Chapter 2 Mountain Rain Forests in Southern Ecuador as a Hotspot of Biodiversity – Limited Knowledge and Diverging Patterns

G. Brehm(∞), J. Homeier, K. Fiedler, I. Kottke, J. Illig, N.M. Nöske, F.A. Werner, and S.-W. Breckle

2.1 Introduction: Why Do We Need Biodiversity Inventories?

Highly complex ecosystems such as the tropical mountain rain forest in southern Ecuador probably harbor tens of thousands of species that interact with each other. It is impossible to understand an ecosystem without knowing the composition of its community. Such knowledge cannot be achieved without the examination of all major groups of animals, fungi, plants, and bacteria. For example, insects such as leaf beetles, ants, or hymenopteran and dipteran parasitoids have a high impact on forest ecosystems (Moutino et al. 2005; Soler et al. 2005), but have not been studied at the RBSF so far. The question of how many species there are on earth is still unresolved. Estimates range from four to 30 million species (e.g. Novotny et al. 2002). Ultimately, only counting and naming species can answer this question.

A hot debate about the methodological approaches, i.e. the usefulness and efficiency of 'traditional' taxonomy versus DNA barcoding approaches is still going on (e.g. Meyer and Paulay 2005; Will et al. 2005). Barcoding techniques provide useful sets of new characters for species descriptions and phylogenies, especially in cryptic species or taxa otherwise poor in morphological characters (e.g. Hajibabaei et al. 2006). However, species definition based on DNA sequence data can be problematic. For example, ribosomal genes can show intraspecific variation in the multinucleate Glomeromycota. The sequence types obtained from the vegetative stage can rarely be related precisely to either morphological or biological species (Sanders 2004). In our opinion, the only strategic way forward can reside on a synthesis of 'classic' and 'modern' approaches with regard to sampling campaigns, application of up-to-date information technology (Godfray 2005), and thorough taxonomic and systematic work. This might include in vitro cultivation, in the case of fungi and bacteria.

Traditional descriptive disciplines such as taxonomy, systematics and natural history provide names, phylogenies, and life history data as a service for other fields of science and their applications. However, these disciplines have suffered a great loss of capacity in past decades (e.g. Breckle 2002; Gotelli 2004). Many species identifications from the RBSF are not the primary result of research efforts in

taxonomy and systematics. Rather, the recently published species checklists (Liede-Schumann and Breckle, 2008) are essentially a by-product of ecological and physiological research. This explains why many lists are still far from being complete (see below) and why only a few species have been newly described from the area thus far. Many (probably many thousands) of species in the RBSF alone are new to science and await description, but specialists are lacking for many taxa. Only some vertebrate groups are well known: All currently recorded bird and bat species are described (Matt 2001; Muchhala et al. 2005; Paulsch 2008). In other groups, however, the proportion of described species drops: from bryophytes (98%; Gradstein et al. 2008), trees (> 5 cm dbh, 90%), lichens (85%; Nöske et al. 2008), to geometrid moths (63%; Brehm et al. 2005), oribatid mites (60%; Illig et al. 2008; Niedbala and Illig 2007) to fungi (5%; Haug et al. 2004; Setaro et al. 2006a;, Suarez et al. 2006; Kottke et al. 2007).

2.2 Inventory Coverage in the RBSF

After eight years of research in southern Ecuador, our knowledge about certain taxa is excellent. The area is one of the most thoroughly investigated neotropical montane forests (see the contributions to this volume). Geometrid and pyraloid moths, and oribatid mites or bush crickets (Tettigoniidae) have never been studied quantitatively in other Andean forests before (Süßenbach 2003; Brehm et al. 2005; Braun 2008; Illig et al. 2008). None of the mycorrhizal fungi has previously been known from the northern Andean forests (Haug et al. 2004, 2005; Setaro et al. 2006a; Suarez et al. 2006; Kottke et al. 2007). However, there is little reason to rest on the laurels. Our knowledge about species richness in the area remains biased and incomplete (Fig. 2.1).

The Bacteria or Archaea have not been investigated in the study area. So far, the only group of single-cell organisms studied are the Testacea (Krashevska 2008; Table 2.1). Due to their dominant role in material and energy flows in ecosystems, plants have received relatively much attention, and groups such as vascular and non-vascular cryptogams have been inventoried across the whole elevational range (see Chapter 10.1). However, botanical collections have focused on the existing trail system that is biased towards ridge sites. Bryophytes and ferns have been collected systematically across the whole altitudinal range (e.g. Kürschner and Parolly 2004a; see Chapter 19; Table 2.1).

Lichens have been sampled intensively at least in the lowermost parts (up to 2100 m) of the area (e.g. Nöske 2005). Moreover, life forms such as trees (Homeier 2004), climbers (S. Matezki, personal communication) and epiphytes (Werner et al. 2005) have been treated in extensive ecological studies, whereas terrestrial shrubs and especially herbs still remain poorly known. Concerning the large group of fungi, only mycorrhiza forming groups were investigated. The molecular diversity of the Glomeromycota forming mycorrhizas with trees and two basal groups of Basidiomycota (Sebacinales, Tulasnellales) forming mycorrhizas with orchids, ericads,

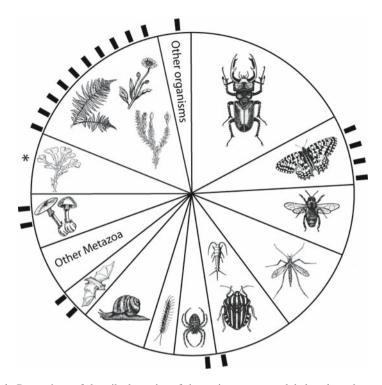


Fig. 2.1 Proportions of described species of the major taxa at a global scale and coverage of inventories at RBSF (see Table 2.1). Taxa (clockwise): Coleoptera, Lepidoptera, Hymenoptera, Diptera, other Insecta, Chelicerata, other Arthropoda, Mollusca, Vertebrata, other Metazoa, Fungi, Stramenopilata + Haptophyta, Embryophyta, other organisms. More than two-thirds of all known species are animals, and more than half of all organisms are arthropods – likely more. The figure covers organisms from all habitats, including marine ecosytems. However, only the brown algae (marked with an *asterisk*) are not expected to be present at the RBSF, whereas all other taxa are. Groups not sorted and identified at species level (e.g. Nematoda) are not included. Only a small proportion of the expected total richness has been covered so far. Data source: Lecointre and Le Guyader (2006). Illustration by G. Brehm

and liverworts, respectively, were studied but are far from being complete (Haug et al. 2004, 2005; Setaro et al. 2006a; Suarez et al. 2006; Kottke et al. 2007; Table 2.1). Saprophytic and plant parasitic fungi remain to be investigated.

Table 2.1 provides an overview of available species lists. Inventories have been carried out on birds, bats, and parts of the arthropod clades Lepidoptera, Orthoptera, and Arachnida. Although Fig. 2.1 gives global numbers of organisms and does not provide the (unavailable) proportions of taxa in an Andean forest, it roughly estimates a reasonable scenario. Thus far, the largest gaps are represented by three of the major insect orders: The Coleoptera (beetles), the Hymenoptera (ants, wasps, bees, etc.), and the Diptera (flies). With the exception of a few selected families of arthropods (see above), no other insect group has been studied (e.g. dragonflies, homopterans). Molluscs (e.g. land snails) as well as aquatic communities as a whole have been

Taxon	Observed species number	References
Chiroptera (bats)	21 (RBSF) 24 (1000–2900 m)	Matt (2001)
Aves (birds)	227 (RBSF)	Paulsch (2008), Rasmussen et al. (1994): old road Zamora–Loja
	379 (1000–2800 m)	
Geometridae (geometrid moths)	1075 (RBSF)	Brehm et al. (2005), Fiedler et al. (2007)
	1266 (1040–2677 m)	
Arctiidae (arctiid moths)	287 (RBSF, 1800–2000 m) 446 (1040–2677 m)	Hilt (2005), Fiedler et al. (2008)
Pyraloidea (pyraloid moths)	748 (1040–2677 m)	Süßenbach (2003), Fiedler et al. (2008)
Sphingidae (hawkmoths)	36	Fiedler et al. (2008)
Papilionoidea (butterflies)	243	Häuser et al. (2008)
Tettigoniidae (bush crickets)	101 (1000–3100 m)	Braun (2002, 2008)
Oribatida (mites)	154 (RBSF) 192 (1050–3000 m)	Illig et al. (2008)
Testacea	78 (RBSF) 110 (1050–3000 m)	Krashevska (2008)
Lichens (lichens)	323 (RBSF)	Nöske et al. (2008)
Glomeromycota	83 (RBSF and afforestation areas, 18S sequences, only four known species)	Haug et al. 2004, Kottke et al. (2007)
Ascomycota	4 (RBSF, sequences, new to science)	Haug et al. 2004
Basidiomycota (Homobasidiomycetes, Heterobasidiomycetes)	90 + 6 (RBSF, sequences, new to science)	Haug et al. 2005, Kottke et al. (2007), Setaro et al. (2006a), Suarez et al. (2006)
Bryophyta (hornworts, liver- worts and mosses)	515 (RBSF)	Gradstein et al. (2008), Kürschner and Parolly (2008)
Spermatophyta (seed plants)	1208 (RBSF)	Homeier and Werner (2008)
Pteridophyta (ferns)	257 (RBSF)	Lehnert et al. (2008)

Table 2.1 Taxa investigated in the RBSF and adjacent areas by October 2007

ignored. Even prominent vertebrate groups such as amphibians or mammals (except for bats; Matt 2001; see Chapter 11.2) have not been studied. A sample of studied and unexplored taxa is provided in Fig. 2.2.

A complete inventory of tropical rain forests such as the RBSF can probably never be achieved, since species-rich tropical communities must be sampled intensively and over very long periods of time. An example is provided by geometrid moths: So far, 35 238 individuals representing 1223 species have been sampled during quantitative assessments at elevations of 1040–2670 m between 1999 and 2003. However, richness estimators (Colwell 2006) indicate that, despite a great sampling effort, ca. 200 more species must be expected in the area

(Brehm et al. 2005). The species checklists of less well sampled taxa therefore often provide observed minimum numbers that do not yet allow serious estimates of the actual richness. Particularly poorly sampled areas outside the RBSF such as the Rio Bombuscaro valley (the lowermost part of Podocarpus National Park, PNP) certainly harbor far more species than the currently available lists of species suggest (e.g. Chapters 11.2, 11.3).

The use of "biodiversity indicators" in "rapid biodiversity assessments" appears to be a tempting shortcut. A good indicator group is supposed to reflect the 'complete' biodiversity. However, the use of indicators is highly problematic along altitudinal gradients because the composition of taxa changes non-linearly throughout the gradient, and patterns of alpha diversity are often discordant, even between closely related groups of organisms (Brehm and Fiedler 2003; see Chapter 11.3 in this volume; Fig. 2.3). Moreover, we have to expect diverging richness patterns in different taxa along the gradient (see Chapter 11.3), and too little is still known about the diversity patterns of most groups to allow general conclusions.

2.3 The RBSF and Podocarpus National Park as Biodiversity Hotspots

It is evident that the tropical Andes are a hotspot of biodiversity (e.g. Rahbek et al. 1995; Myers et al. 2000; Brehm et al. 2005). Using data on vertebrates and vascular plants, Brummitt and Lughadha (2003) ranked the region as the top global biodiversity hotspot. Regarding many groups of organisms, the Neotropical region is more speciose than any other region of the world. However, data from the Andes are still scarce. Two large-scale diversity patterns overlap in tropical mountains in general and in the Andes in particular:

- 1. Species richness of most groups of organisms peaks around the equator and declines towards the poles (Gaston 2000).
- 2. There is a high species turnover along altitudinal gradients and usually a peak of richness not at lowest, but at medium elevations (Herzog et al. 2005; Krömer et al. 2005; Rahbek 2005).

Many hypotheses have been formulated to explain these patterns. Some of the most frequently used explanations are:

- Evolution and biogeography;
- Climate history;
- Biotic and abiotic factors;
- Stochastic effects.

Each of the concepts is plausible to some extent, and it seems most probable that a combination is actually responsible for the observed richness patterns with all their group-specific variations (Brehm et al. 2007).

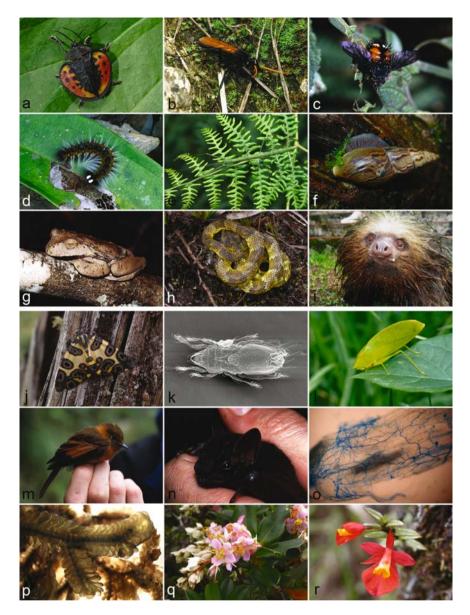


Fig. 2.2 Examples of nine (mostly unidentified) species belonging to taxa that have not yet been investigated or inventoried in the RBSF (a-i), and nine taxa in which inventories have been carried out or started (j-r). a Beetle (Chrysomelidae), b wasp (Pompilidae), c fly (Tachinidae), d *Olceclostera* sp. (Apatelodidae), e stick insect (Phasmatodea), f snail (Orthalicidae), g *Gastrotheca* cf. *testudinea* (Hylidae), h Dusky Lancehead *Bothriopsis pulchra* (Viperidae), i Two-toed sloth *Choloepus hoffmanni* (Megalonichidae), j *Pantherodes colubraria* (Geometridae), k *Dolicheremaeus* sp. (Oribatida), l *Itarissa* sp. (Tettigoniidae), m Cinnamon Flycatcher *Pyrrhomyias cinnamomea* (Tyrannidae), n *Sturnira ludovici* (Chiroptera), o unknown Gomeromycota, p *Frullanoides densifolia* (Marchantiophyta: Lejeuneaceae), q *Purdiaea nutans* (Cyrillaceae), r *Fernandezia subbiflora* (Orchidaceae). Images by: G. Brehm (a-e, j, l, m), J. Homeier (f-h, n, q, r), J. Illig (i, k), A. Beck (o), and N. M. Nöske (p)

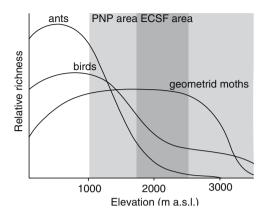


Fig. 2.3 Hypothetical curves of relative species richness of three animal taxa along an altitudinal gradient in the eastern Andes of southern Ecuador using available literature data (see text). Ant richness is expected to peak at low elevations and to decline strongly between 1000 m and 2000 m. In contrast, richness of geometrid moths and birds peaks at higher elevations and is expected to decline only at very high altitudes. Richness of all taxa at the lowest elevations is expected to be lower than at medium elevations. Illustration by G. Brehm

The diversity of the studied organisms in the tropics is usually much higher than in temperate regions, reflecting the latitudinal gradient of species richness. Some groups are exceptionally rich in the RBSF while others are not, probably because they peak at lower elevations (Fig. 2.3). Unfortunately, no hard data are available for the majority of taxa so far (see above).

Comparisons of inventories from the RBSF with other montane neotropical sites are hampered by:

- 1. The scarcity or absence of such inventories;
- 2. Differences in sampling schemes;
- 3. Differences in elevational range and area of the sites.

One of the most suitable approaches is therefore to compare the local (alpha) diversity. Vascular epiphytes in the RBSF are outstandingly speciose. Single trees hosted up to 98 species (Werner et al. 2005), among the highest species number recorded for single trees. Six trees held a total of 225 species (Werner et al. 2005), more than have been recorded for entire Andean sites in Venezuela or Bolivia (Ibisch 1996; Engwald 1999). The RBSF harbors more than 500 species of bryophytes, probably the highest number ever recorded from a relatively small area in the tropics (Gradstein et al. 2007; Kürschner and Parolly 2007). Within the spermatophytes, the orchids are the most speciose family of the RBSF with a total of ca. 340 registered species (many more are expected; Homeier and Werner 2007). So far, this is the highest number recorded for a neotropical forest site. The genera *Stelis* (Orchidaceae) and *Piper* (Piperaceae), and the family Lauraceae show unexpectedly high species numbers (see Chapter 10.1).

Other very speciose groups include the moth family Geometridae. Brehm et al. (2005) observed 1266 morphospecies between 1000 m and 2700 m - a higher number than observed anywhere else in the world. Interestingly, the family did not show a pronounced peak of diversity but a very broad plateau (Fig. 2.3) with a high and regular species turnover (Brehm et al. 2003a, b; but see Brehm et al. 2007). In contrast, pyraloid moth richness peaked around 1000 m (Bombuscaro) and declined with increasing elevation (see Chapter 11.3). Certain taxa of plants and animals are species-rich in tropical lowlands only. Among plants, many families such as Araceae, Arecaceae, and Fabaceae show a high richness in Amazon lowland and Andean foothill forests that quickly drops as elevation increases (Jørgensen and León-Yánez 1999). Elevational richness patterns are far less well known in animals. Ants have not been investigated in the RBSF, but it is evident from qualitative observations that the area is not a hotspot for this group at all, since only a few species occur (Brehm et al. 2005; G. Brehm, J. Illig, K. Fiedler, personal observations). However, ants are obviously far more abundant and speciose at lower elevations such as in the Rio Bombuscaro valley at 1000 m. This corresponds to observations by van der Hammen and Ward (2005) and Mackay et al. (2002) in Colombia who found a pronounced decline in ant species richness along an altitudinal gradient (also, for a palaeotropical altitudinal gradient of ants, see Bruehl et al. 1999). Ant richness might peak at rather low elevations at the foothills of the Andes similarly as observed below 500 m by J.T. Longino (personal communication) in Costa Rica. However, no appropriate data along a complete altitudinal gradient are available from the tropical Andes so far.

Birds are the best known group of animals in Ecuador. The Eastern slope of the Andes is renowned for its outstanding bird diversity (Rahbek et al. 1995; Ridgely and Greenfield 2001a). Paulsch (2008; see Chapter 11.1) observed a total of 227 bird species between 1999 and 2002 in the RBSF. The number increases considerably when lower and higher elevations are included. Rasmussen et al. (1994) recorded a total of 362 bird species along the (old) Loja–Zamora road (1000–2800 m) that passes the RBSF, 292 species from the Rio Bombuscaro area (950–1300 m) and 210 species from the Cajanuma area (2500–3700 m). Only the latter number represents a near-complete list, whereas the other numbers are still underestimations (C. Rahbek, personal communication). The species richness is at the high end for Ecuador, and only some areas in Peru and Bolivia have similar bird diversity (C. Rahbek, personal communication). The elevational pattern of local bird richness in southern Ecuador is not known, but is anticipated to resemble the pattern (a foothill peak, high-elevational plateau) recorded by Herzog et al. (2005) in Bolivia.

Hypothetical curves for three selected animal taxa (geometrid moths, ants, birds) are diverging; and qualitatively similar divergences of species-richness patterns are expected to occur across the whole range of organism diversity. The curves visualize that the RBSF cannot be regarded as a hotspot of biodiversity in general. The richness of many taxa is likely to peak at lower elevations (Fig. 2.3). PNP covers a much broader elevation range (1000–3600 m) and certainly has a far higher biodiversity than the narrow elevational belt of the RBSF alone. Hence, while there is little

doubt that the tropical Andes and PNP can be called hotspots of biodiversity, the RBSF is 'only' a selective hotspot.

From a conservation point of view it would be highly desirable to include lower elevations in a system of protected areas because groups showing a peak of species richness below 1000m currently do not receive legal protection in south-eastern Ecuador. Moreover, the protection of a complete altitudinal gradient similarly as e.g. in Manú National Park in Peru is undoubtedly the best conservation strategy with regard to the threats caused by global warming. Given the dramatic decline of natural habitats in tropical Andean countries and montane forests (Svenning 1998; Hofstede et al., in press; see Chapter 4), biodiversity inventories must play an important role in selecting such areas for conservation.

2.4 Conclusion

Biodiversity inventories combined with systematic and taxonomic work ensure that trustworthy scientific names can be provided for organisms encountered during ecological or experimental work. An excellent knowledge has already been gathered in the RBSF in some groups, e.g. bats, birds, arctiid and geometrid moths, cryptogamic plants, and trees. However, large gaps still remain to be filled, e.g. in groups such as beetles, ants, wasps, bees, dipterans, most other arthropods, and mollusks. Large proportions of species are apparently new to science and particularly many arthropod species need to be described taxonomically. The RBSF is situated in the Eastern Andean hotspot of biodiversity but the species-richness of most taxa in the study area and its surroundings is still unknown. While some groups are extraordinarily diverse (e.g. geometrid moths, orchids), the richness of other taxa is low in the area and peaks far below 1800 m (the lower elevation limit of the reserve). A coordinated sampling and research approach is required to fill the most important gaps of knowledge about the biodiversity of the area in the future.

Acknowledgements Many colleagues generously provided their unpublished data. We would like to thank in particular H. Braun, C.L. Häuser, M. Lehnert, M. Maraun, F. Matt, S. Matezki, G. Parolly, D. Paulsch, and S. Liede-Schumann. M.P. Mackay, D. Paulsch, and C. Rahbek critically discussed parts of the manuscript. V. Wiese, H. Greeney, and L. Dyer (www.caterpillars.org) helped with identifications.