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Vascular Plant Diversity in Natural and Anthropogenic Ecosystems in the Andes of Southern Ecuador

Studies From the Rio San Francisco Valley

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The Andes of Ecuador are one of the world's hotspots of vascular plants. These hotspot characteristics apply particularly to the divergence zone of the study site situated in the Cordillera Real near the Estación Científica San

Francisco (ECSF) in the northernmost part of Podocarpus National Park (3°58' S; 79°04' W). Here, family and species numbers vary considerably between primary mountain forest stands and anthropogenic sites at similar altitudes. The

highest family as well as species numbers (95 and 491, respectively, at 2000–2100 m; 68 and 296 at 2400–2500 m, with sample areas of 400 m² each) document the extraordinarily high plant diversity of primary mountain forest stands. Comparatively, on anthropogenic sites, the analogous numbers are much smaller, with only 64 families/186 species at the lower altitudinal level and 54 families/155 species at the higher altitudinal level.

Keywords: Vegetation; plant diversity; anthropogenic ecosystems; mountain forest ecosystems; Andes; Ecuador.

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Introduction

According to Barthlott et al (2007), the Andes of Ecuador constitute one of the world's 5 megadiversity hotspots of vascular plants. Here, the Andean mountain chain serves as an effective and discrete phytogeographic transition, as well as a barrier zone between the Tumbes–Chocó–Magdalena hotspot in the west and the Amazonian lowlands in the east (Richter et al 2009). Approximately half of the estimated 20,000 Ecuadorian vascular plant species are found between 900–3000 m, although this area covers only 10% of Ecuador's surface (Balslev 1988; Jørgensen and León-Yáñez 1999). These hotspot characteristics apply particularly to the divergence zone of the study site situated in the Cordillera Real, where xeric to hygric climate regimes and a complex topography cause a manifold pattern of vegetation types within a distance of only 35 km. By 2008, the surprising number of 1208 seed plant species and 257 ferns (including fern allies) had been catalogued within a research area of only 1000 ha (Liede-Schumann and Breckle 2008). On this local scale, natural and anthropogenic disturbances have to be considered important additional triggers for the area's outstanding plant diversity.

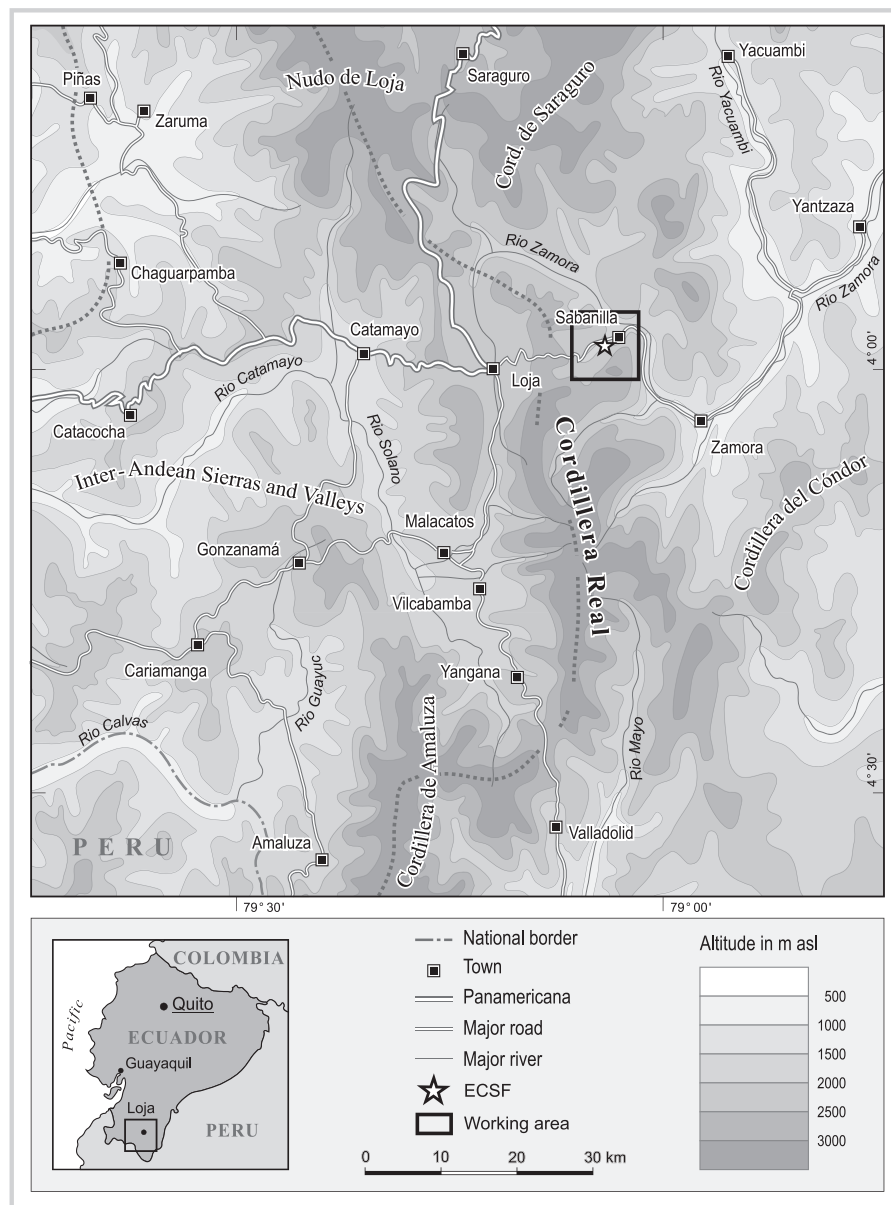
Andean environments have been modified by humans for at least 7000 years (Bruhns 1994; Jokisch and Lair 2002; Sarmiento and Frolich 2002). During the past

50 years, the magnitude of land use has grown at the upper parts of the south Ecuadorian valleys (Ellenberg 1979; Luteyn 1992), and pasture farming is the dominant production system. Between 1960 and 1980, 0.25% of the south Ecuadorian Andean forests were cut down by slash-and-burn practices (Keating 1997; Marquette 2006) annually; Echavarría (1998) showed even higher yearly deforestation rates of 0.25 to 0.46% for the 2 drainage areas of Rio Bombuscaro and Rio Jambue, close to the study area, between 1980 and 1991. Although climate change is intensely debated as a cause of future species extinctions, human land use is currently the most important threat to biodiversity (Pimm and Raven 2000; Köster et al 2009). However, an additional contribution to biodiversity by intentionally introduced and collateral invasive taxa by human impact has been largely ignored. The present article focuses on the latter topic by comparing the local vascular plant diversity on natural and anthropogenic study sites to estimate the human influences on vascular plant diversity on the local scale of the Rio San Francisco valley.

Study area

The study site is located in the steep San Francisco River Valley between Loja and Zamora (Figure 1), which is part of the Andean Depression. This orographic depression

FIGURE 1 Location of the study site in southern Ecuador.



separates the central from the northern Andes and 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). The extreme hygric complexity (eg precipitation amounts from 383 to >6000 mm/y between the inter-Andean basin of Catamayo and the crestline of the Cordillera Real; Richter 2003) facilitates species migration from semiarid open woodlands into clear-cut areas within wetter environments. The study area concentrates on the surroundings of the Estación Científica San Francisco (ECSF), located in the northernmost part of Podocarpus

National Park (3°58'S; 79°04'W) at approximately 1950 m elevation. The particular study sites within the valley itself are located in the “tierra templada” (mean annual temperature $\approx 16^{\circ}\text{C}$ at 2000 masl and $\approx 14^{\circ}\text{C}$ at 2500 m).

The relief is structured by deeply incised ravines, steep slopes of mostly 20–55°, and narrow ridge tops. Frequent translation landslides on schistose and weathered phyllites cause a complex mosaic of plant succession stages (Schrumpf et al 2001). The vegetation extends from a lower evergreen (below approximately 2100 m) and upper montane rain forest to páramo shrubland. Already in 1935 the area was described as follows:

FIGURE 2 Natural and anthropogenic ecosystems in the Rio San Francisco valley near the scientific research station ECSF. (Photo by Karl-Heinz Dierl)



*"During the afternoon of the first day, we arrived at a place called San Francisco, a river, a creek that descends from the Andes and forms the Zamora [...]. It was a rainforest with huge, enormous trees, the finest timber in construction: the romerillo azuceno (*Podocarpus oleifolius*) and the romerillo fino (*Prumnopitys montana*)"* (Serrano Calderón de Ayala 2002: 54).

With the construction of the road from Loja to Zamora in 1957, further settlements were established in the region (Pohle et al 2009). Today, most of the north-facing slopes of the RBSF terrain are still covered by primary mountain rain forest, while beyond the San Francisco River, much of the forest on south-facing slopes has been converted into pastures (Figure 2).

Methods

Vegetation sampling was conducted by investigating sample plots on natural and anthropogenic sites of the Rio San Francisco valley. In accordance with Gentry's rapid inventory methodology for the tropics (Gentry 1982, 1988), a plot size of 50 m × 2 m was selected. The primary mountain rain-forest ecosystem was investigated in regular altitudinal steps of 100 m vertical distance between 2000 m and 3100 m, with 4 transects at each altitude. Within the humanly affected area, transect selections were based on different plant formation types, such as pastures, bracken fern areas, and afforestations of pines and eucalyptus between 1800 m and 2500 m. For comparative studies on both river sides in each case, 8 transects are presented at 2 different altitudinal levels

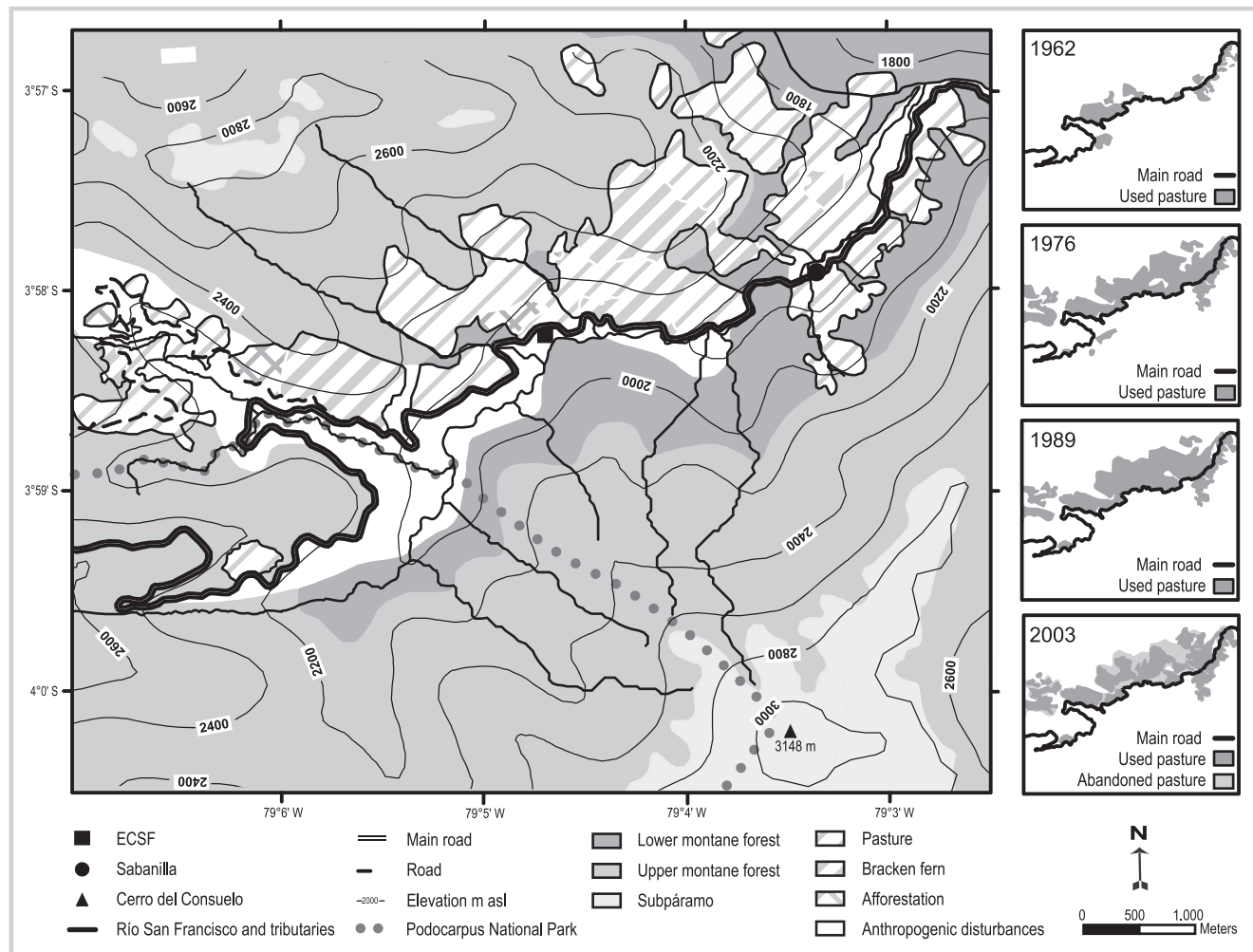
between 2000–2100 m and 2400–2500 m, respectively. The natural forest sites include stands along ravines (2 transects), slopes (4), and ridges (2), while the anthropogenic sites include pastures (2), pine forests (2), and bracken fern areas (4).

All terrestrial vascular plant species and their ground cover (in %) were recorded along each transect. Epiphytes, hemi-epiphytes, lichens, and moss were not sampled. Due to the complex topography of the area as well as the extraordinary high plant richness, Gentry's method was modified. The main differences were in investigating all terrestrial plants, the irregular layout of the 2 × 50 m lines, and investigating only 0.04 ha plots at each altitudinal level and plant formation type. All collected specimens were identified in the herbaria of the universities of Loja (Universidad Nacional) and Quito (Universidad Católica). Statistical analyses were carried out by using PC-Ord 5 (McCune and Mefford 1999) and EstimateS 8.2 (Colwell 2009). Detrended correspondence analysis (DCA) was applied to identify vegetation clusters. Jackknife 2 was calculated to estimate actual species richness (Chao 2005). Furthermore, based on 4 airborne imageries, the spatial distributions of pastures, bracken fern areas, and afforestations between 1962 and 2003 were mapped and analyzed. Fieldwork was finally carried out in 2009 to identify human-induced alterations in land use during the previous 6 years.

Results

Figure 3 verifies the occurrence of pasture systems and afforestations on the northern slopes of the valley, while

FIGURE 3 Overview of principal plant formations in the study area of the Rio San Francisco valley. Record date of the map on the left is July 2009.



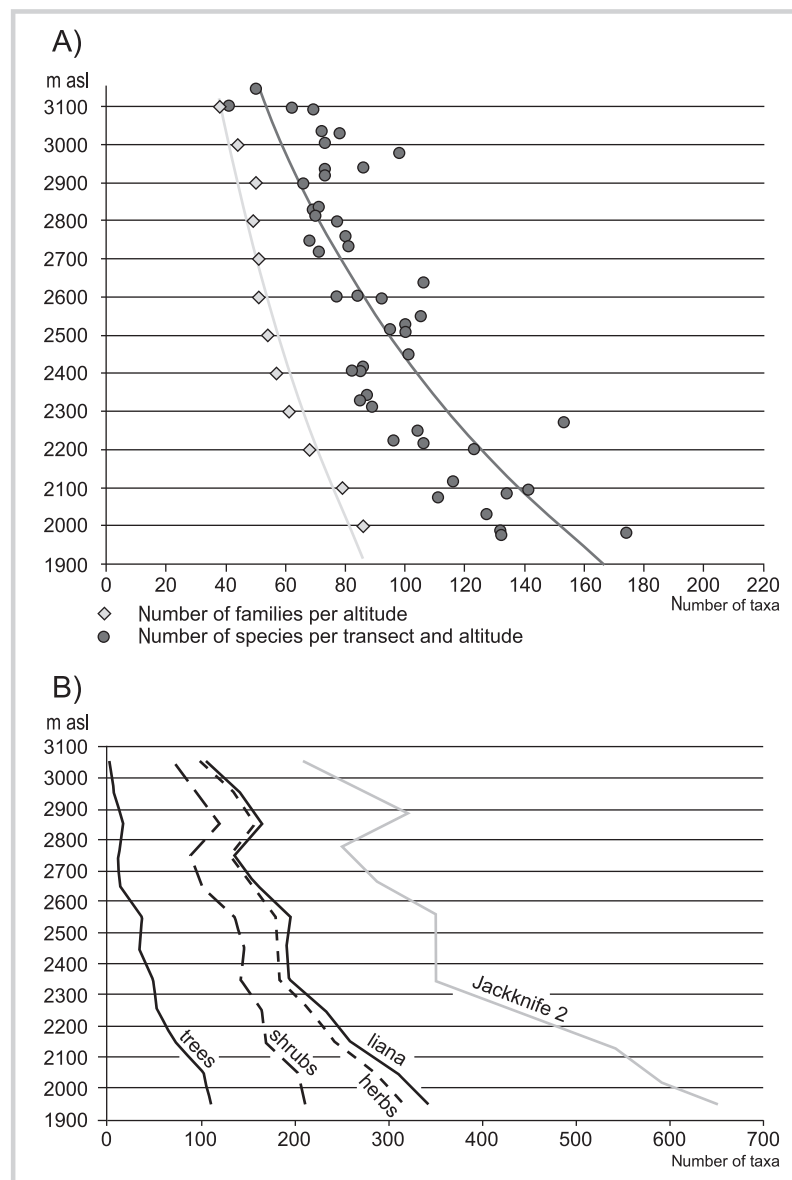
the southern slopes are almost completely covered by primary mountain forest ecosystems. Between 1962 and 1989, pastoral land use increased rapidly, and even small parts of the southern slopes were converted into pastures (Figure 3). With the establishment of the Podocarpus National Park in 1982 (Pohle and Gerique 2008) and the RBSF (Reserva Biológica San Francisco) since 1997, major parts of the southern slopes have been declared protected areas. Land use was intensified on the northern slopes of the valley and on unprotected areas nearby Sabanilla. Since 1998, a reduction of pastures has become apparent, and pasture sites have increasingly been invaded by bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon; Roos et al 2010). Many abandoned pastoral areas on steep slopes are, even after more than 10 years, still characterized by low shrubland and natural vegetation, as well as by secondary forests, which concentrate on scattered patches within narrow bands along ravines. On humanly influenced northern slopes, pine and eucalyptus stands have been planted during the last decades. Here,

timber and the pastoral grass *Setaria sphacelata* are the most evident among the introduced species.

Syntaxonomical studies within the primary mountain forest ecosystem show a notably high species diversity between approximately 1950 m and 3150 m. In block 1006, terrestrial vascular plant species (including 152 morphospecies) of 111 different plant families were identified within 48 transects (eg a total area of only 4800 m²). The families with the highest species numbers are Asteraceae (71 species) and Melastomataceae (66 species), which are widespread at each altitudinal level. Further families such as Araceae, Lauraceae, Rubiaceae, and Piperaceae are mostly restricted to areas below 2600 m, while Symplocaceae, Ericaceae, and Aquifoliaceae prefer higher altitudes. Plant family numbers decrease from 88 per 400 m² at the 2000 m level to 42 families at the highest investigation area (Figure 4A).

This gradient has to be seen in contrast to plant species numbers: in fact, a strong decrease of the latter

FIGURE 4 (A) Altitudinal trends of family and species numbers within the natural forest of RBSF. (B) Species numbers per altitude and life-form. The absolute number of species was calculated by the Jackknife 2 estimator.

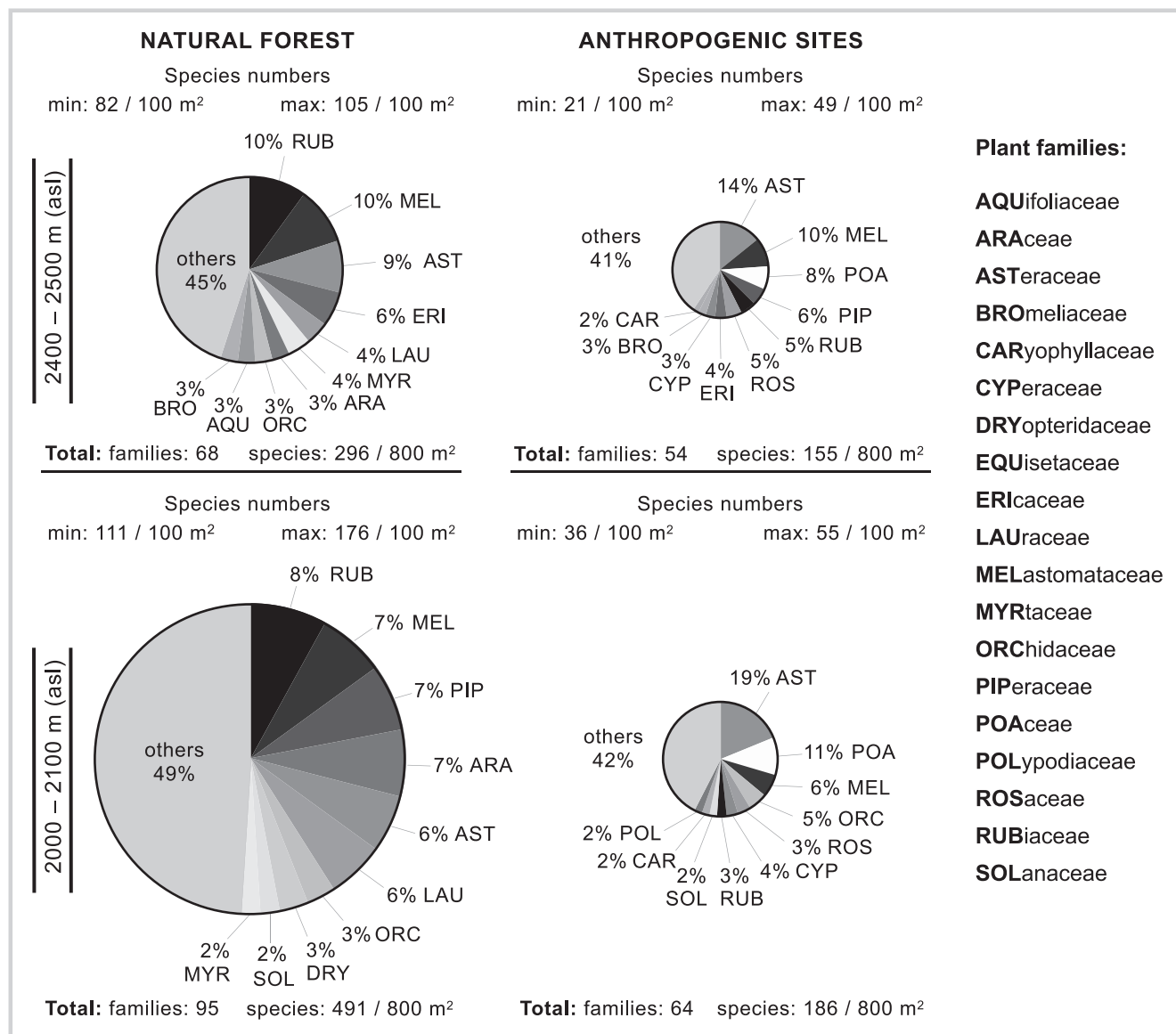


with increasing altitude is apparent. However, the numbers of species per transect fluctuate notably. In particular, some of the elevated *páramo* transects show species richness numbers comparable to those of natural forests at lower altitudes. Maximum turnover rates are located between 2100 and 2300 m. Here, the change from lower to upper montane forest structures becomes obvious. Trees, shrubs, and herbs are represented by roughly the same species numbers at the lowest situated investigation plots (Figure 4B). At higher altitudes, tree species numbers decrease, and shrubs and herbs prevail. A local minimum of shrubs and herbs is identifiable at approximately 2750 m, where the local upper tree-line ecotone is located. Between 1950 m and 2750 m, species

numbers decrease almost linearly, and no mid-domain effect (Rahbek 1995) could be shown (Figure 4B). As calculated by the Jackknife 2 estimator, approximately 50% of the absolute species numbers of the area could be identified within the investigated transects.

On the anthropologically influenced part of the northern valley slopes, 50 and 54 different plant families were recorded on pastures and bracken fern sites, respectively, while the afforested areas had 61 families. The most important families at each of the anthropogenic sites are Asteraceae, Poaceae, and Melastomataceae, even though some must be considered native invaders from disturbed areas. Cyperaceae species are heavily represented on pastures and bracken fern sites, whereas

FIGURE 5 Family composition on natural (left) and anthropogenic sites (right) at 2 different altitudinal levels in the Rio San Francisco valley.



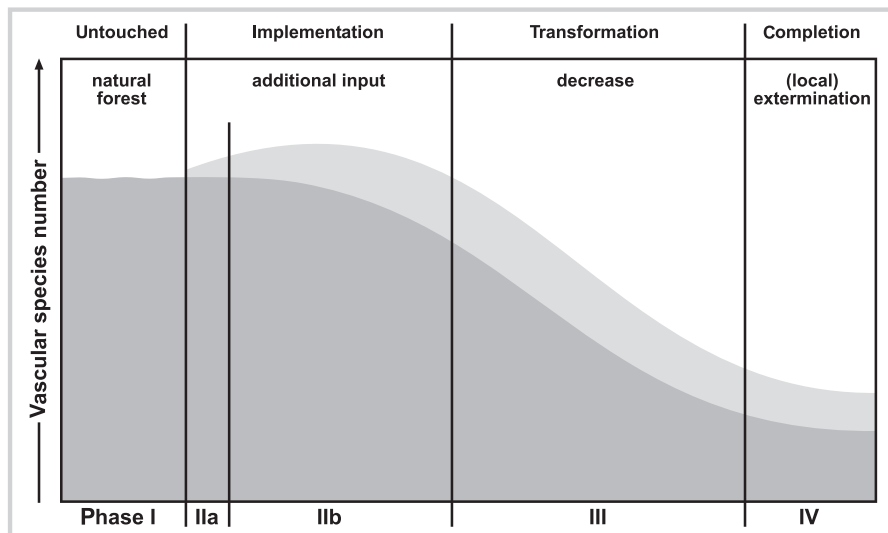
Solanaceae species are characteristic members of afforestation areas.

As indicated in Figure 5, family and species numbers vary considerably between natural and anthropogenic sites at similar altitudes. The greatest family as well as species numbers (95 and 491, respectively, at 2000–2100 m; 68 and 296 at 2400–2500 m) document the extraordinarily high plant diversity of primary forest stands. Comparatively, on anthropogenic sites, the analogous numbers are much smaller, with only 64 families/186 species at the lower altitudinal level and 54 families/155 species at the higher altitudinal level. While for natural sites an altitudinal change of species composition becomes obvious, no significant influence of elevation is stated for the anthropogenic sites due to

the discontinuous pattern of man-made plant communities.

Rubiaceae, Piperaceae, Araceae, and also Lauraceae represent typical families of Neotropical mountain rain forests. Melastomataceae are prominent members, too; however, in contrast to the aforementioned taxa, they also have many heliophilous members, which prefer lightly exposed stands such as the pastures and bracken fern sites. The latter is especially true for Asteraceae and Poaceae, which are most relevant in the man-made communities. While most of these families must first be considered as natural invaders from open plant formations, many of the latter mentioned are consciously or unconsciously introduced Neotropical as well as Paleotropical grasses at lower elevations and even of

FIGURE 6 Influence of anthropogenic disturbances on vascular species numbers of natural ecosystems of the Rio San Francisco valley. The first 2 phases are based on data from the text, whereas phases III and IV present conjectural future scenarios.



European origin at higher elevations. Consequently, there is only a small floristic similarity between primary forest and anthropogenic study sites (*Supplemental material*, Figure S1; <http://dx.doi.org/10.1659/MRD-JOURNAL-D-10-00029.S1>). In particular, pastoral ecosystems differ clearly from primary forest stands and the abandoned pasture systems, whereas the latter show a higher floristic similarity to primary forests and afforestations. This could be mainly ascribed to the appearance of pastoral grasses such as *Setaria sphacelata*, *Melinis minutiflora*, and *Axonopus compressus*, as well as tree species like *Pinus patula*, which were only collected at the anthropogenic sites.

Discussion

Natural as well as anthropogenic ecosystems in the Rio San Francisco valley in southern Ecuador are characterized by extraordinarily high numbers of vascular species. Here, an impressive number of 678 (including 77 morphospecies) vascular plant species on natural sites and 269 vascular plant species (including 41 morphospecies) on anthropogenic sites (including only 67 common species) were identified in 4 sampling areas of only 800 m² each (Figure 5). According to various authors (eg Elton 1958; Naeem et al 2000; Shea and Chesson 2002), highly diverse plant communities generally possess a higher resistibility to exotic invaders than communities with less diversity. Consequently, species numbers in a highly diverse and untouched mountain rain-forest ecosystem do not vary considerably over time (eg 678 species on the primary mountain forest sites; Figure 6, slightly sinuous line in phase I).

Since the implementation of land-use structures through a few small clearings within the mountain rain forest (eg in the Rio San Francisco valley in the early 1960s), species numbers of natural ecosystems have remained largely constant, while introduced and invasive native as

well as non-native species have been added to the environment (Figure 6, phase IIa). Settlement and growth of native and introduced plant species are expected to vary owing to the interaction of plant growth rates and the frequency and intensity of disturbances. After human impact, especially those areas with previously high native plant diversity have also been characterized by a high proportion of non-native plant species. In these cases, advantageous environmental factors as well as anthropogenic disturbances have to be considered as conducive factors for additional plant colonization, since native and exotic species show similar patterns of abundance and species richness (Huston 1994, 2004).

With increasing land consumption, the number of natural species begins to decrease. However, additional native taxa from neighboring warmer and drier climate zones, as well as from open stands such as rock sites or first stages of landslide succession, still immigrate to the newly generated habitats. Consequently, species spill-over persists (eg 202 new established species on the anthropogenic sites; Figure 6, phase IIb), and species numbers for the entire environment remain on a high level regardless of changes in the structure of life-forms and plant formations.

During the prospective transformation period (Figure 6, phase III), natural species numbers are expected to decrease rapidly due to continuous enlargement of the anthropogenic ecosystems, while the number of native and exotic invaders will vary only slightly (Figure 6, phase IV). In the last phase, humans are expected to occupy most of the terrain, and only small fragments of rain-forest sites will remain on steep slopes or along narrow ravines. Even these fragments will still be species-rich islands without any input of alien species. Conversely, only a few native plants will be able to establish themselves in the man-made ecosystems, among them preliminarily taxa from disturbed areas.

To a lesser extent, this scenario resembles the degradation trends in tropical lowland rain forests, where deforestation and subsequent human land use cause extreme species loss. Especially in the coastal plains of Ecuador, only very few and small sheltered areas with natural vegetation stands still persist. Consequently, in such cases, native species numbers might be reduced toward zero. Instead, mountain areas such as the ones investigated bear the advantage of remote and inaccessible terrains, serving as retreat areas for a limited number of native species.

Conclusions

We must assume that the turnaround point for initiation of species loss at the local scale of the Rio San Francisco valley ranges between 10 and 25% of human-impacted terrain. To date, approximately 48% of the natural mountain forest below 2200 m and even 6% of the higher altitudes of the Rio San Francisco valley (Bendix and Beck

2009) are covered by man-made ecosystems. Thus, a coexistence of natural as well as anthropogenic plant formations characterizes the regional landscape of the upper parts of the Rio San Francisco valley. Here, species numbers of primary mountain forests remain almost constant, whereas supplemental exotic species have been added to the valley ecosystem on the anthropogenic sites. On the one hand, triggers for differences in the vulnerability of an existing grade of biodiversity might be given by widely fixed preconditions such as the climate (eg highly biodiverse humid versus less diverse semiarid areas). On the other hand, the height of the apex and the starting point of the reversal are also defined by the type of human impact (eg uniform monocultures versus diversified plantations and gardens).

Disregarding the “quality” of plant diversity, we believe that the additional input of native as well as non-native invaders does not necessarily result in a substantial disadvantage or in a major threat to the investigated area as long as land seizure is limited to its present dimensions.

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Supplemental material

FIGURE S1 Distribution of the sampling plots over the first 2 axes of a biplot as a result of a DCA. The groups of sampling units are separated by circles calculated by a TWINSpan analysis.

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