

Tree Diversity, Forest Structure and Productivity along Altitudinal and Topographical Gradients in a Species-Rich Ecuadorian Montane Rain Forest

Jürgen Homeier^{1,5}, Siegmund-W. Breckle², Sven Günter³, Rütger T. Rollenbeck⁴, and Christoph Leuschner¹

¹ Plant Ecology, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

² Department of Ecology, University of Bielefeld, Germany

³ Institute of Silviculture, Technical University of Munich, Germany

⁴ Laboratory for Climatology and Remote Sensing, University of Marburg, Germany

ABSTRACT

We studied the spatial heterogeneity of tree diversity, and of forest structure and productivity in a highly diverse tropical mountain area in southern Ecuador with the aim of understanding the causes of the large variation in these parameters. Two major environmental gradients, elevation and topography, representing a broad range of climatic and edaphic site conditions, were analyzed. We found the highest species richness of trees in valleys < 2100 m. Valleys showed highest values of basal area, leaf area index and tree basal area increment as well. Tree diversity also increased from ridges to valleys, while canopy openness decreased. Significant relationships existed between tree diversity and soil parameters (pH, total contents of Mg, K, Ca, N and P), and between diversity and the spatial variability of pH and Ca and Mg contents suggesting a dependence of tree diversity on both absolute levels and on the small-scale heterogeneity of soil nutrient availability. Tree diversity and basal area increment were positively correlated, partly because both are similarly affected by soil conditions. We conclude that the extraordinarily high tree species richness in the area is primarily caused by three factors: (1) the existence of steep altitudinal and topographic gradients in a rather limited area creating a small-scale mosaic of edaphically different habitats; (2) the intermingling of Amazonian lowland plant species, that reach their upper distribution limits, and of montane forest species; and (3) the geographical position of the study area between the humid eastern Andean slope and the dry interandean forests of South Ecuador.

Key words: diversity-productivity relationship; Ecuador; Neotropical montane forest; soil nutrients; spatial heterogeneity; tree species richness; tropical tree growth.

TROPICAL MONTANE FORESTS ARE HIGHLY THREATENED ECOSYSTEMS with a rapidly declining area (Doumenge *et al.* 1995, Gentry 1995). For the Andean montane forests, Hamilton (1995) estimated that the original forest cover already has been reduced by 90 percent. These forests show very high species diversities (Henderson *et al.* 1991, Brummit & Nic Lughadha 2003), but they are still among the least-studied tropical ecosystems with respect to the factors that determine their structure and species composition (Brujinzeel & Proctor 1995). A general trend not only found in tropical forests is a decrease in plant species diversity (Gentry 1988, Lieberman *et al.* 1996, Aiba & Kitayama 1999, Kessler 2002) and stature (Grubb 1977, Cavellier 1996, Lieberman *et al.* 1996, Aiba & Kitayama 1999) with increasing elevation. However, topographical variation is a second environmental factor that generates high habitat diversity in montane forests and may partly overlay the altitudinal gradient. Moreover, changes in forest structure along topographical gradients are often quite similar to those along elevational gradients (Tanner 1977, Webb *et al.* 1999, Takyu *et al.* 2002). The mechanisms causing elevational and topographical changes of plant diversity and forest structure in tropical montane forests are still poorly understood. Both are indirect gradients that tend to correlate with variation in a set of interrelated environmental factors, such as soil hydrology, nutrient supply, temperature regime, and wind exposure, which are difficult to disentangle.

A hotspot of biodiversity in tropical montane forests is the Reserva San Francisco (RSF) in the South Ecuadorian Andes. The study area of ca 1000 ha exhibits an outstanding diversity not only of vascular plants (1208 spermatophytes and 257 ferns; Homeier & Werner 2007, Lehnert *et al.* 2007), but also harbors the highest ever recorded species numbers per unit area of bryophytes (> 500 species per 1000 ha; Parolly *et al.* 2004) and of geometrid moths (> 1000 species; Brehm *et al.* 2005).

For identifying possible causes of the remarkable spatial heterogeneity of the vegetation structure and tree species richness at the RSF, we conducted several gradient studies in the forest area covering an altitudinal gradient of 800 m and the transition from valley to ridge. In an array of plots and transects within this environmental matrix, we investigated tree species richness and several stand structural and forest productivity parameters with the aims of: (1) quantifying changes in plant diversity and forest structure along altitudinal and topographical gradients, (2) analyzing interrelations between tree diversity, forest structure and environmental factors, and (3) discussing the putative factors that make the studied forests more species-rich than other tropical montane forests.

METHODS

STUDY AREA.—The study area is located at 1800–2600 m on the eastern slope of the Cordillera El Consuelo in the Andes of southern Ecuador (Fig. S1). The region forms part of the northern Huancabamba depression, where the Andean Cordillera is partly interrupted by the Río Chamaya/Río Maraón system and few

Received 3 June 2008; revision accepted 29 April 2009.

⁵Corresponding author; e-mail: jhomeie@gwdg.de

peaks reach > 4000 m. The study area of ca 1000 ha belongs to the RSF and borders the Podocarpus National Park, between the cities of Loja and Zamora, Zamora-Chinchipe Province (3°58' S, 79°04' W). The main part of the RSF is situated on the steeply sloping (20–50°) north-facing flank of the Rio San Francisco valley, the topography is generally very steep and rugged consisting of ridges and small valleys with only few flat areas. Paleozoic metamorphosed schists and sandstone with some quartz veins are the main source material for soil development. The most abundant soil types are Cambisols at the lower elevations, and Planosols and Histosols at elevations > 2300 m (Wilcke *et al.* 2002). The organic layer is locally very thick (5–35 cm), especially on the ridges and has mostly low pH values and relatively low nutrient contents (Wilcke *et al.* 2008). Increasing C/N-ratios with elevation indicate decreasing decomposition rates (Schrumpf *et al.* 2001, Leuschner *et al.* 2007). The region is characterized by a high heterogeneity in soil conditions with generally better nutrient supply in the valleys compared with ridges and an overall trend to more unfavorable soil conditions for plant growth with elevation (Homeier 2004, Soethe *et al.* 2008, Wilcke *et al.* 2008).

The region is characterized by its particularly high plant diversity (Young & Reynel 1997, Weigend 2002); Podocarpus National Park has the highest number of endemic vascular plant species (> 200) compared with all other protected areas in Ecuador (Valencia *et al.* 2000). In addition, many northern Andean species reach their southern distributional limit while many Central Andean species reach their northern limit in the Huancabamba region (Young & Reynel 1997, Weigend 2002), thereby further increasing species diversity.

Most of the RSF is covered with primary forest, which can be classified as 'bosque de neblina montano,' montane cloud forest (Valencia *et al.* 1999), or as 'bosque siempreverde montano,' evergreen montane forest (Balslev & Øllgaard 2002).

So far, > 280 tree species with a dbh \geq 5 cm are known from the RSF, of which almost 10 percent represented new records for Ecuador, and some were new to science (Homeier & Werner 2007). Lauraceae, Melastomataceae and Rubiaceae are the families with the highest tree species numbers.

Four main types of primary forest were distinguished for the studied elevations of the RSF (Fig. S1), combining different vegetation classification approaches (Paulsch 2002: structural forest parameters; Homeier 2004: tree species composition; Parolly & Kürschner 2004: bryophyte species composition; Homeier *et al.* 2008: synopsis of the previous studies). The tallest and most species-rich forest (forest type I) is located on lower slopes and within the valleys < 2200 m asl, where the canopy reaches 25–30 m with some emergents reaching up to 35 m. Most speciose tree taxa are *Miconia* spp. (Melastomataceae), *Ocotea* spp., *Persea* spp. (Lauraceae), *Ficus* spp. (Moraceae) and *Inga* spp. (Mimosaceae). On nearby upper slopes and ridges (forest type II, 1900–2100 m asl), forest stature and tree species composition is completely different with only few trees reaching a height of > 15 m. Some frequent taxa are *Alzatea verticillata* Ruiz & Pav. (Alzateaceae), *Graffenrieda emarginata* Triana (Melastomataceae), *Podocarpus oleifolius* D. Don (Podocarpaceae) and various Lauraceae. With increasing elevation,

stand height decreases and the canopy becomes more open. Between 2100 and 2250 m asl (forest type III) the trees usually do not surpass 12 m, common species of this forest type include *Clusia* cf. *ducuoides* Engl. (Clusiaceae), *Alchornea grandiflora* Müll. Arq. (Euphorbiaceae), *Licaria subsessilis* van der Werff (Lauraceae), *Eschweilera sessilis* A.C. Sm. (Lecythidaceae) and *G. emarginata* Triana (Melastomataceae). The forest at > 2250 m asl (forest type IV) is dominated by one tree species, *Purdiaea nutans* Planch. (Cyrillaceae). The herbaceous layer of this forest is well developed and principally composed of terrestrial bromeliads. The most abundant tree species of the whole study area at 1800–2600 m asl is *G. emarginata*, which mainly occurs on upper slopes and ridges (forest types II and III).

CLIMATE.—The research area is characterized by a humid tropical montane climate. Mean annual temperature inside the closed forest (measured at 2 m height) decreases linearly by 0.37 K per 100 m of elevation, from 15.7°C at 1850 m to 13.3°C at 2450 m (Homeier 2004). Mean annual precipitation reaches ca 2500 mm (2176 mm at 1960 m asl) with a maximum occurring in June/July (Fig. S2). The higher elevations are significantly wetter with up to 4743 mm (at 3180 m asl) per year and the average gradient yields an increase of 220 mm precipitation per 100 m of elevation (Bendix *et al.* 2008). Further input comes from cloud and fog scavenging, with a potential additional input of up to 1500 mm per year (Rollenbeck *et al.* 2005). The influence of the relatively drier season in October/November is mitigated by this high input of cloud interception water. Furthermore, the site's north-westerly exposure causes a slight lee effect, lowering the intensity of rainfall. In particular, the deep valleys are not as extreme with regard to diurnal temperature variations, wind gusts and exposure to solar radiation. However, the ridges receive the major part of scavenged cloud water and therefore probably have a higher precipitation input than the valleys.

STUDY PLOTS.—We compiled data from two different sampling schemes, thereby covering an environmental matrix, which represents all four main forest types (Fig. S1).

To investigate altitudinal changes in the composition and species richness of trees and the forest structure, we installed 17 permanent plots of 400 m² at 1850–2570 m asl. All plots were situated within homogenous mature forest representative for the elevation in question and without visible recent natural or human disturbance.

The influence of topography on diversity and forest structure was studied in seven of the above mentioned plots, which were assigned either to forest type I (four plots) or forest type II (three plots), all at 1900–2100 m asl (Fig. S1).

Additionally, differences in forest structure between valleys (forest type I) and ridges (forest type II) were explored with a transect inventory using eight transects, each starting at 1900 m asl and ending at 2100 m asl (four located in valleys along tributaries of the Rio San Francisco and four on neighboring ridges, respectively; Fig. S1). All transects had a width of 10 m, but different lengths (170–430 m) according to the topography.

FOREST STRUCTURE AND TREE DIVERSITY.—In the study plots (which differ from the transects), all trees of dbh ≥ 5 cm (at 1.3 m height) were inventoried for their dbh (diameter tape) and heights (calculated trigonometrically; only for the 15 lowermost plots).

Diameter growth of trees with a dbh ≥ 10 cm was measured monthly with self-constructed dendrometer bands (see Homeier 2004) in 11 of the plots at 1850–2450 m asl (285 trees in total). The increase of plot basal area was calculated as the total of the individual tree increments (not including tree deaths, following approach 1 after Clark *et al.* 2001a) by averaging over the years 2001 and 2002.

Tree diversity was calculated after the individual-based rarefaction method (Gotelli & Colwell 2001) as the number of species expected in a sample of 43 trees from a 400-m² plot (43 being the smallest number of trees found in any one of the 17 plots). To analyze canopy openness and leaf area index (LAI), we took four hemispherical images in each of the 15 lowermost tree plots and analyzed them with the Gap Light Analyzer 2.0 software (Frazer *et al.* 1999).

All tree individuals were identified to species where possible (80.7 percent), otherwise to morpho-species. Voucher specimens of sampled species are kept at the herbaria LOJA, QCNE and MO, and images of most species are available at <http://www.visual-plants.de>

In the eight forest structure transects, the abundances and basal areas of all trees with dbh ≥ 20 cm were sampled; the same parameters for trees of dbh ≥ 10 cm were registered in the inner 5 m of the transects only. Total area of all transects was 1.18 ha for dbh ≥ 10 cm and 2.36 ha for dbh ≥ 20 cm in the valleys and 1.13 ha and 2.26 ha along the ridges, respectively.

SOIL PARAMETERS.—At each of the 15 lowermost tree plots, we collected nine independent soil samples from the topsoil (0–10 cm) and analyzed them separately. The pH of the air-dried samples was determined with a glass electrode in deionized water (soil:water ratio 1:5).

To determine total cation concentrations (Ca, K and Mg) the dried soil samples were digested (block digestion) with concentrated HNO₃ (0.15 g soil in 2.0 mL HNO₃) and nutrient concentrations in the extracts measured with flame atomic absorption spectrometry (AAS, PE 5100, Perkin Elmer Corp., Norwalk, CT, U.S.A.) at the Department of Ecology, University of Bielefeld.

For the analysis of correlation between forest parameters and soil parameters, we used additional soil data (total concentrations of nitrogen and phosphorous of the organic layer) from a subset of our study plots from Wilcke *et al.* (2008).

DATA ANALYSIS.—Correlation analyses used the least-squares method. Differences in the means of structural forest parameters and diversity parameters between valley plots and ridge plots were analyzed using the *t*-test after testing for Gaussian distribution (Shapiro–Wilk test). Significance was determined at $P < 0.05$ in all cases. We used ANOVA to compare soil parameters of the 15 sampled plots (Statistica 8, StatSoft Inc., Tulsa, OK, U.S.A.). Partial correlations were calculated to control for the effect of elevation in

the relationships between tree diversity, tree basal area and tree basal area growth and soil parameters.

The Jaccard similarity was computed for every single pair of plots from the forest types I and II using the software EstimateS (Colwell 2008). Subsequently, from the resultant matrix the averages for the similarity within forest types (forest type I–forest type I pairs, forest type II–forest type II pairs) and between the forest types (forest type I–forest type II pairs) were calculated.

RESULTS

ALTITUDINAL GRADIENT.—In the 17 permanent plots, we found 1347 stems (dbh ≥ 5 cm) in total belonging to 190 tree species representing 53 plant families (Table S1). The most important families in terms of tree species were Lauraceae (25 species), Rubiaceae (21) and Melastomataceae (16). In the lower parts of our study area up to 2100 m asl, many typical lowland tree taxa (*e.g.*, Chrysobalanaceae, Moraceae, Sapotaceae, *Quiina* and *Vochysia*) were still present, whereas at higher elevations, typical montane taxa (*e.g.*, Araliaceae, *Ilex*, *Symplocos* and *Weinmannia*) contributed the majority of species. Tree species richness in the RSF decreased significantly with elevation (Fig. 1A). When rarefied species numbers were compared, the trend was the same as with the observed species numbers, but the decrease was not as steep because of the slightly higher tree densities at lower elevations.

The average height of the trees with dbh ≥ 10 cm declined from mean values of 12–16 m at 1850 m asl to 6–8 m at 2450 m asl (Fig. 1B). The total basal area of the stands decreased from values of 30–50 m²/ha at around 2000 m asl to < 12.5 m² on the plots > 2300 m asl (Fig. 1C). On average, trees had a higher height to dbh ratio in the lowermost plots (Fig. 1D). This was also the case for the most common tree species *G. emarginata*. Across the elevation gradient, from 1850 to 2370 m asl its plot average height to dbh ratio declined from 90.0 to 51.7. Annual tree basal area increment of the stands decreased on average from 1850 to 2450 m asl by > 75 percent (Fig. 1E). Variability in annual increment among the plots was highest < 2000 m asl, where we registered values between 0.12 (forest type II) to > 0.70 m²/ha (forest type I). The LAI was highly variable in the stands. Most of the values from < 2250 m asl were 2.5–4 m²/m², while those in the uppermost tree plots were 0.9–1 m²/m² (Fig. 1F). Canopy openness showed a slight increase from < 10 percent at 1800–2000 m asl to around 10–15 percent at *ca* 2200 m asl. Above 2250 m asl, in the *P. nutans*-dominated forest type IV, the canopy openness reached 30–40 percent.

Both pH (H₂O) and total Ca, Mg and K concentrations of the topsoil showed a high spatial variability within the plots as indicated by the standard deviations (Table S2). The soil pH and Mg and K concentrations showed a significant decrease with elevation (Fig. 2).

TOPOGRAPHICAL GRADIENT.—We found a significantly higher tree diversity (rarefied tree species numbers) in the valley (forest type I) relative to ridge forest (forest type II) plots (Table 1). The observed species numbers revealed no significant difference, which is a

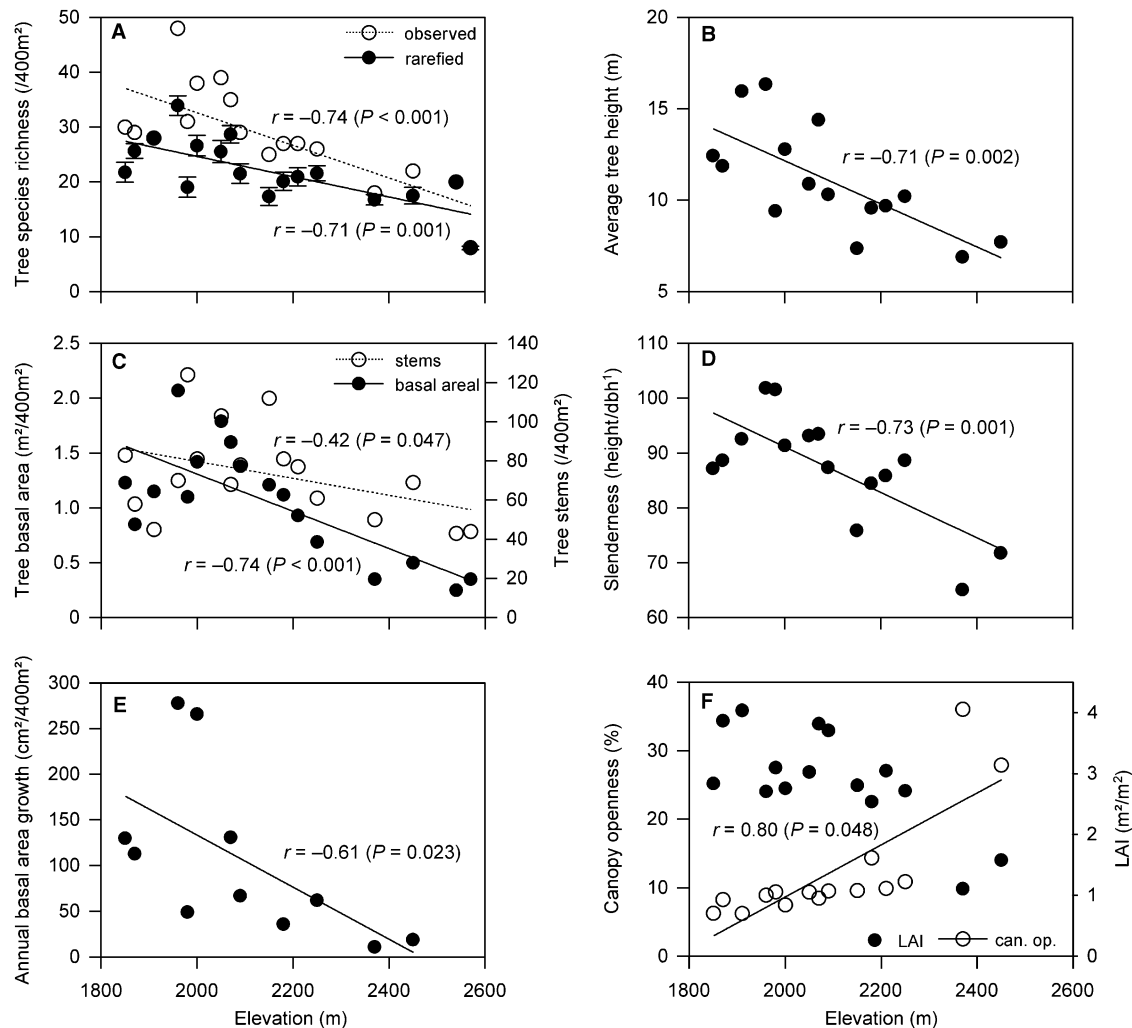


FIGURE 1. Elevational changes in tree diversity and forest structure in the study area. Significant correlations ($P < 0.05$) are indicated by regression lines: (A) observed and rarefied tree species richness (per $N = 43$ trees with SD); (B) average height of trees with dbh ≥ 10 cm; (C) tree basal area and stem density of trees with dbh ≥ 5 cm; (D) stem slenderness (ratio of height : dbh) of trees with dbh ≥ 5 cm; (E) annual basal area increment (mean of the years 2001 and 2002) of trees with dbh ≥ 10 cm; and (F) canopy openness and LAI.

consequence of the higher stem density on the ridges. Among the 139 tree species (dbh ≥ 5 cm) registered in the nine plots < 2100 masl, the fraction of shared species occurring in valleys and on ridges (forest types I and II) was only 9.4 percent. The average Jaccard similarity between plots of the same forest type was 0.18 for forest type I and 0.38 for forest type II, and thus higher than the average of 0.06 between ridge and valley plots.

In total, we recorded 3866 stems (dbh ≥ 10 cm) in the eight transects. Stem density was significantly higher in forest type II than in forest type I (Table 1). The stand tree basal area was significantly higher in the valleys than on the ridges when trees > 10 cm dbh were compared (transect data). If trees with dbh ≥ 5 cm were included (plot data) there was no significant difference, suggesting that small stems contribute notably to total basal area of forest type II.

In both ridges and valleys, the trees of 10–25 cm dbh contributed > 50 percent to the total stand basal area. A significant difference was found for tree height: on average, valley trees ≥ 10 dbh were 4.4 m taller than the ridge trees (Table 1). However, a decrease in slenderness (ratio of tree height to tree dbh), as shown for the altitudinal gradient, was not observed from the valley to the ridge. While LAI for both ridge and valley plots was around 3 (Table 1), canopy openness was significantly higher on the ridge (means: 7.8 vs. 9.4 percent).

RELATIONSHIPS BETWEEN TREE DIVERSITY, ABOVEGROUND PRODUCTIVITY AND SOIL NUTRIENTS.—Tree diversity and basal area increment showed a significant positive relation to each other (Fig. 3). Highest values for both parameters were registered for the lowermost sites (forest type I); they declined with elevation and from valley to ridge

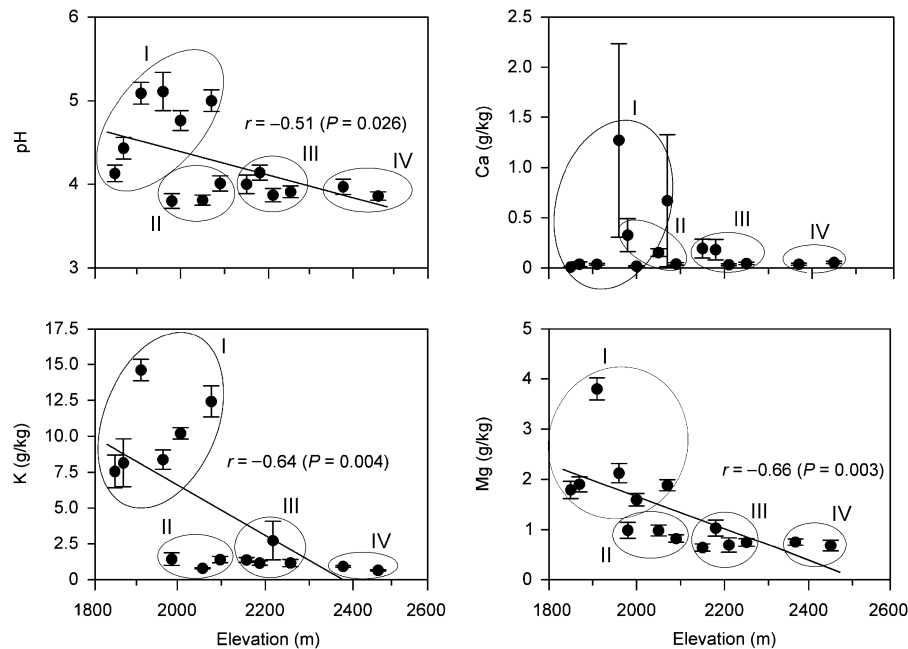


FIGURE 2. Elevational changes in soil pH and total cation concentrations in the study plots. Given are means \pm SE of the nine samples analyzed from each plot. Significant correlations ($P < 0.05$) are indicated by regression lines. Affiliation to the four forest types is indicated by ellipsoids and Roman numerals (I–IV).

at the same elevation. Thus, tree species richness and aboveground productivity were related across a broad range of altitudinal and topographical situations.

Tree diversity showed significant positive correlations with all investigated soil parameters (Table S3). Tree basal area was correlated significantly with total soil concentrations of Ca, N and P, whereas tree basal area increment was correlated with Mg and K concentrations. Moreover, tree diversity showed significant positive correlations with the standard deviations of pH, Ca and Mg of the plots, thus pointing at a positive relationship between tree diversity and small-scale soil heterogeneity. After controlling for the effect of elevation, there remained significant positive correlations of tree diversity with pH and K and Ca concentrations, and with the standard deviation of pH and Ca concentration. Furthermore, tree basal area showed significant partial correlations with the Ca concentrations and their standard deviation.

DISCUSSION

TREE DIVERSITY.—Our results reflect some general trends found in plant diversity of tropical montane forests: First, tree species diversity decreased with elevation in a similar manner as was found in other studies (*e.g.*, Gentry 1988, Lieberman *et al.* 1996, Aiba & Kitayama 1999, Jørgensen & León-Yáñez 1999, Slik *et al.* 2009). Maximum diversity of trees in the Ecuadorian Andes can be expected < 1500 m asl (Jørgensen & León-Yáñez 1999). The high tree species numbers in the plots at 1800–2100 m asl, especially in forest type I, are remarkable, because comparable montane forests in northern Ecuador (Webster & Rhode 2007) have found 125 tree species in total between 1800 and 2100 m asl at Maquipucuna

cloud forest) appear to be much poorer in terms of tree genera and species. For 20 primary forest plots in the Sumaco Biosphere Reserve (NE-Ecuador; 1920–2085 m asl, selected after the same criteria as in the RSF), we found a mean of only 24.5 tree species (dbf ≥ 5 cm) per 400 m² (J. Homeier, unpubl. data).

Second, we observed a higher tree species diversity in valleys/lower slopes (forest type I) in comparison with ridges/upper slopes (forest type II) in a similar manner as described by Takyu *et al.* (2002: Borneo) and Tanner (1977: Jamaica) for two tropical montane forests. The small fraction of shared tree species and the low average Jaccard similarity between the two forest types indicates that most species are restricted in their occurrence to specific sites in the forest. This is corroborated by a study on tree regeneration that found marked differences in the composition of the seedling communities between valley and ridge forests in the RSF suggesting that these contrasts are a consequence of unfavorable germination conditions rather than dispersal limitation in the two forest types (Homeier 2008).

FOREST STRUCTURE AND TREE GROWTH.—The aboveground biomass of the stands (as approximated by tree basal area) decreased with elevation; on the other hand, fine and coarse root biomass have been found to increase (Röderstein *et al.* 2005, Leuschner *et al.* 2007) indicating a large increase of tree root/shoot ratio with elevation. As shown in many other studies, stand height decreased with elevation. However, the average height of 6–8 m found in the *P. nutans*-dominated forests at 2300–2500 m asl is low compared with other montane forests in Ecuador, even for elevations > 2500 m asl. Madsen and Øllgaard (1994) found average heights of 10–12 m (dbf ≥ 5 cm) at 2700 m asl in the nearby Podocarpus

TABLE 1. Structural and diversity parameters (data source in parentheses) for forest type I (valley forest) and forest type II (ridge forest) at elevations 1900–2100 m asl (Reserva San Francisco, southern Ecuadorian Andes). Given are means \pm SE. Significant differences ($P < 0.05$) between the two vegetation types are indicated in bold text.

	Valleys and lower slopes (forest type I)	Ridges and upper slopes (forest type II)
Tree diversity (rarefied species per $N = 43$ trees; /400 m ²) (plots, dbh ≥ 5 cm)	29.3 \pm 1.6	22.0 \pm 1.8
Tree species richness (/400 m ²) (plots, dbh ≥ 5 cm)	37.3 \pm 2.7	33.0 \pm 4.8
Tree slenderness (height/dbh) (plots, dbh ≥ 5 cm)	94.9 \pm 2.4	94.1 \pm 4.1
Tree basal area growth (cm ² /400 m ² /yr) (plots, dbh ≥ 10 cm)	225.0 \pm 47.1	58.0 \pm 9.0
Canopy openness (%) (plots)	7.8 \pm 0.4	9.4 \pm 0.3
Leaf area index (m ² /m ²) (plots)	3.1 \pm 0.1	2.8 \pm 0.1
Tree stem number (/400 m ²) (plots, dbh ≥ 5 cm)	66.0 \pm 7.6	101.7 \pm 13.3
Tree stem number (/400 m ²) (transects, dbh ≥ 10 cm)	31.2 \pm 1.1	36.0 \pm 1.2
Tree basal area (/400 m ²) (plots, dbh ≥ 5 cm)	1.56 \pm 0.19	1.42 \pm 0.20
Tree basal area (/400 m ²) (transects, dbh ≥ 10 cm)	1.04 \pm 0.05	0.95 \pm 0.05
Average tree height (m) (plots, dbh ≥ 10 cm)	14.7 \pm 0.5	10.3 \pm 0.2

National Park, and Valencia and Jørgensen (1992) reported 7.6 m (dbh ≥ 5 cm) at 3300 m asl for the Pasochoa volcano in northern Ecuador. The stunted stature of the forest is associated with low basal area growth rates at elevations > 2000 m asl. We suggest that tree growth at the higher elevations of the studied transect is not only limited by decreasing temperatures, but also by shortage in nutrients and/or adverse soil chemical and physical conditions (Breckle *et al.* 2005, Leuschner *et al.* 2007).

A positive relationship between tree species richness and forest productivity, defined in terms of rates of accumulation of above-ground biomass, has been reported by now for various tropical forest communities (*e.g.*, Phillips *et al.* 1994, Burslem & Whitmore 1999, Waide *et al.* 1999, Aiba *et al.* 2005, Balvanera & Aguirre 2006, Gillman & Wright 2006). However, to our knowledge, this relation has only been shown to exist on larger geographic scales but not for a given rain forest area on the local scale. Local heterogeneity of topography and edaphic conditions could lead to differences in the aboveground biomass and in stem growth between forest stands in close proximity by promoting higher productivity at favorable sites. One possible explanation of the positive species richness–pro-

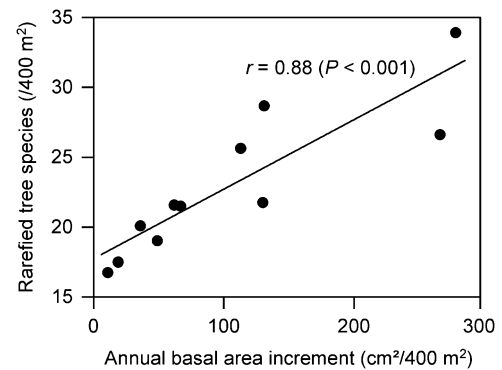


FIGURE 3. Relationship between tree diversity (rarefied species per $N = 43$ trees) and tree growth (mean annual increment of tree basal area of the years 2001–2002) in 11 plots of 400 m².

ductivity relation (Phillips *et al.* 1994) is that more productive sites, in our case the valleys and lower slopes, are also more dynamic, thereby enabling the coexistence of more tree species.

Forest aboveground productivity has been shown to vary strongly across tropical landscapes (Grubb 1977, Clark *et al.* 2001b, Kitayama & Aiba 2002, Malhi *et al.* 2004, Paoli & Curran 2007). Malhi *et al.* (2004) found strong evidence for a positive relationship between aboveground coarse wood (stems ≥ 10 cm dbh) productivity and soil fertility across a matrix of Neotropical forest plots and Paoli and Curran (2007) showed that spatial patterns in productivity of Indonesian lowland forests were positively related to soil nutrients, especially to phosphorus. Tree growth in tropical montane forests in fact seems to be limited by nutrient shortage in many regions as nutrient additions have been shown to enhance tree diameter growth and litter production in Hawaii (Vitousek *et al.* 1993, Vitousek & Farrington 1997), Jamaica (Tanner *et al.* 1990) and Venezuela (Tanner *et al.* 1992). The mean measured annual dbh growth rates of 0.45 (forest type IV)–1.9 mm (forest type I) are in the lower range of tropical montane forests (Tanner *et al.* 1992: Venezuela, 0.5–0.6 mm/yr; Vitousek *et al.* 1993: Hawaii, 0.5–4.6 mm/yr; Felfili 1995: Brazil, 0.6–7.2 mm/yr; Bellingham & Tanner 2000: Jamaica, 0.6–0.9 mm/yr; Homeier 2004: Costa Rica, 1.6–12.3 mm/yr), thereby supporting the assumption of growth limitation especially in the ridge forests of the study area.

PUTATIVE FACTORS CAUSING THE OBSERVED GRADIENTS IN DIVERSITY AND STRUCTURE.—The overall patterns in forest structure and plant species diversity with elevation are similar to those observed in other tropical montane forests and are probably mainly controlled by elevational changes of temperature and precipitation. The consequences of higher rainfall and lower temperatures at higher elevations are a promotion of nutrient leaching, an increasing frequency of waterlogging, a slowing-down of nutrient mineralization and reduced organic matter turnover (Cavelier 1996, Givnish 1999, Leuschner *et al.* 2007, Wilcke *et al.* 2008).

Our results also showed a general decrease in soil nutrient contents and an increase in soil acidity with elevation. Data on fine-

root and foliar nutrient concentrations (Graefe *et al.* 2008, Soethe *et al.* 2008) support these results, indicating that the high-elevation forests of the study area are most likely limited by nutrient shortage, probably by nitrogen.

The positive correlation of tree diversity with soil nutrient concentrations in our sample of stands suggests that nutrient availability is an important factor affecting tree species richness in the RSF, thereby supporting results from earlier studies (Gentry 1988, Ashton 1989, Aiba & Kitayama 1999, Givnish 1999), which reported positive relations between the diversity of tropical trees and soil fertility. Which nutrients are most important in this relationship seems to differ locally, Gentry (1988) reported K to be most closely correlated with Neotropical plant species richness. In Bornean forests, Ashton (1989) found a positive correlation between tree species richness and soil Mg for soil concentrations < ca 1200 ppm. A recent study from Borneo (Slik *et al.* 2009) reported a positive correlation of tree diversity to soil pH, just like in our study. However, the same study found overall higher tree diversity on less fertile soils, thereby supporting the results from Huston (1980) for Costa Rican forests.

The positive relationship between tree diversity and small-scale heterogeneity of pH, and soil Ca and Mg contents hints additionally at an important role for substrate heterogeneity in determining tree species diversity in the RSF. Pereira *et al.* (2007) demonstrated a similar positive effect of the substrate heterogeneity on tree diversity for montane forest stands in Brazil. They found a positive correlation of tree diversity to the heterogeneity of both soil pH and elevation above water-bodies in their comparison of 20 forest fragments. On the other hand, tree species do not only vary in their nutritional requirements, but each species tends to modify its rhizosphere in a particular way (Rothe & Binkley 2001). Therefore, higher species richness may amplify heterogeneity especially of the upper soil.

The observed pattern of high tree species richness at higher levels of soil heterogeneity fits into the 'habitat heterogeneity' hypothesis (Tilman & Pacala 1993, Rajaniemi 2003), which predicts that resource heterogeneity, and thereby the number of species able to coexist, will peak at sites of intermediate resource availability. Moreover, under this hypothesis plant growth at low productivity sites should be entirely limited by a soil resource (high root competition intensity), whereas at high productivity sites plant growth should be limited by light (high shoot competition intensity). Our results support this hypothesis: We found smaller-statured forest, less rich in tree species, in the upper parts of both the elevational and the topographical gradient, associated with low soil heterogeneity. Especially in forest type II, tree growth seems to be primarily nutrient-limited (Wilcke *et al.* 2008) in contrast to the more diverse and taller valley forests at the same elevation (forest type I), where we suppose a higher proportion of light competition.

However, in addition to the poorer and less heterogeneous soils on the ridges, other factors like the stronger exposition to climatic extremes and the higher susceptibility to landslides may also contribute to the observed patterns of species richness. Further studies on foliar nutrients and the experimental manipulation of nutrients could help to clarify the relationship of single nutrients to the variation in tree species richness in the RSF.

Plant species ranges are determined by historical (*e.g.*, altitudinal migrations due to long-term changes in climate) and ecological factors and their interactions. Locally high plant diversity can be the result of species accumulation due to high speciation rates or low extinction rates in the past. For the study area, the former factor seems to be more likely because of the high number of endemics.

In conclusion, the broad matrix of environmental conditions in the rugged mountainous study area generates a high number of different habitats, allowing the co-existence of lowland forest species together with montane species, and 'specialists' adapted to nutrient limitation, like *P. nutans* (Cyrillaceae), together with nutrient demanding species in valleys, within an area < 1000 ha. This floristic mixing is amplified by the geographical position of the reserve in the ecotone between the hyperhumid eastern Andean slope and the dry interandean forest zone of South Ecuador (E–W ecotone) on the one hand (Richter 2003), and the central and the northern Andes each with their characteristic species pools (N–S ecotone) on the other hand.

ACKNOWLEDGMENTS

We would like to thank Nature and Culture International for providing the research station and for logistic support. We are very grateful to the Ministerio del Ambiente for granting the research permits to our projects. Furthermore, we gratefully acknowledge financial support supplied by the Deutsche Forschungsgemeinschaft to several subprojects within the research units FOR 402 and FOR 816. F. Brearley and three anonymous referees provided helpful comments on earlier versions of the paper.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Distribution of the 190 tree species recorded in the 17 study plots in the Reserva San Francisco to the four forest types.*

TABLE S2. *Soil pH and total cation concentrations of the 15 lowermost tree plots.*

TABLE S3. *Pearson correlation coefficients and partial correlations for the relationships between tree diversity, tree basal area, tree basal area growth and soil parameters.*

FIGURE S1. Map of the study area in the Reserva San Francisco showing the locations of the 17 study plots and their affiliation to the four studied forest types and the eight transects.

FIGURE S2. Ecological climate-diagram of the Reserva San Francisco located in the southern Ecuadorian Andes.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

- AIBA, S., AND K. KITAYAMA. 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecol.* 140: 139–157.
- AIBA, S., M. TAKYU, AND K. KITAYAMA. 2005. Dynamics, productivity and species richness of tropical rain forests along elevational and edaphic gradients on Mount Kinabalu, Borneo. *Ecol. Res.* 20: 279–286.
- ASHTON, P. S. 1989. Species richness in tropical forests. In L. B. Holm-Nielsen, I. C. Nielsen, and H. Balslev (Eds.): *Tropical forests: botanical dynamics, speciation and diversity*. pp. 241–251. Academic Press INC, London, UK.
- BALSLEV, H., AND B. ØLLGAARD. 2002. Mapa de vegetación del sur de Ecuador. In M. Z. Aguirre, J. E. Madsen, E. Cotton, and H. Balslev (Eds.): *Botánica Austroecuatoriana. Estudios sobre los recursos vegetales en las provincias de El Oro, Loja y Zamora-Chinchipe*. pp. 51–64. Ediciones Abya-Yala, Quito, Ecuador.
- BALVANERA, P., AND E. AGUIRRE. 2006. Tree diversity, environmental heterogeneity, and productivity in a Mexican tropical dry forest. *Biotropica* 38: 479–491.
- BELLINGHAM, P. J., AND E. V. J. TANNER. 2000. The influence of topography on tree growth, mortality, and recruitment in a tropical montane forest. *Biotropica* 32: 378–384.
- BENDIX, J., R. ROLLENBECK, M. RICHTER, P. FABIAN, AND P. EMCK. 2008. Climate. In E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl (Eds.): *Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies*, Vol. 198, pp. 63–73. Springer Verlag, Berlin, Heidelberg, Germany.
- BRECKLE, S.-W., U. BRECKLE, J. HOMEIER, AND A. SCHEFFER. 2005. Mineral deficiencies in a pine plantation in Southern Ecuador. *Ecotropica* 11: 79–85.
- BREHM, G., L. M. PITKIN, N. HILT, AND K. FIEDLER. 2005. Montane Andean rain forests are a global diversity hotspot of geometrid moths. *J. Biogeogr.* 32: 1621–1627.
- BRUIJNZEEL, L. A., AND J. PROCTOR. 1995. Hydrology and biogeochemistry of tropical montane cloud forests. What do we really know? In L. S. Hamilton, J. O. Juvik, and F. N. Scatena (Eds.): *Tropical montane cloud forests. Ecological studies*, Vol. 110, pp. 38–78. Springer Verlag, New York, New York.
- BRUMMIT, N., AND E. NIC LUGHADHA. 2003. Biodiversity. Where's hot and where's not. *Conserv. Biol.* 17: 1442–1448.
- BURSLEM, D. F. R. P., AND T. C. WHITMORE. 1999. Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forests. *J. Veg. Sci.* 10: 767–776.
- CAVELIER, J. 1996. Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains. In S. S. Mulkey, R. L. Chazdon, and A. P. Smith (Eds.): *Tropical forest plant ecophysiology*. pp. 399–439. Chapman and Hall, New York, New York.
- CLARK, D. B., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, AND J. NI. 2001a. Measuring net primary production in forests: Concepts and field methods. *Ecol. Appl.* 11: 356–370.
- CLARK, D. B., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, J. NI, AND E. A. HOLLAND. 2001b. Net primary production in tropical forests: An evaluation and synthesis of existing field data. *Ecol. Appl.* 11: 371–384.
- COLWELL, R. K. 2008. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0. User's guide and application. Available at: <http://purl.oclc.org/estimates>
- DOUMENGE, C., D. GILMOUR, M. RUIZ PÉREZ, AND J. BLOCKHUS. 1995. Tropical montane cloud forests. Conservation status and management issues. In L. S. Hamilton, J. O. Juvik, and F. N. Scatena (Eds.): *Tropical montane cloud forests. Ecological Studies*, Vol. 110, pp. 24–37. Springer Verlag, New York, New York.
- FELFILL, J. M. 1995. Growth, recruitment and mortality in the Gama gallery forest in central Brazil over a six-year period (1985–1991). *J. Trop. Ecol.* 11: 67–83.
- FRAZER, G. W., C. D. CANHAM, AND K. P. LERTZMAN. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- GENTRY, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Garden* 75: 1–34.
- GENTRY, A. H. 1995. Patterns of diversity and floristic composition in neotropical montane forests. In S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn (Eds.): *Biodiversity and conservation of neotropical montane forests*. pp. 103–126. New York Botanical Garden, Bronx, New York.
- GILLMAN, G. N., AND S. D. WRIGHT. 2006. The influence of productivity on the species richness of plants: A critical assessment. *Ecology* 87: 1234–1243.
- GIVNISH, T. J. 1999. On the causes of gradients in tropical tree diversity. *J. Ecol.* 87: 193–210.
- GOTELLI, N. J., AND R. K. COLWELL. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4: 379–391.
- GRAEFE, S., D. HERTEL, AND C. LEUSCHNER. 2008. Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. *Biotropica* 40: 536–542.
- GRUBB, P. J. 1977. Control of forest growth and distribution on wet tropical mountains, with special reference to mineral nutrition. *Annu. Rev. Ecol. Syst.* 8: 83–107.
- HAMILTON, L. S. 1995. Mountain cloud forest conservation and research. A synopsis. *Mount. Res. Dev.* 15: 259–266.
- HENDERSON, A., S. P. CHURCHILL, AND J. L. LUTEYN. 1991. Neotropical plant diversity. *Nature* 351: 21–22.
- HOMEIER, J. 2004. Baumdiversität, Waldstruktur und Wachstumsdynamik zweier tropischer Bergregenwälder in Ecuador und Costa Rica, PhD Dissertation, University of Bielefeld, Bielefeld, Germany.
- HOMEIER, J. 2008. The influence of topography on forest structure and regeneration dynamics in an Ecuadorian montane forest. In S. R. Gradstein, J. Homeier, and D. Gansert (Eds.): *The tropical mountain forest – Patterns and processes in a biodiversity hotspot. Biodiversity and ecology series*, Vol. 2, pp. 97–107.
- HOMEIER, J., AND F. A. WERNER. 2007. Spermatophyta. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S-Ecuador). In S. Liede-Schumann and S.-W. Breckle (Eds.): *Provisional checklists of flora and fauna of the San Francisco valley and its surroundings (Estación Científica San Francisco)*, Southern Ecuador. *Ecotropical Monographs*, Vol. 4, pp. 15–58.
- HOMEIER, J., F. A. WERNER, S. R. GRADSTEIN, S.-W. BRECKLE, AND M. RICHTER. 2008. Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl (Eds.): *Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies*, Vol. 198, pp. 87–100. Springer-Verlag, Berlin, Heidelberg, Germany.
- HUSTON, M. 1980. Soil nutrients and tree species richness in Costa Rican forests. *J. Biogeogr.* 7: 147–157.
- JØRGENSEN, P. M., AND S. LEÓN-YÁNEZ (Eds.). 1999. Catalogue of the vascular plants of Ecuador. Missouri Botanical Garden Press, St. Louis, Missouri.
- KESSLER, M. 2002. The elevational gradient of Andean plant endemism: Varying influences of taxon-specific traits and topography at different taxonomic levels. *J. Biogeogr.* 29: 1159–1165.
- KITAYAMA, K., AND S.-I. AIBA. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *J. Ecol.* 90: 37–51.
- LEHNERT, M., M. KESSLER, L. I. SALAZAR, H. NAVARRETE, AND S. R. GRADSTEIN. 2007. Pteridophytes. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, Ecuador). In S. Liede-Schumann and S.-W. Breckle (Eds.): *Provisional checklists of flora and fauna of the San Francisco*

- valley and its surroundings (Estación Científica San Francisco), Southern Ecuador. *Ecotropical Monographs*, Vol. 4, pp. 59–68.
- LEUSCHNER, C., G. MOSER, C. BERTSCH, M. RÖDERSTEIN, AND D. HERTEL. 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic Appl. Ecol.* 8: 219–230.
- LIEBERMAN, D., M. LIEBERMAN, R. PERALTA, AND G. S. HARTSHORN. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol.* 84: 137–152.
- MADSEN, J. E., AND B. ØLLGAARD. 1994. Floristic composition, structure, and dynamics of an upper montane forest in Southern Ecuador. *Nord. J. Bot.* 14: 403–423.
- MALHI, Y., T. R. BAKER, O. L. PHILLIPS, S. ALMEIDA, E. ALVAREZ, L. ARROYO, J. CHAVE, C. I. CZIMCZIK, A. DI FIORE, N. HIGUCHI, T. J. KILLEEN, S. G. LAURANCE, W. F. LAURANCE, S. L. LEWIS, M. L. M. MERCADO, A. MONTEAGUDO, D. A. NEILL, V. P. NUNEZ, S. PATINO, N. C. A. PITMAN, C. A. QUESADA, R. SALOMAO, J. N. M. SILVA, L. A. TORRES, M. R. VASQUEZ, J. TERBORGH, B. VINCEIT, AND J. LLOYD. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biol.* 10: 563–591.
- PAOLI, G. D., AND L. M. CURRAN. 2007. Soil nutrients limit fine litter production and tree growth in mature lowland forest of Southwestern Borneo. *Ecosystems* 10: 503–518.
- PAROLLY, G., AND H. KÜRSCHNER. 2004. Ecosociological studies in Ecuadorian bryophyte communities. II. Syntaxonomy of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedwigia* 79: 377–424.
- PAROLLY, G., H. KÜRSCHNER, A. SCHÄFER-VERWIMP, AND S. R. GRADSTEIN. 2004. Cryptogams of the Reserva Biológica San Francisco (Province Zamora-Chinchipe, Southern Ecuador) III. Bryophytes - Additions and new species. *Cryptogamie, Bryol.* 25: 271–289.
- PAULSCH, A. 2002. Development and application of a classification system for undisturbed and disturbed tropical montane forests based on vegetation structure. PhD Dissertation, University of Bayreuth, Germany.
- PEREIRA, J. A. A., A. T. OLIVEIRA-FILHO, AND J. P. LEMOS-FILHO. 2007. Environmental heterogeneity and disturbance by humans control much of the tree species diversity of Atlantic montane forest fragments in SE Brazil. *Biodiv. Conserv.* 16: 1761–1784.
- PHILLIPS, O. L., P. HALL, A. H. GENTRY, S. A. SAWYER, AND R. VÁSQUEZ. 1994. Dynamics and species richness of tropical rain forests. *Proc. Nat. Acad. Sci.* 91: 2805–2809.
- RAJANIEMI, T. K. 2003. Explaining productivity-diversity relationships in plants. *Oikos* 101: 449–457.
- RICHTER, M. 2003. Using epiphytes and soil temperatures for eco-climatic interpretations in Southern Ecuador. *Erdkunde* 57: 161–181.
- RÖDERSTEIN, M., D. HERTEL, AND C. LEUSCHNER. 2005. Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *J. Trop. Ecol.* 21: 483–492.
- ROLLENBECK, R., P. FABIAN, AND J. BENDIX. 2005. Precipitation dynamics and chemical properties in tropical mountain forests of Ecuador. *Adv. Geosci.* 6: 1–4.
- ROTHER, A., AND D. BINKLEY. 2001. Nutritional interactions in mixed species forests: A synthesis. *Can. J. For. Res.* 31: 1855–1870.
- SCHRUMPF, M., G. GUGGENBERGER, C. VALAREZO, AND W. ZECH. 2001. Tropical montane rain forest soils – development and nutrient status along an altitudinal gradient in the South Ecuadorian Andes. *Die Erde* 132: 43–59.
- SLIK, J. W. F., N. RAES, S.-I. AIBA, F. Q. BREARLEY, C. H. CANNON, E. MEIJAARD, H. NAGAMASU, R. NILUS, G. PAOLI, A. D. POULSEN, D. SHEIL, E. SUZUKI, J. L. C. H. VAN VALKENBURG, C. O. WEBB, P. WILKIE, AND S. WULFFRAAT. 2009. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Divers. Distrib.* 15: 523–532.
- SOETHE, N., W. WILCKE, J. HOMEIER, J. LEHMANN, AND C. ENGELS. 2008. Plant growth along the altitudinal gradient – role of plant nutritional status, fine root activity and soil properties. In E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl (Eds.): *Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies*, Vol. 198, pp. 259–266. Springer Verlag, Berlin, Heidelberg, Germany.
- TAKYU, M., S. AIBA, AND K. KITAYAMA. 2002. Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. *Plant Ecol.* 159: 35–49.
- TANNER, E. V. J. 1977. Four montane rain forests of Jamaica: A quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *J. Ecol.* 65: 883–918.
- TANNER, E. V. J., V. KAPO, AND W. FRANCO. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* 73: 78–86.
- TANNER, E. V. J., V. KAPO, S. FRESKOS, J. R. HEALEY, AND A. M. THEOBALD. 1990. Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *J. Trop. Ecol.* 6: 231–238.
- TILMAN, D., AND S. PACALA. 1993. The maintenance of species richness in plant communities. In R. E. Ricklefs and D. Schluter (Eds.): *Species diversity in ecological communities: Historical and geographical perspectives*. pp. 13–25. University of Chicago Press, Chicago, Illinois.
- VALENCIA, R., C. CERÓN, W. PALACIOS, AND R. SIERRA. 1999. Las formaciones naturales de la sierra del Ecuador. In R. Sierra (Ed.): *Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental*. pp. 79–108. Proyecto INEFAN/GEF-BIRF y EcoCiencia, Quito, Ecuador.
- VALENCIA, R., AND P. M. JØRGENSEN. 1992. Composition and structure of a humid montane forest on the Pasochoa volcano, Ecuador. *Nord. J. Bot.* 12: 239–247.
- VALENCIA, R., N. PITMAN, S. LEÓ-YÁNEZ, AND P. M. JØRGENSEN (Eds.). 2000. *Libro rojo de las plantas endémicas del Ecuador 2000*. Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
- VITOUSEK, P. M., AND H. FARRINGTON. 1997. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry* 37: 63–75.
- VITOUSEK, P. M., L. R. WALKER, L. D. WHITEAKER, AND P. A. MATSON. 1993. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry* 23: 197–215.
- WAIDE, R. B., M. R. WILLIG, C. F. STEINER, G. MITTELBACH, L. GOUGH, S. I. DODSON, G. P. JUDAY, AND R. PARMENTER. 1999. The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* 30: 257–300.
- WEBB, E. L., B. J. STANFIELD, AND M. L. JENSEN. 1999. Effects of topography on rainforest tree community structure and diversity in American Samoa, and implications for frugivore and nectarivore populations. *J. Biogeogr.* 26: 887–897.
- WEBSTER, G. L., AND R. M. RHODE. 2007. Inventario de las plantas vasculares de un bosque montano nublado. Flora de la Reserva Maquipucuna, Ecuador. Ediciones Abya-Yala, Fundación Maquipucuna, Corporación SIMBIOE y Conservación Internacional Ecuador, Quito, Ecuador.
- WEIGEND, M. 2002. Observations on the biogeography of the Amotape-Huancabamba zone in northern Peru. *Bot. Rev.* 68: 38–54.
- WILCKE, W., Y. OELMANN, A. SCHMITT, C. VALAREZO, W. ZECH, AND J. HOMEIER. 2008. Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. *J. Plant Nutr. Soil Sci.* 171: 220–230.
- WILCKE, W., S. YASIN, U. ABRAMOWSKI, C. VALAREZO, AND W. ZECH. (2002). Nutrient storage and turnover in organic layers under tropical montane rain forest in Ecuador. *Eur. J. Soil Sci.* 53: 15–27.
- YOUNG, K. R., AND C. REYNEL. 1997. Huancabamba region, Peru and Ecuador. In S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton (Eds.): *Centers of plant diversity, a guide and strategy for their conservation*, Vol. 3. The Americas. pp. 465–469. IUCN Publications Unit, Cambridge, UK.