The Official Journal of the International Association for Landscape Ecology, Chapter Germany (IALE-D)

Landscape Online

International Peer-Review Free-Access Online

Received: 15.03.2009 Received in revision: 29.04.2009 Accepted: 04.05.2009 Published: 16.06.2009

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Landscape Online 12, 1-35. **DOI:10.3097/LO.200912**

Reasons for an outstanding plant diversity in the tropical Andes of Southern Ecuador

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Abstract

Long-term field studies in the scope of a multidisciplinary project in southern Ecuador revealed extraordinary high species numbers of many organismic groups. This article discusses reasons for the outstanding vascular plant diversity using a hierarchical scale-oriented top-down approach (Grüninger 2005), from the global scale to the local microscale. The global scale explains general (paleo-) ecological factors valid for most parts of the humid tropics, addressing various hypotheses and theories, such as the "greater effective evolutionary time", constant input of "accidentals", the "seasonal variability hypothesis", the "intermediate disturbance hypothesis", and the impact of soil fertility. The macroscale focuses on the Andes in northwestern South America. The tropical Andes are characterised by many taxa of restricted range which is particularly true for the Amotape-Huancabamba region, i.e. the so called Andean Depression, which is effective as discrete phytogeographic transition as well as barrier zone. Interdigitation of northern and southern flora elements, habitat fragmentation, geological and landscape history, and a high speciation rate due to rapid genetic radiation of some taxa contribute to a high degree of diversification. The mesoscale deals with the special environmental features of the eastern mountain range, the Cordillera Real and surrounding areas in southern Ecuador. Various climatic characteristics, the orographic heterogeneity, the geologic and edaphic conditions as well as human impact are the most prominent factors augmenting plant species diversity. On microscale, prevailing regimes of disturbance and environmental stresses, the orographic basement, as well as the general role on the various mountain chains are considered. Here, micro-habitats e.g. niches for epiphytes, effects of micro-relief patterns, and successions after small-sized disturbance events are screened. Direct effects of human impact are addressed and a perspective of possible effects of climate change on plant diversity is presented.

Keywords

vascular plant diversity, tropical mountain forests, scale dependent approach, disturbance ecology, Andean Depression

ISSN 1865-1542

1 Integrating the local working area in a global framework of biodiversity

In the context of a scientific project an investigation team of biologists and geographers identified a surprising quantity of animal and plant species within a small mountain rainforest and páramo area of only 11 km2 in southern Ecuador: Preliminary relevés between 1,800 and 3,185 m a.s.l. of the so-called Reserva Biológico San Francisco (RBSF) in the eponymous river valley in southern Ecuador, exhibit around 1,300 seed plants, 250 ferns and fern allies, 320 liverworts and 204 mosses, 311 lichens, 83 Glomeromycota, and 96 Basidiomycota. Furthermore, animal sampling resulted in 21 bats, 227 bird species, 243 butterflies (Papilionoidea), 2396 moths (diversity world record), and among other species-rich animal taxa, 129 soil mites (updated version, further information s. Liede-Schumann & Breckle 2008). Within the large vertical gradient the mountain rainforests deserve particular attention due to their extraordinary biodiversity (Beck & Richter 2008).

Detailed studies of plant diversity in the lowlands and mountains of northeastern Perú und southeastern Ecuador are still in an early stage due to political conflicts in the Mid-1990s. Hence, actual research activities in the border region of the two countries address mainly taxonomic inventories. The few available reports of recent botanical expeditions to the Cordillera del Cóndor, Cordillera Colán and the Andean rainforest refugia in northern Perú, show an enormous potential for new species in that so-called "Amotape-Huancabamba" floristic zone (Dillon et al. 1995, Sagástegui 1994, Weigend 2002 and 2004). On the family level, far above average endemism has been shown for Orchidaceae (55% of the occurring species), Bromeliaceae (50%), Asteraceae (37%), and Piperaceae (37%).

These hints fit well with records of Gentry (1982), who stated that many Neotropical plant groups form a diversity centre in the Chocó, whereas others are concentrated in the western Amazon basin in Ecuador (Barthlott et al. 2007, Pitman et al. 2002). Not least because of that, some spectacular species numbers are reported for the Napo region of the Amazon basin: Valencia et al. (1994) counted 473 tree species and 187 tree genera (> 5 cm/dbh), respectively, on a 1 ha plot of the terra firme at Tarapoa. Nabe-Nielsen (2001) found in the subregion of Yasuni 96 liana species on a 0.2 ha plot and Kreft et al. (2004) recorded an outstanding number of 146 vascular epiphyte species on a 0.1 ha plot, both values presumably the highest numbers ever recorded for comparable lowland plots.

Thus, it is not surprising that the global plant-biodiversity census for vascular plants carried out by Mutke & Barthlott (2005) and Barthlott et al. (2007) points out the tropical Andes-Amazonia transition zone in Ecuador being one of five „megadiverse hotspots". The latter are considered centres with diversity maxima of over 5,000 vascular plants species per 10,000 km^2 (Fig. 1). The entire tropical Andes contain about one sixth of all known plant life in less than one percent of the world's terrestrial area (Mittermeier et al. 1997). The hotspot comprises dry and humid mountain chains up to more than 6,000 m a.s.l. as well as the lowland tropical rainforest. The great variety of ecosystems ranges from elevated, species-poor to complex, species-rich habitats on the eastern foothills of the Andes.

Generally, there is an inverse latitudinal gradient of biodiversity i.e. a decreasing number of species with an increasing distance to the equator. Consequently, the evergreen tropics and subtropics tend to be the most diverse ecozones on earth. In addition, regions with a great variety of environmental conditions are often found to be centres of high biological diversity. This is especially true for mountains and areas with steep topographical and climate gradients (Mutke & Barthlott 2008, Clinebell et al. 1995).

This first overview gives a stepwise perspective on how a small area of extraordinary species richness is embedded in a global biodiversity system by using a simple bottom-up approach. However, for a better understanding of the complex cause-effect-system which helps to explain the outstanding taxonomical spectrum of RBSF we will use a top-down approach from global to local aspects. This proceeding corresponds best with a progressive perception ranking from general to special triggers controlling the vascular plant diversity of the investigation area.

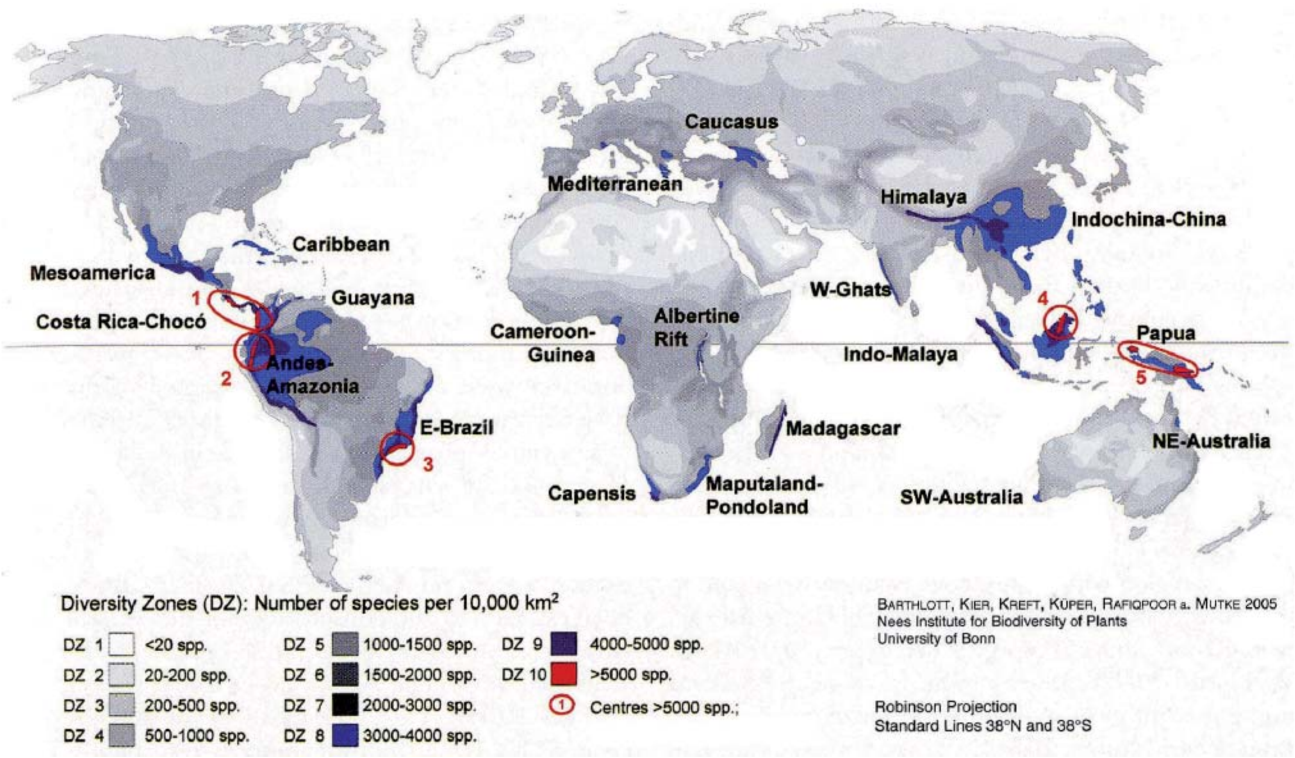


Figure 1: Map of vascular plant species richness. The research area (RBSF) is centered within one of the five world´s megadiversity hotspots. Apart from Ecuador the Costa Rica-Chocó area, south-eastern Brazil, northern Borneo and the New Guinea mountain range are among the other hotspots. From: Barthlott et al. (2007).

2 The study area and a scale dependent approach to explain the outstanding plant diversity

2.1 The study area

The aforementioned study area in southern Ecuador covers an area of around 100 km^2 including a core area of 11 km^2 (Reserva Biológica San Francisco, RBSF) and some satellite areas. The RBSF, situated within the ecozone of the humid tropics in the eastern chain of the South Ecuadorian Andes, belongs to an important transition as well as border zone, which is the Andean Depression (Fig. 2, Fig. 3). This relative orographic depression stretches 500 km N-S between the Girón-Paute drainage basin around Cuenca in southern Ecuador and the Rio Chicama-Rio Huallaga intersection around Cajamarca in northern Peru (Weigend 2004) and separates the central from the northern Andes (Emck et al. 2007). Here, the Andes barely reach 4,000 m a.s.l. and the treeline is as low as 3,000 to 3,400 m a.s.l. (Fig. 3). Despite or exactly for being so low, this part of the Andes is considered an important biogeographical barrier (Weigend 2002). Especially its eastern escarpment comprehends a connotatively and fascinating centre of endemism (Sagástegui et al. 1995, Schulenberg & Awbrey 1997, Young & Reynel 1997, Ayers 1999, Hensold 1999, Neill 2002). For example, many findings suggest a disjunct biogeographical connection between the nutrient poor sandstone massifs of the Cordillera del Cóndor and the isolated summits of the nearly 2,000 km distant Tepuis of the Guayana highlands in southern Venezuela (Neill 2005).

Within the Andean Depression, we focus on the Cordillera Real east of Loja (Fig. 3) to explain the crucial triggers that cause the above-mentioned high biodiversity of the RBSF-area. Here, discrete vegetation belts are at most weakly expressed, which is mainly due to the enormous diversity of species. This feature arises from a primarily random distribution of plant species, in particular of trees in tropical mountain rainforests. Thus the tropical mountain forest of the research area can as well be addressed as a large continuous ecotone (Bach et al. 2007, Richter 2008), which appears to support the so-called Mid-Domain-Effect (Colwell et al. 2004, Herzog et al. 2005, Krömer et al. 2005, Rahbek 2005), i.e. maximum biological diversity at midrange elevations.

Most of the north-facing slopes of the RBSF-terrain are covered by virgin mountain rainforests. Man made environments are restricted to narrow stretches alongside of a power plant channel at 1,900 m a.s.l. ± 50 m as well as of a mountain trail leading up to Cerro de Consuelo (3,185 m a.s.l., Fig. 13), i.e. the highest point in the project area. These habitats are the only ones that are infiltrated by invasive plants from the south-facing slopes on the opposite side of San Francisco River, where managed (as well as abandoned) pastures prevail due to a convenient accessibility through the Loja-Zamora state road.

2.2 A scale dependant top-down approach

Since outstanding plant diversity seems to be a typical feature of the neighbouring ecoregions, the plant diversity of the actual study area can be explained by factors which are effective on different spatial levels. While some of the diversity-triggers are concentrated on micro-sites caused, for example, by activities of small animals others control worldwide distributed ecozones such as the humid tropics. In this context, features of biodiversity must be considered scale dependent. Some of these are of great extension, however show only local effects. In this case we assign such phenomenon

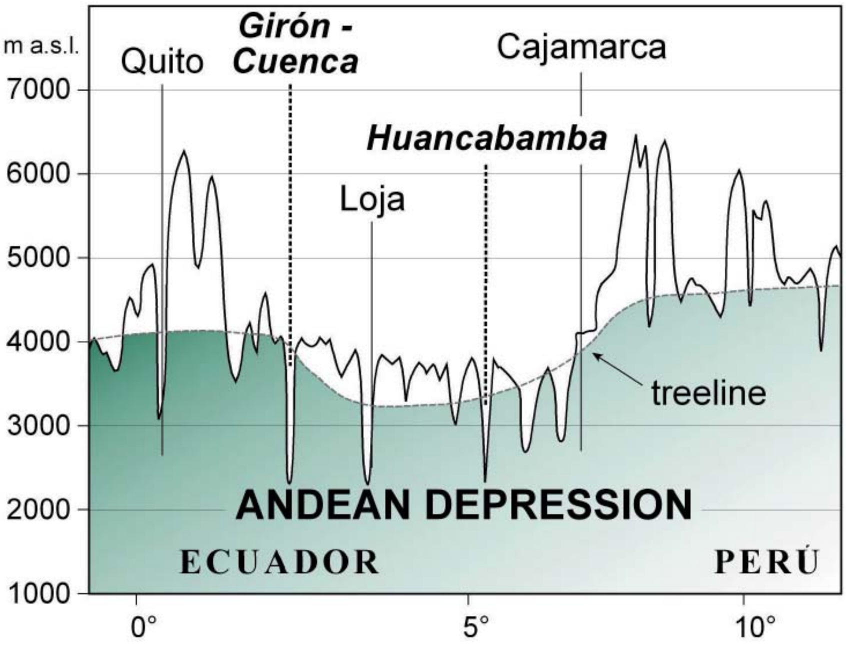


Figure 2: Position of the Andean Depression and its core zone around Huancabamba. The research area is located near the town of Loja. Note the treeline depression in this lower section of the Andes.

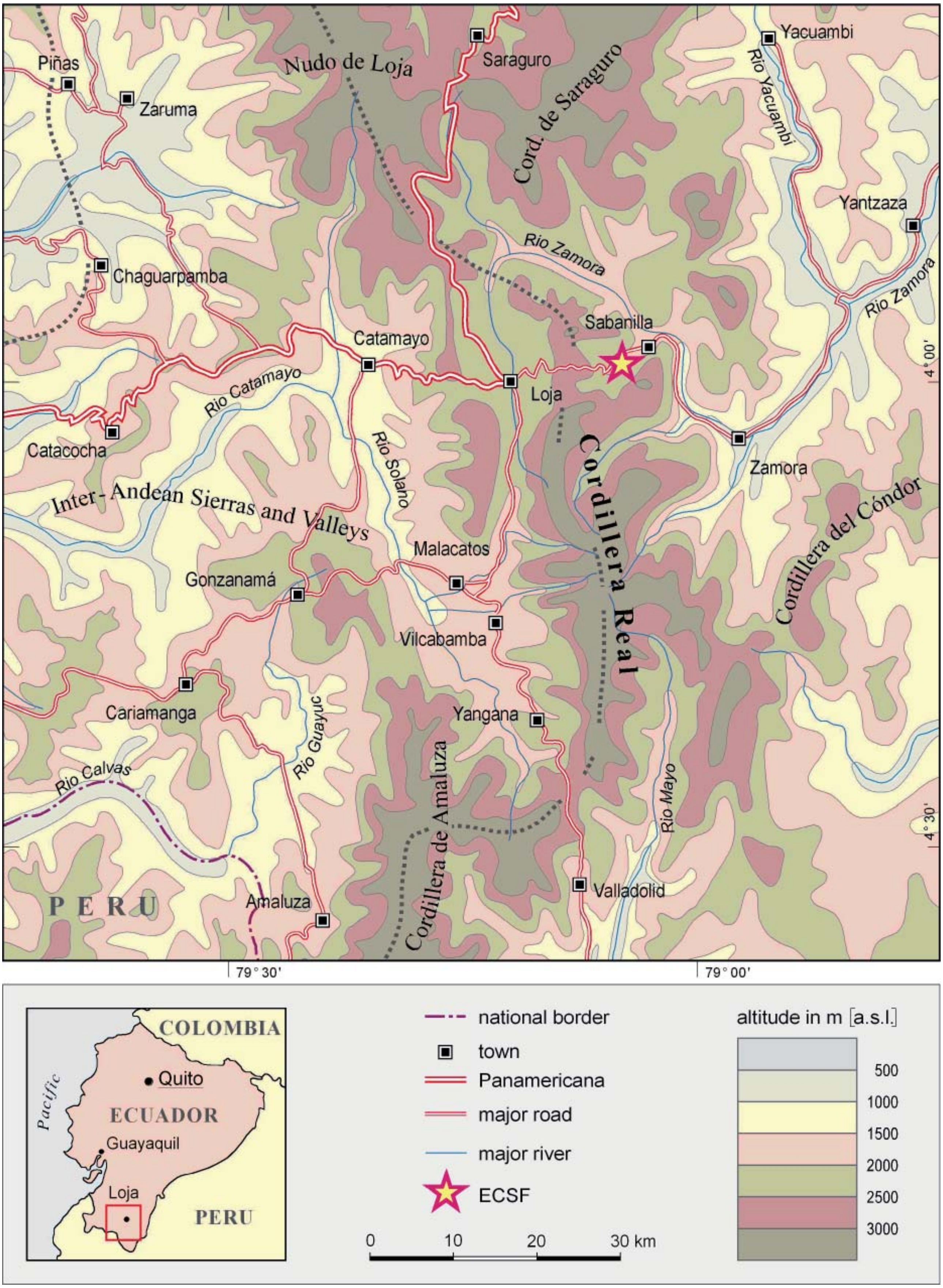


Figure 3: Location of the Cordillera Real and the research station (ECSF) in southern Ecuador.

to a micro-level. Referring to a similar approach developed by Grüninger (2005) we use four different scales to explain the reasons for the outstanding vascular plant diversity of the study area:

- The global scale: general (paleo-) ecological factors associated with the virtually ubiquitous species-rich tropical biodiversity are considered.
- The macroscale: factors typical of the north-western region of South America, including the Andes with their foothills as an essential taxonomical source for the flora of the research area are discussed.
- The mesoscale: environmental factors explaining the species richness of the Cordillera Real and its surroundings in southern Ecuador are highlighted.
- The microscale: small scale factors such as structural patterns and dynamic processes influencing diversity within essential communities of different altitudinal ranges are assessed.

The following considerations focus primarily on taxon or species richness, less so on structural diversity, and will not address functional diversity.

2.2.1 The global scale

A map on global patterns of vascular plant diversity by Kier et al. (2005) shows 51 ecoregions with more than 5,000 species per 10,000 km^2 .Forty-six of these regions are located in the humid tropical broadleaf forest ecozone. Only few tropical rainforests are described as monotonous tree stands (Hart et al. 1989, Müller-Dombois 1998, Richards 1996). However, even these "single-species dominated" forests contain around 20-30 tree species per hectare, so they are still highly diverse by temperate standards. This holds also true for the relatively uniform *Purdiaea nutans* community within the RBSF, which is described by Gradstein et al. (2008).

On global scale, in addition to the variety of trees as the dominant life form, epiphytes and lianas contribute significantly to the enormous tropical species richness. However, the structure of evergreen rainforest formations, normally cited as models for extreme heterogeneity, may vary considerably (Gentry 1982a). Supported generally by the number of tree species, plant diversity of the African Paleotropics involves a greater number of stem-climbers, whereas in the Neotropics, epiphytes play a much more important role. In tropical South America a considerable portion of the area is mountainous which favours epiphytes over lianas and winders. While epiphytism is usually comparatively limited in lowlands with a few larger examples of vascular plants and a low number of bryophytes, there is an increasing epiphytic diversity in mountain and elfin forests (Freiberg & Freiberg 2000, Richter 2001).

For an interpretation of the global aspect of diversity, the so-called „Rapoport‘s Rule“ as consequence of globally effective ecological triggers can be used. The rule states that latitudinal ranges of animal or plant species widen towards the poles (e.g. Willig et al. 2003). This provides a basic explanation for the geographical pattern that marks the two extremes of diversity: „a chemostate-like system tending to become monospecific" on the one hand, "and a Noah‘s ark or museum situation with an infinite number of species each represented by just one specimen“ on the other (Margalef 1994). Some general but decisive factors for "tropical arks" are outlined in the following, since they apparently play a role in the study area.

1. A longer effective evolutionary time since the Mid-Tertiary. This factor comprises both a higher evolutionary rate (at tropical temperatures) and a longer contemporary evolutionary time-span under relatively constant thermic conditions, resulting in higher species numbers in the tropics (Rohde 1992) concomitant with an elevated radiative speciation (Beck & Richter 2008). Fränzle (1994) considers tropical rainforests as highly developed systems with a most efficient entropy flux rendering maximum stability by homogenous climatic and edaphic environments.

2. Low-latitude species typically are less tolerant against environmental stresses than high-latitude species. Furthermore, a higher number of „accidentals“ (i.e. species with a low adaptive capability to various habitats) are typoical of tropical communities. A constant input of such accidentals inflates species numbers in the tropics (Stevens 1989).

3. Present seasonal differences between sites separated by latitude or elevation drive the Rapoport phenomenon, i.e. the observation that low-latitude species are commonly less tolerant of seasonal temperature fluctuations than high-latitude species. The latter produce a more violent competitive evolutionary pressure (Seasonal Variability Hypothesis, according to Stevens 1996), due to a phenological synchronization that inhibits a fast differentiation among species and lowers the opportunities for regeneration (Runkle 1989).

4. The Intermediate Disturbance Hypothesis states that biodiversity is highest at an intermediate degree of (natural) disturbances (Grime 1973, Connell 1978, van der Maarel, 1988). Competitive exclusion and colonization by less competitive species is balanced best at an intermediate frequency and intensity of disturbance. However, this hypothesis has been criticized as being „circular and not particularly useful ... unless the ‘ intermediate frequency ’ of disturbance can be defined independently of its effect on species diversity“ (Huston 1994, p. 122). The hypothesis involves the commonly over-estimated gap-theory, which puts much emphasis on patchiness with regard to dynamics and regeneration processes in rainforests. Instead of the relatively rare toppling of aged overtopping trees in pristine tropical lowland forests these trees usually die while still in an upright position rather than to crash down and create gaps. This observation might have inspired Lieberman et al. (1993) to entitle a paper „Forests are not just Swiss cheese“.

5. Instead, Huston (1994) developed the Dynamic Equilibrium Model for tropical ecosystems, which assumes a dynamic equilibrium achieved by the varying growth rates of individual species, intensity of interspecific competition, and frequency and intensity of disturbance. His model challenges the intermediate disturbance hypothesis inasmuch as species diversity is predicted highest where frequency or intensity of disturbance is lowest, especially when productivity and likelihood of competitive displacement are low.

6. The soil nutrient hypothesis implies an inverse relation between soil fertility and plant diversity in the tropics. Examples of species rich habitats commonly show acidic conditions, low in cations but rich in iron and aluminium, and a lack of pebbles or stones (Fränzle 1994, Kapos et al. 1990, Woodward 1996). According to Huston (1994) competition for the few soil nutrients causes slow growth, although plants often grow all year-round. As a result, fast growing potential competitors are not able to overgrow others and many species can coexist in a non-equilibrium state.

7. Furthermore, a “rainfall-diversity hypothesis”, first stated by Gentry & Dodson (1987) and recently reported by Kreft et al. (2004), seems to address a driving force for epiphyte diversity and possibly also for terrestrial ferns (Kessler 2001). Highest species richness was recorded in humid forests receiving high and largely non-seasonal amounts of annual rainfall. Eco-physiological studies support that hypothesis, showing that epiphytic growth is more water- than nutrient-limited (Laube & Zotz 2003). The situation is different with tree diversity for which mean annual precipitation appears as a weak predictor (Givnish 1999 and ter Steege et al. 2000).

8. Many plant-animal interactions are an outcome of a long standing coevolution and thus strongly related to paleoecology. This comprises flower–pollinator interactions, biotic seed dispersal, ant–plant interactions, or specials patterns of herbivory by insects or mammals (Herrera & Pellmyr 2002, Thompson 2005). The hypothesis interlinks a lower rate of species extinction with an ongoing speciation in areas less affected by Pleistocene climate change supports the idea of the existence of coevolutionary hotspots. This hypothesis is in agreement with the high degree of plant diversity and endemism in the Chocó and in Western Amazonia, where the Upper Napo refuge is considered the largest of the Pleistocene rain forest refugia (Prance 1982) due to an uninterrupted moist paleoclimate (van der Hammen & Hooghiemstra 2000, Kreft et al. 2004).

While some of these general ecological hypotheses and theories may complement each other such as numbers 1 and 2 or 6 and 7, others seem to contradict another, e.g. the hypotheses 4 and 5. Generally, problems caused by conflicting hypotheses can be resolved by applying a conceptual framework that addresses the changing dynamics of non-linear ecological processes over a broad range of interacting environmental conditions. Such a framework implies that the Dynamic Equilibrium Model to some extent fits into the global scale of lowland rainforest ecosystems, in which apart from hurricane prone areas autogenesis can be considered the main mechanism of regeneration (Whitmore 1990). The framework captures critical driving variables for the dynamics of populations, communities, and ecosystems at scales ranging from global ecozones to a local hillside. The Intermediate Disturbance Hypothesis and the gap theory on the other hand can explain species-richness in mountain rain- and cloud forest ecosystems embedded in a rugged terrain as an additional attribute. In corresponding areas natural disturbances might be more effective, as gaps are only frequent in regions, which are prone to them, i.e. where catastrophic events like earthquakes, landslides, floods, or periodic fires contribute to a mosaic of structural phases (Whitmore 1989).

2.2.2 The macroscale

On landscape scale, the northern Andes form an important interface between the Tumbes-Chocó-Magdalena hotspot in the west and the Amazonian lowlands in the east. The uplift of the mountain chain in the Pliocene triggered an extensive evolutionary radiation of the dominating Gondwana elements. Furthermore, the deferred following link between Central and South America by the isthmuses of Nicaragua and Panama facilitated the subcontinental taxanomic exchange (Gentry 1982b). The emerging orographic situation concurred with the formation of mountainous "stepping stones" and boosted the southward migration of subtropical and warm-temperate Nearctic taxa fostered by the cooling since the Miocene. Thus, according to van der Hammen (1989), the mountain forests of the northern Andes form an outstanding meeting point for vascular plant taxa of various origins. Among the non-primordial genera, neotropical elements are represented strongest; they amount to 65%, followed by holarctic elements with 10%. Finally, Austral-Antactic as well as circum-Pacific genera additionally contribute with 5% each to the megadiversity of the northern Andes.

The remaining 15% of genera are considered tropical-Andean and consequently constitute an outcome of accelerated radiative speciation, which explains the high degree of endemism. As a result, the current „Andean-centred elements" significantly contribute to the outstanding plant diversity of northwestern South America. This holds for the various types of mountain and cloud forests extending from 1,000 to 3,300 m a.s.l. as well as for the grass- and scrubland ecosystems at higher altitudes, forming the more humid páramo and drier puna, respectively. In addition, patches of dry woodlands, cactus stands, and thornscrubs regionally reach altitudes of up to 2,500 m a.s.l.

From a paleoecological viewpoint, species migration was frequently stopped by unbearable climatic conditions. For instance, species requiring humid conditions were blocked by dry barriers, which made their further radiation almost impossible. One of the most prominent examples for a widely distributed tropical plant family of humid ecozones that avoids areas with more than seven arid months is that of Melastomataceae (Richter 2003a). If, however, taxa can establish in the new habitat, they become founder populations giving impulses for vivid adaptive radiations. Valleys and adjacent slopes are most favourable to such a development of endemic species swarms ("evolutionary explosion", Gentry 1982a). Gentry and Dodson (1987) provide evidence for rapid genetic transience in evolutionary plastic genera such as *Anthurium, Piper*, and *Cavendishia*. They also point out the importance of site differentiation typical for diverging mountain chains as an important trigger for genetic diversification. Such locations with a dense mosaic of wet and dry habitats in an extremely broken terrain with differently exposed slopes are represented by the convergence zone of the three Columbian cordilleras ("Nudo de Pasto" ≈ 1°N / 77°30'W) as well as at the point of re-divergence of the cordilleras in southern Ecuador ("Nudo de Loja" ≈ 4°S / 79°W).

Gentry (1986, 1995) emphasizes habitat fragmentation and variation in climatic conditions as decisive triggers for high levels of endemism in the tropical Andes. This holds for some subfamilies rich in woody pant life forms such as Vaccinieae (Luteyn 2002) or Clusieae (Gustafsson 2002) at higher elevations and shrubby *Solanum* (Solanaceae, Knapp 2002) or (hemi-) epiphytic Araceae (Vargas et al. 2004) in the lower parts. The latter two confirm Gentry´s suggestion (1982) that distribution centres of understorey families by explosive radiation are located west of, rather than in the Amazon basin. Mountain ridges that are subject to strong wind impact and frequent disturbance regimes of variable size (crown breakage, landslide, drought, fire, and wildlife) can be considered optimum spots for an intensive genetic exchange as a consequence of meso-geographic habitat partitioning. Thus, the specific structure of the tropical Cordilleras seems to conduct an extraordinarily high physiological plasticity of many genera.

While on global level, woody plant life forms with trees of different sizes are main contributors to tropical species richness, some short-lived, mainly herbaceous taxa containing species swarms of endemic plants, increase plant diversity on regional scale. Orchids and Asteraceae are protagonists fo the most "productive" families. They represent around 25 % and 20 %, respectively, of the plant species of Ecuador and Peru (Fig. 4). Also Fabaceae and Piperaceae, the two second strongest families in the area are dominated by non-tree life forms. Hence, most members of these four families are characterised by short generation time-spans, as are many taxa of Araceae, Bromeliaceae, Gesneriaceae, and Scrophulariaceae. This means that many of the herbaceous rainforest taxa increase species richness by high speciation rates, and thus form those "accidentals" of temporary existence.

Actual evolutionary progress can be studied best in modern families with extensive seed production and short regeneration cycles. According to Benzing (1987), epiphytic bromeliads and orchids belong to these r-strategists, as they may react genetically flexible to stressful environments. Gentry and Dodson (1987) observed natural in situ speciation events of various Ecuadorian *Scelochilus*-orchids in as little as 15 years. They also point out nine local endemics of 14 *Telipogon*-orchids, each found in a single valley or on a single slope in the South Ecuadorian junction of the cordilleras. Similarly, Jost (2004) reported a dramatic species radiation within the genus *Teagueia* from the eastern Andes of Ecuador. During the last few years, he discovered 26 new terrestrial species of these fragile

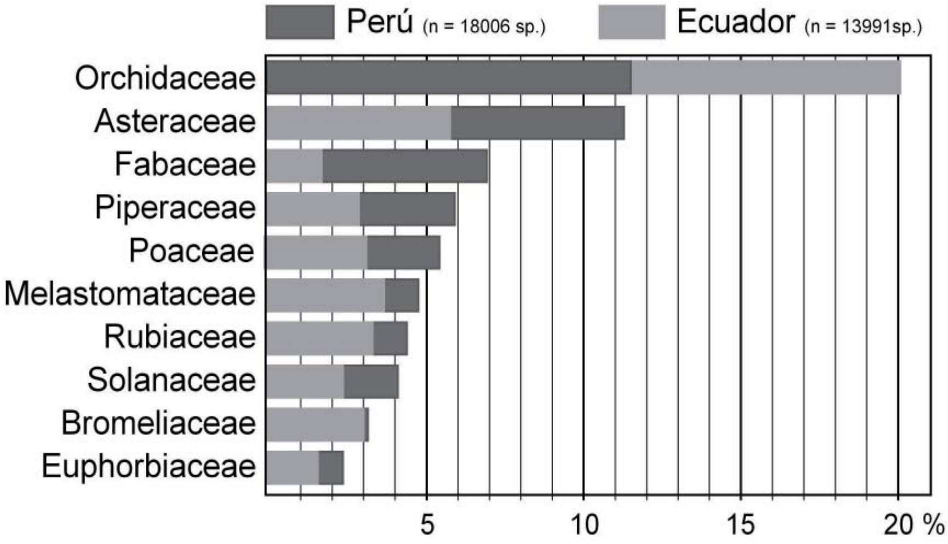


Figure 4: Percentage of the ten most important families of vascular plants in Ecuador and Peru (data base: Jørgensen and León-Yánez 1999, Brako and Zarucchi 1993). The two columns are arranged in layers one behind the other. The investigation area takes a transitory position between these two countries.

miniature orchids on four neighbouring mountains in the Rio Pastaza area. The almost stringent conclusion is that all of them evolved locally from a subrecent common ancestor. A possible factor for their clearly delimited habitats might be the existence or absence of equivalent mycorrhizal partners.

With regard to their extraordinary plant diversity the tropical rainforests in the lowlands of Ecuador and Peru can be considered a relevant genetic resource for plant life in the supra- and altotropical vegetation. However, climbing higher altitudes the different taxa may distribute in discordant patterns. Examining the vertical distribution profiles of representatives of the predominantly tropical families of Melastomataceae and Rubiaceae, a bimodial altitudinal function is registered with a slight secondary maximum at the 2,500 – 3,000 m level, which is at about the same elevation at which the Asteraceae show their distribution peak (Fig. 5). Unlike Melastomataceae and Rubiaceae, which prevail in tropical lowlands, Asteraceae are a worldwide well-distributed family reaching the upper

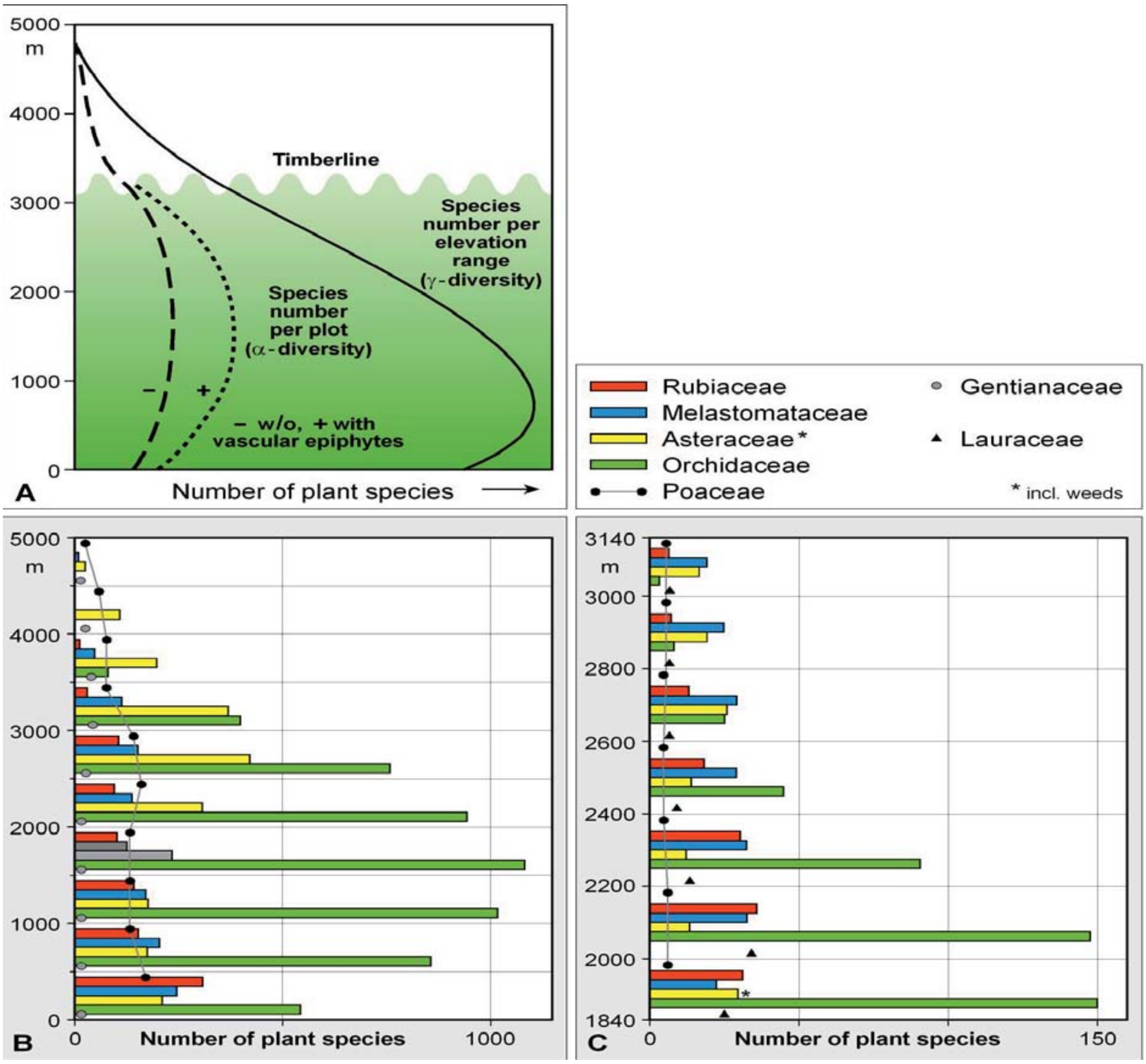


Figure 5: (A) Idealised altitudinal change of vascular plant ?- and ?-diversities in tropical mountains (from: Richter 2001, modified); species richness peaks at medium elevations (Mid-Domain-Effect). (B) Discordant vertical distribution of species numbers of selected plant families in Ecuador (data extracted from Jørgensen & León-Yanez 1999); (C) same as B, but only for the RBSF area (data from Homeier & Werner 2008 and Diertl 2006).

altitudinal limits of plant growth. Orchids are cosmopolitans, too, but their exuberant species diversity concentrates in the warm and humid tropics. In Ecuador, orchids are the dominating family up to 3,000 m a.s.l. Above that altitude, their species richness drops considerably. Representatives of other families show different vertical distributions, for example members of the Gentianaceae, which prefer higher elevations, or grasses, which do not have any significant preference for a specific vegetation belt (for elevation gradients of further Ecuadorian taxa see Kessler 2002). From these observations two essential interpretations for plant diversity in the Ecuadorian mountains can be concluded: The extraordinary genetic resource of the lowland also boosts the species diversity at higher elevations, and thus contributes to the species richness of the total area.

Tropical high mountains provide a meeting platform for tropical lowland and supratropical mountain taxa with extratropical taxa, e. g. in the case of the transition zone between the northern and the central Andean for subantarctic and nearctic taxa.

During the Quaternary, the Andean regions including the Andean Depression were subjected to strong climate changes (Behling 2008). With respect to the vegetation, the change between periods of glaciation of the higher areas and periods of dryness in the low-altitudinal break-through valleys or in upland leeward basins must have limited the migration of plant species, especially from the East to the West and vice versa. Jørgensen et al. (1995) proposed four floristically different regions in the Ecuadorian Andes caused by such barrier effects which can be recognized by their high degrees of endemism (Fig. 6). The main fragmentation or even isolation

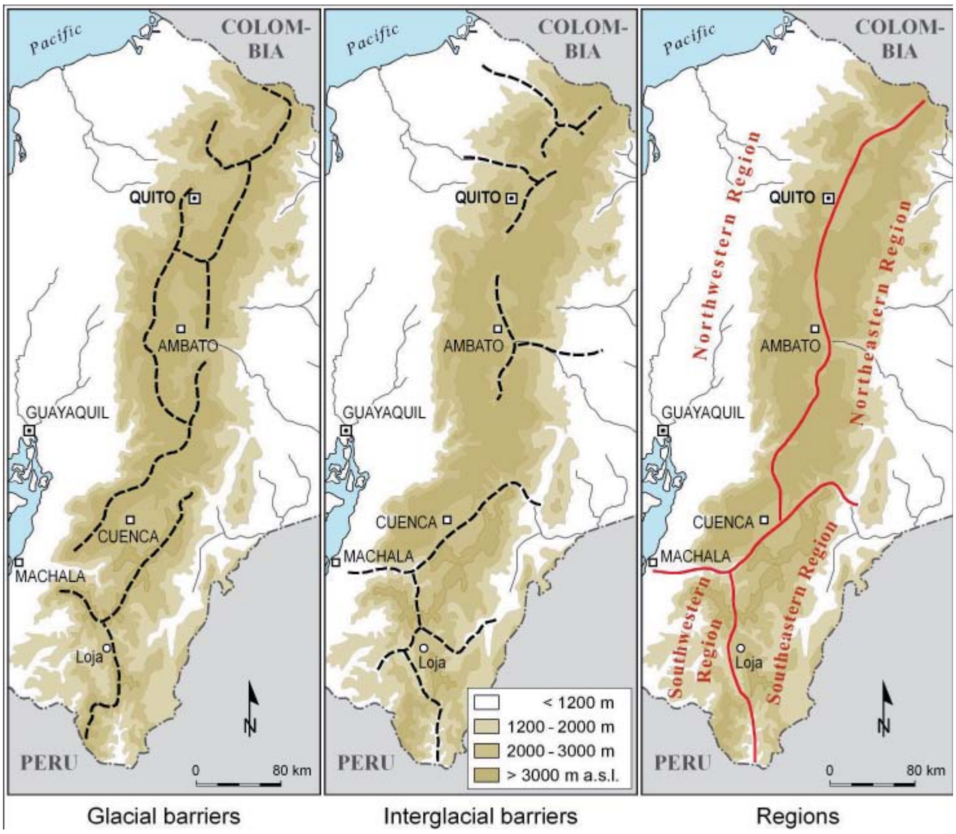


Figure 6: Possible migration barriers for plant species in the Ecuadorian Andes during the Pleistocene. Left: barriers due to Pleistocene glaciations. Centre: barriers due to dry areas in large valleys. Right: recent situation of four regions of endemism. Source: Jørgensen et al. (1995), from: Beck & Richter (2008), slightly modified.

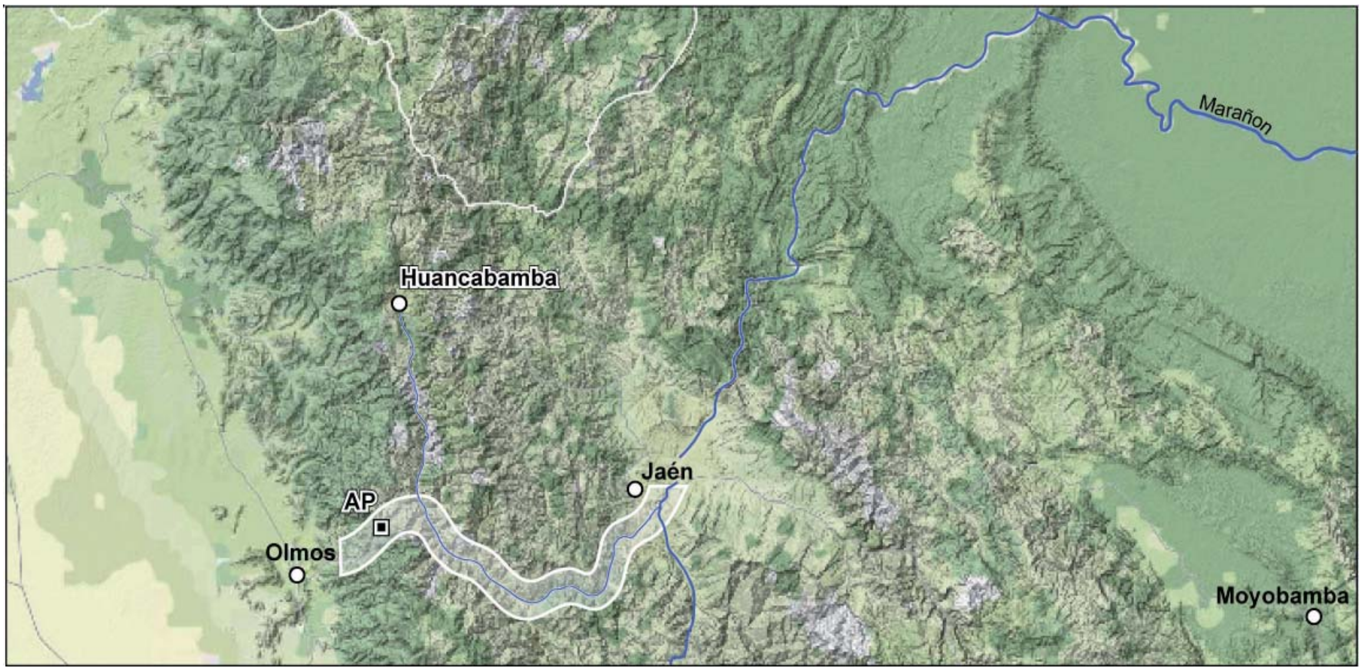


Figure 7: The central part of Andean Depression around the Rio Huancabamba, i.e. the most prominent floristic transition and at the same time barrier zone between the Central and Northern Andes (whitish corridor). AP = Abra de Porculla (terrain map derived from www.maps.google.com).

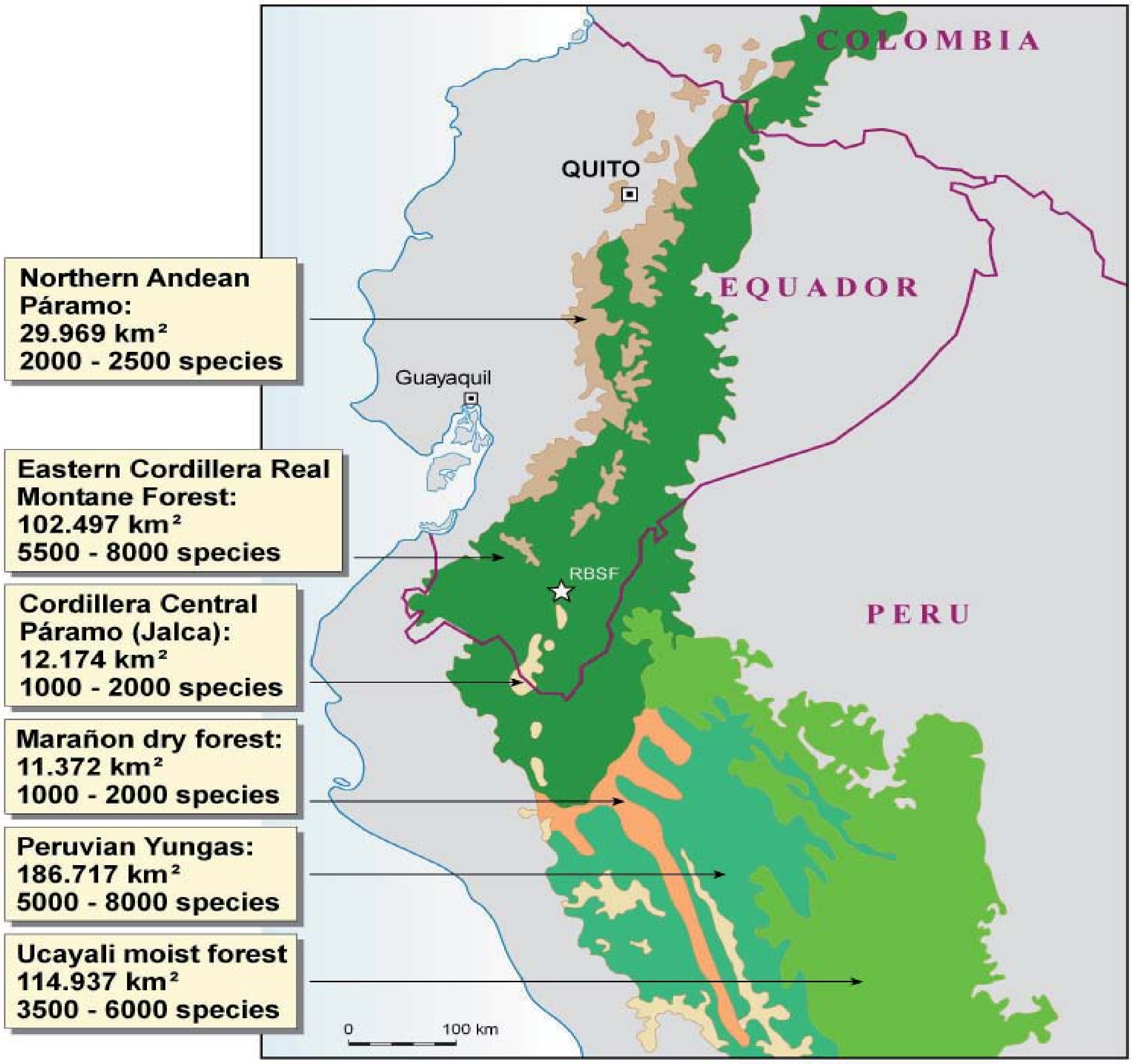
lines of flora elements during the maximum Pleistocene glaciation follows the highest crestlines and is therefore predominantly meridionally oriented. In contrast, interglacial barriers follow the lowest dry valleys and divide the Ecuadorian Cordilleras in a northern and a southern part (Jørgensen et al. 1995). Plant species dissimilarity analyses highlight the Girón-Paute-Valley with its extremely dry western section of the Jubones break-through as the main barrier for a meridional floristic exchange.

2.2.3 The mesoscale

An even stronger barrier for plant migration is the Amotape-Huancabamba-Zone, which is a central incision in the Andean Depression (Fig. 2). It extends from the Marañon breakthrough in the Eastern Cordillera southwards through the basin of Jaen, the lower Rio Huancabamba Valley, then crossing the 2140 m high pass Abra de Porculla (5° 49‘ 60 S, 79° 30‘ 0 W) until Olmos in the West (Fig. 7).

According to the map of ecoregions by Morrison et al. (2001), the northern section of the depression concurs with the eastern Andean escarpment termed “Eastern Cordillera Real Montane Forest”. While the global map shows a homogenous vegetation type consisting mainly of perhumid mountain rainforests (Fig. 8), a complex pattern of natural plant formations appears on the regional scale. In the particular case of upland southern Ecuador, the area west of the mentioned major crest line with its páramo-shrub- and grasslands differs strongly by a mesoscale mosaic of basin-and-range structures with differing climates and impressive environmental changes (s.b.). In general, the Central Andean area south of the Huancabamba corridor is more arid as its northern correspondent, ranging from moist Ucayali mountain forests to dry forests and thorn shrubs in the deeply incised Rio Marañon Valley (Fig. 8).

The flora of the comparatively low corridor in the Andean Depression between the Rio Jubones in Ecuador and the Rio Chamaya in Peru has not yet been investigated well, but its taxonomic uniqueness indicate its significance for phylogenetic studies (Young & Reynel 1997, Hensold 1999, Weigend 2004). Many particular



Northern Andean Páramo:
29.969 km²
2000 - 2500 species

Eastern Cordillera Real Montane Forest:
102.497 km²
5500 - 8000 species

Cordillera Central Páramo (Jalca):
12.174 km²
1000 - 2000 species

Marañon dry forest:
11.372 km²
1000 - 2000 species

Peruvian Yungas:
186.717 km²
5000 - 8000 species

Ucayali moist forest
114.937 km²
3500 - 6000 species

Figure 8: Ecoregions and their vascular plant species numbers in the transition zone between the northern and central Andes. Source: Morrison et al. (2001), from Beck & Richter (2008).

taxa are limited to this area witnessing a situation of isolated patches of moist forests in dry basins, e.g. those of Oña and Catamayo in southern Ecuador or Jaén or along the Rio Marañon in northern Peru. Many areas of the ranges and intermountain valleys reveal a low degree of floristic saturation and thus yields facilities for radiation of plastic taxa of hygric and mesic elements. Among the recently reported neoendemics with very restricted distribution ranges in the area are several members of the Loasaceae, Passiflorae and Grossulariaceae (Weigend 2002). Such elements might have their origin in the higher humid mountain crest regions from where descendants adapting to the drier conditions in the lower parts could migrate north- and southwards. The rendezvous of northern and southern elements, together with the diversity and isolation of habitats as well as a complex tectonic history with its evolutionary challenges, gave and still give rise to the outstanding degree of plant diversification within the particular phytogeographic Amotape-Huancabamba transition zone

On a mesoscale, the complex topography of the region (Fig. 9a) represents the fundamental for the diversity of the petrographic, edaphic, climatic and biogeographic structures. At the northern margin of the region, the

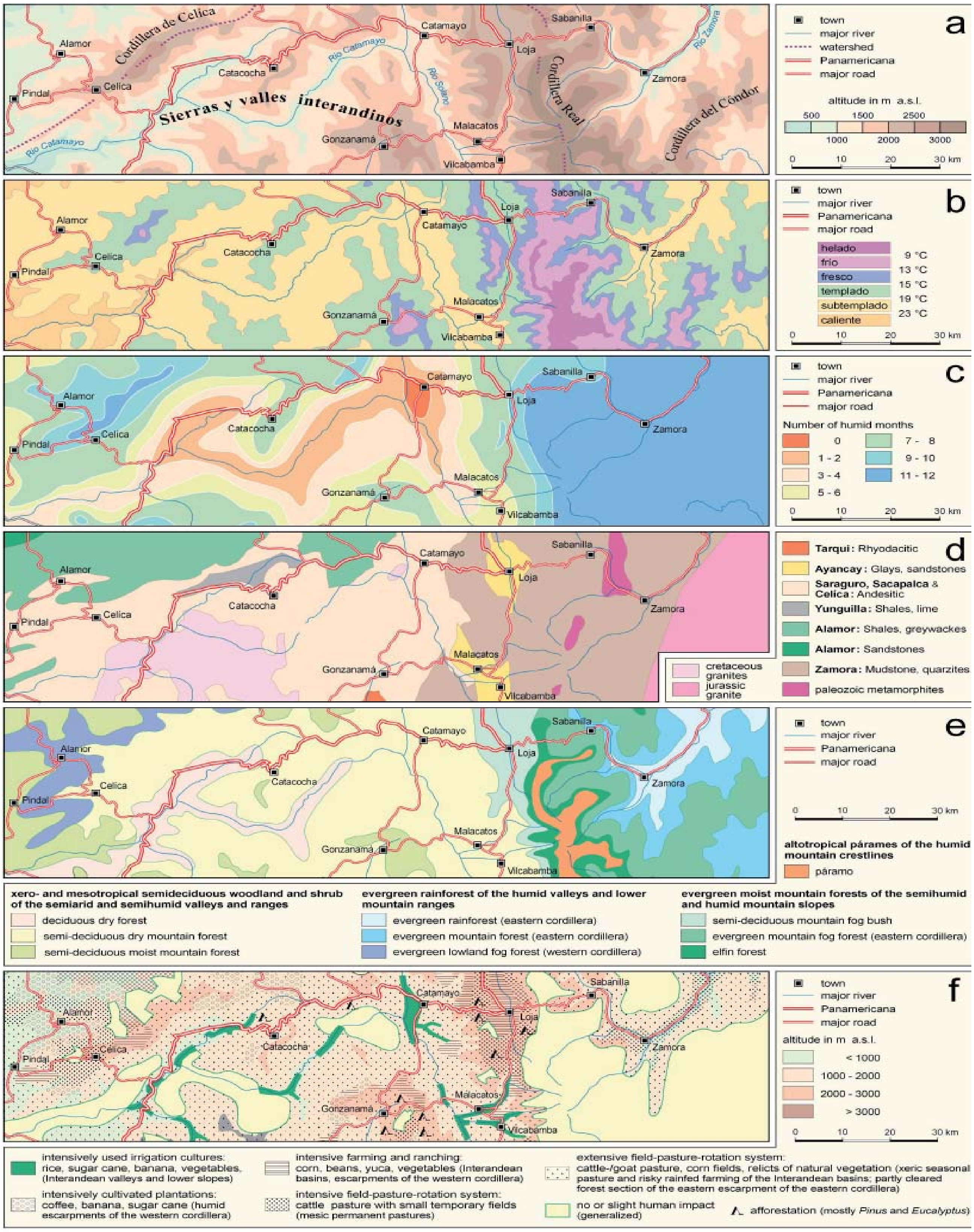


Figure 9: Overview of various ecological components generating and reflecting, respectively, the high "geodiversity" of the research area east and west of the Cordillera Real: (a) orography, (b) temperature belts, (c) number of humid months, (d) petrography, (e) natural vegetation, (f) land use. Source: (a-c) and (e-f) M. Richter 2003, modified; (d) kindly provided by F. Haubrich.

"Nudo de Loja" culminates at 3,800 m a.s.l. in the Fierro Urco and the Cerro Chinchilla. From there, three mountain ranges stretch out towards SW, S and SSE, all of which are interrupted and separated by valleys and basins between smaller inner-Andean Sierras. The altitudinal distances of these topographic structures range from 100 m a.s.l. (Zapotillo-area in the lowermost Catamayo Valley) up to 2,800 m a.s.l. (Sierra de Celíca and S. de Gonzanamá).

According to Neill (2001, p. 5) "…the distribution of plant species in relation to different geologic substrates is a topic that has not received much attention by botanists in Ecuador". Unfortunately the situation has not changed significantly since then. Petrographically, most of the Cordillera Real stretching 60 km north-south is characterised by the Paleozoic Chiquinda unit (Zamora formation in Fig. 9d), consisting of metasiltstones, sandstones and quartzites, interspersed with layers of phyllite and clay (Litherland et al. 1994, Beck et al. 2008a). Soils develop from this kind of rock bed which are poor in plant nutrients and, due to the high precipitation in the eastern Cordillera, are prone to to leaching of nutrients. Special plant communities like the monotypic *Purdiaea*-forests in RBSF (Gradstein et al. 2008) could develop on such soils. However, the historical and edaphic reasons for the establishment of such a forest are not yet clear. In contrast, our investigations at three different timberline sites of the Cordillera Real and eight other mountain areas in the Andean Depression suggest a higher tree species variety on nitrogen-poor and aluminium-enriched soils under perhumid conditions.

Of special interest to explain the high plant diversity of the region is its rugged terrain with an extraordinary multiplicity of landforms. For most of the year, the Cordillera Real is exposed to strong easterly winds carrying large quantities of moisture from the Atlantic Ocean over the Amazon lowlands. Upon uplift on the luff-side of the Andes, this moisture condenses, and almost permanent clouds cover the eastern slopes and the crests of the ranges (Bendix et al. 2006). However, the inner-Andean basin in the rain shadow of both the eastern as well of the western ranges receives only a little precipitation (Richter 2003b, Emck 2007). Nevertheless the intricate topography generates a highly complex climate which is evident from xeric to hygric vegetation types. Cactus shrub and moss-packed elfin forests grow within a distance of less than five kilometers. Especially on the western slope of the Cordillera, vegetation mirrors an extreme altitudinal gradient of precipitation. Figure 9b shows dramatic differences between the moisture regimes on the eastern and western escarpments of the ranges. While the easterlies cause a steady increase of around 300 mm per 100 m on the windward side, foehn effects lead to an abrupt decrease of around 600 mm per 100 m (!) just below the crest line on the leeward slope at the upper level between 3,500 and 3,000 m a.s.l. Towards the inner-Andean basins, the rainfall gradient at the 1,500 -1,000 m level is much more moderate decreasing by around 45 mm per 100 m. An extreme rainfall gradient results from more than 6,000 mm/a at the upper regions of the Cordillera Real, to less than 350 mm of precipitation per year only 30 km further west at Catamayo, where a double rain-shadow effect with frequent sunshine and the dry katabatic winds cause arid conditions (Fig. 10). Climate heterogeneity on an area of approximately 22,500 km² (Fig. 11) spans a sequence from the wet tierra subhelada to the dry tierra caliente.

In spite of the extremely high precipitation in the Cordillera Real, the same localities on top of the mountains are exposed to extraordinary high global irradiance (up to 1,832 W/m², Emck & Richter 2008). Since exclusively radiative effects of clouds have been singled out as the source of the "super-irradiance", UV radiation with its mutagenic potential might reach record levels as well. In the Cordillera Real, some plant families stand out by conspicuous reddish or purple colors of their young organs resulting from an accumulation of anthocyanins or carotenoids in order to protect the cells from photodamage. Among them Blechnaceae, Clusiaceae, and in particular Ericaceae and Huperziaceae are prominently rich in species with a possibly high rate of speciation at higher reaches of the region. Indeed, 221 species on test plots comprising a total of 0.25 ha (Quizhpe et al. 2002) argue for a stupendously high -diversity under the given harsh climate conditions.

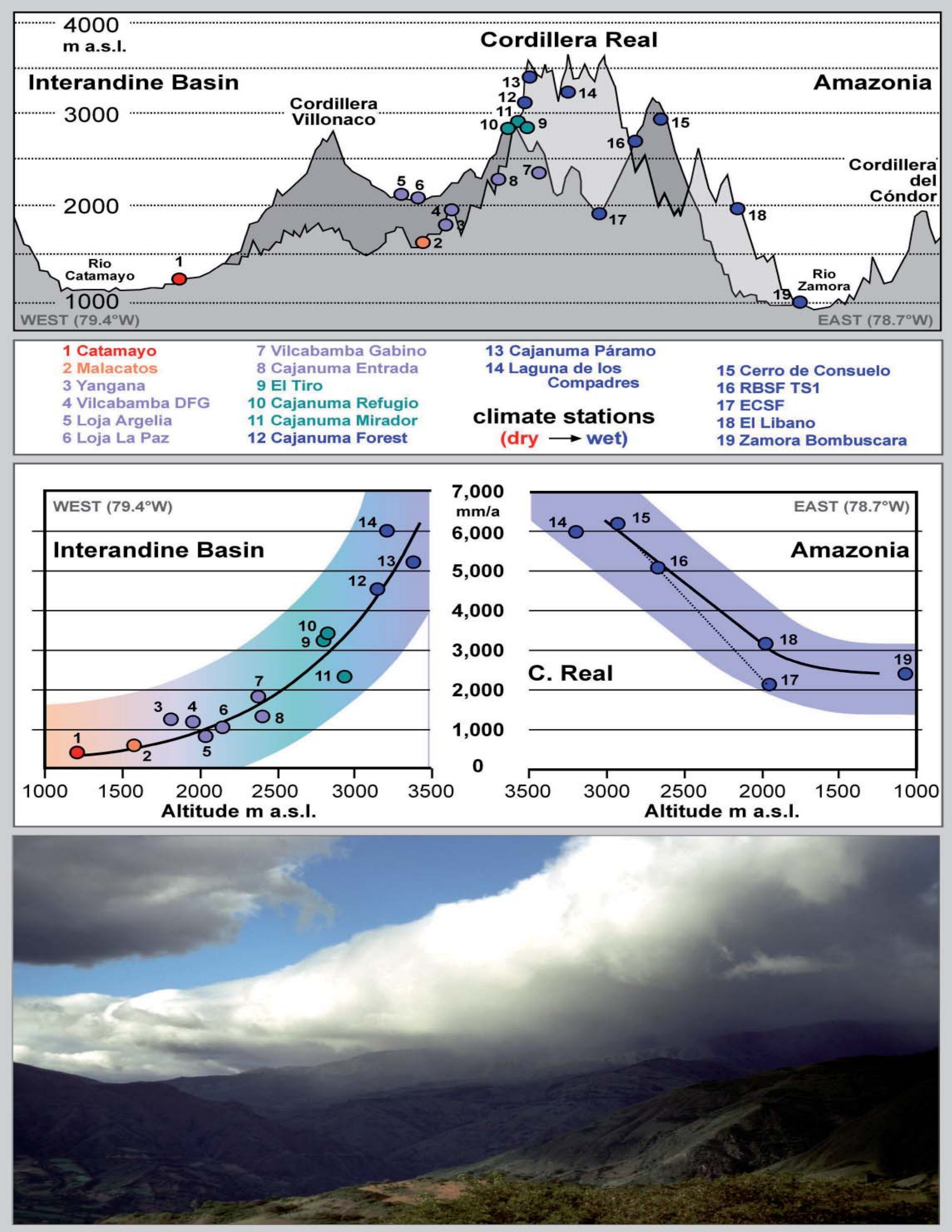


Figure 10: Precipitation gradients east and west of the Cordillera Real (Source: various Figures in Emck 2007, modified) and westward spill-over of the frequent foehn cloud over the crest line (photo: P. Emck).

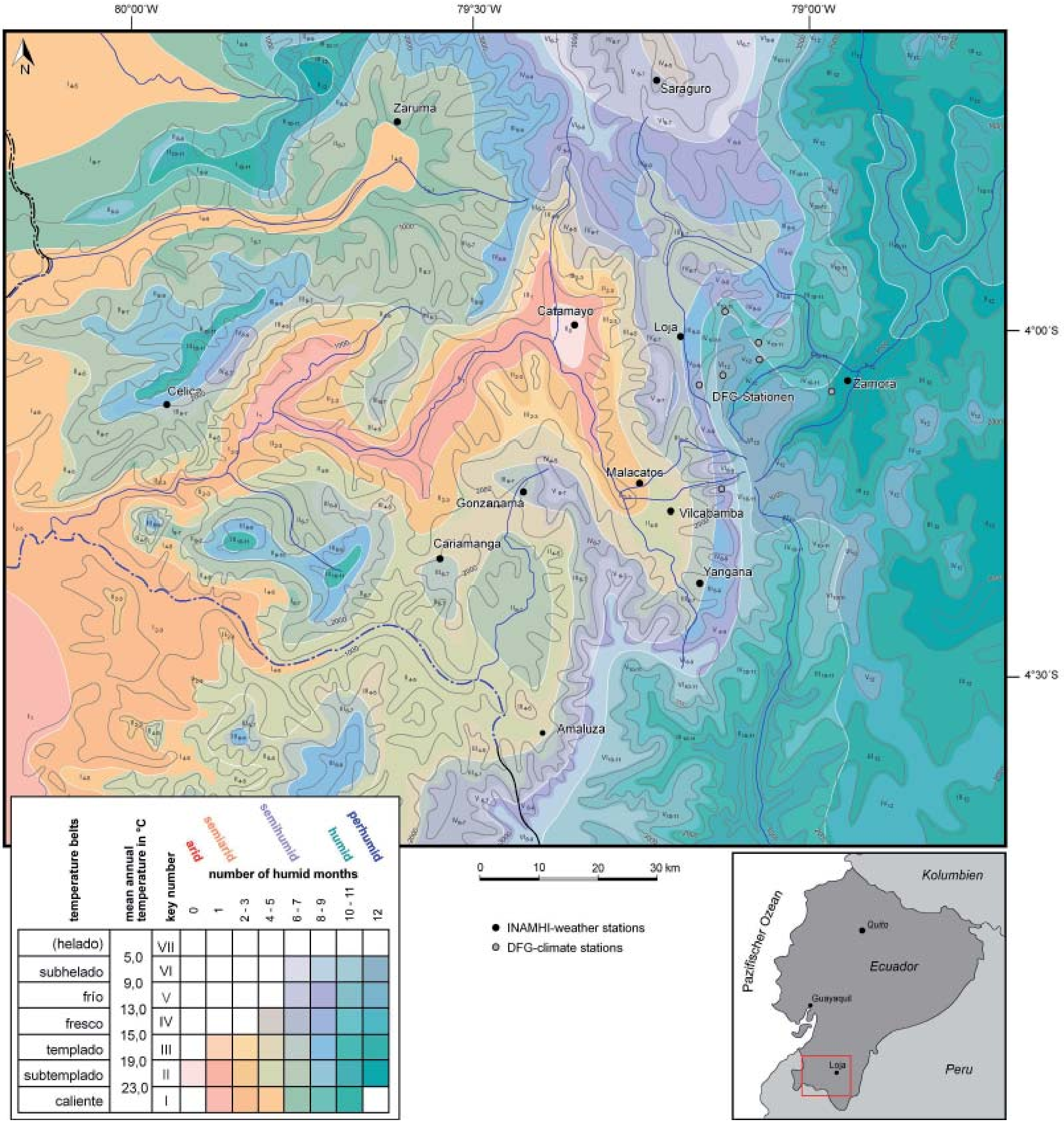


Figure 11: Hygro-thermal climate differentiation of southern Ecuador (source: M. Richter 2003b).

Long-distance pathways on the crests, the heterogeneity of possible invasion areas for taxa, the topographic structure with many habitats and modes of disturbance may contribute to an accelerated adaptive diversity of plant species and community richness at the higher areas of the region. Best examples are the narrow altitudinal belts of the eastern elfin forests and the following bamboo-rich shrub páramos with an outstanding community complexity (Quizhpe et al. 2002). In contrast, the dry inner-Andean valleys are marked by widespread semi-deciduous mountain bush and deciduous open woodland containing bottle trees such as *Ceiba trichistandra* or *Cavanillesia platanifolia*, which extend towards the dry lowlands of north-western Peru. Hence, the variety of climatic conditions has allowed a permanent maintenance of species richness to the region (Richter 2003b).

Figure 9e indicates for the eastern part of the Cordillera Real many remote areas, which are still covered by untouched rainforests or nature near vegetation formations. Reaching up to 3,644 m a.s.l., numerous altitudinal belts on the wet and the drier escarpment are differentiated by a multitude of vegetation types. Comparatively, the central part of the map towards the west appears rather homogenous with its deciduous and semi-deciduous dry and moist forests. Reconstruction of the complex natural vegetation is difficult because of the human impact since (pre-) incaic periods.

Many taxa in the wet rainforests have a broader range of physiological adaptation while those of the drier mountain woodlands are genetically more fixed (Gentry 1982a). Some plant families show notable high frequencies in the investigation area as compared to areas in northern and central Ecuador. More than a third of the total number of Ecuador's Melastomataceae species and around 30 genera reported for southern Ecuador manifest the importance of this plant family for this region (Cotton 2002). While *Miconia* represents by far the largest genus in the rainforests with again a third of all South-Ecuadorian Melastomataceae, the genera *Brachyotum* and *Meriania* concentrate in the upper mountain forests and páramos. Endemism is also very high for various Bromeliads and at least for the Pleurothallidinae of the Orchidaceae. Furthermore, Øllgaard (2002) highlights the eastern Andean slopes with their constantly humid climate (Bendix et al. 2008) and well-drained soils as a centre of extremely high fern diversity forming a hot spot of Polypodiaceae, Grammitidaceae, and possibly also Huperziaceae.

In an assessment of plant diversity, not only speciation but also extinction rates must be considered. They differ considerably between the wet cordilleras and the dry basins. Within the rainforest ecosystems, many species have limited and in some cases even smallest areas of occurrence. Thus, even small-scale deforestation may result in severe losses of taxa. In contrast, areas of most dry forest species areas are much larger and thus their chance to survive human impacts or natural catastrophes is much better. Consequently, extinction of native plant species is less extensive in the inner-Andean section despite the much higher human impact and landscape change. Likewise, encroachment of invasive species and their positive contribution to species enrichment as well as their menacing effect on native taxa can have opposite results. Although considered "trash plants" by conservationists, the amount of alien plant species seems to add up rather than to deplete species richness of the drier areas. However, strongly expanding invaders such as shrubby *Dodonaea viscosa, Tecoma stans* (s. Fig. 12c) and also treelets of *Psidium guajava* undoubtedly tend to marginalize less competitive species. Even stronger are outcompeting effects of introduced pasture grasses. Many of them are of paleotropic origin such as *Melinis minutiflora* with lower and *Panicum maximum, Pennisetum clandestinum*, and *Setaria sphacelata* with higher demands for moisture. Their profoundly negative in situ effect on species depletion is given by its dense sealing structure against seed input of further species. A major problem mentioned by Paulsch et al. (2001) and highlighted by Beck & Hartig (2003) as a serious obstacle for regenerative processes and hence also for a renovation of the original plant diversity causes the long-lasting establishment of the southern bracken fern *Pteridium arachnoideum* and *Pt. caudatum* on abandoned pastureland in mid-altitudes on the wet escarpment of the Cordillera Real.

2.2.4 The microscale

On the microscale, the orographic situation is of specific importance since a complex terrain like the research area provides many combinations of exposure, slope angle, small valleys and ridges (Beck et al. 2008b and Fig. 13). In general, mountain chains have a higher plant diversity due to additional taxonomic elements from cooler climates which inhabit the higher areas. In the vertical dimension the RBSF-terrain extends over 1,335 m. Over this large altitudinal stretch, which is additionally modified by particular topographical sites (valley floor, slope, crest), the range of plant formations varies from different types of mountain and elfin forest, to dwarf forests, bamboo stand, and finally shrub and grass páramos.

Ecotone interdigitations which promote species diversity are not only restricted to the broad transition zones from belt to belt, but are likewise significant between lower and upper parts of the slopes of small catchments. Here, different habitats are mostly connected by smooth transitions without clear borderlines. Figure 14 illustrates such a situation in the tropical mountain forest as compared

Figure 12: While the upper four pictures introduce natural or nature-near vegetation formations of the area shown in Fig. 9, the lower two show typical landscapes changed by human impact. (a) Cajanuma (elfin forest; 3,160 m a.s.l.): trees of *Hedyosmum racemosum* and *Weinmannia rollottii* with herbaceous *Rumex tolimensis;* (b) Cerro Toledo (shrub páramo; 3,240 m a.s.l.): ferns of *Blechnum loxense*, bamboos of *Neurolepis laegardii* and *Chusquea neurophylla,* shrubby Ericaceae of *Gaultheria rigida* and *Macleania rupestris*; (c) Laipuna (dry forest; 630 m a.s.l.): Tecoma stans in the foreground, evergreen *Capparis scabrida* in the center, *Ceiba trichistandra* with green bark, and *Cochlospermum vitifolium* with grey bark; (d) RBSF (mountain rainforest; 1,850 m a.s.l.); (e) semiarid inner-Andean valley around Masanamaca (extensive pasture land and irrigated permacultures in the valley ground; 1,620 m a.s.l.); (f) perhumid eastern escarpment of the Cordillera Real around Sabanilla (extensive pastures; 1,680 m a.s.l.) (photos: M. Richter).

to the extratropical altitudinal zonation of the vegetation. However, this rather random situation applies only to undisturbed areas. On disturbed sites such as natural landslides and gaps by breakdown of overaged trees the borders are sharp. Nevertheless, such temporarily open habitats form a patchwork of various succession stages with their pioneer plant communities contributing additionally to the local plant species richness (Bussmann et al. 2008, Richter 2008).

As a global feature of mountain vegetation, plant families show distribution peaks at specific altitudinal ranges (Fig. 5b & c), which by concordance can lead to an accumulative species summation. Within the RBSF-

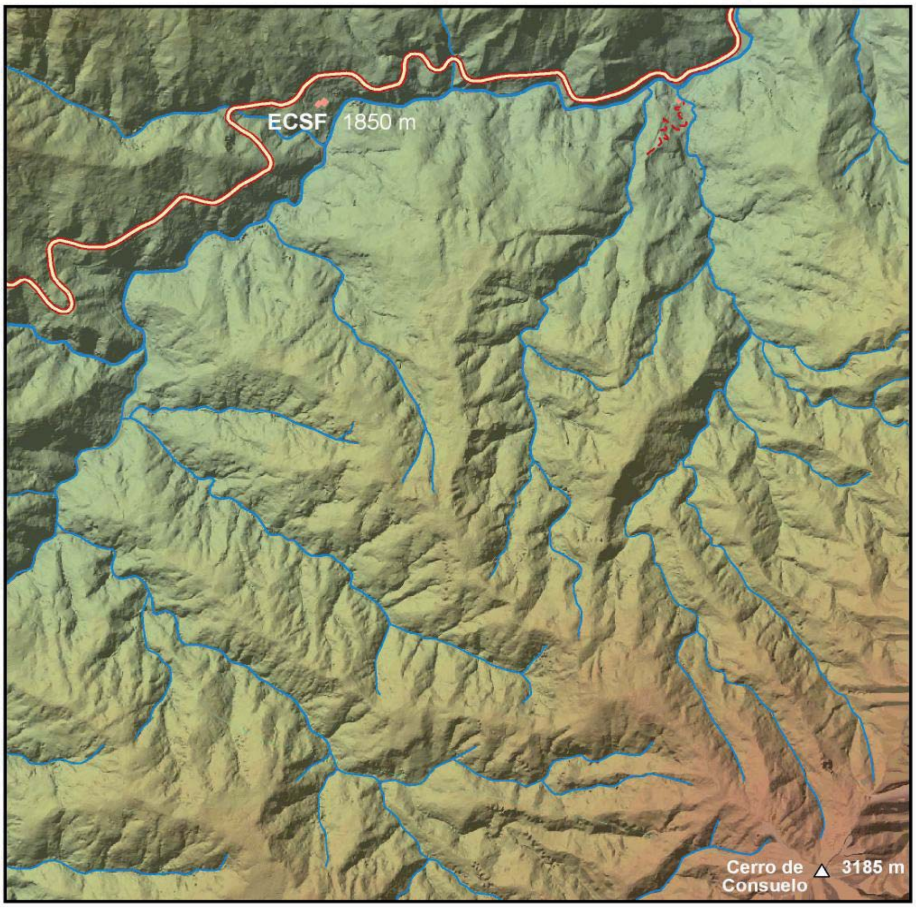


Figure 13: Orography of the RBSF-terrain between the Estacion Científica next to the Rio San Francisco (ECSF) and the mountain top Cerro de Consuelo.

terrain, tree and shrub species of Arecaceae, Euphorbiaceae, Lauraceae, Meliaceae, Piperaceae, and Rubiaceae are more concentrated at elevations below 2,300 m a.s.l. while Aquifoliaceae, Cunoniaceae, Myrsinaceae, and Symplocaceae prefer higher elevations. Other widespread plant families show small peaks of species numbers at the mid-level range, among them shrubs of Melastomataceae, Asteraceae, and Ericaceae (Gálvez et al. 2003, Richter 2008, Homeier & Werner 2008). Epiphytes also increase plant diversity substantially by altitudinal changes of their species (Bussmann 2001). Epiphytic Araceae, Bromeliads (Fig. 15a), Piperaceae, and Orchids are most prominent at lower altitudes, while Lomariopsidaceae, Grammitidiaceae, Hymenophyllaceae (Lehnert, pers. comm.), and Ericaceae are the dominant epiphytic families at medium elevations between 2,500 – 2,800 m a.s.l.

Orchids are extremely abundant, representing nearly 80% of the epiphytic spermatophytes. Among the most important genera in the RBSF *Stelis* (35 species), *Pleurothallis* (32), *Maxillaria* (26), *Lepanthes* (26), and *Epidendrum* (21) take the first five ranks in epiphytic species richness, and also *Masdevallia* (11) and *Elleanthus* (8) are very frequent. Among other families, bromeliads, especially represented by *Tillandsia* (15) and *Guzmania* (8), are common, and of Peperomiaceae, nine species of *Peperomia* have been recorded (database: Homeier & Werner 2008). Scrambling and leaf-climbing ferns are well represented, too, the most abundant genera being *Elaphoglossum* (39), *Hymenophyllum* (16), *Melpomene* (9), and *Serpocaulon* (9). Most of the epiphytic members are small-sized, some of them are tiny, and their multitude suggests appreciable speciation rates as ecological adaptation to highly specified micro-habitats.

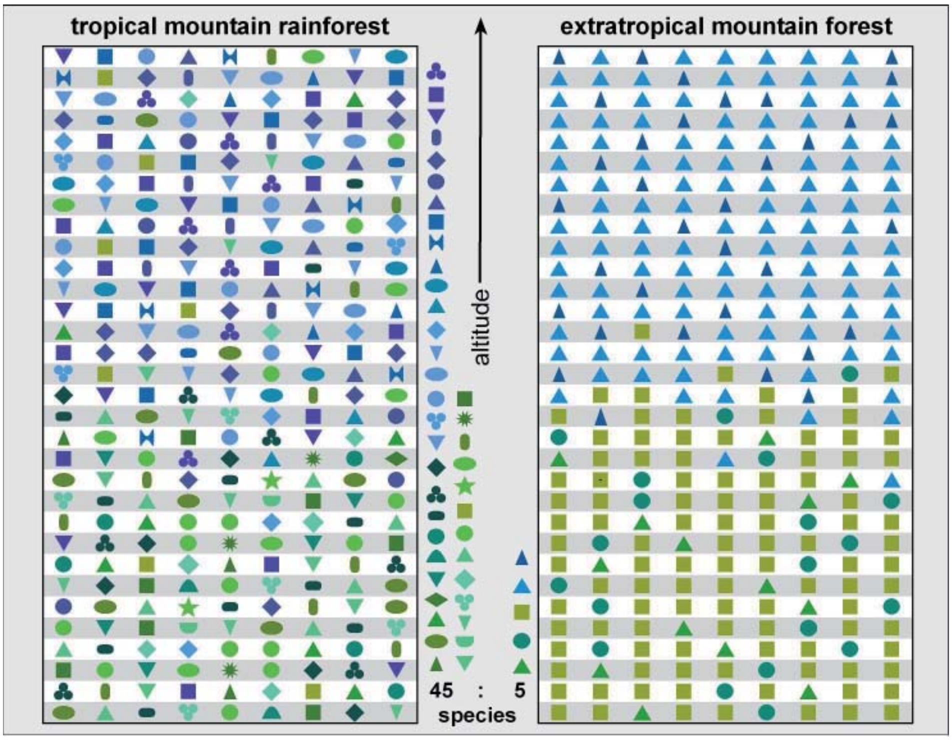


Figure 14: Scheme of the tropical type of random species distribution (left) and smooth zonation transitions versus an extratropical type of sharply delineated altitudinal vegetation belts (right). The distribution of tree species within the two contrasting altitudinal mountain forest transects is symbolized by icons. Note the unequal diversity patterns of tree species in tropical (high species richness, i.e. a typical feature of the RBSF) and extratropical (low richness) regions. Source: M. Richter 2008 modified.

Due to an often extremely high niche complexity, the multitude of structurally different micro-habitats plays an important role in the epiphyte-rich mountain rainforest . In principle, areas below 2,000 m a.s.l. are less rich in vascular epiphytic species (Fig. 5a) because of taller growth forms and a stronger reproductive competition of a few abundant bromeliad and orchid species (Freiberg & Freiberg 2000). This more general observation holds also for the RBSF. At the bottom of the Rio San Francisco Valley, stems and branches of the mountain forests trees are less covered by epithytic mosses rendering the establishment of vascular epiphytes more difficult. In contrast, the ample moss packages on branches and tree trunks in the high altitudinal cloud- and elfin forests facilitate anchoring on the host plants. Thus, cooler climates of high elevation regions have only a marginal effect on epiphytic species numbers in the uppermost forests. On a first glance this is rather surprising since the impact of cold is accompanied by rather uniform microclimatic conditions especially in the elfin forest which is wrapped in quasi-permanent orographic fog. However, due to the smaller size of the trees and their more open crowns living space for epiphytes increases in the high altitudinal forests and epiphytism remains abundant up to the timberline ecotone. Thus, the reduction of the habitat stratification between the foot of the stem and the canopy suface (Johansson 1974) from five in lower mountain rainforests to three in elfin forests is irrelevant for epiphyte richness.

In many páramos, a surprising plant species richness is obvious, forming small-sized communities (Fig. 15 b). This phenomenon results from the coexistence of different micro-habitats generated by the highly variable micro-relief in combination with likewise heterogeneous effects of wind and precipitation. Slightest depressions act as small water catchments while small hills may dry up within a few hours of sunshine and wind. In such a perhumid environment native Gramineae are abundant. Among them Bambusoideae such as *Chusquea* and *Neurolepis* contribute to species diversity, and so do grass genera like *Agrostis, Calamagrostis,* *Cortaderia, Festuca,* and *Muhlenbergia* (Laegaard 2002). Asteraceae are well represented by several species of *Ageratina, Baccharis, Gynoxys, Mikania, Pentacalia,* and *Senecio*, terrestrial Bromeliads by *Puya* and *Tillandsia,* and Ericaceae by *Bejaria, Disterigma, Gaultheria* and *Macleania*. Smaller ferns belonging to the genera *Eriosorus* and *Thelypteris* characterise moss-rich gullies in the perhumid páramos (Øllgaard 2002). The páramo consists of rather species-poor patches inhabited by a few dominant vascular species while adjacent habitats exhibit a highly diverse plant cover (Diertl 2006, Richter et al. 2008). Dominance by fast growing species of *Neurolepis, Chusquea* or *Rumex* usually takes place after natural or anthropogenic disturbances.

On top of the vertical turnover of species composition azonal horizontal gradients from the wet gorges over the slopes to the protruding crests multiply the species diversity on the microscale. For example, flattened crest-sites around 2,300 m a.s.l. may carry rather monotonous open forests of *Purdiaea nutans* and *Graffenrieda* emarginata together with a variety of scattered bushes. In contrast, forests of the narrow gorges at the same altitude show a high tree diversity, heavily loaded with cryptogamic epiphytes but, due to low light intensity a less diverse undergrowth, especially with respect to the herb layer. In contrast climbers and winders encounter favourable conditions and therefore show a remarkable diversity. The horizontal floristic gradients result primarily from changes in microclimate and edaphic conditions. Gorges have a higher air and soil humidity, more balanced temperatures and efficient wind-shelter. Oesker et al. (2008) report higher nutrient concentrations of the soils as well as of the rain throughfall in the gorges as compared to the ridges.

The geologic structure and petrographic situation of the RBSF-terrain giving rise to the formation of steep slopes promote an ongoing landslide activity, which is obvious on 8,5 % of the area shown in Figure 13 (Brenning 2005, based on data from Stoyan 2000). On the north exposed escarpment by far most of the mass movements represent shallow transitional slides and debris flows. On the opposite escarpment in the vicinity of the Loja-Zamora road rotational sliding and block subsidence dominate. Triggered by high amounts

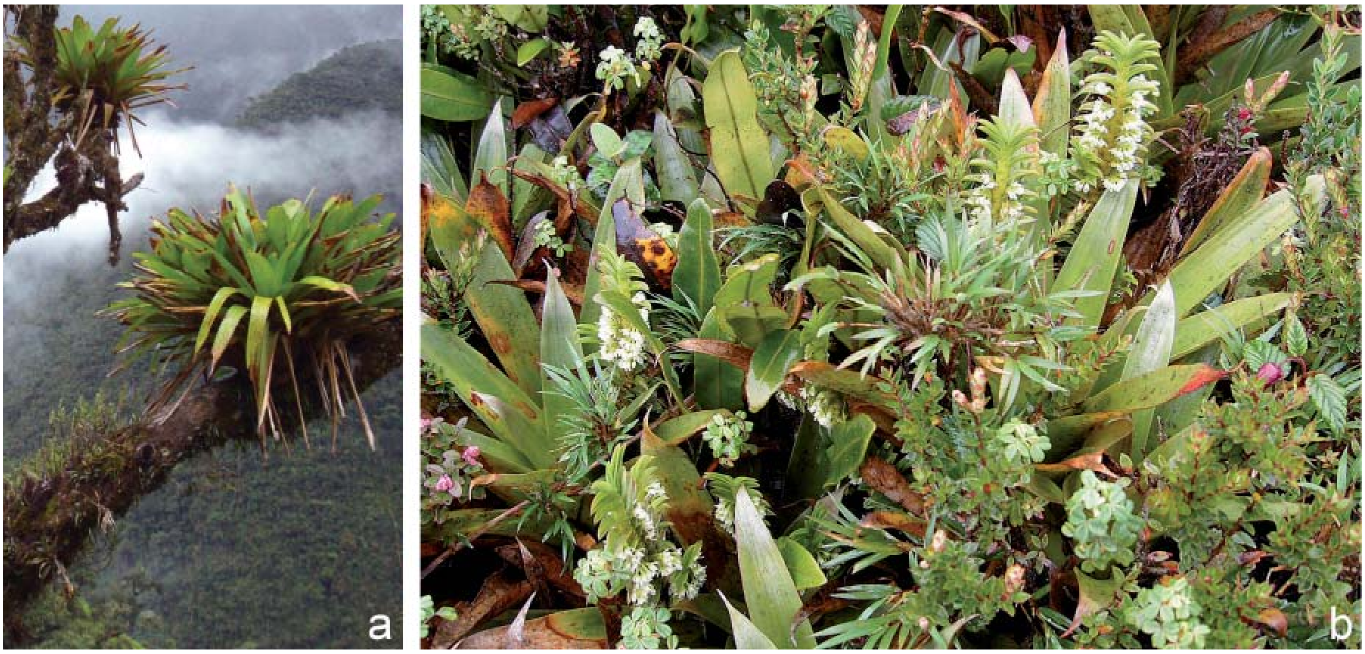


Figure 15: Small habitats such as epiphytic communities on trees (a) as well as slight level differences from the micro-relief in páramos (b) harbour a considerable number of herbaceous vascular plants and contribute additionally to enhanced species numbers (photos: M. Richter).

of rainfall and sometimes by earthquakes, sliding in mountain rainforests of RBSF results among others from labilization of thick, water-soaked humus layers and the weight of the trees (Stoyan 2000). The spatiotemporal pattern of differently old landslide areas results in a „mosaic cycle“ which is typical of that particular forest ecosystem. The chronology of sliding is mainly subject to biotic and to a lesser degree to hydrological circumstances (Zimmermann & Elsenbeer 2008), which finally engender an oscillation between slope stability and instability (Fig. 16c). Destabilization increases with the increasing weight of the growing forest, while after the slide the initial regeneration steps accomplished by a non-woody vegetation stabilize the new soil surface.

On landslide sites, first pioneers are cryptogams including algae and fungi. According to Lozano et al. (2008), mosses and lichens build up a complete coverage facilitating the establishment of ferns (Gleicheniaceae, Dryopteridaceae,

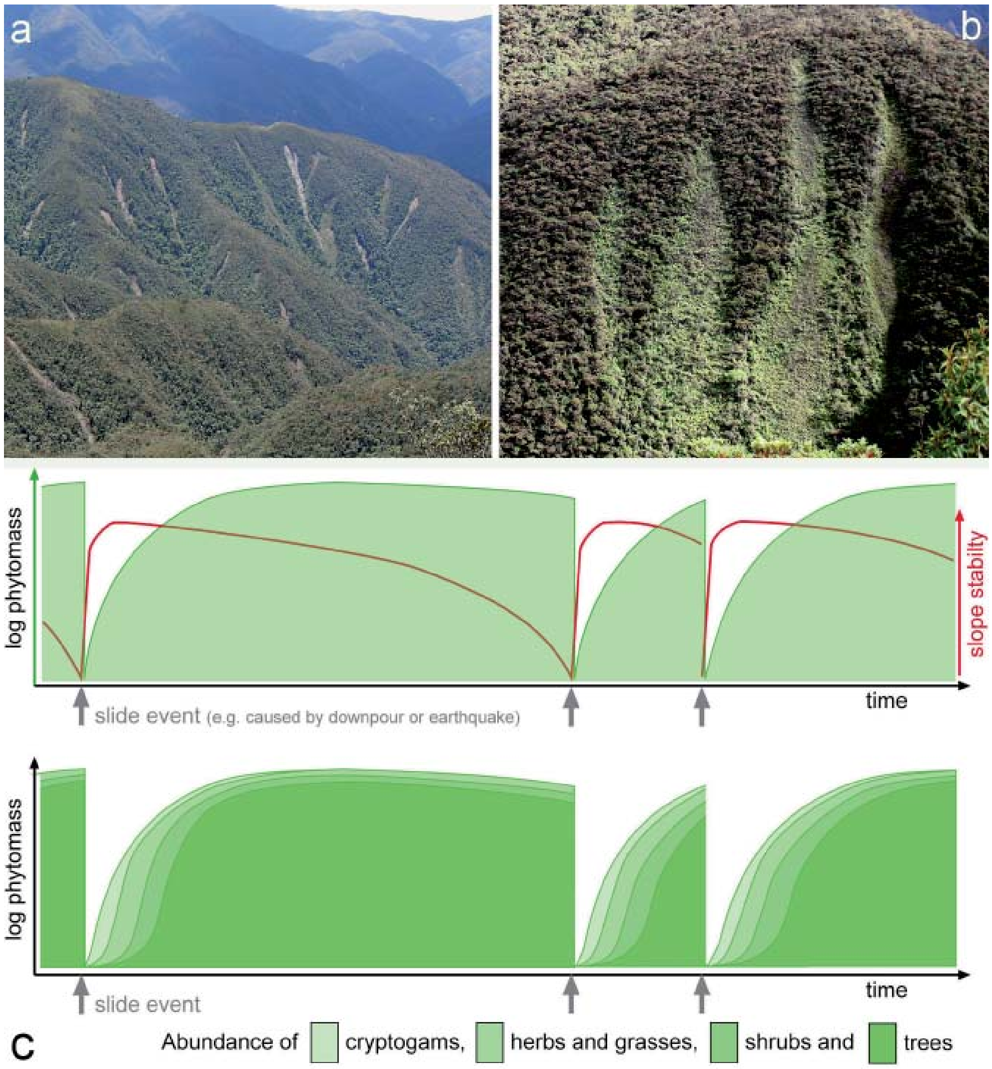


Figure 16: Landsliding as triggers of a dynamic mosaic of plant cover regeneration stages in the mountain rainforest. Active sliding zone between 2,300 and 2,600 m a.s.l. on the RBSF-terrain (a) and plant recovery 20-40 years after slide processes near the research area at around 2,300 m a.s.l. (b). The upper sketch in (c) indicates the relationship between total plant biomass (green field) and slope stability (red line); biomass increase causes weight increment and leads to slope instability (sketch design partly by Elsenbeer, pers. comm.). Arrows indicate landslide events. The lower sketch illustrates non-linear trajectories describing changes in the abundance of different functional groups of plants through time (area under each curve). The time scale is in the order of few centuries. (photos: M. Richter)

Figure 17: Cohort mortality of Chusquea scandens (b) and subsequent plant succession of herbaceous and shrubby pioneers (c-f) at about 3,080 m a.s.l. in Cajanuma. 14 inclined trees marked by orange lines indicate the debris creeping effect, while 4 (green) apparently are not affected by the slow mass movement process (a). Photo+s b-f were taken between October 2004 and 2008 (photos: M. Richter).

and at higher elevations Blechnaceae) and herbs (species-rich genera of the Orchidaceae, e.g. *Epidendrum* and *Elleanthus,* of Asteraceae e.g. *Ageratina* and *Munnozia*, and several grasses, especially *Cortaderia jubata*) during the first years. Little later, several dwarf shrubs accrue to that kind of pioneer vegetation, among them many Ericaceae (*Gaultheria* spp. and higher up *Bejaria* spp.) and once again Asteraceae (*Baccharis* spp. and *Gynoxys* spp.). Secondary shrub starts with the appearance of Melastomataceae (*Tibouchina lepidota* and various species of *Miconia* and *Graffenrieda*) and Piperaceae (*Piper* spp.) followed later on by members of Rubiaceae, Lauraceae and Myrtaceae as initially dominant tree taxa. Although the sequence of successional stages is quite clear the investigations so far do not allow for a temporal perspective of the one cycle. The situation is complicated by the fact that many of the interactive parameters vary considerably.

In contrast to fast moving slides, soil or debris creep is another example for destructive mass movement processes that enhance plant diversity. Figure 17 documents a five year survey of a site on a mobile debris layer in Cajanuma at 3,080 m a.s.l. . By far most of the tree trunks are slant (orange dots in Fig. 17a) due to the downward flow of the debris. Before 2003 the site was covered by a monotypical bamboo cohort of *Chusquea scandens* that died after flowering (Fig. 17b). Since 2003, the fast recolonisation by pioneer trees generated a completely different and heterogeneous aspect from transitory assemblages of high floral diversity (17c-f).

While the described landslide and soil creep processes produce medium-sized disturbances with local effects on ecosystems, other perturbative forces act on much larger or smaller scale. Figure 18 gives a qualitative overview of prominent disturbance regimes by identifying their impact on floral replacement against altitude. Herbivorous mammals such as the Andean bear *Tremarctos ornatus* and the mountain tapir *Tapirus pinchaque* are effective endozoochorous seed dispersers, especially for the numerous Bromeliad species. Although their actions are locally confined they cover wide areas of páramo and elfin forest as indicated by abundant bite marks or destroyed plants and by feces containing seeds and pieces of plant tissue. Also crown breaking or partial dieback of single trees can be addressed as small-scale disturbances. Larger clearings from breakdowns of overtopping trees are rare in the mountain forest of the RBSF. Small gaps, however, created by e.g. heavy, moss-covered branches that occasionally crash down are quickly occupied by heliophilous specialists waiting in the seed bank for their chance.

Contrasting to the addressed, spatially rather isolated disturbance regimes, some regional climate peculiarities such as droughts and strong wind have wide spread impact with partially long-lasting effects. In this context it is important to note that the ecological stress by droughts and wind is assigned to the microscale factors because its effect is, in most cases, confined to few individuals, small sites, or maximally to a particular topographic aspect of some mountain ridges.

Droughts are restricted to the “Veranillo del Niño” during late October and November and are characterised by sunny, westerly weather situations, which may last for

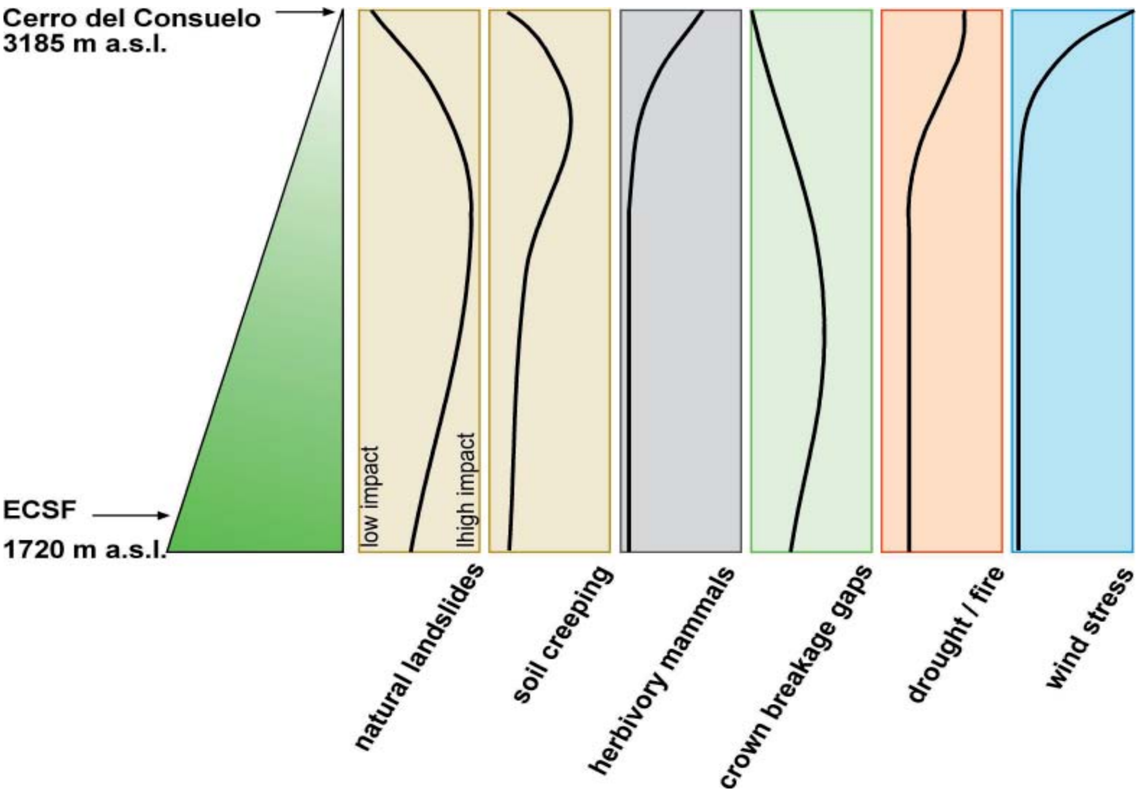


Figure 18: Important disturbance regimes in the RBSF-terrain and their relevance along the altitudinal gradient.

two to four weeks without any precipitation. Such fairly regular situations occur during a combination of low pressure at low latitudes (0°~15°S) along the east Andes, relatively high pressure over the equatorial Pacific and a trough at mid-level. Westerlies and air subsidence especially at the upper levels of the South Ecuadorian mountains reduce relative humidity here to less than 20% while significantly boosting evaporation (Emck 2007). The aridity is strongest in the summit regions and, surprisingly, strongest at night. Long Veranillo del Niño periods like at the end of the ENSO-year 1998 as well as in November 2000 and 2005 (Fig. 19) not only kill trees by drying out (e.g. at the timberline at Cajanuma in 1998). They also facilitate the outbreak and spread of mostly man-made fires as in 2005 when the terrestrial Bromeliad vegetation at the pass El Tiro was affected. The majority of the páramo plant species display xeromorphic traits, e.g. small coriaceous leaves, which can be interpreted as an adaptation to drought as well as a protection against the destructive mechanical force of permanent high wind speeds. While droughts and wind may favour physiological adaptation, high radiation boosts genetic mutation, which once again explains the extraordinary wealth of endemics in the páramo flora.

While droughts and wind do not enrich plant diversity, another stress factor must be mentioned, which is the soil nutrient scarcity. The terrain with its rampant layers of sandstones, metasiltstones, and quartzites with interspersed layers of phyllites and argillaceous schists gives rise to soils which are poor in nutrients, especially nitrogen, phosphorus and calcium (Wilcke et al. 2008). Above 2,200 m a.s.l., the mineral substrate is mostly covered by thick layers of organic material, representing a huge C-reservoir (Soethe et al. 2008). Precipitation of 4,000 to more than 6,000 mm/a (at higher elevations) result in waterlogged soils which are unfavourable for plant growth. Water-logging occurs predominantly on flat areas and depressions, where no trees are found, although with regard to the altitude tree growth would be possible. Where the timberline drops down to altitudes of only 2,600 m (Diertl 2006, Beck & Richter 2008, Richter 2008), it is the combination of the stress factors water-logging and nutrient scarcity, which challenge the ecological plasticity of plant taxa, resulting in an increased rate of speciation.

3 Conclusions

The approach of a top-down scaling of plant diversity issues (Grüninger & Fickert 2003, Grüninger 2005) was applied to evaluate the decisive factors for the outstanding of species richness in the biodiversity hotspot of southern Ecuador. Unlike many other Andean areas, species richness in the Cordillera Real appears to be connected to nearly each of the mentioned ecological factors (Fig. 20). Only few are without effect or off small impact, either by low intensity or frequency. For example, human impact is still moderate at the microscale, i.e. in the RBSF-area itself, where in accordance with the moderate disturbance hypothesis it may even contribute to plant diversity enrichment (Martinez et al. 2008). On the mesoscale, human impact already causes a loss of species, due to deforestation and subsequent agricultural or pastoral use of the areas below 1,800 m a.s.l. on the windward and below 2,500 m a.s.l. on the leeward side of the Cordillera. On the macroscale, both extinction of species and encroachment of invaders probably exceed the potential of speciation. The exuberant land use in the lowlands of northwestern South America requires clearing of the tropical forests and as a consequence, many positive macro- or global scale factors such as a rapid genetic transience, species explosion by accidentals, vivid plant-animal interactions, or intermediate disturbance impacts do no longer apply there.

Clearly, the direct, human impact on biodiversity must be considered much more harmful than man's indirect impact via a changing climate. In the latter context, Urrutia & Vuille (2008) predict a considerable warming for the tropical Andes using regional climate models. Taking one of the worst case scenarios (A2) of IPCC-SRES, an increase in the order of 4-7° could be expected for the end of the 21st century for parts of the Central Andes. This trend is already obvious from the recent rapid retreat of glaciers (e.g. Jordan et al. 2005). Temperature in the northern Andes has increased by approximately 0.1

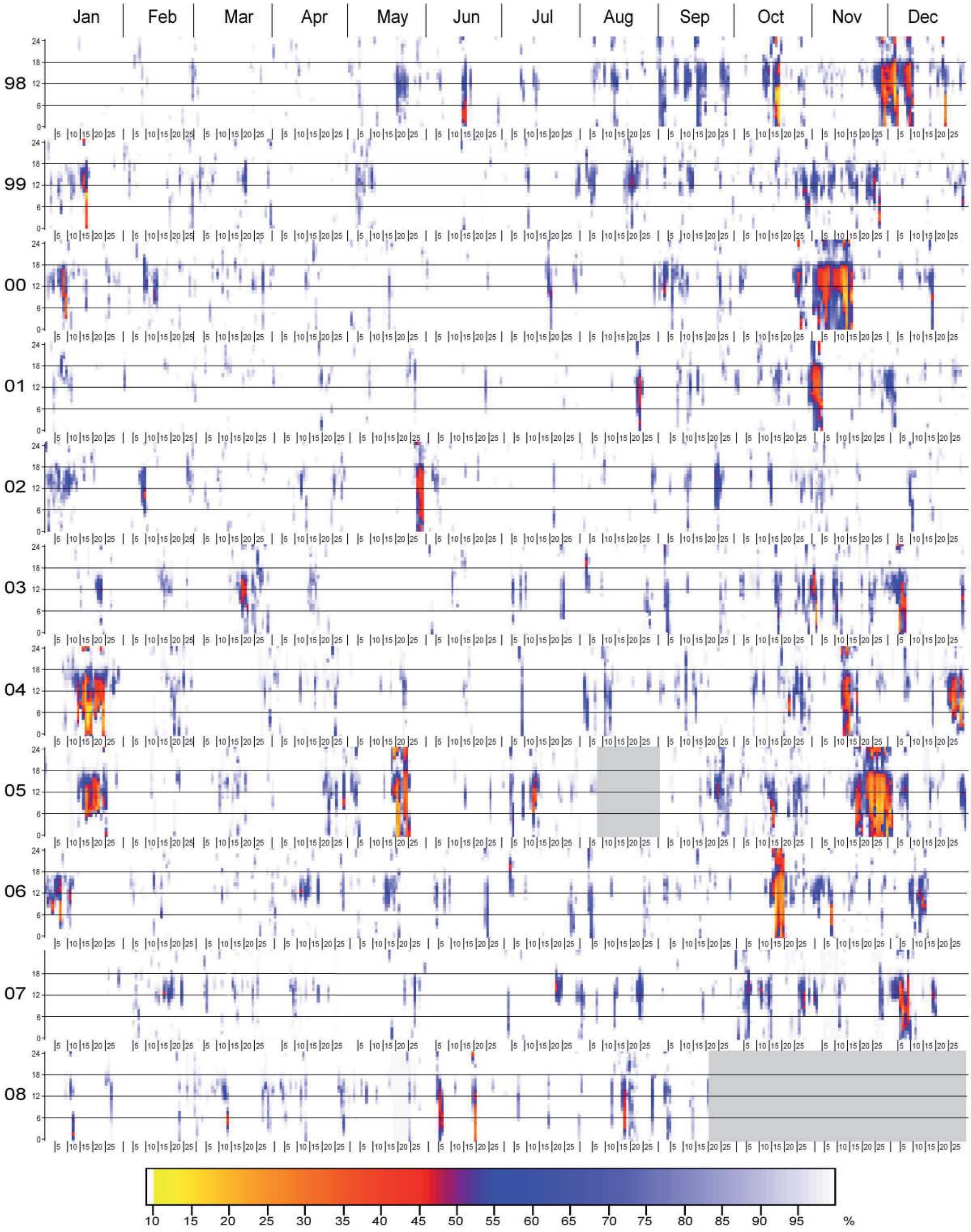


Figure 19: Long-term course of relative humidity on the crest of the Cordillera Real (climate station "Páramo" above Cajanuma, 3,400 m a.s.l.). The y-axis displays data of every hour of each day (x-axis); note the dry periods at the end of year 1998 (El Niño-year), 2000 and 2005.

C/decade during the second half of the 20th century (Vuille et al. 2008). Within this period climate warming was also associated with the more frequent occurrence of El Niño events (Garreaud et al. 2008). While mitigation of mid- and upper tropospheric easterlies and strengthening of westerlies may cause decreasing precipitation in the Central Andes, the prognosis for the dry area in south-western Ecuador suggests slightly increasing rainfall. In that case, various fundamental floral changes can be anticipated: Increased precipitation could advance the migration of native and alien invaders from moister areas into the dry basins near the Peruvian border. Due to warming, many moist forest species could extend their areas into higher reaches of the inner-Andean ranges; many endemics of limited distribution areas may face range shift gaps. Rising temperatures could also cause lowland rainforest species to invade higher reaches of the Cordillera Real, but increased intensity and frequency of drought will eliminate non resistant taxa. Especially

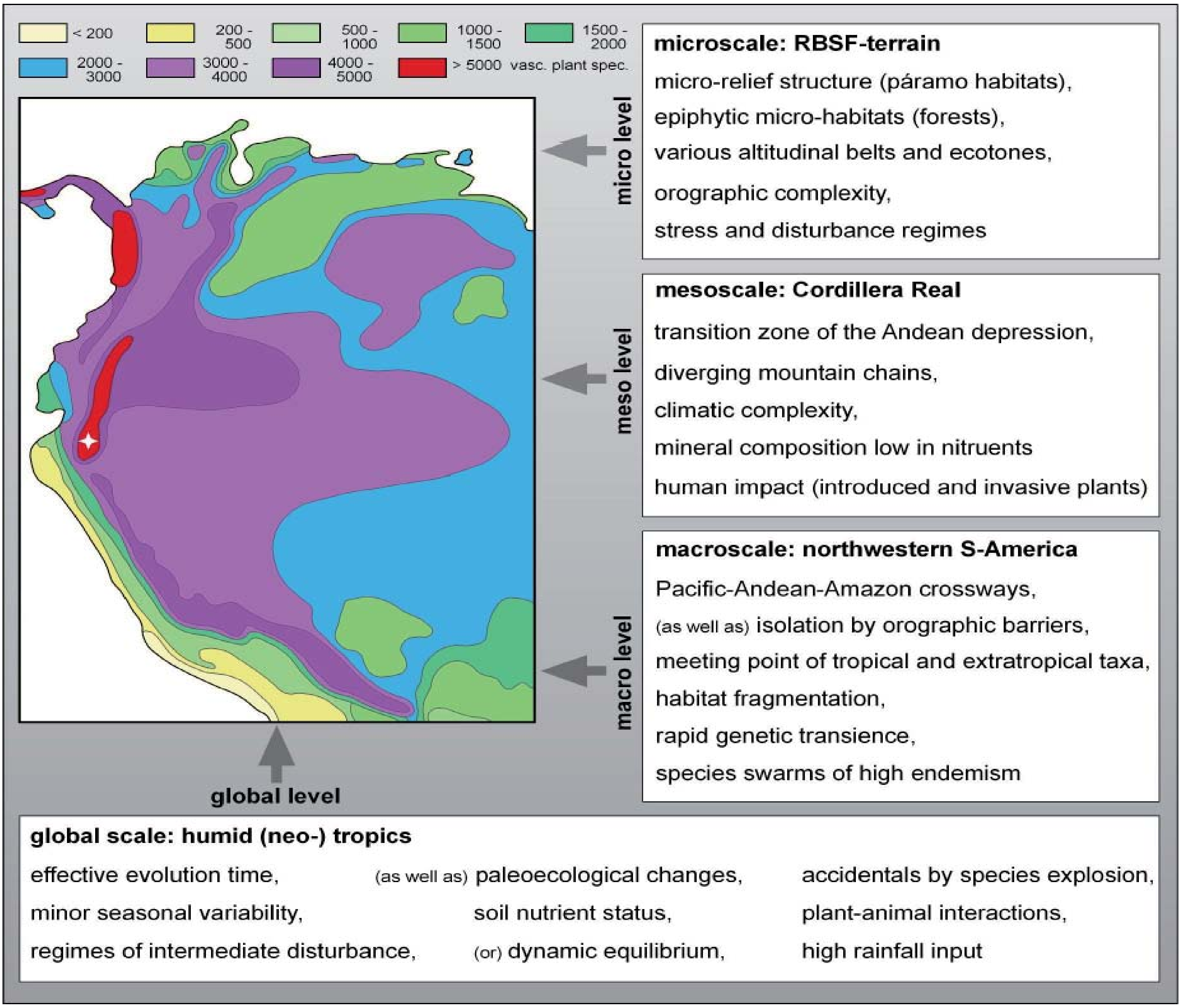


Figure 20: Scale dependent factors contributing to plant diversity in the study area in southern Ecuador. The four levels from global to microscale are expressed by boxes. The plant diversity map on the upper left is based on a section of a recent world map by Barthlott et al. (2007).

in the páramos an uplift of the treeline could displace species whose altitudinal ranges will shrink, in worst cases to nil. However, an elevational shift of the treeline may be counteracted by the strong easterlies, as discussed above.

There is concern that especially small-ranged species adapted to cool environments become eliminated by climate warming (Colwell et al. 2008). Deforestation, however, will continue to be the major threat for the biological megadiversity of the Andean Depression, because "deforestation rate and, presumably, loss of biodiversity in Ecuador are highest in South America" (Mosandl & Günter 2008). Therefore, in accordance with the main aims of the UNESCO MAB Biosphere Reserve "Podocarpus-El Condor", finding and establishing sustainable strategies to release human pressure from pristine mountain rainforests are more urgent than ever.

4 Acknowledgements

The authors gratefully thank the German Research Foundation (DFG) for funding our projects in the scope of the research units FOR 402 and FOR 816.

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