

# Chapter 17

## Conclusions, Synthesis, and Future Directions



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### 17.1 Conclusions

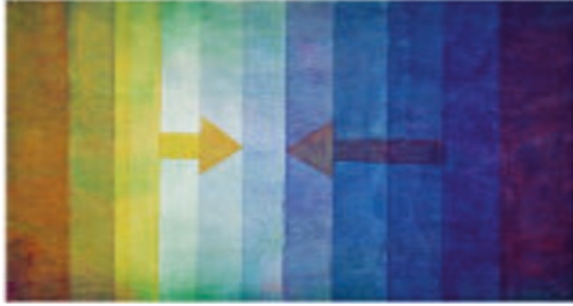
In the first chapter, I defined the Neotropics as a tropical area in the Western hemisphere with hard boundaries that have ecological meaning. Within those boundaries, the Neotropics is also defined by three large spatial gradients measured on coordinate series of elevation, latitude, and longitude. 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 Neotropical 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  $60^{\circ} 44' 8.27''\text{N}$  and latitude  $5^{\circ} 48' 27.58''\text{E}$ ) 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 discipline 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 Rohlf (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 Rohlf 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 discipline 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 ( $H_0$ ) 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 Rohlf 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, Rohlf FJ (1981) Biometry. Freeman and Co, New York