

## Ecological aspects of a biodiversity hotspot in the Andes of southern Ecuador

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**Abstract.** Results and conclusions obtained by several research groups in the tropical mountain rainforest of the Reserva Biológica San Francisco, southern Ecuador, are used to reflect upon this exceptional hotspot of biodiversity from an ecosystem point of view. Features of functionality are emphasized while addressing the following questions: (1) What is a "biodiversity hotspot"? Can a relatively small area like the Reserva Biológica San Francisco be considered a hotspot of biodiversity? Does the term hotspot pertain to all groups of organisms of the area? How can we interpret species turnover along gradients? (2) Which geographical and ecological factors may have contributed to the accrual of the extraordinary organismic diversity of the area? (3) Which factors may be important for the maintenance of the hotspot? Which role does disturbance play? (4) Is there a feedback of biodiversity on ecosystem processes? (5) Is there redundancy of species in the South Ecuadorian hotspot?

## Introduction

This chapter reflects upon the incidence of biodiversity hotspots from an ecosystem perspective. Biodiversity on a global scale has been censused for vascular plants (Barthlott et al. 2005) and based on this, centres of plant biodiversity with more than 5000 species of vascular plants per 10,000 km<sup>2</sup> have been identified. One of these centres, commonly called "biodiversity hotspots", is the tropical Andes-Amazonia region. It comprises dry and humid mountain areas up to more than 6000 m a.s.l. as well as lowland rain forests, and thus a great variety of ecosystems. These areas have not been examined in detail with respect to underlying, ecologically significant factors.

The first question arising is whether a specific ecosystem, or an ecologically explorable part of that ecosystem, may be considered representative of the biodiversity hotspot. We will present a "bottom-up" approach to deal with this question.

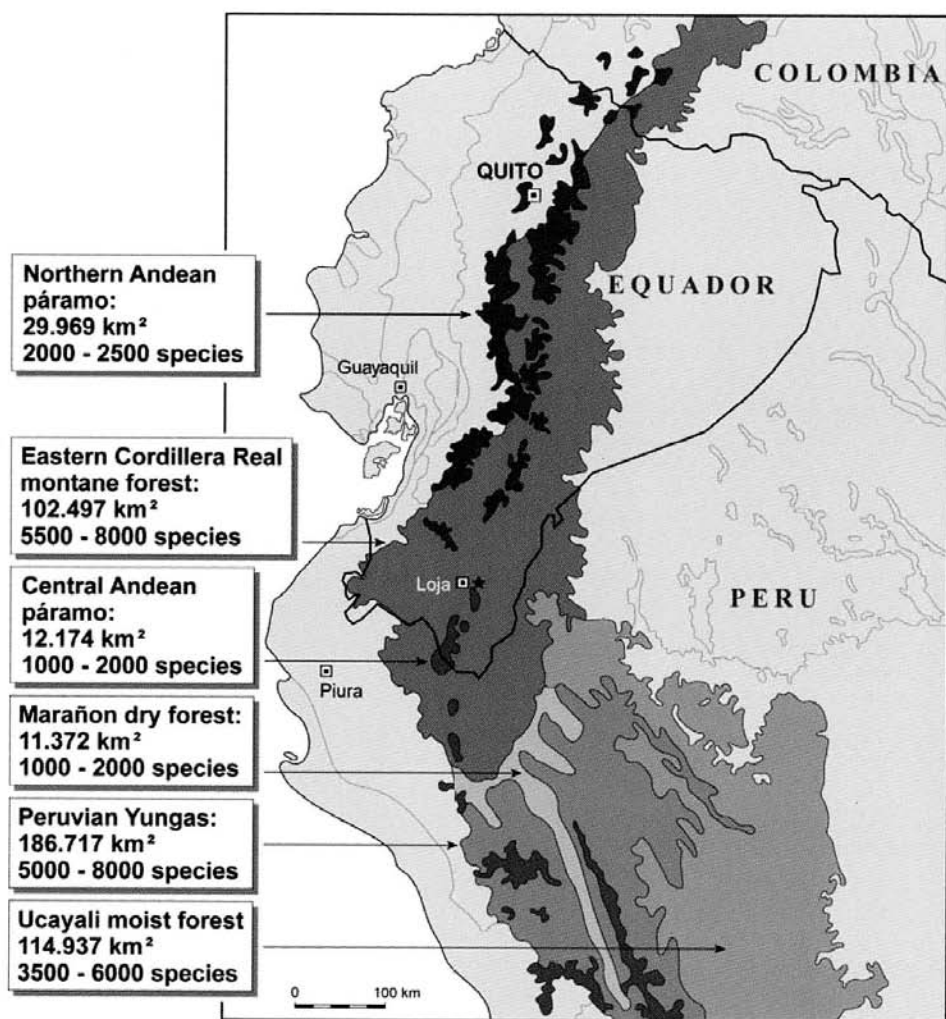


Figure 1. Ecoregions in the Neotropics (from Kier et al. 2005, based on Morrison et al. 2001). The black star indicates the location of the Reserva Biológica San Francisco.

On a global scale, distribution of terrestrial biodiversity has been systematically dealt with on the basis of plant species diversity. Ecosystem aspects, however, address interactions, e.g. of plants and animals. The question, therefore, is posed whether the term "hotspot" pertains to all groups of organisms of that area. When considering a biodiversity hotspot under environmental aspects, geographical, ecological and historical factors which may have contributed to the accrue of that extraordinary diversity are of special interest, as are factors important for the maintenance of the hotspot. Finally, it is tempting to examine the influence of

biodiversity on ecosystem processes and explore whether, under the aspect of ecosystem functionality, redundancy of species can be assessed.

In the following these questions will be discussed using the results of a unique, comprehensive study of a tropical mountain rainforest in the southern Ecuadorian Andes. This study has been carried out by an interdisciplinary group of researchers over a period of ten years. The results of the investigations have been synthesized in a recent volume of "Ecological Studies" (Beck et al. 2008) and in a comprehensive species checklist (Liede-Schumann & Breckle 2008). A brief description of the research area, the "Reserva Biológica San Francisco" (RBSF), is given below.

### **Is the RBSF representative of the biodiversity hotspot "Tropical Andes of Ecuador"?**

The studies of the research group in southern Ecuador covered an area of maximally 100 km<sup>2</sup>, including a core area of 11 km<sup>2</sup> (the Reserva Biológica San Francisco, RBSF) and some satellite areas. The question arises whether this area is representative of the Andes-Amazonia hotspot and whether it can be addressed as a hotspot of biodiversity in a more general sense. For this purpose, a scale-down approach aimed at estimating the degree of biodiversity of the RBSF was performed, making use of the "ecoregion" concept. Ecoregions (Fig. 1) are relatively large units of land delineated to reflect boundaries of natural communities of animal and plant species. Using plant species richness data of 1800 "operational geographical units", 867 terrestrial ecoregions have been recognized on a world-wide basis (Kier et al. 2005). Highest richness is in the Borneo lowlands ecoregion (10,000 species), followed by nine ecoregions in Central and South America with  $\geq 8000$  species each. All of these are within the tropical and subtropical moist broadleaf forests biome. To compare the richness of plant species in a geographical region with that of an ecoregion, the number of species and the size of the respective areas are related using the following equation:

$$S_e = S_u \left( \frac{A_e}{A_u} \right)^z$$

where  $S_e$  = number of species in the ecoregion (here 8000);  $S_u$  = number of species in the geographical unit (see Table 1);  $A_e$ ,  $A_u$  = area sizes (102,000 km<sup>2</sup> for Ecoregion NT 0121; 100 km<sup>2</sup> for the extended RBSF, respectively);  $z$  = a richness parameter (0.32 for tropical forests of South America) (Kier et al. 2005).

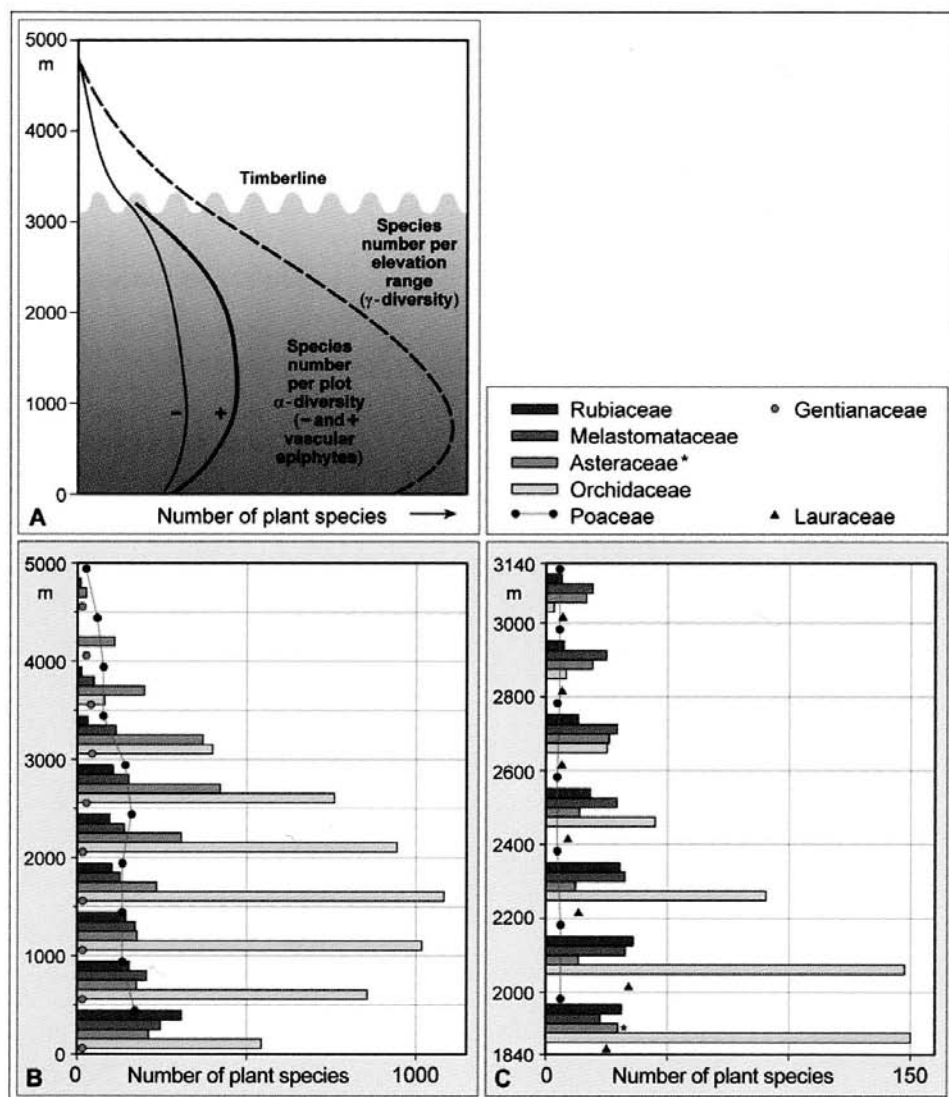
As shown in Table 1, more than 1450 species of vascular plants have been identified in the RBSF. According to the above equation, only 900 species would

be required to meet the number of the ecoregion. In spite of the presumably better knowledge of the plant diversity of the RBSF, this relatively small area turned out an outstanding hotspot of plant diversity. Although ecoregion data are not available for cryptogams, the total of more than 500 species of bryophytes (mosses, liverworts, hornworts; Table 1) recorded from the RBSF may also be considered outstanding.

**Table 1.** Species diversity in the RBSF area and the San Francisco Valley, respectively. \* RBSF only; (x) San Francisco valley, 1000-3000 m; \*\* world record.

	families	species	reference
seed plants	131	1208	Homeier & Werner (2008)
ferns and ferns allies	22*	250*	Lehnert et al. (2008)
hornworts	2*	3*	Gradstein et al. (2008)
liverworts	30*	320*	Gradstein et al. (2008)
mosses	40	204	Kürschner et al. (2008)
lichens	46*	311*	Nöske et al. (2008)
Glomeromycota		83*	Haug et al. (2004), Kottke et al. (2008)
Ascomycota		4*	Haug et al. (2004)
Basidiomycota		96* (102)	Haug et al. (2004)
bats		21* (24)	Matt (2001)
birds		227* (379)	Paulsch (2008), Rasmussen et al. (1994)
moths		(2396)**	Brehm et al. (2005), Hilt (2005), Brehm et al. (2003), Fiedler et al. (2008)
butterflies (Papilionidae)		(243)	Häuser et al. (2008)
Bush crickets		(101)	Braun (2002)
soil mites (Oribatidae)		129* (167)	Illig & Maraun (2008)
soil amoebae (Testacea)		78* (110)	Krashevskay et al. (2008)

Only few other groups of organisms of the RBSF have been investigated in similar detail as plants. An extraordinary species-rich group are moths, for which a world record of species diversity has been recorded (Table 1; Brehm et al. 2005). With respect to vertebrates, only birds and bats have thus far been investigated; these groups likewise show outstanding diversity. Fungi have not been systematically surveyed and the species numbers given in Table 1 are by no means exhaustive (I. Kottke, pers. com.).



**Figure 2.** Rapoport's Rule along the elevational gradient and the Mid-Domain-Effect. **A**, altitudinal change of vascular plant  $\alpha$ - and  $\gamma$ -diversities in tropical mountains (from Richter 2001, modified); species diversity and altitude are inversely correlated but there is usually a peak of richness at medium elevations (Mid-Domain-Effect). **B**, discordant vertical distribution of species numbers of selected plant families in Ecuador (data from Jørgensen & León-Yáñez 1999). **C**, same as B, but for the RBSF area (data from Homeier & Werner 2008, supplemented by recent findings of K. H. Dierl, pers. com.).

Other groups of organisms such as litter decomposers, however, are relatively poor in species. Only a few earthworms have been found (M. Maraun, pers. com.), and soil mites (*Oribatidae*) and soil amoebae (*Testacea*), which have been carefully investigated, are disappointingly species-poor (Illig et al. 2005, Maraun et al. 2008; Table 1; see also chapter 6 of this volume). The available data, thus, show that the investigated area in spite of its small size can be considered to represent a hotspot of neotropical biodiversity, but not for all groups of organisms.

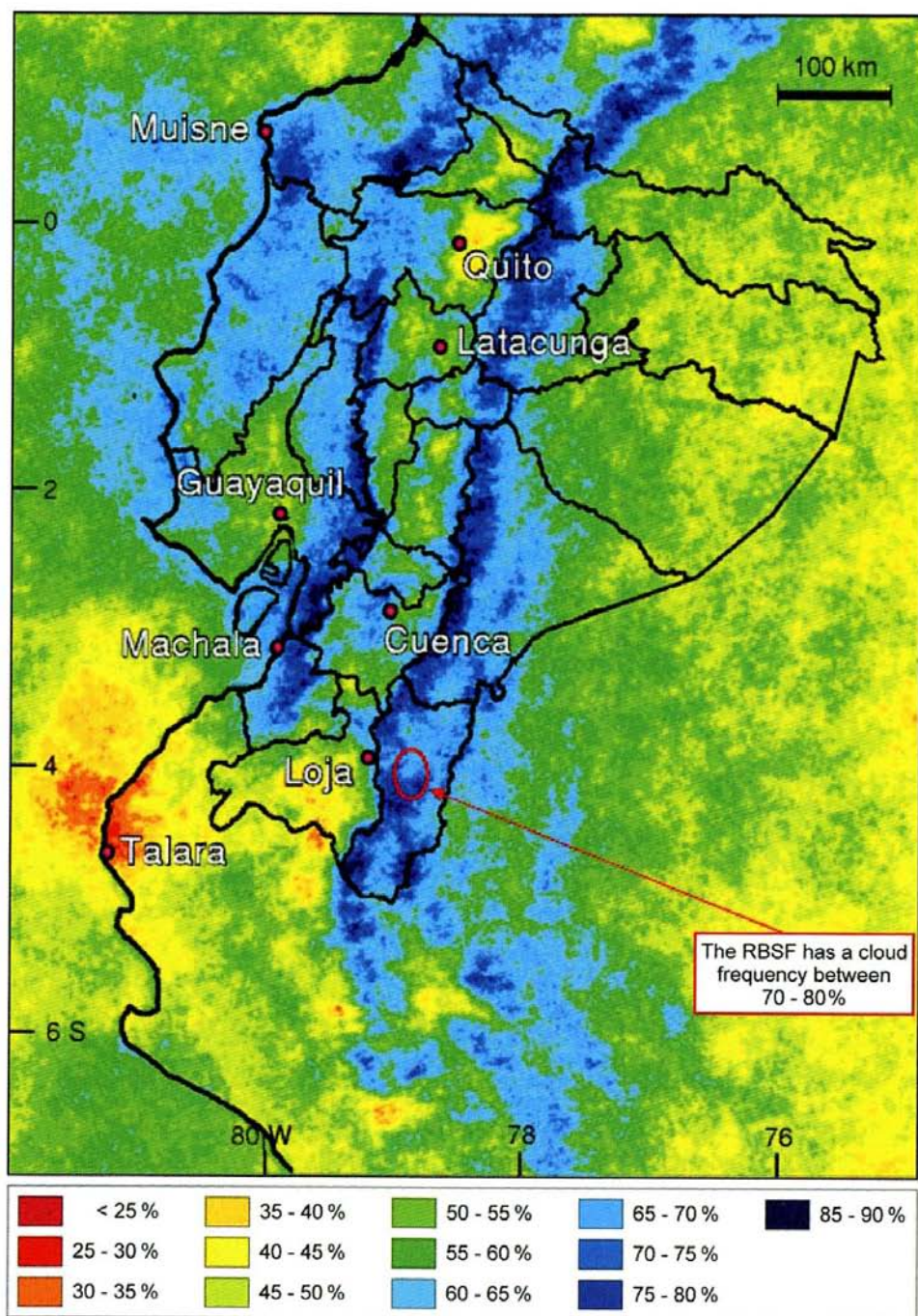
## Why is it hot?

To explain high biodiversity, one has to differentiate between factors that have contributed to the development of this diversity and those that have contributed to its maintenance. Both types of factors are not always separable because those effective in maintaining biodiversity may also have been effective its accrument.

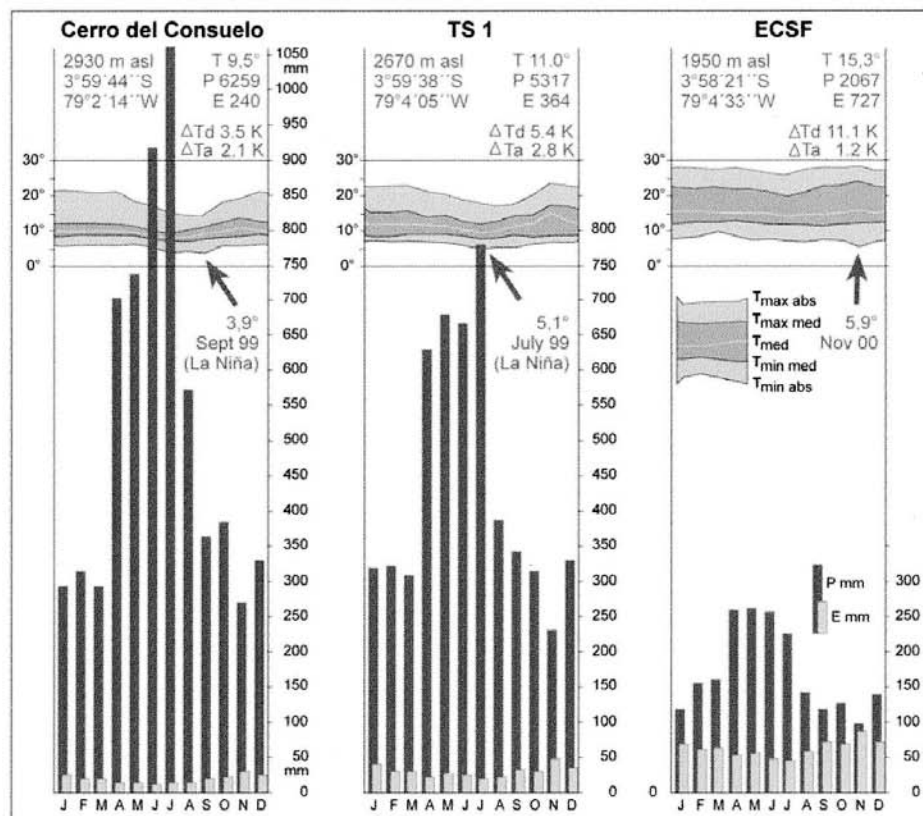
**Positional effects in general: Rapoport's rule and the mid-domain effect.** Rapoport's rule as exemplified by Stevens (1989, 1992, 1996) states that latitudinal ranges of plant and animal species are generally smaller at low than at high latitudes. Narrow ranges, as are typical of the Tropics, facilitate more species to coexist and thus result in higher species richness. It is evident that Rapoport's rule is subject to modification by factors such as drought or elevation.

The tropical regions also experienced a longer evolutionary time period since the Tertiary as compared with temperate regions and, thus, an elevated radiative speciation can be expected. Due to mostly favourable conditions for plant and animal life, newcomers or new ecotypes have better chances and thus the percentage of accidentals is comparatively high. Rapoport's rule may also apply to altitudinal gradients, posing that species ranges increase with altitude concomitantly with a decrease of species richness (Fig. 2). However, many studies on the altitudinal dimension of species diversity have shown that there is usually a peak of richness at medium elevations, the so-called Mid-Domain-Effect (Herzog et al. 2005, Krömer et al. 2005, Rahbek 2005; Fig. 2A; see also chapter 3 of this volume). Expectedly (taking into account the different ecological demands of certain plant families), the altitudinal distribution of various plant families is discordant, i.e. their mid-elevation peaks occur at different altitudes (Fig. 2B). The RBSF, at only some 450 kilometres south of the equator, occupies a latitudinal as well as an altitudinal range (1000–3200 m) where species richness can be assumed to be at its highest, as will be discussed below.





**Figure 3.** Relative cloud frequency for Ecuador (2002-2003) and adjacent areas derived from NOAA-AVHRR data. From Bendix et al. (2004).



**Figure 4.** Climate diagrams of the RBSF showing the altitudinal gradients (monthly means) of precipitation, evaporation, amplitude of air temperature as well as the annual means. Temperature minima are highlighted by arrows. From Bendix et al. (2006), modified.

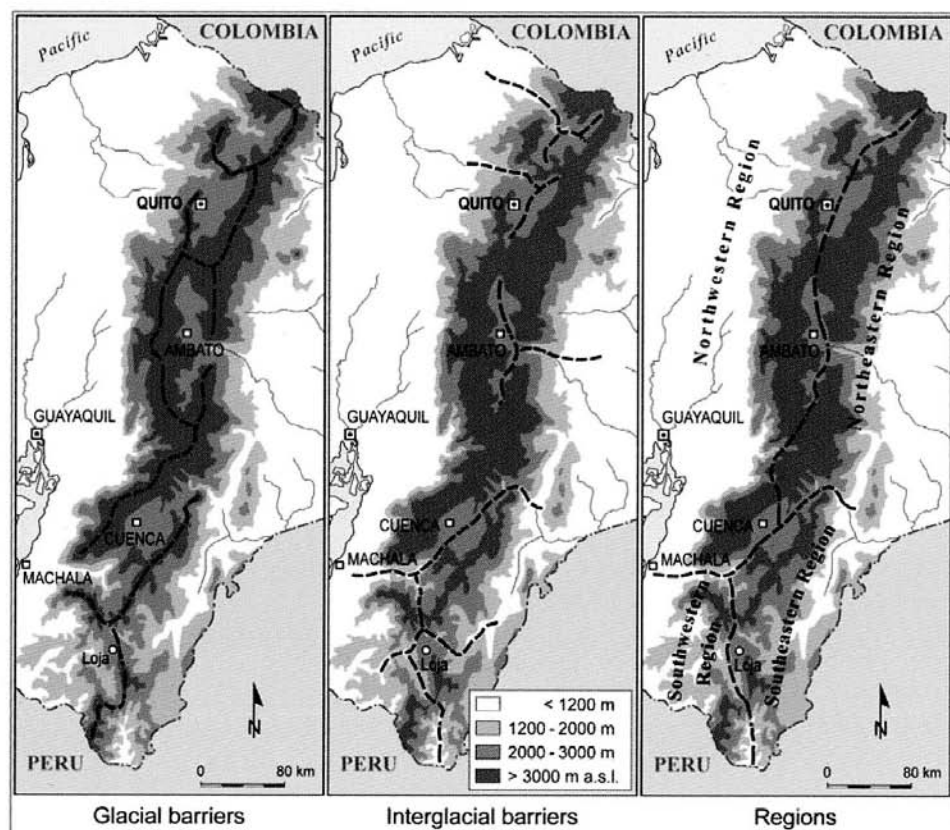
**Positional effect of the RBSF.** Located in the eastern range (= Cordillera Real) of the South Ecuadorian Andes, the RBSF belongs to the zonobiome of the humid tropics. The reserve is in the Amotape-Huancabamba depression, stretching from southern Ecuador to northern Peru, where the Andes barely reach 4000 m and the treeline is as low as ca. 3000 m. The geological setting of the Cordillera Real is rather monotonous and belongs to the paleozoic Chiquinda unit, consisting of metasilstones, sandstones and quartzites, interspersed with layers of phyllite and clay (Litherland et al. 1994; Beck et al. 2008b). However, the terrain of this depression is extremely broken, e.g. in the "Nudo de Loja" from where several mountain ranges are stretching south- and southeastward with a great variety of differently exposed slopes. This rugged landscape harbours an extraordinary multiplicity of geomorphological microsites. For most of the year the Cordillera Real is subjected to strong easterly winds carrying a lot of moisture from the Atlantic Ocean over



the Amazon. When reaching the Andes this moisture condenses with the rising air masses, causing the eastern slopes and the crest to be more or less constantly covered by clouds. A similar situation exists on the western escarpment of the Andes, which is subjected to the westerly winds from the Pacific Ocean. However, the Inner-Andean basin in the rain shadow of both wind systems receives only a small amount of precipitation as is shown by the cloud frequency (Fig. 3). With respect to the area of the Cordillera Real and the RBSF, an extraordinarily steep gradient of annual precipitation occurs over a short distance of not more than 30 km (Fig. 4). Likewise, a steep altitudinal precipitation gradient has been demonstrated in the area, from 2400 mm at 1850 m to over 6000 mm at 3100 m (Richter et al. 2008; chapter 1 of this volume).

The multiplicity of morphological microsites in combination with the strong climatological gradients result in a great variety of habitat types, enhancing the development of a high biological diversity. The incidence of a biodiversity hotspot in the South Ecuadorian Andes is in line with a recent model of plant diversity based on climate-driven growth conditions (Kleidon & Mooney 2000).

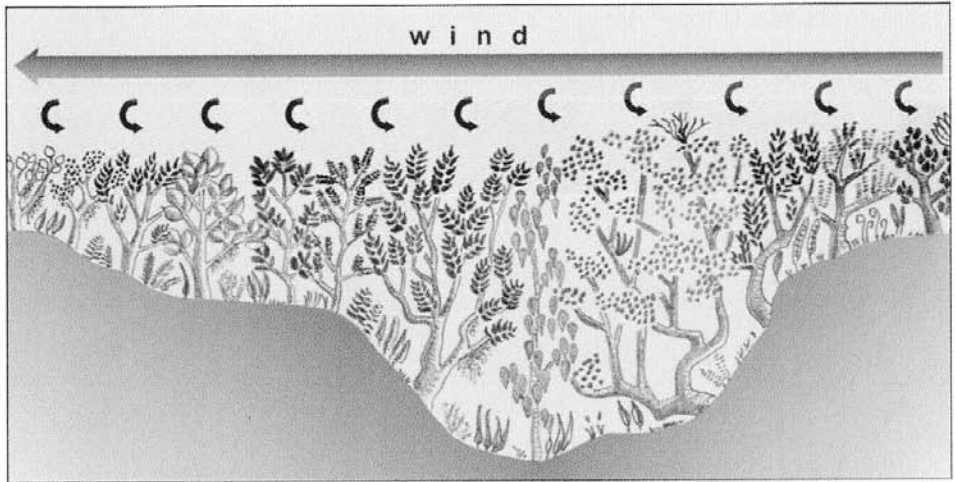
**Landscape history.** During the Quaternary, the Andean area including the Amotape-Huancabamba depression was subjected to strong climate changes (Niemann & Behling 2007; chapter 2 of this volume). With respect to plant diversity, the alternating glaciations and interglacial dry periods must have affected the local spreading of plant species, especially from the East to the West and *vice versa*. Jørgenson et al. (1995) described putative pleistocenic migration barriers of plants in the Ecuadorian Andes and recognized four regions of endemism (Fig. 5). Thus, the conceivable idea of the Amotape-Huancabamba-depression as a corridor for species exchange between the Amazon and the Pacific area as well as between the northern and the southern part of the central Andes, is less likely. Nevertheless, it cannot be ruled out that climatic changes resulted in periods of contact and separation between these areas, relative to the absence or presence of migration barriers. The Amotape-Huancabamba-depression might thus have functioned as a meeting point for the extraordinary genetic variety of the lowlands and as a centre of explosive radiation, e.g. in the genera *Anthurium*, *Piper* and *Cavendishia* (Gentry & Dodson 1987). Accrue ment of gene flow barriers by habitat fragmentation likewise results in enhanced genetic diversification and fosters endemism. Reports of recent expeditions by botanists exploring the flora of the Cordillera del Condor, Cordillera Colán and the Andean rainforest refugia in northern Perú have yielded large numbers of new species, all from the so-called "Amotape-Huancabamba floristic zone" (Dillon et al. 1995, Sagástegui et al. 1999, 2003, Weigend 2002, 2004). On the plant family level, far above-average degrees of local endemism have been demonstrated for Orchidaceae (55% of the occurring species), Bromeliaceae (50%), Asteraceae (37%), Piperaceae (37%) and Solanaceae (percentage not known).



**Figure 5.** Possible migration barriers for plant species in the Ecuadorian Andes during the Pleistocene. *Left:* barriers due to Pleistocene glaciation. *Centre:* barriers due to dry land areas in large valleys. *Right:* recent situation: 4 regions of endemism. From Jørgensen et al. (1995), slightly modified.

An impressive account of the effects of climate change on the vegetation of the southern Ecuadorian Andes during the Holocene has been given by Niemann & Behling (2007; see also chapter 2 of this volume). Based on pollen analysis data these authors showed a change of the páramo vegetation in the San Francisco valley area from a grass-dominated herbaceous formation to the current shrubby subpáramo dominated by bushes and small trees. Climate warming after the disappearance of the glaciers caused an uplift of the treeline by presumably several hundred meters. Nevertheless, the recent treeline around 3000 m a.s.l. on the mountains of the Amotape-Huancabamba-depression is about 1000 to 1500 m lower than the treeline North and South of the depression. The comparatively low elevation of the treeline can be attributed to the continuous strong easterly winds and the extremely high precipitation in the eastern ranges, resulting in large areas of water-logged soil which prevent the growth of deep-rooting trees. This explanation

is corroborated by two observations: (1) The treeline in the depression is composed of a great variety of woody plants, on average 70 species (Richter et al. 2008), whereas beyond the depression the treeline is formed only by *Pohlylepis* spp. (Rosaceae) occurring up to 4500 m and even higher; (2) Species-rich islets of small trees can be found in local, wind-sheltered hollows well above the treeline in the depression, indicating wind as an important factor inhibiting the growth of the taller plants (Fig. 6).



**Figure 6.** The treeline in the Amotape-Huancabamba depression is subjected to continuously strong easterly winds forcing treelets into hollows and ravines, with only dwarf shrubs thriving on slopes and crests. From Richter (2001), modified.

**Vegetation dynamics.** In contrast to the very effective long-term climatic changes, short-term changes apparently are of lesser significance. In the eastern mountains of South Ecuador, the recurrent El Niño and La Niña periods result in an transitory decrease of precipitation (Holmgren et al. 2001), which may enhance plant growth in the area (Cueva et al. 2006). However, there are other dynamic phenomena which could have an effect on plant diversity. First, tropical forests like those of the RBSF exhibit a so-called mosaic-climax characterized by a pronounced patchiness of different successional stages. The simultaneous coexistence of early and late pioneers and species characteristic of a mature forest enhances an increased plant diversity. Furthermore, the research area shows a high frequency of landslides, presumably due to the instability of the water-soaked soils and the steepness of the slopes. It has been hypothesized that the weight of the mature forest triggers the incidence of these landslides (Bussmann et al. 2008). Where a landslide has occurred, the topsoil containing the organic layers and the humic horizon is removed and the deeper soil horizons or even the bedrock become exposed. Since these are very poor in nutrients, plant re-growth starting with cryp-

togams, a few orchids and ericaceous species, is usually very slow (Ohl & Bussmann 2004, Hartig & Beck 2003). Nevertheless, landslides apparently contribute significantly to the dynamics of the vegetation of the RBSF and thus may enhance plant diversity even though representing an element of landscape instability. This observation is in agreement with the "intermediate disturbance hypothesis" (Levin & Paine 1974, Connell 1978, Huston 1994), which states that medium disturbances increase biodiversity. The impact of vegetation dynamics on plant diversity has been well exemplified for the RBSF (chapters 4 and 7 of this volume). In addition, recent studies by Hilt & Fiedler (2006) have shown that the species patterns of moths differ substantially between areas of undisturbed and disturbed forests, the latter being more diverse. The diversity of herbivorous insects apparently is likewise increased by vegetation dynamics.

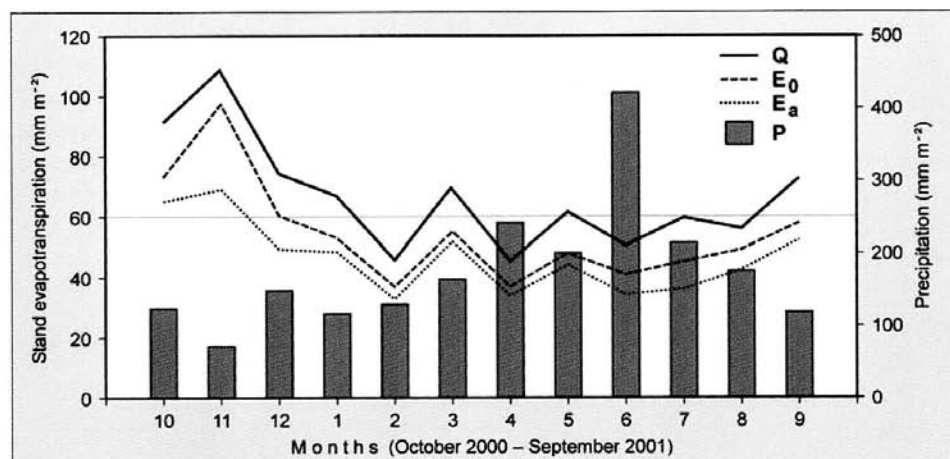
### Factors contributing to the maintenance of high biodiversity

Limitation of resources, especially of macronutrients prevents the dominance of particular species which by excessive biomass production could outcompete others. This interrelation is known as the "soil nutrient hypothesis" of biodiversity (Kapos et al. 1990, Huston 1994, Woodward 1996). The C:N - and the C:P - ratios of leaves increases with elevation indicating substantial N- and P-deficiencies as compared to other forest types, especially the tropical lowland forest (Table 2).

**Table 2.** N- and P-content in leaves of trees ( $n = 5 \pm \text{SE}$ ) in the RBSF compared with data (a) from McGroddy et al. (2004). Different upper case letters indicate statistically significant differences; n = number of studies. From Soethe et al. (2006).

location/forest	C:N ratio	C:P ratio
RBSF (1900 m)	$23.3 \pm 1.2^a$	$232 \pm 21^a$
RBSF (2400 m)	$38.2 \pm 3.8^b$	$430 \pm 44^b$
RBSF (3000 m)	$44.7 \pm 1.1^b$	$372 \pm 19^b$
temperate broadleaved forest (a)	30.4 (n = 29)	357 (n = 28)
tropical lowland forest (a)	30.1 (n = 7)	951 (n = 12)

Wilcke et al (2008) showed an increase of soil organic matter, carbon stocks and the C/N-ratio with elevation in the RBSF, while mineralization was negatively correlated with altitude. Even the organic soil layer is quite poor in macronutrients. As a likely consequence, woody plants at higher elevations invest more of their biomass into the root system (Leuschner et al. 2007; chapter 8 of this volume). In addition, the establishment of an effective mycorrhiza is of utmost importance for the perennial plants. Very high colonization rates of arbuscular mycorrhiza were



**Figure 7.** Stand parameters of the natural lower montane forest of the RBSF. Monthly sums of evapotranspiration, precipitation ( $P$ ) in mm and monthly net radiation balance ( $Q$ ), here also expressed in mm as equivalent to vaporization.  $E_a$  = monthly actual,  $E_0$  = monthly potential evapotranspiration. During the wet months,  $E_a$  almost equals  $E_0$ . Low evapotranspiration rates contribute to low nutrient acquisition, in particular of mobile nutrients like nitrogen. From Motzer et al. (2007).

found not only in trees at all altitudes but also in hemi-epiphytic ericads, epiphytic orchids, ferns, and even in some groups of liverworts (Kottke et al. 2008; chapter 5 of this volume). The density of the litter-decomposing soil fauna, especially of the primary decomposers in the RBSF, is generally low and declines with altitude. In addition to low mineralization rates, nutrient uptake is also low. Because of the high degree of cloudiness together with a high relative humidity, evapotranspiration and, in turn, water and nutrient uptake rates are low (Fig. 7). During extremely wet months tree growth is even suspended. However, due to the elevational increase in precipitation leaching of nutrients increases with altitude, adding to the deterioration of the litter quality of the upper montane forest.

**Table 3.** Leaf area index as an indicator of the abiotic resource light in various habitats of the RBSF. Competition for light is especially strong in the lower montane forest. From Motzer et al. (2007) and Oesker (unpubl.).

site	gully	gully → slope	slope	slope	elfin forest
altitude [m]	2050	1950	1975	2125	2240
LAI [m <sup>2</sup> /m <sup>2</sup> ]	9.8	6.7	6.4	5.9	3.0

Reduced light intensities (Table 3) in the dense forest, on the other hand, favour the occurrence of plant life forms such as lianas and epiphytes, which considerably



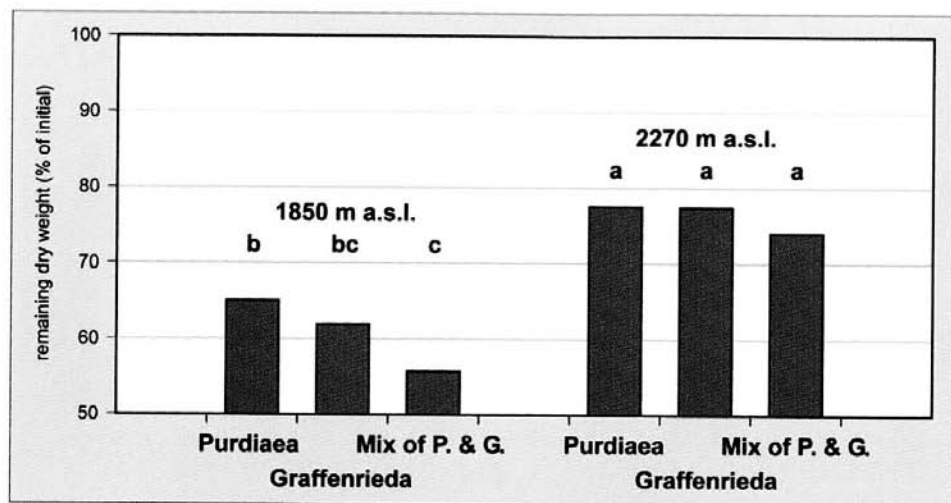
contribute to plant diversity of the area. Favoured by the perhumid climate the wealth of epiphytic species is staggering: Up to 98 vascular epiphyte species have been counted on one single tree – the highest number ever recorded – and 225 on six trees (Werner et al. 2005). A very important result of the research reported here is the fact that keystone species of plants or animals could not be identified in the natural forest. Rather, a variety of up to 160 plant species share one hectare with only very few individuals of any one species present (Martinez 2006). The scattered populations of discrete tree species in the dense forest pose the question of the specificity of the biotic interactors, e.g. pollinators, seed dispersers and mycorrhizal fungi. *Vice versa* the outstanding diversity of herbivorous insects, e.g. moths, should also be reflected by a similar diversity of fodder plants. Although several specific interactions have already been detected, e.g. of bats or humming birds with particular flowers (Wolff 2006), biotic interaction is still an open field for further investigation. It should be borne in mind, however, that it is the multitude of rather weak biotic interactions which stabilizes the outstanding biodiversity of the ecosystem.

### **The influence of biodiversity on ecosystem processes and the question of redundancy**

Ecosystems channel and circulate matter and energy, and exchange these with their surroundings. As most ecosystem processes are accomplished via food webs, the question arises as to the influence of the degree of diversity and food-web complexity on element cycling and matter balance.

With regard to an ecosystem we may differentiate two categories of elements, essential and luxury (redundant) components. In his security hypothesis, Schulze (1989; see also Schulze et al. 1999) compared these components and their functions with the parts of a car and their intended functions – upon normal use – and in emergency situations. A luxury part may facilitate normal driving, e.g. a brake booster, but will become a lifesaver in an emergency situation. For an ecosystem an emergency situation may result from a change in its abiotic setting or from a biological calamity. In the case of a biodiversity hotspot the question arises which species are necessary (and sufficient) for the "normal" functioning of the ecosystem: Which species may function in alternative processes ("exchangeability" of species), which as emergency components, and which may be redundant and dispensable (Gitay et al. 1996). In a more general sense the question is posed as to the resilience of a hotspot of biodiversity to unpredictable changes or events.

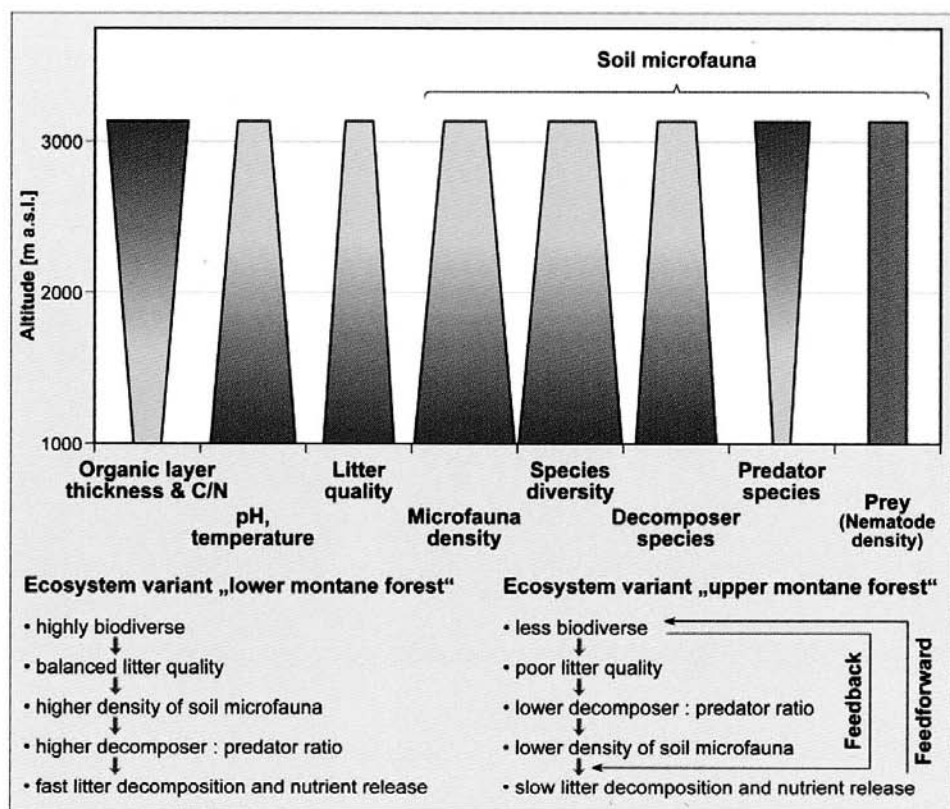
Ecosystems are commonly described by the flux of matter, including water, and of energy. The balance of these fluxes can be taken as a measure of the stability of the ecosystem. Characterization of the ecosystem, however, is by its biotic components and their interactions, i.e. of individuals in populations. These interac-



**Figure 8.** Effect of litter quality (C/N-ratio) and elevation on litter decomposition (measured as remaining dry weight). Leaf litter of *Graffenrieda emarginata* (C/N 42), *Purdiaea nutans* (C/N 74), and a mixture of both (mix) was exposed in the field for 12 month at two different altitudes. Bars sharing the same letter are not significantly different (Tukey's HSD test;  $P > 0.05$ ). From Maraun et al. (2008), slightly modified.

tions may be strong in an ecosystem with a few keystone species (few degrees of freedom) but weaker and more variable in species-rich ecosystems (many degrees of freedom).

A nectar-licking bat (3 of at least 21 bat species in the RBSF belong to this guild, see Matt et al. 2008) must change its diet several times in the course of the year, as most perennial plants (e.g. *Macrocarpaea* and some Marcgraviaceae) show a pronounced seasonality of flowering. A high phytodiversity favours weak plant-animal interactions, i.e. counteracts a too tight specialization, thus reducing the risk of missing a special partner in a low density population. Recent work on host-plant relationships showed that in spite of, or even because of the narrower tropical habitat ranges, herbivores in tropical lowland forests are not generally more specialized than in temperate-zone ones, supporting the idea of preponderance of weak and often asymmetric biological interactions (Novotny et al. 2006). As already mentioned, keystone species with a wide habitat range could not be identified in the hotspot ecosystem represented by the RBSF. But the general attenuation of species diversity with increasing elevation poses the question whether the ecological functions and ecosystem services provided by many lower-montane species are taken over by a smaller number of less specific upper-montane species, or whether the lower montane and the upper montane forests represent different variants of the ecosystem (Fig. 9). Irrespective of the extreme cases, a gradual change of the ecosystem with increasing altitude appears to reflect the situation



**Figure 9.** A possible feedback of biodiversity on ecosystem processes in lower montane (1850 m) and upper montane (2270 m) forest. A faster flux of resources in the lower montane forest promotes plant biodiversity, which in turn produces a more balanced litter quality.

best, concomitantly with a gradient of indispensability for individual components and their interactions.

Wilcke et al. (2008) and Iost et al. (2008) showed an accumulation of organic soil material at higher altitudes, which cannot only be attributed to a temperature-triggered decrease of the mineralization rate but is also caused by poorer litter "quality", i.e. lower nutrient contents (Table 2, Fig. 8). This concurs with an elevational change in the guild compositions of the soil fauna but also with a decrease of the population densities of litter decomposers. Comparison of the soil organic layer and carbon stocks of the lower and the upper mountain forest ecosystem of the RBSF reveal an effect of biodiversity on the respective matter fluxes. Due to a higher litter quality, the higher biodiversity encountered in the lower montane forest accomplishes a faster flux of the resources (nutrients) through the ecosystem, which in turn favours diversity of plant species (Homeier et al. 2008). In this case,

a feedback of biodiversity on the ecosystem processes can be inferred (Fig. 9). Conceivably, such an effect could stabilize the tropical lower montane rainforest ecosystem, but we still lack empirical data. The fast recovery of a highly diverse secondary forest in the RBSF (Martinez et al. 2008) inhabited by an extraordinary diversity of herbivorous insects (Hilt & Fiedler 2008) nevertheless shows a substantial resilience of that ecosystem against small-scale disturbances, as long as recolonization by organisms lost through disturbance is possible.

The lower and upper montane forests demonstrate the existence of such a feedback, but we are not yet able to nail this effect down to the species level. This situation is best characterized by the "rivet"-hypothesis (Ehrlich 1994), which assumes that removal of a number of rivets (guild components) rather than of a specific rivet (a key species) will destabilize an airplane's wing (an ecosystem) to the point where it breaks. As a consequence, we cannot yet state whether or not there is species redundancy in our biodiversity hotspot.

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