may affect metacommunity structure along elevational gradients. These effects are an aspect of processes associated with species sorting, as other species represent part of the environment to which particular species respond (Leibold and Chase 2018). Species sorting requires taxa to perform (i.e., survive and reproduce) differently under different conditions. Within the context of elevational gradients, different habitat types represent the environmental setting and can contribute to the outcome of interspecific interactions such as competition (e.g., species A excludes species B from montane rainforest, but species B excludes species A from cloud forest). Such mutual exclusion may be actively maintained via competitive interactions or may represent habitat associations due to the legacy of historical competition (i.e., the "ghost of competition past"; Connell 1980).

Metacommunity structure along Neotropical elevational gradients has been evaluated for gastropods in northeastern Puerto Rico (Presley et al. 2011; Willig et al. 2011; Willig et al. 2021), for bats, rodents, and passerines in the Peruvian Andes (Presley et al. 2012), and for amphibians, bats, and nonvolant small mammals in Mexico (Ochoa-Ochoa and Whittaker 2014; López-González and Lozano 2015). These metacommunities exhibited a number of structures, including nested

(Peruvian bats), Clementsian (Peruvian rodents, Mexican amphibians, Mexican bats, and Puerto Rican gastropods), quasi-Clementsian (Puerto Rican Gastropods and Peruvian passerines), Gleasonian (Puerto Rican gastropods, Mexican amphibians, and bats of the Mexican Sierra Madre Occidental), and quasi-Gleasonian (Puerto Rican gastropods, Mexican amphibians, and small mammals of the Mexican Sierra Madre Occidental) patterns. Despite this variety of structure, transitions between habitat types (i.e., ecotones) along elevational gradients were important for defining the elevational ranges and elevational range boundaries of species in many metacommunities. In general, Neotropical metacommunities have shown distinctive lowland and upland faunal compartments, with the transition between rainforest and cloud forest often defining the boundary between compositionally distinct communities (Terborgh 1985; Patterson et al. 1998; Willig et al. 2011; Presley et al. 2012).

In Puerto Rico, gastropods were evaluated along paired elevational transects designed to decouple underlying environmental mechanisms (Willig et al. 2011): a palm forest transect was restricted to forest dominated by sierra palm, which occurs along the length of the gradient, whereas a mixed forest transect included montane rainforest, cloud forest, and elfin forest (Willig et al. 2011; Willig et al. 2013). The palm forest metacommunity was quasi-Gleasonian, with structure determined by species-specific responses to elevational variation in abiotic factors (Willig et al. 2011). However, when elevational variation in forest type was superimposed on the gradient of abiotic variation in the mixed-forest transect, gastropods exhibited a Clementsian structure with compartmentalization associated with changes in forest type (Barone et al. 2008; Willig et al. 2013). In the absence of elevational variation in forest type (i.e., along the palm forest transect), gastropod species exhibited broader elevational distributions than in the mixed forest transect. This arose in part because of relaxed energetic constraints, as palm forest sites have greater primary production and concentrations of essential nutrients compared to sites from mixed forest transects at the same elevation (Willig et al. 2011). Importantly, these differences in structure between transects were maintained through time, with sampling a decade later indicating quasi-Clementsian and Gleasonian structure for the mixed forest and palm forest transects, respectively. For gastropods, abiotic variation gave rise to positive turnover along the gradient and variation in forest types contributed to the location of range boundaries, indicating that both biotic and abiotic components of elevational variation structure these metacommunities.

Metacommunity structure was evaluated for trees along the same mixed-forest transect that was used for gastropods (Barone et al. 2008). Trees along this transect exhibited Clementsian structure, with boundary clumping suggesting the locations of three compartments distinguished by ecotones between montane rainforest and cloud forest, as well as between cloud forest and elfin forest. This combination of results for trees and gastropods suggests that the metacommunity structure of plants may play a critical role in affecting metacommunity structure of animals.

Although the same ecotone (e.g., the transition between montane rainforest and cloud forest) can be a catalyst for compositional change in faunas along elevational gradients, the ways in which metacommunities are structured by such ecotones can

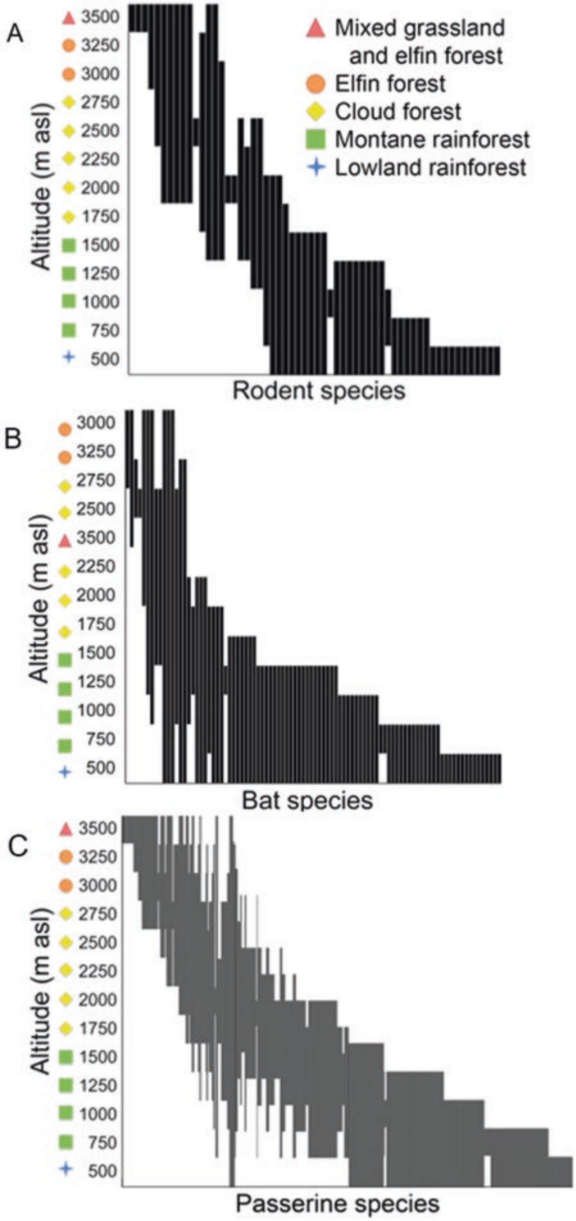

Fig. 15.2 Distributional profiles of each species (black vertical bars) as ordered via reciprocal averaging for (**a**) rodents, (**b**) bats, and (**c**) passerines along an elevational gradient in Peru. Placement of sites (identified by elevation) along the primary axis of correspondence exactly maintained elevational order after reciprocal averaging for rodents and birds, and closely approximated it for bats. (Modified from Presley et al. 2012)

be taxon-specific (Fig. 15.2). The rainforest-cloud forest ecotone in Manu (Peruvian Andes) is an important boundary for compositional change of rodents, bats, and passerines, but different metacommunity structures arose due to autecological differences among faunas (Presley et al. 2012). Rodents have low vagility compared to their volant counterparts (birds and bats), resulting in greater habitat specialization.

Rodents in Manu were specialists of lowland rainforest, montane rainforest, cloud forest, or elfin forest. Even rodents that are habitat generalists only spanned portions of the gradient, generally occupying habitats that were exclusively above or exclusively below the cloud condensation point. Indeed, the cloud condensation point represents a critical biotic feature of the elevational gradient that contributes to the Clementsian structure of the rodent metacommunity (Fig. 15.2a). Bats in the Peruvian Andes generally do not specialize on particular forest types: nearly all bats occur in the lowland rainforest, with species loss occurring with increasing elevation, resulting in a nested structure (Fig. 15.2b). Even so, range boundaries of bats are clumped in the nested structure, with the most dramatic loss of bat species occurring at the ecotone between montane rainforest and cloud forest. The nested structure of bats is a function of direct (colder temperatures) and indirect (reduced resource diversity and abundance) effects of elevational variation in climate (Speakman and Thomas 2003; von Helversen and Winter 2003). Passerines in the Peruvian Andes formed two compartments (Terborgh 1985; Patterson et al. 1998; Presley et al. 2012): one below the cloud condensation point (lowland and montane rainforests) and one above the cloud condensation point (cloud and elfin forests; Fig. 15.2c). However, the transition zone between low- and high-elevation compartments for passerines was relatively broad and indistinct compared to that of rodents (Fig. 15.2). This broad transition zone for birds may arise from the relaxation of environmental constraints during particular seasons, allowing birds to move up or down the gradient for short time periods to track seasonal changes in resources.

15.5.2 Landscape Structure

The Anthropocene is characterized by pervasive and increasingly dominant effects of human activities on the world's biomes (Monastersky 2015). One of the defining human activities of the Anthropocene is habitat conversion for agricultural, urban, or suburban land uses. Habitat loss and fragmentation have resulted in a considerable loss of biodiversity (Newbold et al. 2015) and altered species distributions (Brown et al. 2016). Consequently, understanding how changing landscapes affect populations, communities, and metacommunities is a grand challenge of the twenty-first Century (National Research Council 2001).

Landscape ecology examines the influence of spatial heterogeneity on ecological systems, and explicitly addresses the importance of landscape composition (i.e., the relative proportions of different land cover types within a focal area) and configuration (the spatial arrangement of land cover types within a focal area) in determining ecological patterns and processes (Presley et al. 2019a). Humans have reshaped over 77% of the terrestrial biosphere (Ellis et al. 2010), resulting in natural (e.g., primary or mature forest) and seminatural (e.g., secondary forest) lands that are embedded within a mosaic of land converted for human use (Fig. 15.3). In general, three anthropogenic landscape-level processes affect the abundance and distribution of species: (1) loss of native vegetation, (2) fragmentation (i.e., formation of

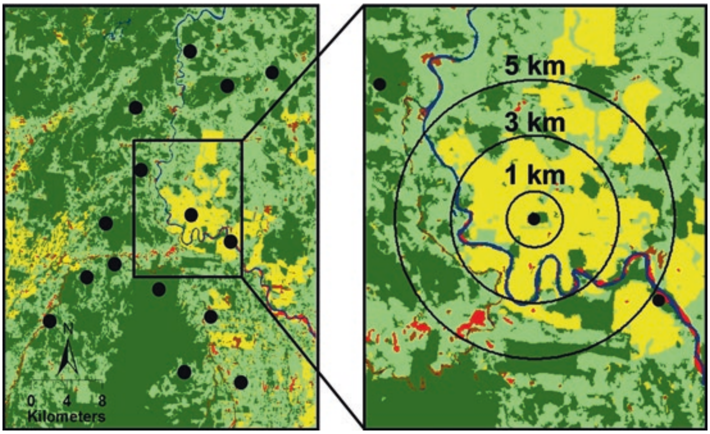

Fig. 15.3 An example of sites distributed in a heterogeneous landscape that are subject to various forms of land use (left), and an example of multiple focal scales for evaluation of effects of landscape structure on populations, communities, or metacommunities in a focal patch (right). Black dots represent sampling locations, dark green is forest, light green is pasture, yellow is agriculture, blue is water, and red is human settlements

isolated patches of habitat), and (3) matrix quality (i.e., utility of anthropogenically modified habitats to species). Landscape composition reflects the proportion of natural and anthropogenically modified land cover types, whereas landscape configuration measures their spatial arrangement and fragmentation, as well as the connectivity between habitat patches (Fahrig 2003; Tscharntke et al. 2012). Because species perceive their environment at different spatiotemporal scales, landscape dynamics are inherently scale sensitive (Gorresen et al. 2005; Lyra-Jorge et al. 2010). Consequently, a multiscale approach is necessary to ensure that the scale of response to landscape structure is included in experimental designs (Fig. 15.3).

Few studies have evaluated effects of landscape structure on the metacommunity structure of Neotropical biotas. In human-modified landscapes, the a priori assumption is that metacommunities will be nested, with more sensitivity to disturbance forming a gradient in which heavily modified landscapes harbor communities that are perfect subsets of communities from less disturbed landscapes (Meyer and Kalko 2008; Struebig et al. 2008). However, Neotropical metacommunities in disturbed landscapes generally do not exhibit nested subsets. This is true for bats in Costa Rica (Cisneros et al. 2015) or the Amazon (Martins 2016), as well as for small mammals (de la Sancha et al. 2014; Delciellos et al. 2018) or amphibians (Schiesari and Corrêa 2016) in Atlantic Forest. In contrast, nested structure did manifest for bats in Atlantic Forest (Teixeira 2019; Gomes 2020). In Caribbean Lowland Forests of Costa Rica, phyllostomid bats exhibited Gleasonian structure during the dry season and Clementsian structure during the wet season (Cisneros et al. 2015). Distance between forest patches and forest edge density were the most important factors in structuring Costa Rican bat metacommunities during the dry and wet seasons, respectively. Rather than nested distributions along a landscape-modification gradient, some species (mostly gleaning animalivores of the subfamily Phyllostominae) occurred primarily in less modified, highly forested landscapes, whereas other species (mostly frugivores and nectarivores of the glossophagine and stenodermatine subfamilies) occurred primarily in highly modified landscapes dominated by agricultural land covers (Cisneros et al. 2015).

Small mammals in the highly fragmented Atlantic Forest exhibited Clementsian structure (de la Sancha et al. 2014). Despite the loss of ~90% of the original extent of Atlantic Forest to human activities (Ribeiro et al. 2009), small mammal metacommunity structure reflected the presence of multiple centers of endemism (Costa and Leite 2012). These areas of endemism correspond to locations of historical refugia and vicariance events associated with large rivers. The maintenance of historical patterns is particularly noteworthy, because many small mammal species of Atlantic Forest effectively disperse through matrix habitats to other forest fragments and can maintain populations in nonforest habitats as well (Umetsu and Pardini 2007; Umetsu et al. 2008). In a smaller-scale study of small mammals within a single center of endemism in Atlantic Forest, Clementsian structure also manifested, driven primarily by small mammal responses to patch size and to variation in vertical forest structure (Delciellos et al. 2018). In combination, these studies demonstrate that the same metacommunity structure may occur at multiple spatial scales, but with different mechanisms driving structure at each scale.

In a large-scale study of Atlantic Forest, phyllostomid bats exhibited a quasi-Clementsian structure that was associated with spatially structured environmental variation, as well as the habitat loss from human activities (Gomes 2020). However, structure was foraging guild specific: analyses of only herbivores and of only carnivores exhibited Clementsian and nested structures, respectively. Nonetheless, spatially structured environmental variation was the driving force behind each of these structures (nested and Clementsian), showing that the same process can give rise to different metacommunity structures in the same system. In a small-scale study of the effects of fragmentation on metacommunity structure of bats in Atlantic Forest, nested (phyllostomid bats) and quasi-nested (animalivorous bats) structures manifested (Teixeira 2019). For both groups of bats, species found in smaller fragments represented a subset of species occurring in larger fragments or in continuous forest, and metacommunity structure reflected a combination of disturbance tolerance and inter-fragment dispersal ability of species (Teixeira 2019).

Bats in a fragmented landscape in southern Amazonia exhibited noncoherence, failing to respond to a shared environmental gradient, whereas herbivorous bats (frugivores and nectarivores) exhibited quasi-Clementsian structure (Martins 2016). Interestingly, this fragmented landscape was just south of intact, continuous Amazonian forest, with that forest likely harboring source populations for most of the 44 species of bat captured in forest fragments. Consequently, herbivorous species generally formed three groups based on their responses to open habitats and forest fragment sizes: (1) species that preferred large fragments and landscapes near the intact continuous forest (e.g., *Chiroderma trinitatum*, *Vampyressa pusilla*, *Platyrrhinus brachycephalus*); (2) species that preferred small forest fragments with an abundance of forest edges and secondary forest (e.g., *Artibeus concolor*, *A. anderseni*, *A. glauca*, *Lichonycteris obscura*, *Platyrrhinus lineatus*), which produce an abundance of fruit and flowers on which these bats feed, and (3) species that were ubiquitous (e.g., *A. lituratus*, *A. planirostris*, *Carollia perspicillata*, *Rhinophylla pumilio*), using all forest fragments regardless of size or location (Martins 2016). However, forest fragments do not only differ in size, they also differ in plant species composition and in physical structure, and this variation in forest physiognomy has differential effects on bat populations (Martins et al. 2017). Gleaning animalivorous phyllostomines are particularly sensitive to vertical forest structure, as they require an open stratum between the understory and canopy to forage effectively (Meyer et al. 2008). These multidimensional and complex responses of bats to this fragmented landscape likely account for the lack of coherence when the entire fauna was considered as a group. This demonstrates that even random metacommunity structure may arise from ecological responses and that autecological knowledge is paramount for understanding the species- or guild-specific responses within a single fauna.

15.5.3 Biogeographical Variation

Metacommunity structure can be evaluated at multiple spatial scales as well as in a hierarchical fashion (Presley et al. 2010). The crucial aspects of scale in a metacommunity context are that the definitions of a site (i.e., community) and the extent of the environmental domain are consistent with the theoretical questions addressed in the analysis, as well as with the explanatory factors and mechanisms invoked to account for empirical patterns. For example, to evaluate effect of landscape structure on metacommunity structure of forest fragments (Cisneros et al. 2015; Schiesari and Corrêa 2016; Delciellos et al. 2018), communities are restricted to forest fragments, explanatory variables are characteristics of fragments and the surrounding landscape, and the spatial extent of the metacommunity is confined to one habitat type to ensure that only variation in landscape structure, and not variation in habitat type, affects the composition of communities. In contrast, to evaluate biogeographical attributes on metacommunity structure in an island system (Presley and Willig 2010), communities are defined by islands, explanatory variables are island characteristics, and the spatial extent is a group of islands that represent variation in important biogeographical factors (e.g., area, habitat heterogeneity, distance to source populations). Moreover, focal scale and extent are critical a priori considerations, because metacommunities may evince distinctive structures corresponding to different spatial extents, with different underlying mechanisms associated with each extent (Presley and Willig 2010; López-González et al. 2012; Brasil et al. 2017; Alves-Martins et al. 2019).

Clementsian metacommunity structures that occur at large spatial scales may represent an agglomeration of structures that occur at smaller spatial scales, with distinctive structures associated with each compartment (Fig. 15.4). Because Clementsian metacommunities are defined by compartments (i.e., groups of species

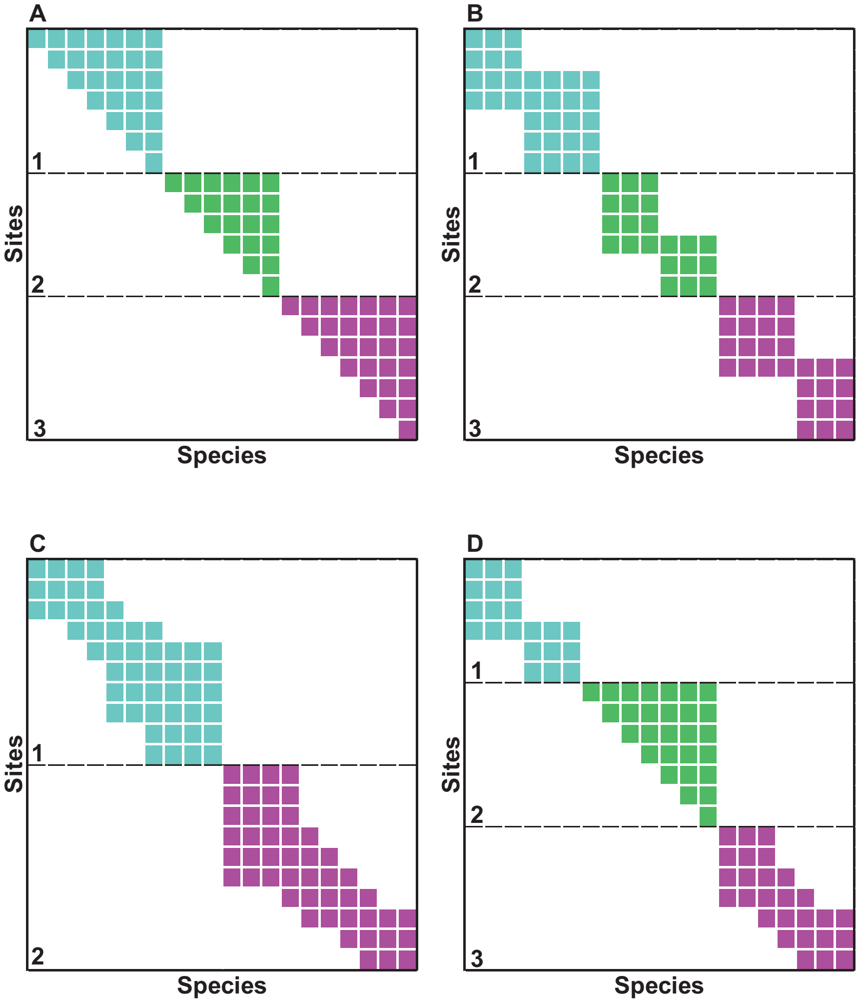

Fig. 15.4 Four exemplar metacommunities comprising 20 species and 20 sites that evince Clementsian structure (perfect coherence, positive turnover, and clumped range boundaries), but that exhibited different types of structure within compartments. Compartments within each metacommunity are delineated by dashed horizontal lines. Species in metacommunity (**a**) exhibit nested structure (negative turnover), with evenly spaced species loss in each compartment. Species in metacommunity (**b**) exhibit Clementsian structure (positive turnover and clumped boundaries) in each compartment. Species in metacommunity (**c**) exhibit Gleasonian structure (positive turnover and randomly distributed boundaries) in each compartment. Species in metacommunity (**d**) exhibit Clementsian (compartment 1), nested (compartment 2), or Gleasonian (compartment 3) structure. (Modified from Presley et al. 2010)

with similar distributions, which typically results in groups of sites with similar species composition; Lewinsohn et al. 2006), identification of compartments provides the basis for multiscale analysis of metacommunity structure. Natural biogeographical divisions are often an ideal basis for identifying compartments, because they generally have distinct species pools (Presley and Willig 2010; López-González et al. 2012; de la Sancha et al. 2014; Brasil et al. 2017; Alves-Martins et al. 2019; González-Trujillo et al. 2020). When easily identifiable biogeographical divisions are not available, cluster analysis (Legendre and Legendre 2012) can be used to identify compartments for analysis at smaller spatial scales. The structure of each compartment in a Clementsian metacommunity, particularly for analyses done at large spatial scales, may be analyzed independently to uncover additional gradients or structures at smaller spatial scales that are embedded within the larger structure.

Caribbean bats exhibited strong Clementsian structure with compartments corresponding to three island groups (the Bahamas, Greater Antilles, and Lesser Antilles; Fig. 15.5a). Each compartment had distinctive bat species composition, and this was true for all bat species, for only herbivorous species, and for only carnivorous species (Presley and Willig 2010). The continental sources of colonization were unique for each island group, contributing to their distinctive assemblages (Koopman 1989). For analyses restricted to only one island group, the structure and number of compartments was related to the number of primary sources of colonization and the geographical relationships of those sources of colonization to islands (Fig. 15.5a), all of which represent biogeographic mechanisms.

The Lesser Antillean bat fauna had two primary sources of colonization (Greater Antilles and northern South America), resulting in Clementsian structure with two compartments for analyses based on only carnivorous bats or on only herbivorous bats. However, the relative influence of each source of colonization was guild specific. Carnivore compartments spanned the northern half of the Lesser Antilles, south to Guadeloupe (bats of Greater Antillean origin), and islands south of Guadeloupe (bats of South American origin), whereas, the transition between herbivore compartments was considerably further south, with the southern compartment restricted to Grenada, St. Vincent, and the Grenadines (Fig. 15.5b). The unique geographical patterns associated with each guild created three distinct bat communities when considering all Lesser Antillean bat species: (1) Grenada, St. Vincent, and the Grenadines, (2) northern islands south to and including Guadeloupe, and (3) islands between and including Marie Galante and St. Lucia (Fig. 15.5b). Because bats are highly vagile, it is likely that most species capable of dispersal from continental sources to newly formed and inhabitable islands colonized those areas during the same geological timeframe. As a result, distinct communities of bats from opposite ends of an archipelago would systematically colonize islands until they met. In this transition area, priority effects (Paine 1977) may allow species to prevent further dispersal of ecologically similar species.

Greater Antillean bats had nested structure, with most (26 of 38) bat species from this island group having evolved on the large islands such as Cuba, Hispaniola, or Jamaica (Baker and Genoways 1978). The ranges of Greater Antillean bats formed nested subsets, with a core group of widespread species that is augmented by

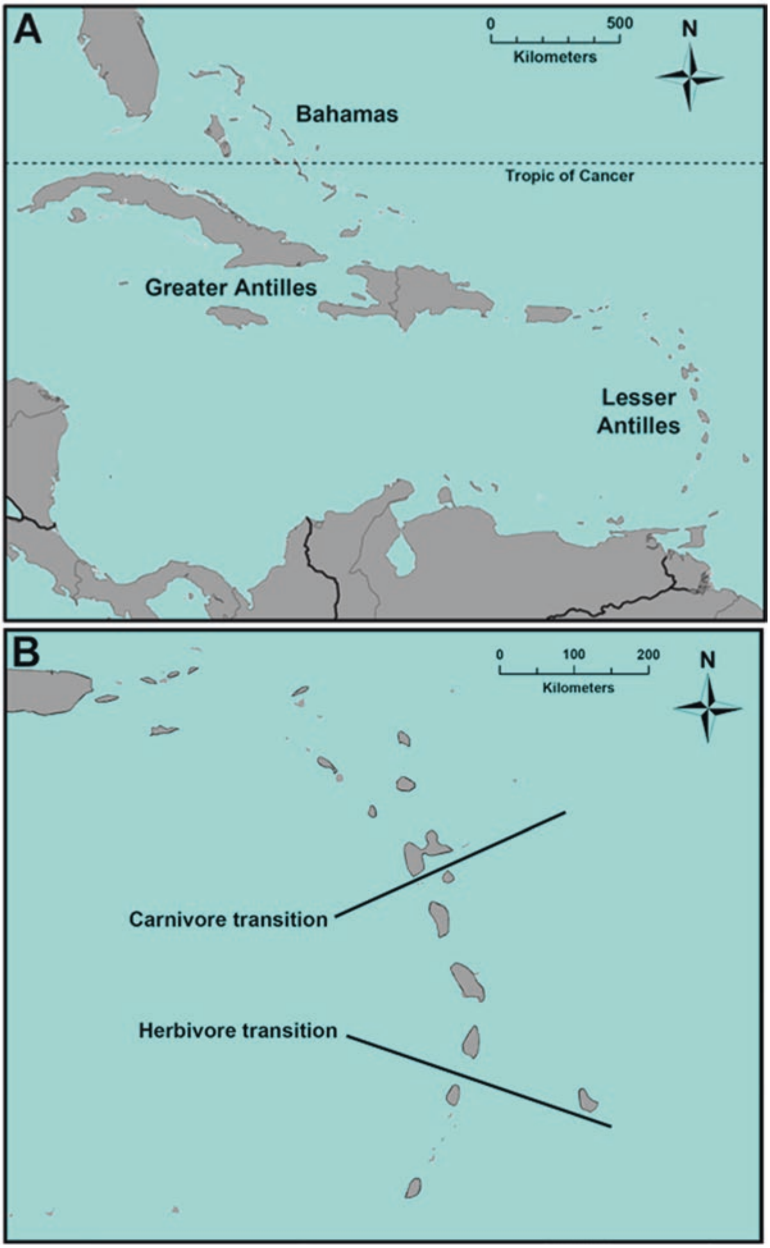

Fig. 15.5 Maps of (**a**) the Caribbean Islands, indicating the locations of the Bahamas, Greater Antilles, and Lesser Antilles in relation to continental America, and (**b**) the Lesser Antilles indicating the different locations of transitions between northern and southern compartments associated with carnivorous and herbivorous bats in their respective Clementsian structures. (Modified from Presley and Willig 2008)

restricted-range species that occur only on the large islands on which they originated as well as on some nearby small islands. The geographical configuration of the Greater Antilles may predispose the creation of nested subsets via speciation and the subsequent dispersal of those species. The greater area represented by larger islands can support more individuals and more habitat types, increasing the number of species that can maintain sustainable populations (Rosenzweig 1995). These factors increase the likelihood that larger islands served as sites of species origination more often than did smaller islands. Finally, larger islands in the Greater Antilles were closer to continental sources of colonization (Florida, Yucatán Peninsula) than were smaller islands. Consequently, populations on larger, western islands replaced continental populations as the primary sources of colonization for smaller, eastern islands of the Greater Antilles. Differential dispersal of species, specialization on locally abundant resources, and size-mediated hierarchical habitat distributions on islands are mechanisms that likely enhanced nestedness for the Greater Antillean bat metacommunity (Presley and Willig 2008).

Mexican bats exhibited Clementsian structure with two compartments associated with a distinct boundary at the tropical-temperate transition zone (López-González et al. 2012). This metacommunity was structured by spatial variation in vegetation and climate, with dry, seasonal, and temperate habitats at one end of the gradient (temperate compartment), and with wet, aseasonal, and tropical habitats at the other end (tropical compartment). This Nearctic-Neotropical dichotomy characterizes much of the Mexican biota (Ortega and Arita 1998). Separate analyses of metacommunity structure for each compartment revealed structures along a heterogeneity gradient associated with topography traversing relatively flat homogeneous regions to topographically heterogeneous regions. Nonetheless, each compartment exhibited distinct structure. The temperate compartment evinced a nested structure, with communities in elevationally heterogeneous sites being species rich, and communities in flat regions being species poor. Widely distributed species were largely temperate in origin and able to persist in deserts, tropical lowlands, and xeric highlands, whereas restricted range species were of tropical origin and occurred only in tropical lowland habitats. In contrast, the tropical compartment exhibited Clementsian structure with a lowland rainforest compartment inhabited by species of tropical origin, and a distinct compartment comprising montane and lowland habitats, including montane rainforests, dry semideciduous forests, wetlands, and tropical scrubland. The second compartment harbored tropical species that occur in a wide range of habitats, as well as species of temperate origin that are euryecious and inhabit tropical highlands.

Amazonian metacommunities comprising damselflies (Zygoptera) or dragonflies (Anisoptera) exhibited Clementsian or quasi-Clementsian structures at large spatial scales that spanned multiple biogeographical regions (Brasil et al. 2017; Alves-Martins et al. 2019). In general, compartments represented areas of endemism: two compartments representing two biogeographical regions (Brasil et al. 2017) or four compartments representing four biogeographical regions (Alves-Martins et al. 2019). Random structures manifested when metacommunities associated with each compartment (defined by areas of endemism) were analyzed separately, indicating that the distributions of species within biogeographical regions were not structured by a common gradient (Brasil et al. 2017; Alves-Martins et al. 2019). These legacies of biogeographical history persist despite the pervasive impact of human activities as reflected in the water quality of streams, including centuries-long effects associated with a densely populated farming community that has inhabited one region since pre-Colombian times. Streams in each region were classified as negligibly or heavily impacted by human activities (Brasil et al. 2017). The negligibly impacted metacommunity produced the same two-compartment Clementsian structure that was detected when all communities were considered together; however, the heavily impacted metacommunity exhibited a quasi-nested structure, despite including streams from two areas of endemism. This indicates a change in metacommunity structure due to human activities that has erased historical patterns of species distribution. The communities from the region that has hosted farming communities for centuries are nested within those of the region that have only recently been impacted by agricultural activities, presenting evidence of the long-term effects of human activities on the composition and distribution of species.

Between the Amazon and Atlantic Forest are drier habitats (e.g., Cerrado and Caatinga) that isolate these two large wet forests from each other. However, the hilltops in Caatinga and Cerrado often receive greater rainfall and support wet forests, called “brejos de altitude,” which act as high-elevation forest refugia surrounded by open and drier habitats. Metacommunity structure of rodents was studied at small and large spatial scales in this dry zone (Braga 2016). At the smaller scale, rodents in the Brazilian State of Pernambuco exhibited nested structure with clumped species loss. All species occurred in brejos, with a subset of those species occurring in surrounding Caatinga. The species that occurred only in brejos represented remnant populations of species of Atlantic Forest origin. In contrast, at the larger spatial scale, the rodent metacommunity spanning the Brazilian States of Cearâ, Pernambuco, and Alagoas exhibited quasi-nested structure with clumped species loss. Again, brejos harbored greater species richness with surrounding drier and open habitats supporting only a subset of the species found on hilltops (Braga 2016). However, the structure in this case revealed three compartments: (1) one at end of the gradient comprising species of Amazonian origin that are restricted to northwestern brejos (in Cearâ) as well as species found in the surrounding Caatinga, (2) one at the other end of the gradient comprising species of Atlantic Forest origin that are restricted to southeastern brejos (in Pernambuco and Alagoas) as well as species found in the surrounding Caatinga, and (3) one in the middle of the gradient comprising only species found in lowland xeric habitats of the Caatinga (Braga 2016). This analysis supports the idea that both the Amazon and Atlantic Forests were more expansive in the past, and that brejos represent refugia that support remnant hilltop populations of Amazonian and Atlantic Forest species amidst a xeric habitat that acts as a barrier to dispersal between the two mesic forest types. This observation corresponds to the hypothesis of Mares et al. (1985) for small mammals of the Caatinga, which posits that species persist by inhabiting climatic interstices, those microhabitats that retain moisture for much of the year.

15.5.4 Other Environmental Gradients

Metacommunities may be structured along environmental gradients that are not associated with topography, anthropogenically induced changes to landscapes, or historical biogeography. For example, gradients may be associated with heterogeneity in edaphic features, patterns of seasonality, or gradients of disturbance. Moreover, these types of gradients may be spatially structured (Bloch and Klingbeil 2016) or may represent ecological gradients that are spatially interspersed (i.e., not spatially structured) or spatiotemporally dynamic throughout the landscape (Willig et al. 2021). Importantly, multiple gradients may independently or interactively structure metacommunities in complex manners (Presley et al. 2009).

Paraguayan bats exhibited different metacommunity structures along each of two environmental gradients (Presley et al. 2009). Paraguay exhibits strong east-west precipitation and temperature gradients that combine with edaphic heterogeneity to create complex patterns of habitat distribution that range from sand dunes and thorn-scrub forests in the northwest, to seasonally flooded palm savannahs and marshlands near the Paraguay, Paraná, and Pilcomayo Rivers, to tall humid evergreen forests in the east (Hayes 1995). This temperature-precipitation gradient supported two compartments, with insectivorous bats, particularly molossids, dominating communities in dry and flooded habitats, and frugivorous bats dominating communities in evergreen forests (Presley et al. 2009). In contrast, a gradient of edaphic features supported three compartments: one associated with the well-drained western habitats, one associated with seasonally flooded habitats, and one associated with eastern evergreen forests. Although insectivores and frugivores dominated the well-drained and evergreen forest compartments, respectively, the compartment associated with seasonally flooded habitats harbored distinctive communities comprising combinations of insectivores, frugivores, piscivores, and sanguinivores. Such complexity is unsurprising, as Paraguay represents a subtropical-temperate nexus within which a number of phytogeographic regions (e.g., Cerrado, Chaco, Interior Atlantic Forest, and Pantanal) interdigitate (Willig et al. 2000).

The tabonuco rainforest in northeastern Puerto Rico is a disturbance-mediated environment that experiences frequent hurricane-induced disturbances (Brokaw et al. 2012). Over the past few decades, this forest has experienced a combination of press (climate change) and pulse (Hurricanes Hugo in 1989, Georges in 1998, and Maria in 2017) disturbances that significantly altered the structure of the forest (Uriarte et al. 2019). Nonetheless, terrestrial gastropods have consistently maintained compartmentalized structures (Clementsian or quasi-Clementsian) despite repeated, severe pulse disturbances and secondary succession occurring in the midst of droughts and increasing temperatures associated with global climate change

(Willig et al. 2021). All gastropods in this metacommunity have geographical ranges that extend beyond the study area; however, species specialize on particular ecological niches in the forests that are differentiated by plant composition and physiognomy related to successional stage after major hurricanes. Consequently, compartments in the metacommunity are dynamic in space and time, with one group of species occurring primarily in mature, closed-canopy habitats and another group of species occurring primarily in early successional habitats. Both groups of species effectively track their preferred microhabitats through space and time to maintain the same ecological compartments and same metacommunity structure (Willig et al. 2021). In contrast to many of the examples presented here, this environmental gradient represents small-scale environmental variation within a single forest type and an annual pattern that has persisted for almost three decades.

Similar to the stable metacommunity structure of Puerto Rican gastropods, the metacommunity structure of semiarid plant communities in the Zapotitlán Valley of Puebla, México, evinced consistent Clementsian structure over a 23-year period (Jiménez et al. 2020). This metacommunity consistently comprised three compartments associated with cardonal (unbranched columnar cacti), tetechera (branched columnar cacti), and shrubland plant formations that occur along a gradient of soil characteristics (e.g., texture, soil class, organic matter). However, the proportion of communities that represent each plant formation changed through time. Although the number of cardonal communities remained unchanged over the past 23 years, 75% of tetechera communities (the most common community type in 1980) were classified as shrubland communities in 2003. This conversion of tetechera to shrubland may represent a natural successional progression, as columnar cacti change soil characteristics, making them more suitable for the shrubs, legumes, and agave that characterize shrublands. Both of these long-term studies (tropical gastropods and semi-arid plants) indicate the importance of supplementary analyses to understand temporal dynamics, even when emergent metacommunity structures do not change through time.

Benthic metacommunities in Todos os Santos Bay (Bahia, Brazil) generally exhibited nested structures along a salinity-contamination gradient (Teixeira Alves et al. 2020). Sites in marine environments supported high species richness; as salinity decreases along the gradient, sites progressively lost species, and were relatively depauperate at freshwater sites. The majority of species in these communities are of marine origin, with tolerance for low salinity and shallow water determining the extent of their incursions into estuarine environments. Although most structures were nested or quasinested, the strongest patterns of nestedness occurred in the estuary with the greatest level of anthropogenic activity and contamination (Teixeira Alves et al. 2020). Some species were intolerant of freshwater itself, whereas other species were intolerant of contamination from the freshwater sources. The combination of low salinity and high contamination resulted in strongly nested patterns, with particularly depauperate communities in proximity to contaminated, freshwater sources. Biogeographical effects may inhibit the ability to detect effects of human activities on metacommunity structure at large spatial scales (e.g., Atlantic Forest Bats and nonvolant small mammals), requiring smaller-scale studies of communities that share a single species pool to effectively evaluate anthropogenic effects on the distributions of species and emergent metacommunity structures.

In a study of the invertebrates of intertidal habitats of Puerto Rico, the metacommunity exhibited Gleasonian structure (Bloch and Klingbeil 2016). Because coastal habitats in Puerto Rico are human-dominated systems, anthropogenic effects were expected to affect the biodiversity and composition of communities, as well as the structure of the metacommunity. This was not the case. Rather, a gradient of wave exposure, a combination of wave power and wave height, structured the metacommunity, with species evincing idiosyncratic responses to tidal variation. Wave action subjects intertidal organisms to strong hydrodynamic forces that mediate biological interactions and define physical aspects of intertidal habitats. These factors continue to structure Puerto Rican intertidal communities and metacommunities despite increasing anthropogenic activity in these habitats.

15.5.5 Empirical Neotropical Metacommunities: Summary

Metacommunity approaches have revealed spatial structures associated with many types of environmental gradients in the Neotropics, and have done so from small to large spatial scales and in a hierarchical fashion. Neotropical metacommunities are structured by gradients associated with abiotic variation, edaphic features, habitat type, disturbance, contamination, land use, or by the legacies of historical factors. The flexibility of the EMS approach has been used to generate and test hypotheses associated with a wide range of ecological, biogeographical, evolutionary, and conservation questions by simultaneously evaluating mechanisms that affect spatial patterns at vastly different time scales (e.g., biogeographical history versus modern land use change). Large-scale metacommunity structures are typically associated with historical factors (evolutionary histories, biogeography), whereas smaller-scale patterns arise in response to variation in local factors (e.g., habitat type, disturbance history) or anthropogenic activities (e.g., habitat loss and fragmentation, pollution, and contamination). Finally, ecological differences between taxa have resulted in taxon-specific structure, confirming that the study of multiple metacommunities in the same system may be required to understand the relative influence of historical and contemporary mechanisms.

15.6 Future Directions for Metacommunity Research in the Neotropics

Future research on metacommunities in the Neotropics will no doubt contribute to ecological understanding, because the region (1) includes some of most dramatic and extensive elevational gradients in the world; (2) represents an extensive latitudinal gradient, spanning nearly 47°, from 23.44° S to 23.44° N Latitude; (3) harbors some of the greatest biological diversity on Earth, strongly contributing to comparative understanding; (4) comprises a broad diversity of terrestrial biomes within which gradients can be studied; (5) is home to a broad variety of freshwater systems, ranging from the Amazon and its tributaries, to the world's largest wetland, the Pantanal; and (6) reflects a complex biogeographical history, including the formation of many island systems, recent connection of North and South American continents, and orogeny of several mountain ranges. This unique combination of complex and extensive environmental gradients combined with high biodiversity makes the Neotropics ideal for conceptual and empirical advancements in metacommunity ecology.

Conducting structured, preplanned, large-scale ecology has always been a challenge, and that challenge remains today. As a consequence, the majority of metacommunity ecology in the Neotropics is born of opportunity rather than design. Two aspects of biodiversity monitoring in the Neotropics can improve our understanding of metacommunity dynamics. First, long-term studies that entail repeated sampling at regular intervals to quantify the extent and nature of changes in metacommunities along gradients subject to combinations of press (e.g., eutrophication, contamination, pollution, climate change) and pulse (e.g., extreme weather events, logging) disturbances are necessary to understand spatiotemporal dynamics. Such studies would benefit from concomitant monitoring of salient abiotic, biotic, or climatic factors so that the nature of latent environmental gradients can be identified with confidence. Second, comparative studies of multiple taxa (e.g., bats, rodents, birds, amphibians, arthropods, trees, fungi) along the same spatial or environmental gradients should be executed to determine which groups are particularly vulnerable to changing environmental conditions, as well as to identify emerging conservation concerns. In addition to new strategies for documenting metacommunities through space and time, development of new approaches for understanding both the spatial structure of metacommunities as well as the processes and mechanisms that give rise to them would benefit metacommunity ecology. Of particular utility would be development of new quantitative methods to objectively identify suites of sites that comprise compartments within Clementsian metacommunities or within nested metacommunities that evince compartmentalized species loss. The three elements of metacommunity structure are all aspects of species distributions; however, the abundances of species vary throughout those distributions. Development of quantitative methods that can characterize metacommunity structure based on considerations of species abundances rather than only their incidence would lend greater insight into spatial structure of metacommunities. Finally, metacommunity ecology would benefit from the incorporation of manipulative studies to facilitate the identification of particular mechanisms that underly the structure of current or future metacommunities.

Metacommunity ecology has made great strides in understanding patterns along environmental gradients, and work in the Neotropics has been crucial to many of these developments. The continued development of methods for characterizing spatial patterns and identifying the local and regional mechanisms that give rise to them should be leveraged by dedicated long-term research programs (e.g., the Long-Term Ecological Research program of the U.S. National Science Foundation, Pesquisas Ecolôgicas de Longa Duraçâo of the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico) in Neotropical areas to provide unprecedented opportunity to understand ecological dynamics and its causation at multiple spatial scales. This is particularly urgent as the tempo and mode of human-induced disturbances associated with the Anthropocene will likely have great impact on the structure and functioning of vital ecological systems in the New World tropics, and beyond.

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References

Alves-Martins F, Brasil LS, Juen L, de Marco JP, Stropp J, Hortal J (2019) Metacommunity patterns of Amazonian Odonata: the role of environmental gradients and major rivers. PeerJ 7:e6472

Baker RJ, Genoways HH (1978) Zoogeography of Antillean bats. In: Gill FB (ed) Zoogeography of the Caribbean. Special Publications, Academy of Natural Sciences, Philadelphia, pp 53–98

Barone JA, Thomlinson J, Anglada-Cordero P, Zimmerman JK (2008) Metacommunity structure of tropical forests along an elevational gradient in Puerto Rico. J Trop Ecol 24:1–10

Barry RG (2008) Mountain weather and climate, 3rd edn. Cambridge University Press, Cambridge, MA

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Belmaker J, Ziv Y, Shashar N, Connolly SR (2008) Regional variation in the hierarchical partitioning of diversity in coral-dwelling fishes. Ecology 89:2829–2840

Bloch CP, Klingbeil BT (2016) Anthropogenic factors and habitat complexity influence biodiversity but wave exposure drives species turnover of a subtropical rocky inter-tidal metacommunity. Mar Ecol 37:64–76

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055

Braga CAdC (2016) Estrutura de metacomunidades de rodentia das regiões serranas do nordeste do Brasil: uma análise ecológica e biogeográfica. PhD Dissertation, Universidade Federal do Rio de Janeiro, Rio de Janeiro

Brasil LS, Vieira TB, de Oliveira-Junior JMB, Dias-Silva K, Juen L (2017) Elements of metacommunity structure in Amazonian Zygoptera among streams under different spatial scales and environmental conditions. Ecol Evol 7:3190–3200

Brokaw N, Crowl TA, Lugo AE, McDowell WH, Scatena FN, Waide RB, Willig MR (eds) (2012) A Caribbean Forest tapestry: the multidimensional nature of disturbance and response. Oxford University Press, New York

Brown CJ, O'Connor MI, Poloczanska ES, Schoeman DS, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Pandolfi JM, Parmesan C, Richardson AJ (2016) Ecological and methodological drivers of species' distribution and phenology responses to climate change. Glob Chang Biol 22:1548–1560

Chase JM, Leibold MA (2003) Ecological niches. University of Chicago Press, Chicago

Cisneros LM, Fagan ME, Willig MR (2015) Season-specific and guild-specific effects of anthropogenic landscape modifications on metacommunity structure of tropical bats. J Anim Ecol 84:373–385

Cisneros LM, Fagan ME, Willig MR (2016) Environmental and spatial drivers of taxonomic, functional, and phylogenetic characteristics of bat communities in human-modified landscapes. PeerJ 4:e2551

Clements FE (1916) Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, DC

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261

Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138

Costa LP, Leite YLR (2012) Historic fragmentation shaping vertebrate diversification in the Atlantic Forest biodiversity hotspots. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: the history and geography of recent Neotropical mammals. University of Chicago Press, Chicago, pp 283–306

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett 8:1175–1182

Dallas T, Presley SJ (2014) Relative importance of host environment, transmission potential, and host phylogeny to the structure of parasite metacommunities. Oikos 123:866–874

de la Sancha N, Higgins CL, Presley SJ, Strauss RE (2014) Metacommunity structure in a highly fragmented forest: has deforestation in the Atlantic Forest altered historic biogeographic patterns? Divers Distrib 20:1058–1070

Delciellos AC, Borges-Júnior VNT, Prevedello JA, Ribeiro SE, Braga C, Vieira MV, Cerqueira R (2018) Seasonality in metacommunity structure: an empirical test in the Atlantic Forest. Landsc Ecol 33:1769–1783

Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JL (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, MA, pp 342–444

Ellis EC, Goldewijk KK, Siebert Lightman SD, Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700–2000. Glob Ecol Biogeogr 19:589–606

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Freestone AL, Inouye DB (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. Ecology 87:2425–2432

Gauch HG, Whittaker RH, Wentworth TR (1977) A comparative study of reciprocal averaging and other ordination techniques. J Ecol 65:157–174

Gering JC, Crist TO (2002) The alpha–beta–regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. Ecol Lett 5:433–444

Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:7–26

Gomes LAC (2020) Estrutura de Metacomunidade de Morcegos Filostomídeos (Mammalia, Chiroptera) na Mata Atlântica Brasileira. PhD Dissertation, Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro

González-Trujillo JD, Donato-Rondon JC, Muñoz I, Sabater S (2020) Historical processes constrain metacommunity structure by shaping different pools of invertebrate taxa within the Orinoco basin. Divers Distrib 26:49–61

Gorresen PM, Willig MR, Strauss RE (2005) Multivariate analysis of scale-dependent associations between bats and landscape structure. Ecol Appl 15:2126–2136

Hayes FE (1995) Status, distribution, and biogeography of the birds of Paraguay. Monogr Field Ornithol 1:1–230

Higgins CL (2010) Patterns of functional and taxonomic organization of stream fishes: inferences based on α, β, and γ diversities. Ecography 33:678–687

Holt RD (1993) Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs R, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 77–88

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Jackson HB, Fahrig L (2014) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24:52–62

Janzen DJ (1967) Why mountain passes are higher in tropical montane landscapes. J Anim Ecol 78:315–327

Jiménez M, Zavala-Hurtado JA, Martorell C, Vega E, Sandoval-Palacios E, Hernández-Cárdenas IG, Rendón-Aguilar B (2020) Despite dramatic local changes, the metacommunity structure of a semiarid scrub remains unaffected after 23 years. Bot Sci 98:264–277

Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439

Koopman KF (1989) A review and analysis of the bats of the West Indies. In: Wood CS (ed) Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Gainesville, pp 635–643

Legendre P (2007) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. J Plant Ecol 1:3–8

Legendre P, Legendre L (2012) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. J Plant Ecol 1:3–8

Legendre P, Borcard D, Roberts DW (2012) Numerical ecology. Elsevier, Oxford

Leibold MA (2011) The metacommunity concept and its theoretical underpinnings. In: Scheiner SM, Willig MR (eds) Theory of ecology. University of Chicago Press, Chicago, pp 163–184

Leibold MA, Chase JM (2018) Metacommunity ecology. Princeton University Press, Princeton

Leibold MA, Mikkelson GM (2002) Coherence, species turnover, and boundary clumping: elements of meta-community structure. Oikos 97:237–250

Leibold MA, Holyoak M, Mouquet M, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613

Lewinsohn TM, Inácio Prado P, Jordano P, Bascompte J, Olesen JM (2006) Structure in plant–animal interaction assemblages. Oikos 113:174–184

López-González C, Lozano A (2015) Metacommunity structure of small mammals in western Mexico: is the San Pedro-Mezquital River a biological Corridor? Southwest Nat 60:327–335

López-González C, Presley SJ, Lozano A, Stevens RD, Higgins CL (2012) Metacommunity analysis of Mexican bats: environmentally mediated structure in an area of high geographic and environmental complexity. J Biogeogr 39:177–192

López-González C, Presley SJ, Lozano A, Stevens RD, Higgins CL (2015) Ecological biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta diversity, and environmental gradients to species richness and composition patterns. Ecography 38:261–272

Lyra-Jorge MC, Ribeiro MC, Ciocheti G, Tambosi LR, Pivello VR (2010) Influence of multiscale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. Eur J Wildl Res 56:359–368

MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. Ecology 53:330–342

Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S (2010) Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Glob Chang Biol 16:3171–3175

Mares MA, Willig MR, Lacher TE Jr (1985) The Brazilian Caatinga in South American zoogeography: tropical mammals in a dry region. J Biogeogr 12:57–69

Martin PH, Sherman RE, Fahey TJ (2007) Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. J Biogeogr 34:1792–1806

Martins ACM (2016) Morcegos em paisagens fragmentadas na Amazônia: uma abordagem em múltiplas escalas. PhD Dissertation, Universidade de Brasília, Brasília

Martins ACM, Willig MR, Presley SJ, Marinho-Filho J (2017) Effects of forest height and vertical complexity on abundance and biodiversity of bats in Amazonia. For Ecol Manag 391:427–435

Meyer CFJ, Kalko EKV (2008) Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. Divers Distrib 14:644–654

Meyer CFJ, Fründ J, Pineda Lizano W, Kalko EKV (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. J Appl Ecol 45:381–391

Monastersky R (2015) Anthropocene: the human age – editorial. Nature 519:144–147

Mori AS, Isbell F, Seidel F (2018) β-diversity, community assembly, and ecosystem functioning. Trends Ecol Evol 33:549–564

National Research Council (2001) Grand challenges in the environmental sciences. National Academic Press, Washington, DC

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Díaz S, Echeverria-Londoño S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann JPW, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520:45–50

Ochoa-Ochoa LM, Whittaker RJ (2014) Spatial and temporal variation in amphibian metacommunity structure in Chiapas, Mexico. J Trop Ecol 30:537–549

Ortega J, Arita HT (1998) Neotropical-nearctic limits in middle America as determined by distributions of bats. J Mammal 79:772–783

Paine RT (1977) Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory, vol 12. Special Publications of the Academy of Natural Sciences, Philadelphia, pp 245–270

Patterson BD, Atmar A (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. Biol J Linn Soc 28:65–82

Patterson BD, Stotz DF, Solari S, Fitzpatrick JW (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. J Biogeogr 25:593–607

Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625

Peres-Neto PR, Leibold MA, Dray S (2012) Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. Ecology 93:14–30

Presley SJ (2020) On the detection of metacommunity structures. Community Ecol 21:103–106

Presley SJ, Willig MR (2008) Composition and structure of Caribbean bat (Chiroptera) assemblages: effects of inter-island distance, area, elevation, and hurricane-induced disturbance. Glob Ecol Biogeogr 17:747–757

Presley SJ, Willig MR (2010) Bat metacommunity structure on Caribbean islands and the role of endemics. Glob Ecol Biogeogr 19:185–199

Presley SJ, Higgins CL, López-González C, Stevens RD (2009) Elements of metacommunity structure of Paraguayan bats: multiple gradients require analysis of multiple axes of variation. Oecologia 160:781–793

Presley SJ, Higgins CL, Willig MR (2010) A comprehensive framework for the evaluation of metacommunity structure. Oikos 11:908–917

Presley SJ, Willig MR, Bloch CP, Castro-Arellano I, Higgins CL, Klingbeil BT (2011) A complex metacommunity structure for gastropods along an elevational gradient. Biotropica 43:480–488

Presley SJ, Cisneros LM, Patterson BD, Willig MR (2012) Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents and birds. Glob Ecol Biogeogr 21:968–976

Presley SJ, Cisneros LM, Klingbeil BT, Willig MR (2019a) Landscape ecology of mammals. J Mammal 100:1044–1068

Presley SJ, Mello JHF, Willig MR (2019b) Checkerboard metacommunity structure: an incoherent concept. Oecologia 190:323–331

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142:1141–1153

Ricklefs RE (2006) Evolutionary diversification and the origin of the diversity-environment relationship. Ecology 87:S3–S13

Ricklefs RE (2008) Disintegration of the ecological community. Am Nat 172:741–750

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Scheiner SM, Cox SB, Willig MR, Mittelbach GG, Osenberg C, Kaspari M (2000) Species richness, species-area curves and Simpson's paradox. Evol Ecol Res 2:791–802

Schiesari L, Corrêa DT (2016) Consequences of agroindustrial sugarcane production to freshwater biodiversity. GCB Bioenergy 8:644–657

Schmera D, Podani J, Botta-Dukát Z, Erős T (2018) On the reliability of the elements of metacommunity structure framework for separating idealized metacommunity patterns. Ecol Indic 85:853–860

Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 430–490

Stevens RD, López-González C, Presley SJ (2007) Geographical ecology of Paraguayan bats: spatial integration and metacommunity structure of interacting assemblages. J Anim Ecol 76:1086–1093

Stone L, Roberts A (1990) The checkerboard score and species distributions. Oecologia 85:74–79

Struebig MJ, Kingston T, Zubaid A, Mohd-Adnan A, Rossiter SJ (2008) Conservation value of forest fragments to Palaeotropical bats. Biol Conserv 141:2112–2126

Teixeira TSM (2019) Bats in a fragmented world. Doctoral Dissertation, Queen Mary University of London

Teixeira Alves A, Petsch DK, Barros F (2020) Drivers of benthic metacommunity structure along tropical estuaries. Sci Rep 10:1739

Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179

Ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Adv Ecol Res 18:271–317

Terborgh J (1971) Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52:23–40

Terborgh J (1977) Bird species diversity on an Andean elevational gradient. Ecology 58:1007–1019

Terborgh J (1985) The role of ecotones in the distribution of Andean birds. Ecology 66:1237–1246

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biol Rev Camb Philos Soc 87:661–685

Umetsu F, Pardini R (2007) Small mammals in a mosaic of forest remnants and anthropogenic habitats—evaluating matrix quality in an Atlantic forest landscape. Landsc Ecol 22:517–530

Umetsu F, Metzger JP, Pardini R (2008) Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. Ecography 31:359–370

Uriarte M, Thompson J, Zimmerman JK (2019) Hurricane Maria tripled stem breaks and double tree mortality relative to other major storms. Nat Commun 10:1362

von Helversen O, Winter Y (2003) Glossophagine bats and their flowers: costs and benefits for plants and pollinators. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 346–397

Willig MR, Presley SJ (2013) Latitudinal gradients of biodiversity. In: Levin S (ed) Encyclopedia of biodiversity, vol 4, 2nd edn. Academic, Waltham, pp 612–626

Willig MR, Presley SJ (2016) Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. J Trop Ecol 32:421–436

Willig MR, Presley SJ (2018) Latitudinal gradients of biodiversity: theory and empirical patterns. In: DellaSala DA, Goldstein MI (eds) The encyclopedia of the Anthropocene, vol 3. Elsevier, Oxford, pp 13–19

Willig MR, Presley SJ (2019) The spatial configuration of taxonomic biodiversity along a tropical elevational gradient: α-, β-, and γ-partitions. Biotropica 51:104–116

Willig MR, Presley SJ, Owen RD, Lopez-Gonzalez C (2000) Composition and structure of bat assemblages in Paraguay: a subtropical-temperate interface. J Mammal 81:386–401

Willig MR, Presley SJ, Bloch CP, Castro-Arellano I, Cisneros LM, Higgins CL, Klingbeil BT (2011) Tropical metacommunities along elevational gradients: effects of forest type and other environmental factors. Oikos 120:1497–1508

Willig MR, Presley SJ, Bloch CP, Alvarez J (2013) Population, community, and metacommunity dynamics of terrestrial gastropods in the Luquillo Mountains: a gradient perspective. In: González G, Willig MR, Waide RB (eds) Ecological gradient analyses in a tropical landscape, ecological bulletins, vol 54. Wiley, Oxford, pp 117–140

Willig MR, Presley SJ, Cullerton EI (2021) A canonical metacommunity structure in a hurricane-mediated system: an environmentally consistent but spatially dynamic pattern. Oecologia 196:919–933

Wilsey BJ, Chalcraft DR, Bowles CB, Willig MR (2005) Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. Ecology 86:1178–1184

Yu DW, Wilson HB, Pierce NE (2001) An empirical model of species coexistence in a spatially structured environment. Ecology 82:1761–1771

Chapter 16
Socioecological Gradients: Contesting Traditional Ecoclines to Explain the High Biocultural Diversity of the Andean Verdant

Fausto Sarmiento, Andreas Haller, Domenico Branca, Christiam Aguirre, Vladimir Kremsa, Carla Marchant, and Masahito Yoshida

16.1 Introduction

There is consensus to advance science with unorthodox narratives generated with new discoveries, different perspectives, or challenging innovation altogether. However, it is also consensual that these mountain narratives, like the waves in fluid

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water or air, move along the time scales with different dynamics and distinctive rhythms, generating a symphony of knowledge, which can only be integrated with the crosscutting ability of montology as a convergent science (Sarmiento 2020). Indeed, applied montology is the appropriate avenue for developing an environmental awareness of the whole mountainscape. With the wise trend of *consilience* (Wilson 1998) and the untested hype of noetic science (Nickell 2010), we contribute this chapter with the objective of increasing our epistemology of mountains to include them as socioecological landscapes and not as mere ecosystems.

To achieve our objective, we need to emphasize on scaling, as scalar considerations – whether in space or in time – are at the crux of our understanding of the mountain environment, hence one of the most important indicators for geographical inquiry. Geographers know that most tangible entities, and particularly the intangible ones, require intervention of design, construction, usage, or neglect due to the political ecology exerted at the research onset (Zimmerer and Bassett 2003). Therefore, along with Sauer (1925) and Head (2017) they agree that mountains are cultural landscapes and that the time scale is not important only for the passing of time –be hours, days, months or years, as phenology would put it– but also, and mainly, for the *historicity* that affected the current state of affairs. We concur and offer cases whereby the cultural heritage is intimately linked with natural heritage in the minds and hearts of mountain communities (Aguirre et al. 2021).

16.1.1 Geographic Inquiry

Geographers also know that the physical characteristics define abiotic conditions that explain the community structure, composition, and change of floral and faunal assemblages (Austin et al. 1994). However, Myster (2018) points out that the two *physicalities* are explicit and can be established with haptic methods, but the third factor is a dynamic two-way errand and could be delimited with thresholds. However, the significance of the declivity, is the difficulty of using indirect gradient analysis for questions on instrumentation, monitoring, and bias offered by the ways in which the biota or co-inhabitants of the mountains (including humans and other than humans) have transformed the mountain space to create a meaningful and protected place. Thus, *placialities* of mountains differ widely depending on the cultural background, scientific affiliation, worldview, and territorial appropriation, in what Haller and Branca (2022) call “cosmophany” and are the culprits for the rich biocultural diversity observed in socioecological production landscapes and seascapes (SEPLS). These are the result of the *natureculture*, “a synthesis of nature and culture that recognizes their inseparability in ecological relationships that are both biophysically and socially formed” (Malone and Ovenden 2016, see also Fuentes 2010; Haraway 2003), something that is particularly important to detect along the Andean crescent and, in general, along the extent of the Andean cordillera (Escobar-Mamani et al. 2020).

In the neotropics, the local *bohios*, or hilltops of equatorial Andes, occupied by elite settlers, are places where you find that "coquito" palms (*Parahubea cocoides),* now survive exclusively in the town boulevards or central plazas of Andean towns – as they cannot be found in the "wilderness." Something similar can be said about the peach palm (*Bactris gasipaes*) that can be found as a testament of abandoned *chacras* of the swidden agriculture practiced in the Andean Amazonian piedmont. Other clear indicators of the socioecological identity of tropandean landscapes are easy to find, when the "tree of Peru," or *molle (Schinus molle),* is found decorating the avenues of Mexico: the reeds of California that are found in the settled Andean lakes with totora, (*Schoenoplectus californicus*) cultivated and harvested for handcrafts, or the pollen grains of corn (*Zea maiz*) that are found in the Amazonian lowlands. In summary, there exists direct paleoecological evidence of an active exchange of plants and animal species between Mesoamerica and the Andes, as well as between Amazonia and the coastal plains; this represents a socioecological gradient that cutcross the altitudinal variation of the mountain chain.

Most plant ecologists based their findings of gradual changes on measuring the size of leaves, the size of tree trunks, or the amount of rain or temperature that is registered along the ecocline as elevation-dependent gradients (EDGs), often relating to minimum, average, optimum, or maximum values that allow qualifying a threshold, after which the fluid gradient changes into some hard terminus or fixed state. Where concentration of elements diminishes gradually –such as with the adiabatic lapse rate– the presence/absence of "indicators" hints the zoning of hyperabundance of species, or a contrasting lack thereof. This was clearly articulated by Al Gentry (1988) describing a mid-elevational "bulge" in the presence of arboreal taxa in the montane zone when he discussed the geographical gradients that could explain tropandean diversity. We argue that he was right, but incomplete, as the bulge of trees is mimicked by the bulges from other taxa in different elevations, such as the bryophytes' bulge in the high Andean forests, the bulge of shrubs in the Patagonian and Magellan Andes, the bulge of lichens in the upper paramo, the bulge of fords in puna zones, or the pteridophytes' bulge in the Andean flank of the verdant, or even the suspected bulge of underground soil biota, exemplified by the giant earthworm that lives furrowing the mossy surfaces and sandy soils of the talus and scree. A bulge of socioecological factors could be discerned from archaeological evidence of ancient socioecological productive landscapes of the Andean flanks (de la Cadena & Legoas 2012; Sarmiento & Sarmiento 2021). Furthermore, we argue that SEPLS are good examples of biocultural diversity that often survive in isolated microrefugia in the hinterland (Minga et al. 2019), rural fringes occupied by both traditional and indigenous people. These new mixed territories of the "rurban" landscape are the productive zones, economic and otherwise, that are in the tipping point either to lose their identity or to reinforce their sense of microrefugium.

16.1.2 Task at Hand

Notwithstanding the difference between Amazonian or Pacific slopes, these “indicator” species could give the explorer an idea of altitude, precipitation, temperature, and other meteorological climate factors, justly noted in the “Humboldtian” paradigm of altitudinal zonation as elevation increases. Some of the tenets of this “Humboldt law” are still valid to elucidate the “Humnboldt’s enigma” (Rahbbek et al. 2019); however, a newer narrative emerged from the highland-lowland dynamics observed across the altitudinal belts affected by economic, religious, military, investment, and other climates experienced in the region (Table 16.1), and the indelible human tracks observable within the slopes of Andean forests (Sarmiento 2000). Increasing scholarly interest is now devoted to clarifying the “Andean-Amazonian divide” (Pearce et al. 2020, see also Cavalcanti-Schiel 2014). Now it is accepted that most places are indeed fusion landscapes, in many cases manufactured landscapes by “bioengineers” of the past, better assessed with transdisciplinary research (TDR) as conduits of mountain transformation and meaning (Harden and Fernández 2022). These SEPLS are now showing the intrinsic relationship of natureculture, whether in the Araucanian slopes (Ibarra et al. 2020), the Mesoamerican mountains (Kremsa and Zigrai 2021), the Japanese satoyamas (Brown et al. 2022), the urban-rural fringe of central- (Haller 2019) and southern -Peru (Branca 2019), and Ecuador (Kingman and Bretón 2017), the páramo mountainscapes (Sarmiento 2012) or the Chocoan or Amazonian junglescapes (Sarmiento et al. 2022).

Table 16.1 Gradual changes associated with differential altitude as registered by field studies and literature reviews of factors affecting the dynamic of Andean flanks based on traditional ecological and alternative socioecological studies

Elevation Dependent Gradients (EDGs)	
Ecological	Socioecological
Temperature	Agriculture output (biomass)
Precipitation	Agrobiodiversity (heirlooms)
Soil humidity	Mining ores (metals)
Acidity	Water capture (hydroenergy)
Photosynthate output	Wind capture (eolic energy)
Evapotranspiration	Sun capture (solar energy)
Luminosity	Human settlements (towns)
Cloudiness	Terracing (slope adaptation)
Sun radiancy	Aqueducts (irrigation)
UVß radiation	Timber harvesting (wood)
Water opacity	Urban expansion (amenity)
Water supply	Transportation network
Root exudate	Animal husbandry (grazing)
Particulate/aerosol	Transhumance (seasonality)
Carbon sequestration	Disturbance (clearing)

Thus, a new narrative must come into play to promote the ontology of Elevation Dependent Gradients (EDGs) based on altitudinal ecoclines to problematize the socioecological reality of mountains (Haller and Branca 2020). We plan to include examples of cases in different latitudes, longitudes, or altitudes, so that the graticule used in our analysis be a good indicator for the important places that SEPLS have in our understanding of ecological legacies, based on anthropic "indicators" that place the mountain slope and aspect, as a focus of significant human intervention. We will end by helping to claim, with Sarmiento and Sarmiento (2021), the need to reclassifying the Andean flanks as an ecoregion on its own right, instead of a mere transitional cline that changes gradually from the highlands to the lowlands. We need to acknowledge that further research on sociobiological and ecological processes is needed, and particularly the TDR study about the cryptic cultural bulge of the verdant.

16.2 Methodologies

Albeit most likely not comprehensive, we tried to incorporate several methodological options to cover different themes, in what is considered a multimethod approach. We based our criteria in several parameters, including participatory research, critical discourse analysis, observational, and survey-based information, contrast-and-compare adaptations, analyses of paleothemes, including pollen fossil, phytoliths, protein separations from excavated samples, chronosequence analysis of repetitive photographs, aerial orthophotography and drone-based estimations, and the old but proven effective "boots on the ground" for ground truthing of both remote and literary observations.

The information generated by the review of socioecological themes published in mountain journals shows that there is a preponderance of sources about EDGs dealing with physical parameters with both direct and indirect gradient analyses. The few sources of related papers are augmented when including other social science outlets not specifically identified as "mountain" research journals, but with comprehensive and areal foci of transformed mountainscapes. The bibliometrics of socioecological gradients is not significantly different from the generally low number of social-science studies about mountains.

16.3 Results

The presence of megalithic constructions associated with places where closed-canopy forests now exist in the Andean flanks gives the paradox of biocultural diversity, while currently, the forest formation seems mature, even old growth and pristine-looking, but, in reality, harbors evidence of heavy human use in the past. Examples abound in recent literature as more and more sites of the caliber of citadels, fortresses, terraces, temples, open fields, channel-based irrigation, etc. are incorporated in the repertoire of Andean cultural landscapes (Erikson 2020). The communities have created ancestral ways of dealing with the sloppy terrain and in some cases, they have conserved it as traditional ecological knowledge, such as the yearly construction of a suspension bridge over the *Urubamba* river using tussock grasses (*Stipa ichu, Calamagrostis* sp.) to braid a strong interlocked cord that sustain the pedestrian bridge in *Q'eswachaka*, near *Qosqo,* now a UNESCO declared intangible world heritage. In some areas of the wet grasslands of Tucumán, Argentina, the páramo-like formation is maintained by the withered practice of transhumance of cattle. Just as in northern reaches of the cloud forest belt, the effects of trampling and herbivory of grazers are the driver of the maintenance of the upper treeline, blurring the boundaries between the forest and the pastures (Dávalos et al. 2021).

16.3.1 Cultural Bulge in Andean Flanks

One of the most significant socioecological gradients of the EDGs is the differential resource use preference that increase in the mid-elevation mountains as a result of terracing, building of irrigation channels, and other transportation networks. In fact, most of the successional dynamics of the cloud forest is a direct consequence of road construction and talud breakage, hence providing for landslides (e.g., Myster and Sarmiento 1998), rockslides, or the feared "*waiku*"or destructive mudflow that washes downstream-bound catastrophes. Huge floods of the piedmont are directly related to the changes in forest cover and resource use of the headwaters. The socio-ecological hybridity is manifested mainly in the concentration of terraced geoforms distributed along the incline, but concentrated in the mid-elevation bulge observed in the plotting of the number of findings at different elevations. Certainly, incomplete archaeological studies are showing now the occupancy of the mid-elevation montane zone with the dry terraces and stone terraces built in the Andean arc (Fig. 16.1), such as in *Wuapaula*, by the *Upano* river, in the shadow of the *Sangay* volcano in Ecuador.

Sites distributed in the isolated slopes of the *Sierra Nevada* de Santa Marta, and throughout the *Quindío* in Colombia, provide evidence that human occupation abounds in this mid-elevation cultural bulge. Recent findings on the *Quijos* Andean flank, even within the most pristine of National Park in Ecuador, *Llanganati* the stone walled terraces are an evident signal of past occupations. Northern Peru also boasts a significant number of archaeological sites that confirm the rich variety of human occupation in the mid-elevation bulge with impressive fortresses (or *pukarakuna)* and even whole citadels, such as *Kuelap* in Chachapoyas, or *Chuquiquiraru* in *Sabancay* towards *Cuscu* in southern Peru. The majority of the Andean flank in Bolivia is peppered with archaeological sites with either mounds, channels, or walls (or *pirkakuna*) that tell about ancient heavy usage of the verdant. The best known example of this cultural bulge is Bingham's "discovery" in 1911 of what is now the

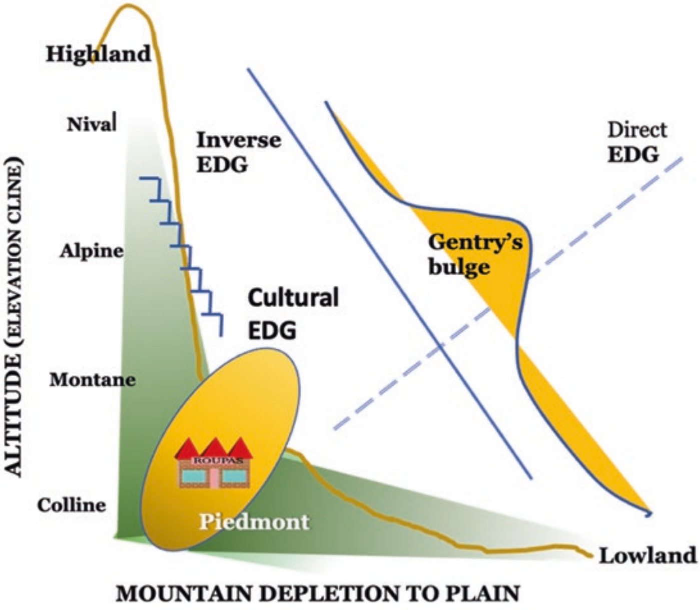

Fig. 16.1 Representation of the interaction of Elevation Dependent Gradients (EDGs) in the ecological and socioecological consideration. Notice that the presence of elements at a certain altitude is no longer correlated to the gradual change and most cultural EDGs show erratic socioecological gradients

National Sanctuary of *Machu Picchu*, when the area looked like a pristine mountain forest with continuous canopy, just to show a masterful architecture when the excavation and restoration practices finished, ancient stoneworks that helped to appreciate it as one of the "modern wonder of the world."

Many other sites throughout the Andean Arc – sometimes called "Andean Crescent" tell of previous civilizations and indigenous groups lost in history, such as the *Quixus*, the *Bracamoros*, the *Awaruna*, or the *Ashwar*. With the use of the new LIDAR technology, the discovery of the oldest human settlement in the whole of the Amazon has been located in *Wuapula*, near the *Sangay* volcano in the mid-elevation areas of tropandean landscapes, making the point of considering a cultural bulge in the EDGs much stronger than before.

16.4 Conclusions and Discussion

Our conclusion is that the SEPLS conditions are evidence often perceived as indicators of elevational gradients with ecoclines that confirm the well-known physical estimates of clinal variation. However, we claim the need of reclassifying the Andean flanks as a proper ecoregion, instead a mere transitional cline that changes gradually from the highlands to the lowlands. This prompts an urgent change in textbooks, maps, magazines, and even in scientific circles, to move urban montology and critical biogeography into a new height, literally! (Sartori and Moreira-Muñoz 2022). Also, we claim the imperative to study more about the cryptic cultural bulge of the verdant to identify the true natureculture hybridity of these heritagescapes (Sarmiento et al., 2023).

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References

Aguirre CP, Córdova JD, Piqué R (2021) Agriculturización: la alquimia de un paisaje precolombino Kañari en la cuenca alta del río Chanchán, Andes del Ecuador. Estud Atacameños 67:1–11

Austin MP, Nicholls AO, Doherty MD, Meyers JA (1994) Determining species response functions to an environmental gradient by means of a β-function. J Veg Sci 5:215–228

Branca D (2019) The urban and the rural in Puno, highland Peru. Anthropol Today 35(6):18–20

Brown J, Yoshida M, Inaba N (2022) Mountain landscapes as "lifescapes": sustaining traditional biocultural heritage and supporting resilience in Asia-Pacific region. In: Sarmiento FO (ed) Montology palimpsest: a primer of mountain geographies. Springer-Nature/Switzerland

Cavalcanti-Schiel R (2014) Cómo construir y sobrepasar fronteras etnográficas. Entre Andes y Amazonía, por ejemplo. Chungara Rev Antrop Chil 46(3):453–465

de la Cadena M, Legoas PJ (2012) Introduction: Cosmopolitiques dans les Andes et en Amazonie comment l'autochtone politique influence-t-il la Politique? Researches amerindiennes au Québec 42(2–3):5

Dávalos LM, Dávalos E, Holmes J, Tucker C, Armenteras D (2021) Bosques, coca y conflicto: la dinámica de la frontera de pasturas y deforestación en la Amazonía andina. JIED 3(1):74–98

Erikson CL (2020) The domesticated landscapes of the Andes. In: Seligman LJ, Fine-Dare KS (eds) The Andean world. Routledge, London/New York

Escobar-Mamani F, Branca D, Haller A (2020) Investigación de montaña sobre y para la región andina. Rev Investig Altoandin 22(4):1–3

Fuentes A (2010) Naturalcultural encounters in Bali: monkeys, temples, tourists, and ethnoprimatology. Cult Anthropol 25:600–624

Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann Mo Bot Gard 75(1):1–34

Haller A (2019) Impacts of urban growth on Andean smallholders. A study of perception in the rural-urban zone of Huancayo, Peru. Espac Desarro 29:37–56

Haller A, Branca D (2022) More than landscape: towards cosmophanic diversity in environmental planning and governance. Soc Nat Resour 35(10):1123–1133

Haller A, Branca D (2020) Montología: Una perspectiva de montaña hacia la investigación transdisciplinaria y el desarrollo sustentable. Rev Invest Altoandin 22(4):313–322

Haraway DJ (2003) The companion species manifesto: dogs, people, and significant otherness, vol 1. Prickly Paradigm Press, Chicago

Harden C, Fernández A (2022) Mountain waterscapes: geographies of interactions, transformations and meanings. In: Sarmiento FO (ed) Montology palimpsest: a primer of mountain geographies. Springer-Nature/Switzerland

Head L (2017) Cultural landscapes and environmental change. Routledge

Ibarra JT, Barreau A, Marchant C, González JA, Oliva M, Donoso-Correa ME, Sarmiento FO (2020) Montology: an integrative understanding of mountain foodscapes for strengthening sovereignty in the Andes. In: Sarmiento FO, Frolich LA (eds) The Elgar companion to geography, transdisciplinarity and sustainability. Edward Elgar Publisher, London

Kingman E, Bretón V (2017) Las fronteras arbitrarias y difusas entre lo urbano-moderno y lo rural-tradicional en los Andes. J Lat Am Caribb Anthropol 22(2):235–253

Kremsa V, Zigrai F (2021) Landscape ecology in Mexico: evolution, research, education and future (selected theoretical and meta-scientific aspects). J Landsc Ecol 14(2):82–114

Malone N, Ovenden K (2016) Natureculture. In: The international encyclopedia of primatology. Wiley, Hoboken, NJ

Minga D, Cordero P, Donoso M, Montesinos K, Jimenez M, Antaki B, Sarmiento F (2019) The *Uchucay* microrefugium: an Interandean forest relict with an important arboreal richness in Southern Ecuador. Pirineos J Mt Ecol 174:1–16

Myster RW (2018) The nine classes of plant-plant replacement. Ideas Ecol Evol 11:29–34

Myster RW, Sarmiento FO (1998) Seed inputs to microsite patch recovery on two Tropandean landslides in Ecuador. Restor Ecol 6(1):1–10

Nickell J (2010) ‘Noetic science’ in the lost symbol. Skept Inq 34(1):60–61

Pearce AJ, Beresford-Jones AG, Heggarty P (eds) (2020) Rethinking the Andean-Amazonian divide: a cross-disciplinary exploration. UCL Press

Rahbbek C, Borregaard MK, Colwell RK, Dalsgaard BO, Holt BG, Moreuela-Holme N, Nogues-Bravo D, Whittaker RJ, Fjeldså J (2019) Homboldt’s enigma: what causes global patterns of mountain biodiversity? Science 13–365(6458):1108–1113

Sauer CO (1925) The morphology of landscape. Foundation Papers in Landscape Ecology (2007). Pp. 36–70

Sarmiento FO (2020) Montology manifesto: echoes towards a transdisciplinary science of mountains. J Mt Sci 17(10):2512–2527

Sarmiento FO (2012) Contesting Paramo: critical biogeography of the Northern Andean Highlands. Kona Publishing, Higher Education Division, Charlotte

Sarmiento FO (2000) Breaking mountain paradigms: ecological effects on human impacts in managed tropandean landscapes. AMBIO J Hum Environ 29(7):423–431

Sarmiento FO, Inaba N, Iida Y, Yoshida M. (2023). Mountain Graticules: Bridging Latitude, Longitude, Altitude, and Historicity to Biocultural Heritage. Geographies 3(1):19–39

Sarmiento FO, Sarmiento EV (2021) Flancos Andinos: Paleoecología, Biogeografía Crítica y Ecología Política en los Climas Cambiantes de los Bosques Neotropicales de Montaña. Editorial INDES_CES/UNTRM. Universidad Nacional Toribio Rodríguez de Mendoza, Amazonas. Chachapoyas

Sarmiento FO, Rodríguez J, Yépez A (2022) Forest transformation in the wake of colonization: the Quijos Andean-Amazonian Flank, past and present. Forests 13(11):1–19

Sartori M, Moreira-Muñoz A (2022) Biogeography of knowledges in the mountain anthropocene: hybrid conceptual and practical spaces within the GeoHumanities. In: Sarmiento FO (ed) Montology palimpsest: a primer of mountain geographies. Springer-Nature/Switzerland

Wilson EO (1998) Consilience: the unity of knowledge. Vintage Books, Random House Inc, New York

Zimmerer KS, Bassett TJ (eds) (2003) Political ecology: an integrative approach to geography and environment-development studies. Guilford Press, New York

Chapter 17
Conclusions, Synthesis, and Future Directions

Randall W. Myster

17.1 Conclusions

In the first chapter, I defined the Neotropics as a tropical area in the Western hemisphere with hard boundaries that have ecological meaning. Within those boundaries, the Neotropics is also defined by three large spatial gradients measured on coordinate series of elevation, latitude, and longitude. I also gave a precise definition of gradients as laid out on spatial, temporal, or spatiotemporal coordinates (Fig. 17.1) and, for ecological gradients, consisting of measured physical, chemical, or biological quantities. Those gradients work within ecosystems, and I gave several examples of how they can overlap and interact to produce structure, function, and dynamics, where understanding dynamics is of key importance. Finally, I suggested how this book can help in the development of a theory of gradients.

Subsequent chapters have continued in showing gradients in Neotropic ecosystems (like in the mountains of Ecuador: Fig. 17.2), including the entire gradient spectrums of physical versus chemical versus biological, spatial versus temporal versus spatiotemporal, and elevation versus latitude versus longitude. For example, the powerful capacity of bracken ferns to acclimate and become adapted to extreme conditions on elevational gradients in the Andes. We saw field-based physical characteristics, growth rate and selected xenobiotic and polyphenolic-based solar UV-B screens responses to well-defined climatic conditions measured systematically along a variety of altitudinal gradients. Also details of the understudied insect community on Neotropical *Pteridium* fronds in connection with species diversity were explored. Then we reviewed how the effects of native terrestrial ecosystem conversion to agriculture in the Neotropics impact the structure and composition of aquatic invertebrate communities. This led to a recommendation to create stakeholder-based Neotropical stream conservation strategies and to rehabilitate disturbed areas altered

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Fig. 17.1 Gradient with arrow, by Swiss painter Paul Klee. I suggest that this could represent the interaction of spatial gradients (the gradual increasing/decreasing in the wavelength of colors in the background) and temporal gradients (the arrows)

Fig. 17.2 Working across the elevational gradient in Ecuador is my friend and field assistant Arcenio Barras, here at Maquipucuna Reserve in the Andes

by agricultural activities and ranching. Continuing with aquatic macroinvertebrates, we looked at the drivers of aquatic macroinvertebrate diversity along the altitudinal gradients of Colombian rivers. Models were developed using the relationship of the trophic network structure of aquatic insects with an altitudinal gradient and anthropogenic effects. We also saw how savanna vegetation in the Orinoco savannas (Llanos) of Venezuela has a several-fold gradient in soil fertility and rainfall where specific leaf areas and photosynthesis rates of both the grass *Trachypogon spicatus* and the tree *Curatella americana* increase with water availability and their leaf N and P are positively associated with soil fertility. In addition growth rate and leaf thickness and longevity set *T. spicatus* and *C. americana* at the “fast-slow” extremes of the leaf economics spectrum.

Next we investigated how suitable are the Bergmann’s rule, and the Rapoport’s effect in explaining latitudinal trends in scorpion diversity in the Brazilian Atlantic

Forest and found scorpion richness in the Atlantic Forest does not adhere to the Rappaport's effect, being more similar to the assumptions of the Inverse Rapoport' rule, and latitudinal diversity gradient hypothesis, and a comprehensive pattern in the spatial distribution of scorpion body sizes in the Atlantic Forest seems to be absent, or at least, its complexity cannot be explained by well-known ecogeographical rules such as the Bergmann's rule. Then we examined the latitudinal and elevational gradients in Scarabaeinae species richness and found a clear triangular pattern in which maximum values of species richness are reached at the equator and in the lowlands with an elevational decline in the number of species. We saw that a metacommunity is a network of communities or sites that are potentially connected to each other via dispersal of individuals among constituent communities, which may correspond to underlying environmental gradients such as abiotic variation, biotic interactions, edaphic features, habitat type, disturbance, contamination, land use, or legacies of historical factors. Two approaches to biodiversity monitoring in the Neotropics are needed to improve our understanding of metacommunity dynamics: (1) long-term studies that repeatedly sample at regular intervals to quantify changes in metacommunities along gradients subject to combinations of press (e.g., eutrophication, contamination, pollution, climate change) and pulse (e.g., extreme weather events, logging) disturbances and (2) comparative studies of multiple taxa (e.g., bats, rodents, birds, amphibians, arthropods, trees, fungi, microbes) along the same spatial or environmental gradients to determine which groups are particularly vulnerable to changing environmental conditions.

Land use was explored assessing the species diversity of amphibians, dung beetles, and ants along a successional gradient formed by cattle pasture, a 13-year-old regenerating secondary forest, a 23-year-old regenerating secondary forest, and a mature cloud forest remnant located in a mountainous landscape of central Mexico. For amphibians, species richness and abundance increased from cattle pasture to cloud forest; for dung beetles species, richness was greater in the cattle pastures than in the three forests, while abundance was greater in cloud forest and cattle pasture compared to secondary forests and for ants species, richness and occurrence frequency did not differ among the vegetation types. Next we analyzed the distribution patterns of soil organic carbon and nutrients along an altitudinal gradient in the Luquillo Experimental Forest, northeastern Puerto Rico as a way to investigate climate change, and found clay content decreased but water content increased with elevation. In addition, soil carbon content, nitrogen, phosphorus, and C:N ratio also increased with elevation. The elevational distribution of diverse leaf-litter fauna, from coastal dry forest through rain forest into the cloud forest at the montane peaks of the Andes, was also examined and the cold, historically temperature invariant cloud forests are rapidly heating, while the hot low elevation dry forests are not cooling off during the rainy season as they would have historically. Researchers also found that the connection between alpha diversity and elevation was very dependent on the taxa in question (along elevation: some increased, some decreased, some displayed mid-elevational peaks, and some no relationship). However, changes in betadiversity occurred with dramatic speed and were remarkably similar for the same taxa.

Finally, we saw a novel narrative of socioecological gradients that show alternative behaviors to the frequency curves associated with linear tendencies of direct relations between altitude differential of physical factors. The evidence of a so-called cultural bulge in the mid-elevation zone of the incline calls for the inclusion of socioecological gradients driving our understanding of gradients in the Andes' rich biocultural diversity. Results suggest the need to develop more studies with the transdisciplinary research of urban montology to assess the validity of reformulating past geographical theory to include a new ecoregion of the Andean flanks.

17.2 Synthesis

Most chapter authors used direct gradient analysis rather than indirect, but several authors only graphed their gradients. Those gradients were mainly spatial but included physical, chemical, and biological measured quantities. Authors have shown that any place in the Neotropics, or on the earth itself, has spatial and temporal coordinates (e.g., the village of Myster – named after my family and nestled between two fjords in the province of Hordaland in Norway – has the spatial coordinates of longitude 60° 44′ 8.27″N and latitude 5° 48′ 27.58″E) and thus could be places where quantities are measured to make a gradient.

Within any terrestrial ecosystem – including those in the Neotropics – both abiotic and biotic components and processes move, primarily, in and out of the plant phytomass (the biomass [Myster 2003] and necromass of all plants in ecosystems taken together). In all my books, I have presented a view of terrestrial ecosystems as plant-centered, where biogeochemical components of ecosystems cycle in and out of – or flow through, like energy – the total plant phytomass. No other component or components of the Neotropics, except the phytomass, can assume this central role as a conduit for physical, chemical, and biological parts of the ecosystem (Myster 2001). Only the phytomass can mediate and integrate among biogeochemical cycles (including cycles of productivity and decomposition: Myster 2003) while also conducting most of an ecosystem's energy processing. In addition, because the phytomass occupies the phytospace, and outside the phytospace there are neighborhood spaces, which the plant controls and where it may interact with other plants, it largely controls space in ecosystems. Taken all this together then I posit that the phytomass should be put in the center in our conceptual models of terrestrial ecosystems, as opposed to say nutrient availability and cycling (NAC) where, apparently, living things merely respond passively to NAC. Whatever the models, we cannot lump species together (especially plants that make up >90% of the biomass in terrestrial ecosystems), because evolution creates species that are different from each other, with unique traits, adaptations, and functions (Darwin 1859), and thus, we cannot reduce the biota (mainly plants) to a "green box" in ecosystem conceptual diagrams and models.

The dynamics of that phytomass (a key research objective) is best captured as an *individual* plant-plant replacement process, which is a fundamental temporal gradient of terrestrial ecosystems (Myster 2012b), and where the most critical mechanisms determining the plant-plant replacements are at the seed and seedling stages of the plant life-cycle (Grubb 1977; Myster 2012c; Myster 2015) usually without dispersal limitation (Myster 2017). These regeneration mechanisms determine what individual plants are present, where they grow, and to a large extent their entire life-cycle (i.e., survivorship, growth, allocation of biomass, architecture, and reproduction) after the seed/seedling stage. This plant-plant replacement process has nine classes (Myster 2018) from "none" where no new plant recruits into that now available patch of space but neighboring plants may grow into it, to "one" where one new plant recruits into that now available patch of space and may grow to occupy additional space in that patch, and/or to "many" where more than one plant as a group recruits into that now available patch of space and may grow to occupy additional space in that patch.

While natural disturbances may lead to plant-plant replacements like none => none, none => one, none => many (Myster 2018), human-caused disturbances – because they remove relatively larger amounts of biomass – may lead to replacements like many => none, many => one, many => many (Table 17.1). If so the plant-plant replacements in an area could indicate the level and kind of past disturbance, just like crops and/or associated species still growing in an agricultural field after abandonment indicate the crop that was growing there before abandonment. Also after abandonment from agriculture, plants are often replaced by plants with the same size or larger seeds (Myster 2007). There may also be a tendency for responses to match their disturbances (parallelism), where none => none, one => one, and many => many replacements are most common. Because there are multiple plants in an ecosystem, their neighborhoods spaces may overlap and I define a zero degree no overlap/open space, a 1° two trees overlap, a 2° three trees overlap, etc., where the more overlap the less likely other plants can use the space. While these replacements involving individual plants may produce species replacement, species themselves do not replace each other. I posit that dynamics are the reality of the phytomass and the key to ecosystems, and so, ecosystems do not coexist, have a steady state, or achieve equilibrium.

A significant part of this book is devoted to the methodology adopted: how best to measure and analyze gradients. This is part of the larger issue of methodology in the entire disciple of ecology and here I would like to state my skepticism regarding the use of analysis of covariance (ANCOVA) in experiments which adjusts group means to try and produce significance when other methods like analysis of variance (ANOVA) have not. I find myself in agreement with Sokal and Rohl (1981) that instead of resorting to ANCOVA, most biologists would (I suggest should) look at the results, change their experimental design, repeat the experiment, and try ANOVA again ("a valid, commonsense approach, which is part of the experimental method": p.495 Sokal and Rohl 1981). My skepticism extends to (1) some treatments and the levels of treatments applied in an experimental design, because they may not occur in nature and/or are applied in such a way that make responses likely to occur, and (2) whether experiments in some cases are the best way to test a hypotheses comparing to just measuring out in the field.

Table 17.1 The nine classes of plant-plant replacement (Reprinted from Myster 2018)

Replacement class	Description and example
none => none	No plant died and no new plant joined the neighborhood. New phyto space and/or new neighborhood space may, however, be replaced by a pre-existing plant and reoccupied by the same or another pre-existing plant. For example, when a branch falls off a tree and another tree gives rise to a branch into that space(s).
none => one	No plant died and one new plant joined the neighborhood. The new plant may reoccupy space(s) that was released by a pre-existing plant. For example, when a branch falls off a tree and a tree seedling recruits into that space(s).
none => many	No plant died and more than one new plant joined the neighborhood. These new plants may reoccupy space(s) that was released by a pre-existing plant. For example, when a branch falls off a tree and more than one tree seedling recruits into that space(s).
one => none	One plant died and no new plant joined the neighborhood. The space(s) released by the now dead plant may be reoccupied by a pre-existing plant. For example, when a tree dies and another tree grows a branch into that space(s).
one => one	One plant died and one new plant joined the neighborhood. The space(s) released by the now dead plant may be reoccupied by the new plant. For example, when a tree dies and another tree recruits into that space(s).
one => many	One plant died and more than one plant joined the neighborhood. The space(s) released by the now dead plant may be reoccupied by the new plants. For example, when a tree dies and more than one tree recruits into that space(s).
many => none	More than one plant died and no new plant joined the neighborhood. The combined or collective space released by the now dead plants may be reoccupied by a pre-existing plant. For example, when a tree dies and as it falls, it pulls down another tree with it. Then another tree grows a branch into that collective space.
many => one	More than one plant died and one new plant joined the neighborhood. The combined or collective space released by the now dead plants may be reoccupied by this new plant. For example, when a tree dies and as it falls, it pulls down another tree with it. Then another tree recruits into that collective space.
many => many	Can be decomposed into the other replacement classes.

In fact there may be an even deeper problem with experiments and the treatment group, because once you apply a treatment to individuals, they may no longer be the same *kind* of individuals as in the control group, and thus, the two groups cannot be compared statistically (like trying to compare apples and oranges). That is to say the control group is made up of individuals but the treatment group is made up of individuals + treatments. This may be especially true when a treatment can be assimilated into the individual organisms it was applied to, for example, when adding N to plants (D. Schaefer, pers. comm.).

All these considerations/factors together point to a need for more healthy skepticism (Fig. 17.3) in the disciple of Ecology. That is to say, less acceptance of results, concepts, and ideas just because they are published by a well-known scientist and/or widely cited, without critical analysis. It is good to remember that the scientific

Fig. 17.3 Skepticism

method itself is fundamentally skeptical (Shermer 2009) when, for example, the null hypothesis (H_o) is never accepted, only rejected, or not rejected (Popper 1952) and then only within a given error level of being wrong (the *p* value: Sokal and Rohl 1981). I further suggest that some concepts need to be eliminated outright such as (1) communities (I prefer individual species associations, which can be proven statistically and then combined hierarchically into larger groups: Myster 2012a) and distinctions among communities such as successional, climax, primary, secondary, etc. (Clements 1916; Gleason 1926), and (2) a species' "niche" (I prefer just listing important species traits and justifying them) (Bazzaz 1996). Finally, journal editors need to be more independent in reading and critically analyzing submitted papers by themselves, before looking at reviewer comments. Indeed I find reviewers often critique not the paper I send them but instead, a paper they have in mind or a paper they would have written themselves about the topic, or a paper that "should" have been written about the topic etc. I ask my colleagues to consider these points, made in order to help make our scientific method work better in ecology (Shermer 2009).

17.3 Future Directions

The Neotropics is vast and its ecosystems are key to the functioning of the earth that sustains all of us. There is much research that needs to be done in the Neotropics, and soon. Funding agencies (including those in the USA like the National Science Foundation) need to find ways to get money *directly* into the hands of researchers in Central and South America (Myster 2007). I have found that even small grants – in the \$5–\$10 k/year range like those given by the Fulbright Foundation – can be quite effective. This book has made clear that understanding how gradients work in Neotropical ecosystems must be central to that research. The structure, function, and dynamics of those ecosystems must be investigated across their gradients, in particular, those found on latitude, longitude, and altitude coordinate series. In particular, we need to understand how the dynamics (plant-plant replacements are key) varies across gradients.

And so future research should first include the setting up of large plots on Neotropical gradients (like those I set up in Ecuador to sample spatial and temporal gradients after abandonment from banana and sugarcane cultivation: Myster 2007) and then sampling ecosystem components of structure, function, and dynamics over space and time in those plots, with an emphasis on links among those components. That plot data can later be used to design field experiments that explore the ecosystem dynamics of those components and what causes them. I have argued that for a focus on plant-plant replacements (Table 17.1) and mechanisms that control the early parts of regeneration (i.e., recruitment of seeds and saplings), which would include the ecophysiology of key plants and other species found in the plots. Restoration experiments should also be included.

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References

Bazzaz FA (1996) Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridge
Clements FE (1916) Plant succession: an analysis of the development of vegetation. Publ. No. 242. Carnegie Institution, Washington, DC
Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London
Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:1–20
Grubb PJ (1977) The maintenance of the species-richness in plant communities: the importance of the regeneration niche. Biol Rev Cambridge Philo Soc 52:107–145
Myster RW (2001) What is ecosystem structure? Caribb J Sci 37:132–134
Myster RW (2003) Using biomass to model disturbance. Community Ecol 4:101–105
Myster RW (2007) Post-agricultural succession in the Neotropics. Springer, Berlin
Myster RW (2012a) Plants replacing plants: the future of community modeling and research. Bot Rev 78:2–9
Myster RW (2012b) A refined methodology for defining plant communities using data after Sugarcane, Banana and pasture cultivation in the Neotropics. Sci World J 2012:365409. https://doi.org/10.1100/2012/365409
Myster RW (2012c) Spatial and temporal heterogeneity of light and soil water along a *terra firma* transect in the Ecuadorian Amazon. Can J For Res 42:1–4
Myster RW (2015) Seed predation, pathogens and germination in primary vs. secondary cloud forest at Maquipucuna Reserve, Ecuador. J Trop Ecol 31:375–378
Myster RW (2017) Does the seed rain limit recruitment, regeneration and plant community dynamics? Ideas Ecol Evol 10:1–12
Myster RW (2018) The nine classes of plant-plant replacement. Ideas Ecol Evol 11:29–34
Popper K (1952) The Logic of Scientific Discovery. Routledge
Shermer M (2009) I want to believe. Sci Am 301:33–35
Sokal RR, Rohl FJ (1981) Biometery. Freeman and Co, New York

Correction to: Elevational and Latitudinal Species Richness Patterns of Dung Beetles in North and South America and the Role Played by Historical Factors

Jorge M. Lobo

Correction to:
Chapter 13 in: R. W. Myster (ed.), *Neotropical Gradients and Their Analysis*, https://doi.org/10.1007/978-3-031-22848-3_13

Chapter 13 was inadvertently published with the second author "Jose Gutierrez". The second author name "Jose Gutierrez" has been removed from the chapter.

The updated original version of this chapter can be found at https://doi.org/10.1007/978-3-031-22848-3_13

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