

Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador

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Summary

1 We mapped and identified all trees ≥ 10 mm in diameter in 25 ha of lowland wet forest in Amazonian Ecuador, and found 1104 morphospecies among 152 353 individuals. The largest number of species was mid-sized canopy trees with maximum height 10–20 m and understorey treelets with maximum height of 5–10 m.

2 Several species of understorey treelets in the genera *Matisia* and *Rinorea* dominated the forest numerically, while important canopy species were *Iriartea deltoidea* and *Eschweilera coriacea*.

3 We examined how species partition local topographic variation into niches, and how much this partitioning contributes to forest diversity. Evidence in favour of topographic niche-partitioning was found: similarity in species composition between ridge and valley quadrats was lower than similarity between two valley (or two ridge) quadrats, and 25% of the species had large abundance differences between valley and ridge-top. On the other hand, 25% of the species were generalists, with similar abundance on both valley and ridges, and half the species had only moderate abundance differences between valley and ridge.

4 Topographic niche-partitioning was not finely grained. There were no more than three distinct vegetation zones: valley, mid-slope, and upper-ridge, and the latter two differed only slightly in species composition.

5 Similarity in species composition declined with distance even within a topographic habitat, to about the same degree as it declined between habitats. This suggests patchiness not related to topographic variation, and possibly due to dispersal limitation.

6 We conclude that partitioning of topographic niches does make a contribution to the α -diversity of Amazonian trees, but only a minor one. It provides no explanation for the co-occurrence of hundreds of topographic generalists, nor for the hundreds of species with similar life-form appearing on a single ridge-top.

Key-words: Amazonian Ecuador, catena, habitat partitioning, topographic niche, tropical forest diversity, tropical trees, Yasuni National Park

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Introduction

Amazonian forests are species rich. There are usually 200–300 tree species co-occurring at a single site (Gentry

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1982, 1992; Phillips *et al.* 1994; Sierra *et al.* 1999; Ter Steege *et al.* 2000), and these estimates are based only on trees larger than 10 cm in stem diameter over a single hectare. The total number of species could be higher than this (Valencia *et al.* 1994). A variety of hypotheses have been proposed to account for high diversity (Hubbell *et al.* 2001; Wright 2002), and one explanation has to do with local variation in soil resources caused by topography. There is ample evidence that individual species partition

topographic ridge-valley gradients, or 'catenas' as they are sometimes called, and that tree species distributions are affected by underlying geological variation as well (Lieberman *et al.* 1985; Kahn 1987; Basnet 1992; Tuomisto & Ruokolainen 1994; Ruokolainen *et al.* 1997; Clark *et al.* 1999; Svenning 1999; Harms *et al.* 2001; Romero-Saltos *et al.* 2001; Phillips *et al.* 2003; Tuomisto *et al.* 2003ab). Few studies, however, quantify the degree to which species abundances are controlled by soil characteristics, and it thus remains possible that random forces as well play an important role in community composition (Hubbell 2001). For example, many neotropical tree species are generalists, occurring across many soil types (Hubbell & Foster 1986; Pitman *et al.* 1999, 2001), and for these species, factors controlling abundance remain unknown.

The importance of soil gradients to tree diversity is thus a quantitative proposition: some species respond strongly to soil type, while others are generalists, and just how much each species' abundance is limited by soil variation is the key. Here we attempt a quantitative evaluation of how individual tree species respond to a soil catena with a large-scale, complete forest inventory in Amazonian Ecuador. All trees, treelets and shrubs were located and identified over 25 ha of forest, spanning two ridge systems. From the first census of this plot, we have precise maps of every tree of every species, and with these we seek a quantitative description of diversity and how it varies from shrubs to tall trees, and of how much the tree community varies across the catena. Which growth-forms are most diverse? Do species partition the topography finely? Or are most species generalists? To evaluate the catena, we must also consider the degree to which tree species composition changes with topographic position as well as with geographical distance (Borcard *et al.* 1992; Legendre 1993; Ruokolainen *et al.* 1997; Condit *et al.* 2002; Phillips *et al.* 2003). We use the variation in abundance of individual species to evaluate how important the soil catena might be in maintaining diversity.

Materials and methods

STUDY SITE

Yasuni National Park and Biosphere Reserve and the adjacent Huaorani Indian territory cover 1.6 million ha of forest and form the largest protected area in Amazonian Ecuador. Within the park, there are extensive oil reserves that are ceded for prospecting and exploitation. Several oil roads enter the park from the north, and there are a few permanent oil camps. Huaorani Indians also inhabit small settlements in the park, and they hunt wild meat. North of the park and the Napo River are more extensive settlements of Quichua Indians and other Ecuadorians, people who clear forest for agriculture; some Quichua have been colonizing oil roads close to the park. There is also evidence of past Native American settlements within the park, but whether there were ever extensive clearings is unknown (Netherly 1997). Overall, human

influences are currently sparse, and most of Yasuni National Park is undisturbed wilderness covered by unbroken forest, home to the most sensitive megafauna of tropical South America, such as jaguar (*Panthera onca*), harpy eagle (*Harpia harpyja*), giant otter (*Pteronura brasiliensis*) and white-lipped peccary (*Tayassu pecari*).

The park is nearly level at about 200 m above sea level, but crossed by numerous ridges rising 25–40 m above the intervening forest streams. At wider intervals, large rivers flow east to meet the Napo and the Amazon. Except for swampy areas and floodplains of the larger rivers, the vegetation is a visually homogeneous tall, evergreen, terre firme forest, lacking large disturbances or clearings. The canopy is 10–25 m high punctuated with emergents to 40 and rarely 50 m tall as well as with small gaps created by fallen trees.

The 25-ha plot is located inside the park, at 0°41' S latitude, 76°24' W longitude, just south of the Tiputini River. It is within a kilometre of the Yasuni Research Station, which is operated by the Pontificia Universidad Católica of Ecuador (Fig. 1). Access to the research station and thus the plot is via an oil road. There are a few Huaorani settlements on this road, north of the station, and there has been some recent hunting near the research station and even inside the plot.

Soils of the Yasuni area are poorly known. Most are fluvial sediments originating in the Andes, and a geological map indicates that the area south of the Tiputini River is a single Miocene sediment (Malo & Arguello 1984). Korning *et al.* (1994) described the soils of one site in Yasuni National Park as udult, clayey, kaolinitic and aluminium-rich. Tuomisto *et al.* (2003a) found soils in and around the 25-ha plot to be rich in exchangeable bases compared with other Amazonian sites, with a texture dominated by silt. They concluded that two broad soil types cover Yasuni; our plot lies entirely within one.

At a finer scale, the 25-ha plot ranges from 216 to 248 m a.s.l., and includes two ridges and an intervening valley, plus a small section of another valley on the north boundary (Fig. 2). The valley occasionally floods, but only for brief periods. Nothing about soil variation within the plot is currently known.

CLIMATE

Rainfall and temperature are aseasonal at Yasuni. During 53 months of records at the research station, the longest rainless period was 3 weeks and the least rainy month was August. The mean annual rainfall was 2826 mm, and none of the 12 calendar months averaged < 100 mm, although three of the 53 months received < 100 mm. Mean monthly temperatures were a high of 34 °C and a low of 22 °C.

CENSUS

A 50-ha plot was fully surveyed in 1995 by a professional team. Between June 1995 and June 2000, all free-standing woody plants ≥ 10 mm in stem diameter were

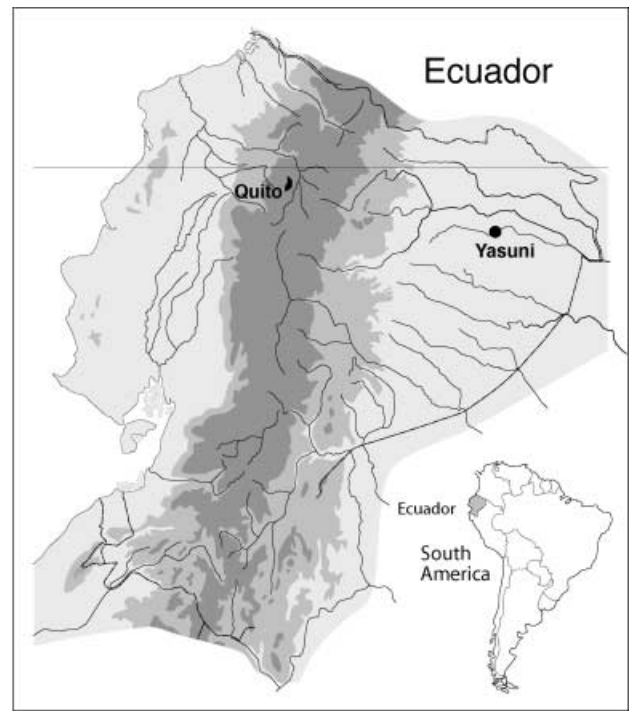
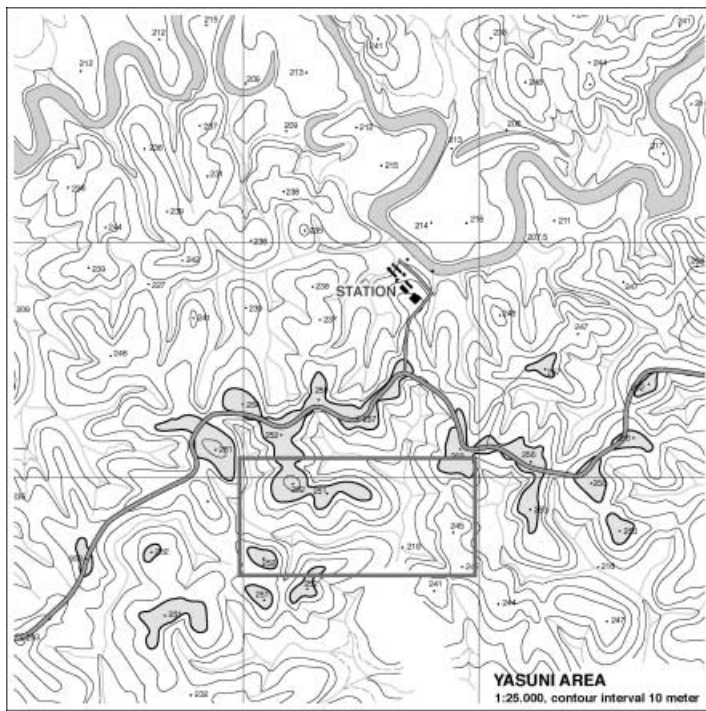


Fig. 1 Map of Ecuador and the plot location in Amazonia. The map on the left shows the entire 50-ha region that was surveyed, 1 km × 0.5 km. The 25-ha region that was censused is the left-hand (west) half of this rectangle.

tagged, mapped and identified to morphospecies in the western half of the 50 ha. The diameter of every individual was recorded at 1.3 m above the ground, unless the stem was swollen or buttressed; measurements were taken just below small swellings, or at least 0.5 m above large buttresses. Regardless of the height-of-measure, we refer to these as d.b.h. (diameter at breast height). These methods are described in detail in Condit (1998).

The taxonomy of the 25-ha plot was far more difficult than first anticipated, with many more species encountered than expected. In particular, there were many groups with very similar species that could only be sorted accurately in the laboratory. A complete set of collections from the plot is now deposited in the Herbarium of the Pontificia Universidad Católica of Ecuador, Quito (QCH is the herbarium code), and duplicates of most of the specimens are in the Field Museum in Chicago (F). We have compared specimens from the plot with collections at Ecuador's National Herbarium (QCNE), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the Smithsonian Natural History Museum (US) and the Field Museum, and 335 collections have been sent to specialists. Romoleroux *et al.* (1997) published a list of all the species and morphospecies and their corresponding vouchers; an updated version is now available on the web (<http://www.puce.edu.ec/herbario> and <http://ctfs.si.edu>).

There remain morphospecies for which we have seen only one or two individuals, so a number of identifications remain tentative. As the taxonomic work is ongoing and far from complete, we froze a data base of species assignments in June 2001, and here report on it:

152 353 individual trees tagged and identified in the 25-ha plot, with 145 406 sorted into morphospecies and 6947 that could not be assigned; 1104 total morphospecies, with 548 fully identified and 471 identified to genus. The number of morphospecies we have segregated has been climbing slowly since, and additional taxonomic work will probably expand the species count to 1130 or possibly 1150.

LIFE-FORM CATEGORIES

We grouped species into four life-forms, defined by the maximum height they usually attain: shrubs (< 5 m), treelets (≥ 5 and < 10 m), mid-canopy trees (≥ 10 and < 20 m), and tall-canopy trees (≥ 20 m). The typical maximum height of 273 Yasuni species was obtained from florulas and taxonomic treatments (Croat 1978; Prance 1979; Sleumer 1980; Pennington *et al.* 1981; Berg *et al.* 1990; Pennington 1990; Brako & Zarucchi 1993; Rohwer 1993; Vásquez 1997). Life-forms for the remaining species (all but one, which might be a liana) were assessed from our own observations in the plot. For common species, these categories are reasonably accurate, but for rare species, they should be considered provisional. We believe, however, that the general patterns we present will not be greatly affected by errors in life-form categorization.

HABITAT CATEGORIES

Habitats were defined with topographic information only, as this was the basis for prior hypotheses about tree distribution. The topography was based on elevation

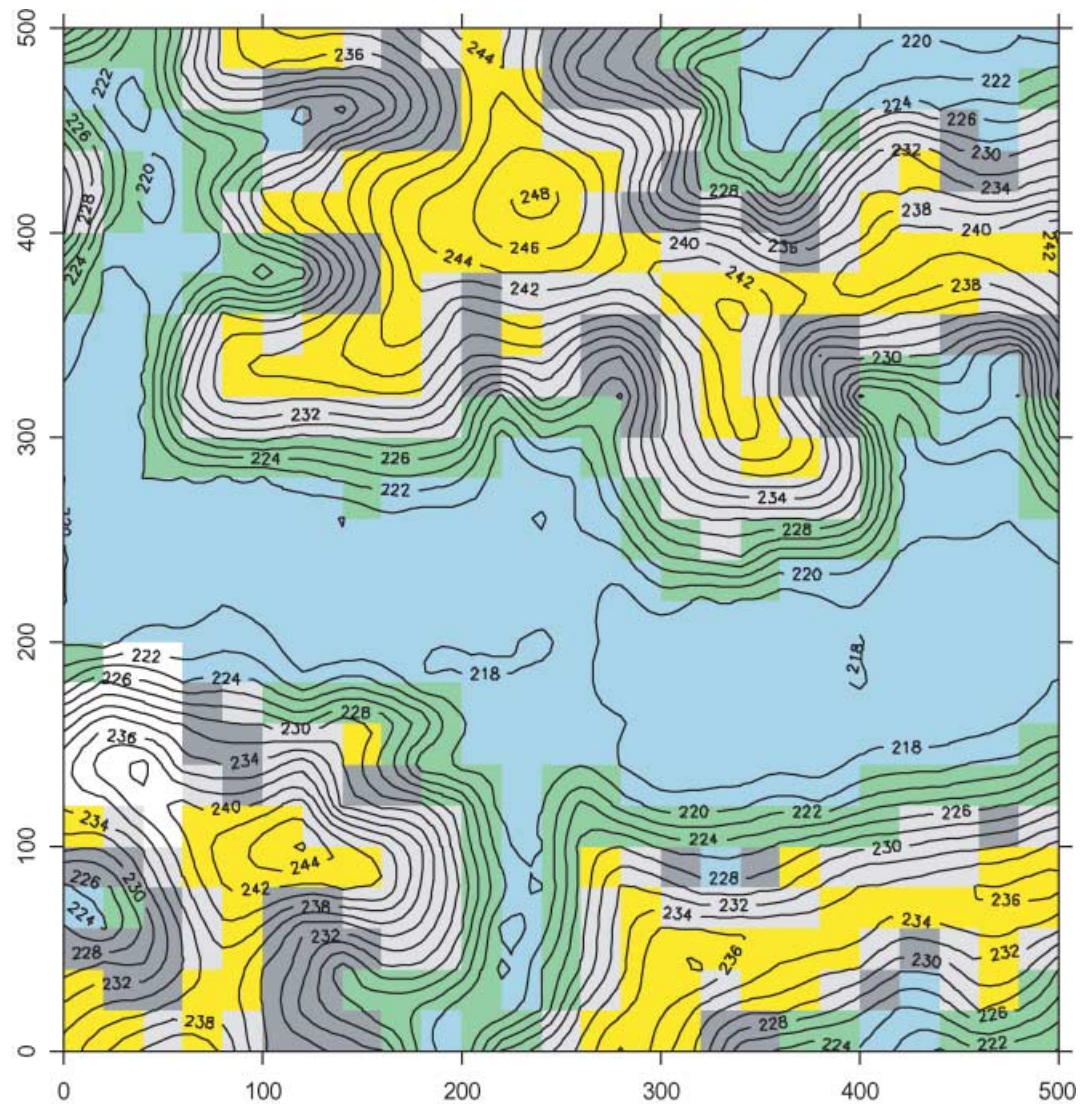


Fig. 2 Topographic map of the 25-ha plot, with 2-m contour intervals. Numbers marking each line are metres above sea level. Six habitats are indicated: valley (blue), low-slope (green), high-gully (dark grey), upper-slope (light grey), ridge-top (yellow), and secondary forest (white). Axes are marked in metres; north is up.

estimated at each point on a 20×20 m grid by the professional survey team (Fig. 2). Each 20×20 m quadrat was assigned three topographic attributes to assist in categorization: elevation, convexity and slope. Elevation of a quadrat was defined as the mean elevation at its four corners, and convexity as the elevation of a focal quadrat minus the mean elevation of the eight surrounding quadrats. For edge quadrats, convexity was defined as the elevation of the centre point (10 m from all corners) minus the mean of the four corners; the elevation of the centre point was estimated by kriging (using Spyglass software for Macintosh). Slope was calculated as in Harms *et al.* (2001), and is the single average angle from the horizontal of the entire quadrat.

Quadrats were divided into five topographic habitats, splitting the plot around median values of elevation and slope and around zero convexity:

- valley (slope $< 12.8^\circ$, elevation < 227.2 m);
- low-slope (slope $\geq 12.8^\circ$, elevation < 227.2 m);

- high-slope (slope $\geq 12.8^\circ$, elevation ≥ 227.2 m, convexity > 0);
- high-gully (slope $\geq 12.8^\circ$, elevation ≥ 227.2 m, convexity < 0);
- ridge-top (slope $< 12.8^\circ$, elevation ≥ 227.2 m, convexity > 0).

The distribution of habitats is shown in Fig. 2.

A sixth habitat category was defined as well, due to an accident of plot layout. After selecting the plot site, we made crude estimates of the positions of plot corners, then chose a location for the northern boundary. Only later, after precise surveying, did we discover that a small portion of the south-west part of the plot included a former helicopter landing, probably cleared in the past 20 years during oil exploration. The abundance of *Cecropia sciadophylla*, a typical roadside tree otherwise rare in the old forest, is the clearest indication of this disturbance. Twelve quadrats where *C. sciadophylla* was very dense were separated and classified as secondary forest (Fig. 2).

FOREST STRUCTURE AND DIVERSITY

We use tree density (individuals) and basal area to describe forest structure. Basal area was calculated by summing the cross-sectional area of each stem at breast-height, including secondary stems that split from a main stem below breast-height (Condit 1998). We define diversity either as the total number of species, or the mean number of species per unit squares (either 20×20 m quadrats or hectares). To correct for sample-size differences between habitat, the diversity index Fisher's α was used (Rosenzweig 1995; calculated from the routine given in Condit *et al.* 1998). Statistical confidence was calculated using the variance across 20×20 m quadrats within a single habitat, or across hectares in the entire plot, based on *t*-statistics. The quadrats in this and every analysis presented are the non-overlapping 20×20 m squares between grid-posts set down by the survey team, or non-overlapping square hectares composed of 25 of the 20×20 m quadrats (Condit *et al.* 1996).

IMPACT OF HABITAT VERSUS GEOGRAPHICAL DISTANCE ON SPECIES COMPOSITION

To separate the effect of habitat from the effect of geographical distance, we started with the similarity in species composition between pairs of 20×20 m quadrats. We used the Sørensen similarity index 'without cover' (Barbour *et al.* 1987), defined as $\frac{S_{12}}{0.5(S_1 + S_2)}$, where S_{12} is the number of species common to the two quadrats and S_i the total found in quadrat i . We also used the version of Sørensen that incorporates abundance data, known as the Sørensen index 'with cover' (Barbour *et al.* 1987) or the Steinhaus index. Similarity was calculated for all $\frac{625 \cdot 624}{2} = 195\,000$ quadrat-pairs in the plot. Next, the geographical distance between each pair of quadrats was defined as the distance from quadrat centre to quadrat centre. Then mean similarity for all pairs whose distance fell in a 20-m bin (≥ 0 and < 20 , ≥ 20 and < 40 , ≥ 40 and < 60 , etc.) was calculated; this mean was graphed as a function of distance. Similarity-distance graphs were drawn for quadrat-pairs within a given habitat and for pairs that included one quadrat in one habitat and the second quadrat in a different habitat. The similarity-distance graph within a habitat shows how geographical distance affects species composition; a habitat effect is indicated if the similarity-distance curve between habitats is lower than the curve within a habitat, at a given distance.

To assess similarity between pairs of habitats i and j while correcting for distance, a standardized mean similarity was defined as $\frac{100 \times \text{SOR}_{ij}}{0.5(\text{SOR}_{ii} + \text{SOR}_{jj})}$. Here, SOR_{ij} is the mean Sørensen similarity between quadrat pairs where one quadrat is in habitat i and the other in habitat j , but only considering cases where the distance between the two quadrats is 150–500 m. At this range, the impact of distance on similarity was slight. The

denominator, based on quadrat pairs from within a habitat (but never a quadrat with itself), does the standardizing: if quadrat pairs between habitats are just as similar as quadrat pairs within a habitat, the standardized index is 100%. Values less than 100% demonstrate habitat difference that is independent of geographical distance.

We used a jackknife resampling approach to generate confidence limits on mean similarity. A subset of 312 of the 625 quadrats was drawn at random, without replacement, and the similarity-distance analysis was repeated. We sampled without replacement because if replacement was allowed, quadrats would appear more than once in each sample, and a quadrat's similarity to itself provides no information. Sampling was repeated, and the standard deviation from 100 replicates was divided by $\sqrt{2}$ to generate an estimate of the standard error for all quadrats (dividing by $\sqrt{2}$ because the jackknife sample was half the original); the standard error was multiplied by 1.96 to estimate 95% confidence limits.

SPECIES ABUNDANCE DIFFERENCES ACROSS HABITATS

The most abundant species are often used to define forest composition, and we considered the top-10 ranking species in density or basal area as dominant. Abundance differences between two habitats for all species are illustrated with a graph of density in one habitat vs. density in a second habitat, with one point for each species. If all species have identical density in two habitats, the points fall on a one-to-one line. The r^2 from these regressions provide an index of habitat similarity. Density was calculated by adding one to the total number of individuals for a given species in a given habitat, then dividing by the habitat's area; this was then log-transformed. Confidence in density estimates and regressions was judged by bootstrapping from the 625 quadrats and calculating density of each species in each habitat every time; the standard deviation of 100 bootstrap estimates was multiplied by 1.96 as an estimate for 95% confidence limits.

Confidence limits on both abundance and similarity were thus based on bootstrapping quadrats, not individuals. This means we consider a single quadrat as a sampling unit, and individuals within that quadrat are not treated as independent. Spatial autocorrelation in tree distributions in many tropical forests is strongest at scales < 20 m (Condit *et al.* 2000), so by treating 20×20 m quadrats as sampling units, we remove at least part of the problem of spatial autocorrelation in assessing statistical confidence (Harms *et al.* 2001).

To judge differences in species' abundances between habitats, we tallied species in three categories: those with density differing by < 1.5 -fold, by ≥ 1.5 -fold and < 5 -fold, or by ≥ 5 -fold. The factor 1.5 corresponds roughly to cases where 95% confidence limits on density did not overlap; the cut-off of 5 was arbitrary, meant to indicate extreme density variation. These tallies were restricted

Table 1 Tree abundance and diversity in the Yasuni 25-ha plot, in three d.b.h. categories. The rows labelled 'full plot' give complete counts for all 25 ha pooled. Mean and standard deviations come from the 25 1-ha (100 × 100 m) samples. Fisher's α was calculated using the number of identified individuals, which is lower than the total number of individuals

	d.b.h. category	Basal area	Individuals	Species	Fisher's α
Full plot	≥ 10 mm	833.8	152353	1104	162.4
Mean ha ⁻¹		33.4	6094.1	654.9	190.5
SD ha ⁻¹		4.0	821.0	31.8	12.9
Full plot	≥ 100 mm	684.0	17546	821	180.8
Mean ha ⁻¹		27.4	701.8	251.4	147.6
SD ha ⁻¹		4.0	52.7	18.2	19.1
Full plot	≥ 300 mm	335.2	2036	398	150.8
Mean ha ⁻¹		13.4	81.4	55.0	88.5
SD ha ⁻¹		4.0	17.0	10.5	26.9

to species that had at least 10 individuals in all 25 ha; below this cut-off, confidence intervals on density were so broad that comparisons between habitats were essentially meaningless. Comparisons of abundance between habitats are uncorrected for distance, but the impact of distance on similarity was generally only pronounced within 50 m, and pooled habitat categories on which we based comparisons are considerably larger than this. In particular, upper-ridge and valley are more than 50 m apart, and this is the habitat comparison we emphasize.

Results

TOTAL DIVERSITY AND ABUNDANCE

There were 6094 individual trees and saplings ha⁻¹ in the 25-ha plot, and 702 ha⁻¹ were ≥ 100 mm d.b.h. (Table 1). Total basal area was 33.4 m² ha⁻¹, with 27.4 ha⁻¹ ≥ 100 mm d.b.h. Total diversity was 1104 species, including 11 previously undescribed species, of which four were Lauraceae and two Burseraceae. Assigning Latin names to the 556 unnamed morphospecies, especially the notoriously difficult Myrtaceae and Lauraceae, will require years more work, and we anticipate additional newly described species.

The most abundant species was *Matisia oblongifolia*, an understorey shrub of the Bombacaceae; with 4581 individuals, it represented 3% of the individuals ≥ 1 cm d.b.h. (Table 2). The most abundant tree ≥ 100 mm d.b.h. was the palm *Iriarteia deltoidea*, with 1808 individuals (10.3% of the total); *Iriarteia* also had the highest basal area (1.98 m² ha⁻¹, 5.9% of the total). *Eschweilera coriacea* (Lecythidaceae) was the most abundant tree ≥ 300 mm d.b.h. (Table 2). Among species over 1 m in diameter, *Cedrelinga cataeniformis* (Fabaceae) was the most numerous; with only 40 individuals it ranked sixth in basal area (Table 2); the largest *Cedrelinga* was 1540 mm d.b.h., but the largest individual in the plot was *Ficus gomeillera* (Moraceae) at 1542 mm d.b.h. The dominant families were Bombacaceae, with several abundant *Matisia* species, Violaceae, with several abundant *Rinorea* species, and the Fabaceae, with several abundant genera (Romoleroux *et al.* 1997).

At the other extreme, nearly 40% of the species, 433 of 1104, had fewer than 25 individuals in 25 ha, and 64 were represented by just a single individual. As these rare species are most likely to see taxonomic changes (just 14 of the 64 rarest have confirmed Latin names), we consider the count of singletons very preliminary.

IMPACT OF HABITAT VERSUS GEOGRAPHICAL DISTANCE ON SPECIES COMPOSITION

The Sørensen similarity index without cover between pairs of 20 × 20 m quadrats declined with the distance between quadrats, even if the two quadrats were within one topographic habitat (Fig. 3). The decline was abrupt for 50–100 m, then gradual or absent. All patterns indicated by the Sørensen index without abundance (Fig. 3) were also indicated by the version of the index that uses abundance information, and we present data only for the index without cover. The decline with distance within a habitat was also observed using a probability index of similarity (Condit *et al.* 2002).

Similarity also declined across habitat boundaries, even after correcting for distance: between-habitat pairs of quadrats were less similar than within-habitat pairs at the same distance. The ridge-valley contrast was the most pronounced (Fig. 3a): two ridge-top quadrats averaged 36% species in common, whereas ridge-valley quadrats averaged just 27% in common (Table 3). The standardized similarity between ridge-top and valley was 78%; statistically, this is very different from 100% (Table 3). Most other habitat pairs were distinguishable, that is, with standardized similarity statistically different from 100% (Table 3). The valley was most like the low-slope and least like the ridge-top. Secondary forest was most like the ridge and least like the valley.

Two habitat-pairs could not be distinguished (Table 3). The low-slope and high-gully habitats had cross-habitat similarity identical to within-habitat similarity at all distances (Fig. 3b), and the standardized similarity was close to 100% (Table 3; the value over 100% indicates that quadrats in different habitats were actually more similar than quadrats in the same habitat). Likewise, the

Table 2 Dominant species in the Yasuni 25-ha plot. A species is in the table if it ranked among the top-10 in at least one of four categories: total count (*n*) in three d.b.h. categories, or total basal area (BA). Thus, all 10 of the top ranks in all four categories are in the table; species are ordered by abundance in the first category. Ranks of half indicate ties in abundance; because of a tie for ranks 9–12 in abundance ≥ 300 mm, 12 species are included in that category. The highest rank is number 1; very low ranks are included because a species high-ranking in one category might be low ranking in another. The life-form is given in parentheses (T = tall tree, M = mid-sized tree, U = treelet, S = shrub). Three species have not been identified yet and are designated with temporary descriptive names

Species	Family	≥ 10 mm d.b.h.		≥ 100 mm d.b.h.		≥ 300 mm d.b.h.		≥ 10 mm d.b.h.	
		<i>n</i>	Rank	<i>n</i>	Rank	<i>n</i>	Rank	BA	Rank
<i>Matisia oblongifolia</i> (S)	Bombacaceae	4581	1	13	262.5	0	751	3.50	42
<i>Rinorea lindeniana</i> (S)	Violaceae	3239	2	7	397.5	2	218.5	3.08	49
<i>Matisia malacocalyx</i> (M)	Bombacaceae	2323	3	426	3	2	218.5	11.06	8
<i>Iriartea deltoidea</i> (M)	Arecaceae	2313	4	1808	1	0	751	49.38	1
<i>Brownia grandiceps</i> (M)	Fabaceae	2156	5	405	4	0	751	8.57	10
<i>Memora cladotricha</i> (U)	Bignoniaceae	2075	6	3	574	0	751	1.50	125
<i>Piper</i> 'obchic' (S)	Piperaceae	2074	7	2	649.5	0	751	0.55	310
<i>Marmaroxylon basijugum</i> (U)	Fabaceae	1913	8	11	293	0	751	3.16	47
<i>Zygia schultzeana</i> (U)	Fabaceae	1764	9	7	397.5	1	327	1.88	92
<i>Inga auristellae</i> (M)	Fabaceae	1701	10	127	17	1	327	4.09	35
<i>Pourouma bicolor</i> (T)	Cecropiaceae	1545	11	197	9	49	5	10.66	9
<i>Eschweilera coriacea</i> (T)	Lecythidaceae	1374	13	462	2	114	1	24.88	2
<i>Gustavia longifolia</i> (M)	Lecythidaceae	1032	21	224	6	0	751	4.90	20
<i>Siparuna decipiens</i> (U)	Monimiaceae	918	26	206	7	0	751	4.53	23
<i>Matisia bracteolosa</i> (M)	Bombacaceae	705	33.5	186	10	2	218.5	4.85	21
<i>Inga</i> '6cuadra' (T)	Fabaceae	680	38	68	43	22	10.5	5.03	19
<i>Protium sagotianum</i> (T)	Burseraceae	670	40	133	15.5	27	7.5	6.08	15
<i>Pseudolmedia laevis</i> (T)	Moraceae	586	52	157	11	22	10.5	6.13	14
<i>Apeiba aspera</i> (T)	Tiliaceae	477	71	142	12.5	68	4	13.24	7
<i>Cecropia sciadophylla</i> (T)	Cecropiaceae	457	76	363	5	40	6	15.34	5
<i>Otoba glycyarpa</i> (T)	Myristicaceae	376	85.5	203	8	87	2	17.05	4
<i>Alchornea triplinervia</i> (T)	Euphorbiaceae	299	112.5	114	21.5	85	3	21.86	3
<i>Inga</i> '3oscuro' (T)	Fabaceae	188	184	49	72	27	7.5	7.53	12
<i>Virola duckei</i> (T)	Myristicaceae	129	275	67	45.5	22	10.5	5.52	16
<i>Cedrela fissilis</i> (T)	Meliaceae	103	327	32	119.5	22	10.5	7.81	11
<i>Cedrelinga cateniformis</i> (T)	Fabaceae	40	567	26	144.5	18	20	14.59	6

Table 3 Mean Sørensen similarity (without cover) between 20×20 m quadrats, by habitat, with distance controlled. Each entry is the mean \pm 95% confidence range of similarity between all pairs of 20×20 m quadrats separated by 150–500 m, with one member of the pair in habitat *i* and the other in habitat *j*. Above the diagonal is the original Sørensen index between two different habitats ($i \neq j$). On the diagonal is the index for quadrat pairs within a habitat ($i = j$, excluding a quadrat's similarity to itself). Below the diagonal is standardized similarity: the Sørensen similarity expressed as a percentage of self-similarity (see Methods). The confidence limits were calculated from a jackknife analysis (see Methods); entries in bold indicate cases where confidence intervals of standardized similarity did not reach 100%. There is no self-similarity and thus no standardized similarity for secondary forest because no quadrat pairs were ≥ 150 m apart

Habitat <i>i</i>	Habitat <i>j</i>					
	Valley	Low-slope	High-gully	High-slope	Ridge-top	Secondary
Valley	0.320 \pm 0.005	0.301 \pm 0.005	0.298 \pm 0.004	0.282 \pm 0.005	0.269 \pm 0.006	0.272 \pm 0.017
Low-slope	95.18 \pm 1.13	0.313 \pm 0.007	0.318 \pm 0.005	0.320 \pm 0.006	0.314 \pm 0.007	0.302 \pm 0.016
High-gully	92.52 \pm 1.31	100.05 \pm 0.80	0.324 \pm 0.007	0.330 \pm 0.006	0.320 \pm 0.007	0.316 \pm 0.018
High-slope	83.17 \pm 1.52	95.56 \pm 1.34	96.84 \pm 1.15	0.358 \pm 0.007	0.360 \pm 0.005	0.338 \pm 0.019
Ridge-top	78.45 \pm 1.84	92.64 \pm 1.56	93.03 \pm 1.64	99.64 \pm 0.59	0.364 \pm 0.009	0.340 \pm 0.019
Secondary	–	–	–	–	–	–

high-slope and the ridge-top were indistinguishable, having standardized similarity close to 100%.

COMBINED HABITAT CATEGORIES

The four proposed ridge habitats can thus be collapsed into two: we combined ridge-top plus high-slope as the

upper-ridge habitat, and low-slope plus high-gully as the mid-slope habitat. This provides larger sample sizes per habitat and also reduces the number of comparisons and thus makes presentation clearer. Valley and secondary habitats were not changed. All further analyses are based on this four-habitat classification, not the original six.

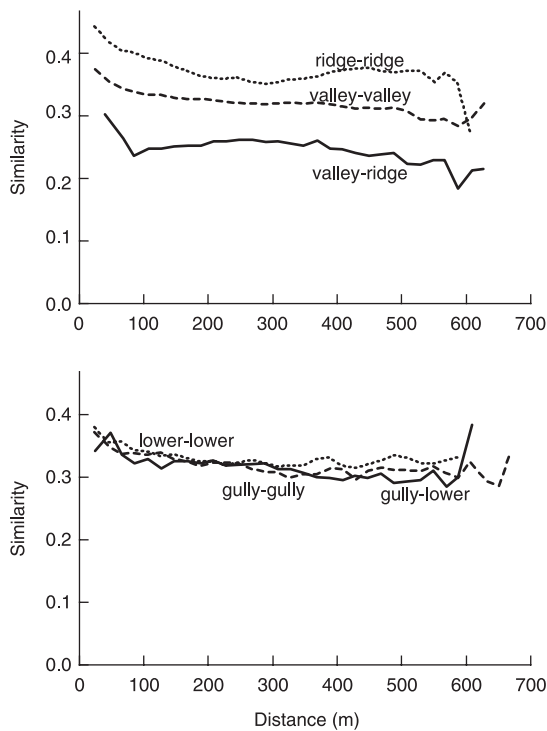


Fig. 3 Sørensen similarity index (without cover) between pairs of 20×20 m quadrats vs. distance between the quadrats. Each point is the average of Sørensen indices within a 20-m distance interval (e.g. 40–60 m), for a single habitat comparison. That is, the ridge-ridge line includes only quadrat pairs where both members of the pair were on the ridge-top habitat, while valley-ridge means one quadrat of the pair was in the valley, the second on the ridge-top. ‘Lower’ means the low-slope habitat, and ‘gully’ means the high-gully habitat.

HABITAT DIFFERENCES IN FOREST STRUCTURE

The valley had lower basal area and lower tree density than the slope and ridge habitats (Table 4). Both basal area and stem density were intermediate on the mid-slope, and highest on the upper-ridge. Higher stem density on the upper-ridge held for all life-forms, shrubs to tall trees, but there was a habitat difference in the way basal area was distributed among life-forms: the upper-ridge had more tall trees, whereas basal area in the valley was mostly in medium-sized trees. Thus, most of the increase in basal area from valley to ridge-top was in tall trees.

The secondary forest contrasted sharply in structure from all other habitats. Stem density was very high, especially in tall trees, and basal area was highly concentrated in tall tree species. This concentration, though, was due entirely to a single species, *Cecropia sciadophylla*, which made up half the basal area in this small patch (17.5 of $35 \text{ m}^2 \text{ ha}^{-1}$).

HABITAT DIFFERENCES IN DIVERSITY

All habitats had high species number, over 985 in all except the secondary forest (which was less than half a hectare). Thus, no habitat, apart from secondary forest, had less than 89% of the forest’s total diversity. Species richness was especially high in understory treelets and mid-sized trees (Table 4).

Many differences in diversity are due to differences in sample size, as suggested by the low species count in

Table 4 Density, basal area and diversity of different habitats within the Yasuni 25-ha plot. Mid-slope is the combined lower-slope plus high-gully habitats, and the upper-ridge is combined high-slope plus ridge-top. For abundance and basal area, the sum of four life-form categories is always less than the total for all life-forms, because the latter includes unidentified individuals. Species count or Fisher’s α over an entire region refers to all 20×20 m quadrats pooled; species count or Fisher’s α per quadrat is the mean (or standard deviation, SD) per 20×20 m quadrat

	Habitat Area (ha)	Valley 7.88	Mid-slope 7.68	Upper-ridge 8.96	Secondary 0.48	Total 25
Density (individuals ha^{-1})	All species	5150.0	5963.8	6878.1	9031.3	6093.9
	Tall trees	599.7	658.5	748.0	2629.2	709.9
	Mid-sized trees	1291.2	1417.6	1629.2	1937.5	1463.6
	Treelets	1751.1	2226.4	2687.3	2639.6	2249.7
	Shrubs	1275.1	1391.3	1507.0	1220.8	1392.9
Basal area (ha^{-1})	All species	27.06	35.10	37.30	35.00	33.35
	Tall trees	8.87	13.00	15.70	22.81	12.86
	Mid-sized trees	9.97	12.61	11.79	5.33	11.35
	Treelets	5.77	6.68	7.08	4.39	6.50
	Shrubs	1.34	1.28	1.15	0.92	1.24
Species number (entire region)	All life-forms	986	1001	990	546	1104
	Tall trees	142	143	139	82	160
	Mid-sized trees	295	307	305	156	333
	Treelets	363	370	372	215	403
	Shrubs	186	180	174	93	207
Species/quadrat (all life-forms)	Mean/ 20×20	118.6	129.7	138.7	147.3	129.8
	SD/ 20×20	19.3	22.0	17.4	20.7	21.3
Fisher’s α (all life-forms)	Entire region	182.2	180.7	167.5	165.2	161.1
	Mean/ 20×20	130.0	128.7	122.9	107.7	126.6
	SD/ 20×20	29.5	29.8	26.7	36.6	29.0

secondary forest. Based on Fisher's α , which at least partially corrects for sample-size differences, the most diverse habitat was the valley, with $\alpha = 182$ for the full species count or 130 per quadrat. The other habitats, however, were only slightly less diverse, and based on α , no habitat differences in diversity were significant (Table 4). For the life-form comparison, Fisher's α did not change the trend shown by total species: mid-sized trees and treelets had α about double that for tall trees and shrubs.

HABITAT DIFFERENCES IN DENSITY OF DOMINANT SPECIES

Dominant species of upper-ridge and mid-slope habitats were very similar (Table 5). The mid-slope shared eight of the 10 dominant species with the entire plot, and the upper-ridge nine of 10. None of the top-10 species forest-wide had a density below 50 trees ha^{-1} on either of the ridge habitats, and no dominant species varied by more than threefold in density between those two habitats (*Piper* 'obchic' differed the most). This consistency holds further down Table 5 as well.

Mid-slope and upper-ridge were not, however, always similar. *Matisia longiflora* had high density in the valley and mid-slope, but was much less abundant on the upper-ridge. *Rinorea viridifolia* showed a similar pattern.

In the valley, dominant species were quite different. Just three of the 10 dominant valley species were also dominant in the whole forest, and abundances varied by as much as 10-fold between valley and ridge habitats. *Neea* sp., for instance, ranked fifth in the valley with a density of 85.5 ha^{-1} , but 184th on the upper-ridge with a density of just 8 ha^{-1} . *Rinorea lindeniana* also varied more than 10-fold in density from valley to ridge, and *Marmaroxylon basijugum* by fivefold (Table 5). On the other hand, *Brownea grandiceps* and *Pourouma bicolor* had similar density on both valley and ridge (Table 5, Fig. 4). *Brownea* was the clearest generalist among dominant species, being very similar in density from valley to ridge and secondary forest (Table 5).

Ridge-valley abundance differences are evident in distribution maps. *Rinorea lindeniana*, *Matisia malacocalyx* and *Memora cladotricha* were strongly associated with the ridge, avoiding the valley except in small patches (Fig. 4). Conversely, *Matisia obliquifolia* and *M. longiflora* were associated with valley and high-gully. Other maps (Fig. 4) illustrate generalists, the patch of secondary forest (*Cecropia sciadophylla*), and a rare species (*Cedrelinga cataeniformis*).

Still, differences between valley and ridge were not great when considering the entire range of abundance in the plot. Of the 10 forest-wide dominants, none had a density below 18 ha^{-1} on any habitat. Although the eighth

Table 5 Dominant species in four different habitats of the Yasuni 25-ha plot, based on abundance ≥ 10 mm d.b.h. Mid-slope is the combined lower-slope plus high-gully habitats, and upper-ridge the combined high-slope plus ridge-top. All species ranking in the top-10 in abundance in at least one of the four habitats are listed; the final column gives the abundance rank over the entire plot, and the table is sorted by that rank. Family names not given in Table 2: *Acidoton* and *Aparisthmium* (Euphorbiaceae), *Cordia* (Boraginaceae), *Neea* (Nyctaginaceae), *Pentagonia* (Rubiaceae), *Pseudoptadenia* (Fabaceae)

Species	Valley		Mid-slope		Upper-ridge		Secondary forest		Full plot	
	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank
<i>Matisia oblongifolia</i> (S)	172.3	1	263.7	1	123.9	4	183.3	5	183.2	1
<i>Rinorea lindeniana</i> (S)	19.5	53	114.3	3	242.9	1	64.6	28	129.6	2
<i>Matisia malacocalyx</i> (M)	35.7	22	76.3	8	157.5	2	93.8	16	92.9	3
<i>Iriartea deltoidea</i> (M)	89.2	4	124.5	2	71.0	14	37.5	43	92.5	4
<i>Brownea grandiceps</i> (M)	91.0	3	84.6	6	84.2	10	72.9	21.5	86.2	5
<i>Memora cladotricha</i> (U)	25.3	36	101.2	4	117.4	5	97.9	15	83.0	6
<i>Piper</i> 'obchic' (S)	26.1	33	54.0	14	156.5	3	106.3	12	83.0	7
<i>Marmaroxylon basijugum</i> (U)	18.7	57.5	81.9	7	115.2	7	218.8	4	76.5	8
<i>Zygia schultzeana</i> (U)	24.7	39	62.1	9	116.1	6	108.3	11	70.6	9
<i>Inga auristellae</i> (M)	32.7	26	50.7	16	109.8	8	145.8	6.5	68.0	10
<i>Pourouma bicolor</i> (T)	44.8	10	56.0	12	71.8	13	247.9	3	61.8	11
<i>Rinorea viridifolia</i> (S)	104.1	2	59.2	10	17.6	78	0.0	825.5	57.3	12
<i>Rinorea apiculata</i> (U)	25.1	37.5	92.7	5	48.9	20	2.1	465.5	54.0	14
<i>Acidoton nicaraguensis</i> (S)	13.3	88	50.0	17	94.4	9	12.5	143	53.6	15
<i>Cordia nodosa</i> (S)	49.7	8	47.9	18	34.4	38	45.8	34.5	43.6	17
<i>Matisia longiflora</i> (U)	57.4	7	58.6	11	18.5	72	0.0	825.5	42.7	18
<i>Gustavia longifolia</i> (M)	64.0	6	36.5	25	25.8	55	35.4	46	41.3	19
<i>Neea</i> 'bajio' (S)	85.5	5	24.5	43	8.0	184.5	10.4	171.5	37.6	21
<i>Pentagonia</i> 'subauric' (S)	47.7	9	30.7	30	9.2	162	4.2	330.5	27.8	25
<i>Aparisthmium cordatum</i> (U)	7.6	165	19.8	59	28.1	49	145.8	6.5	21.4	36
<i>Apeiba aspera</i> (T)	19.4	54	17.2	70	13.7	96.5	143.8	8	19.1	55
<i>Cecropia sciadophylla</i> (T)	3.9	289	6.4	216	6.1	241.5	670.8	1	18.3	71
<i>Alchornea triplinervia</i> (T)	3.6	310	4.6	289	8.4	177	335.4	2	12.0	76
<i>Cecropia ficifolia</i> (M)	6.6	189	4.2	314	1.9	521.5	129.2	9	6.5	112.5
<i>Pseudoptadenia suaveolens</i> (T)	1.0	595.5	3.4	363	6.9	218	116.7	10	6.1	217

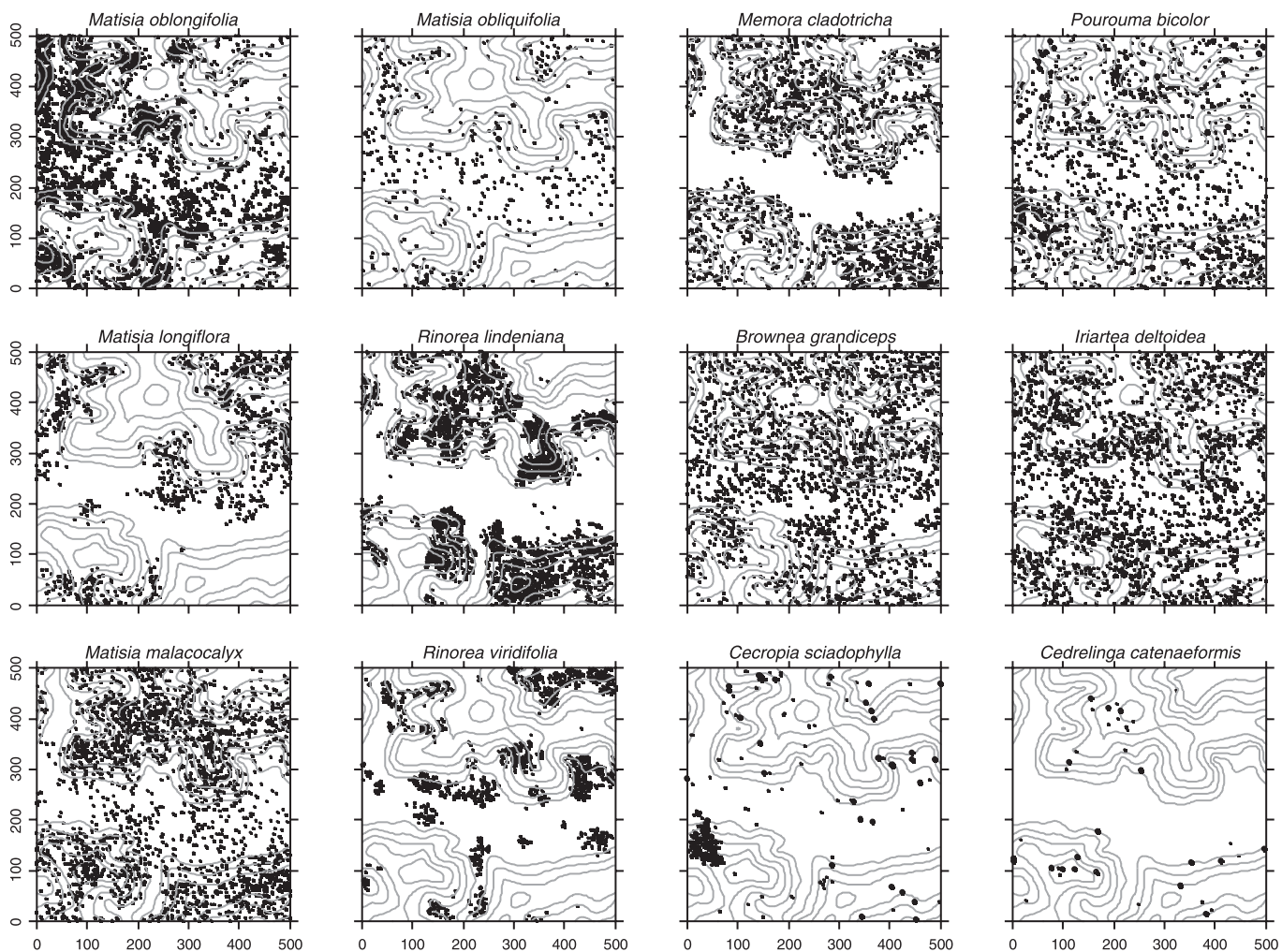


Fig. 4 Species distribution maps overlain on 5-m contours. Points come in three sizes: the largest indicate trees with d.b.h. ≥ 300 mm, medium indicate d.b.h. ≥ 100 and < 300 mm, and the smallest indicate d.b.h. ≥ 10 and < 100 mm.

ranking species in the whole plot, *Rinorea lindeniana*, fell to 53rd in rank in the valley, one should recall that the forest had 1104 species, so the 53rd rank is still well above the median.

The small bit of secondary forest was most distinct in terms of dominant species. The two most abundant species, *Cecropia sciadophylla* and *Alchornea triplinervia*, were 100 times denser than in any other habitat. To some extent, though, these widely differing densities should be attributed to the small size of the secondary forest patch.

HABITAT DIFFERENCES IN DENSITY OF ALL SPECIES

Graphical display allows abundance of all 1104 species to be compared across habitats (Fig. 5). Mid-slope and upper-ridge were very similar, with most species clustered near the one-to-one line and not significantly different in density (red points). More than 40% of species differed by < 1.5 -fold in density, and fewer than 8% had extreme (> 5 -fold) abundance differences (Table 6).

The upper-ridge and valley differed considerably more: 23% of species differed more than fivefold in density

(Table 6); and more of these were associated with the upper-ridge (126 species) than with the valley (72). Another 25% of the species differed less than 1.5-fold in density between upper-ridge and valley (Table 6). The remaining 52% of the species had a moderate density difference; of these, 262 species favoured the upper-ridge and 177 the valley.

Abundance differences between habitats were similar when only trees ≥ 100 mm d.b.h. were considered (Table 6). However, there was a markedly different pattern when only dominant species were considered: few of the abundant species differed much between habitats in density ≥ 100 mm d.b.h. (Table 7). Only one of the top-10 species in abundance, for instance, differed by fivefold between upper-ridge and valley (Table 7). The dominant species in the plot that showed a strong ridge-valley contrast in density were mostly shrubs or treelets, and do not appear in counts ≥ 100 mm d.b.h. (Table 4).

NORTH VERSUS SOUTH RIDGES

The north and south ridges were more similar to each other than to the intervening valley (Fig. 6). Moreover,

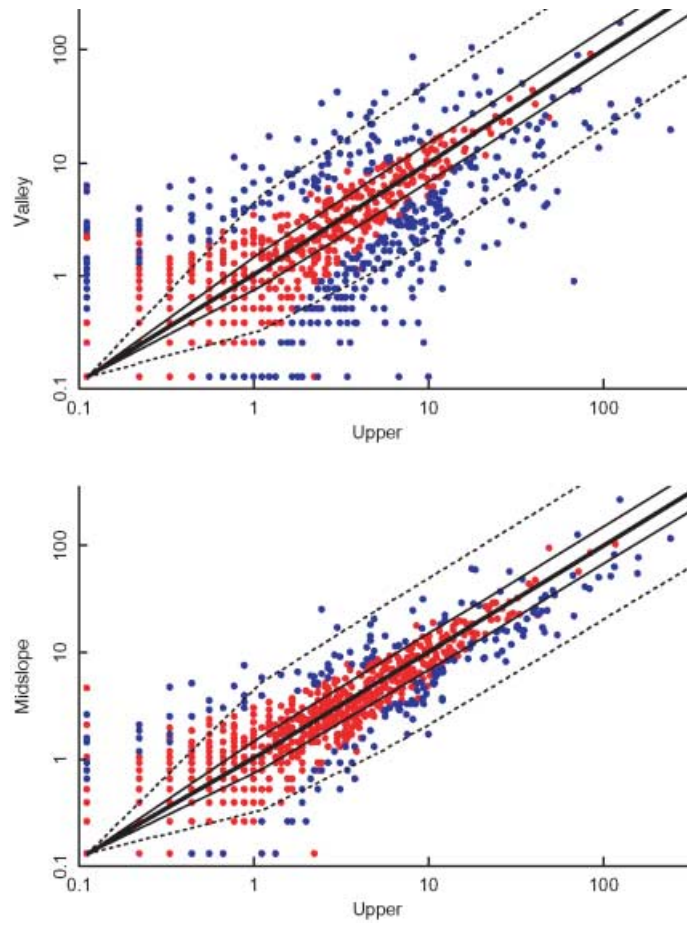


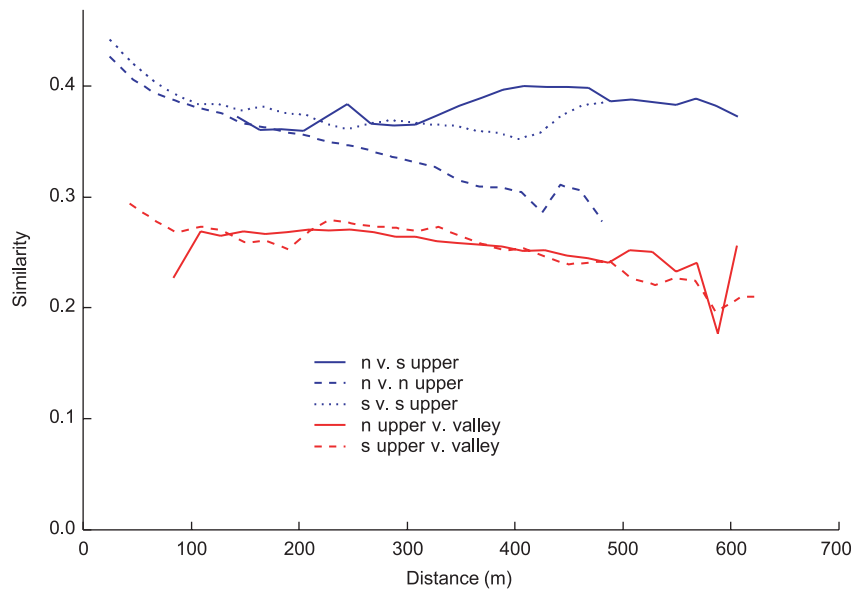
Fig. 5 Scatter diagrams of species density (abundance + 1 ha⁻¹; abundance based on individuals ≥ 10 mm d.b.h.) in one habitat vs. density in a second habitat. Axes are logarithmic. Top panel, density on upper-ridge (combined ridge-top plus upper-slope habitats) vs. the valley. Lower panel, density on mid-slope habitat (combined low-slope plus high-gully) vs. the valley. The lines on each figure are not regression lines, but mark density differences: the central line indicates equal density in each habitat; the outer (dashed) lines indicate 5-fold density differences; the intermediate (thin solid) lines indicate 1.5-fold density differences. On logarithmic axes, these lines would be straight: the bending is caused by adding 1 to abundance before calculating density. Blue points indicate significant differences in density, based on bootstrap confidence; red are non-significant.

Table 6 Comparison of abundance of individual species between habitats, in two different d.b.h. categories. The upper-ridge refers to the combination of ridge-top and high-slope; mid-slope to the combination of high-gully and low-slope; north refers to the section north of the valley, and likewise for south. The four columns under abundance give the percentage of species that had at least 10 individuals in the entire 25 ha (854 species for d.b.h. ≥ 10 mm; 317 for d.b.h. ≥ 100 mm). Similar in abundance means that density differed by < 1.5-fold between a pair of habitats; moderate indicates a density difference ≥ 1.5-fold but < 5-fold; and very different indicates ≥ 5-fold; those three columns add to 100%. Significant difference indicates species whose bootstrap confidence intervals (95%) in two habitats did not overlap. The final column is the *r*² from a regression of all species' log-densities across two habitats; in this case, all 1104 species were included; density was calculated from abundance + 1 before being log-transformed

Habitat comparison	d.b.h. (mm)	Percentage of species				<i>r</i> ²
		Similar in abundance	Moderately different in abundance	Very different in abundance	Significantly different in abundance	
Upper-ridge (north) vs. upper-ridge (south)	≥ 10	40.5	42.4	17.1	12.3	0.743
	≥ 100	32.2	49.8	18.0	0.0	0.650
Upper-ridge (total) vs. mid-slope (total)	≥ 10	43.6	49.2	7.3	18.1	0.791
	≥ 100	42.3	49.8	7.9	0.0	0.686
Valley vs. mid-slope (total)	≥ 10	39.5	50.8	9.7	19.8	0.747
	≥ 100	36.0	51.7	12.3	0.0	0.612
Upper-ridge (total) vs. valley	≥ 10	25.2	51.5	23.3	37.6	0.549
	≥ 100	25.2	51.7	23.0	0.0	0.513

Table 7 Dominant species in four different habitats of the Yasuni 25-ha plot, based on abundance ≥ 100 mm d.b.h. See Table 5 legend. Family names not given above: *Grias* (Lecythidaceae), *Astrocaryum* (Arecaceae), *Solanum* (Solanaceae), *Jacaranda* (Bignoniaceae), *Tapirira* (Anacardiaceae), *Miconia* (Melastomataceae)

Species	Valley		Mid-slope		Upper-ridge		Secondary forest		Full plot	
	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank	$n \text{ ha}^{-1}$	Rank
<i>Iriartea deltoidea</i> (M)	70.3	1	100.1	1	52.8	1	25.0	5	72.3	1
<i>Eschweilera coriacea</i> (T)	13.2	3	21.7	2	21.1	3	4.2	19.5	18.5	2
<i>Matisia malacocalyx</i> (M)	5.5	14.5	15.4	4	29.4	2	4.2	19.5	17.0	3
<i>Brownea grandiceps</i> (M)	14.1	2	20.3	3	15.1	4	6.3	13	16.2	4
<i>Cecropia sciadophylla</i> (T)	2.9	41.5	5.5	18	4.7	23	533.3	1	14.5	5
<i>Gustavia longifolia</i> (M)	11.0	4	8.6	7	7.8	8	2.1	45	9.0	6
<i>Siparuna decipiens</i> (U)	4.2	24	8.3	8.5	11.8	5	6.3	13	8.2	7
<i>Otoba glycyarpa</i> (T)	6.5	9	11.1	5	7.3	9	4.2	19.5	8.1	8
<i>Pourouma bicolor</i> (T)	8.6	7	8.3	8.5	6.7	14.5	10.4	8	7.9	9
<i>Matisia bracteolosa</i> (M)	10.3	5	6.4	12.5	6.0	18	4.2	19.5	7.4	10
<i>Pseudolmedia laevis</i> (T)	4.6	20	5.3	19.5	8.8	7	2.1	45	6.3	11
<i>Apeiba aspera</i> (T)	6.3	10	5.7	15.5	5.4	20.5	0.0	585.5	5.7	12.5
<i>Siparuna cuspidata</i> (U)	2.4	53	3.0	39.5	11.2	6	0.0	585.5	5.7	12.5
<i>Grias neubertii</i> (M)	2.2	61.5	7.4	10	6.9	11.5	0.0	585.5	5.4	14
<i>Matisia obliquifolia</i> (U)	9.8	6	7.0	11	0.2	429.5	0.0	585.5	5.3	15.5
<i>Rinorea apiculata</i> (U)	2.2	61.5	10.2	6	3.2	42	0.0	585.5	5.0	19
<i>Alchornea triplinervia</i> (T)	1.6	81.5	3.6	29	7.0	10	20.8	6	4.6	21.5
<i>Aparisthium cordatum</i> (U)	1.0	140	4.7	23	6.9	11.5	12.5	7	4.5	23
<i>Cecropia ficifolia</i> (M)	4.3	23	2.6	56	1.0	158	66.7	2	3.8	30.5
<i>Astrocaryum murumuru</i> (U)	6.7	8	2.6	56	1.1	139.5	0.0	585.5	3.3	35
<i>Solanum 'scabrosa'</i> (U)	0.6	207.5	0.9	163	1.7	93.5	27.1	4	1.6	91
<i>Jacaranda copaia</i> (T)	0.8	175	0.5	259	0.7	224	43.8	3	1.5	101
<i>Tapirira 'comun'</i> (T)	1.0	140	1.3	111	1.1	139.5	8.3	9.5	1.3	119.5
<i>Miconia poeppigii</i> (S)	0.0	854	0.0	873.5	0.4	296.5	8.3	9.5	0.3	361.5

**Fig. 6** Mean Sørensen similarity vs. distance, as in Figure 3. Here, 'n upper' means the upper-ridge (combined ridge-top plus high-slope habitats), but only north of the valley; 's upper' means the same combination south of the valley.

ridge habitats on opposite sides of the valley were much more similar to each other in terms of dominant species than they were to the valley. For instance, the north upper-ridge and south upper-ridge shared 8 of 10 dominant species, but each shared only two dominant species with the valley (Table 8).

Despite overall similarity, there were examples of species that differed substantially in abundance between north and south ridges. One case was *Brownea grandiceps*,

which was similar in abundance on the north ridge and the valley, but differed on the south ridge. Across all species, 17% differed by more than fivefold in abundance between north and south ridges.

Discussion

Topography predicts tree species composition of the Yasuni plot in Amazonia. Many species changed in

Table 8 A comparison of dominant species on the north and south ridges. The upper-ridge refers to the combination of ridge-top and high-slope. All species that had a rank in the top-10 on either north or south sections are included

Species	North upper-ridge		South upper-ridge		Valley	
	Abundance	Rank	Abundance	Rank	Abundance	Rank
<i>Rinorea lindeniana</i>	246.0	1	233.8	1	19.5	53
<i>Matisia malacocalyx</i>	166.1	2	140.3	4	35.7	22
<i>Matisia oblongifolia</i>	132.8	3	104.3	8	172.3	1
<i>Piper</i> 'obchic'	132.1	4	184.7	2	26.1	33
<i>Memora cladotricha</i>	122.8	5	104.8	7	25.3	36
<i>Acidoton nicaraguensis</i>	117.6	6	65.6	15	13.3	88
<i>Zygia schultzeana</i>	112.3	7	116.5	6	24.7	39
<i>Marmaroxylon basijugum</i>	104.0	8	125.0	5	18.7	57.5
<i>Brownea grandiceps</i>	100.2	9	59.1	17	91.0	3
<i>Inga auristellae</i>	87.0	10	143.2	3	32.7	26
<i>Guarea fistulosa</i>	74.3	13	91.8	9	20.1	51
<i>Pourouma bicolor</i>	60.0	16	86.4	10	44.8	10

abundance along the ridge-valley catena, and there are impressive pairs of species in the genera *Rinorea* and *Matisia* that partitioned the topographic niche very precisely (see Fig. 4). The fact that two separate ridges were conspicuously more similar to each other than to the intervening valley confirms that the abundance differences were caused by soil and not by unrelated patchiness in species distributions. The ridge-valley difference is not surprising: catenas are fundamental in plant ecology in general and in the tropics in particular (Gartlan *et al.* 1986; Weaver 1991; Tuomisto & Ruokolainen 1994; Tuomisto *et al.* 1995; Clark *et al.* 1999; Svenning 1999; Webb 2000). Corresponding with species turnover, forest structure also changed from valley to ridge; the valley had smaller-stature species, fewer individuals, less basal area, and a lower canopy.

We initially tested five topographic sections, but the evidence did not support this many. Instead, we found essentially three topographic habitats (two ridge, plus the valley). We quantified the abundance differences across these habitats, and classified species relative to the catena using the contrast between upper-ridge and valley. A quarter of the species differed less than 1.5-fold in density from ridge-top to valley, and thus appear to be generalists. At the opposite extreme, 15% of the species were much denser on the upper-ridge and 8% were much denser in the valley; it seems reasonable to conclude that most of these species are specialists to topographic differences. The remaining half of the species were more difficult to classify, as they favoured one habitat (> 1.5-fold density difference), but still occurred at both (< 5-fold density difference).

We conclude that at least a quarter of the species are generalists with respect to the catena, another quarter are specialists to ridge or valley, and a very small number are narrowly restricted to gullies or lower ridge. The bulk of the species fall in a grey area and cannot be classified on present data; they might be generalists whose density varies due to dispersal limitation or other factors, or they might be specialists with some individuals occurring in poor habitat as a sink population. More

observations or experiments would be required to establish topographic preferences of these species. This illustrates limitations of estimating habitat requirements from a single census, that is, of judging process from pattern. In defence of pattern analysis, though, there are so many sites and so many species in Amazonia that pattern analyses are all we are ever likely to have for most.

Among the dominant species, the clearest habitat specialists were small-stature treelets or shrubs. Duque *et al.* (2002) found the same pattern in the Colombian Amazon. Many other tree surveys in Amazonia are based on trees ≥ 100 mm d.b.h., and these would miss the small-statured specialists at Yasuni.

We also found a distance effect on tree species composition, even within areas of uniform topography, suggesting patchiness in distributions not related to topography. A number of species had large abundance differences between north and south ridge-tops, also suggesting patchiness not related to topography. Svenning (1999, 2001a) suggested that decay of similarity within palm assemblages is caused at least partly by limited seed dispersal. Condit *et al.* (2002) tested for the importance of dispersal limitation using a theory describing how dispersal should influence similarity; they found that dispersal might play some role, but that other factors are involved in the rapid decay of similarity at short distances. Interestingly, habitat effect on tree species composition at Yasuni, as measured by Sørensen similarity, was on a par with the distance effect: both led to a moderate reduction in similarity. To make predictions about forest composition at this scale, it is equally important to know what is nearby as it is to identify the topographic habitat.

It is possible that fine-grained variation in soil within topographic habitats provided further habitat partitioning, and we have begun detailed studies of soils within the plot that can test this hypothesis. Tuomisto *et al.* (2003a), however, found evidence for variation in soil chemistry and texture only at wider scales at Yasuni. They concluded that there are two main soil types, with corresponding variation in vegetation, in

the area of their study; the 25-ha plot fell within one. We thus doubt that we will find much partitioning due to soil variation within the 25 ha, beyond the topographic patterns described here. Maximum tree height (which we refer to as life-form) provides another deterministic avenue by which species can coexist (Kohyama 1993, 1996), but we found hundreds of species with similar life-form coexisting in close proximity. It appears unlikely that this is a major diversifying force, but more precise evaluation of growth, reproduction and height are needed (Kohyama *et al.* 2003). Variation in light within the forest provides colonization-based niches (Grubb 1986; Pacala & Rees 1998; Rees *et al.* 2001), and the small patch of secondary forest that fell inside the plot demonstrates that species composition in high light differs conspicuously from the rest of the forest. Svenning (2000) also demonstrated species associations with smaller gaps in undisturbed forest at Yasuni. We have not yet evaluated light-based niches across the entire community.

We found high tree species diversity for all life-forms in all habitats. More than 100 species occurred in individual 20 × 20 m quadrats, and 370 species of understorey treelets coexisted on a topographically uniform ridge-top *c.* 200 m across. We acknowledge that our categorization of species into growth forms is preliminary, and that some of those 370 species may exist only as sink populations; however, it seems clear that a very large number of very similar species occupy homogeneous topographic and soil conditions. We conclude that topography does not provide a niche axis that is finely partitioned by hundreds of species; rather, it provides three niches. Moreover, many of the thousand-plus species in the forest are generalists with respect to topography. Thus, although topography explains some of the tree α -diversity, its contribution is minor. Harms *et al.* (2001), Svenning (2001b) and Wright (2002) drew similar conclusions from tree distribution studies.

Abundance fluctuations of generalists and patchiness within topographic habitats could be due largely to chance or to unpredictable events. Given so many generalist species, a description of forest dynamics cannot ignore randomness (Van der Maarel & Sykes 1993; Dewdney 1997; Bell 2001; Hubbell 2001) nor dispersal limitation (Hurt & Pacala 1995; Silman 1996; Hubbell *et al.* 1999). On the other hand, there are species specialized to topographic habitats, and a full understanding of the forest cannot ignore patchiness in soil resources (Terborgh *et al.* 1996; Svenning 2001a; Condit *et al.* 2002).

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References

- Barbour, M.G., Burk, J.H. & Pitts, W.D. (1987) *Terrestrial Plant Ecology*. Benjamin/Cummings, Menlo Park, California.
- Basnet, K. (1992) Effect of topography on the pattern of trees in Tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. *Biotropica*, **24**, 31–42.
- Bell, G. (2001) Neutral macroecology. *Science*, **293**, 2413–2418.
- Berg, C.C., Akkermans, R.W. & van Heusden, E.C. (1990) Cecropiaceae: *Coussapoa* and *Pouroma*, with an introduction to the family. *Flora Neotropica*, **51**, 1–208.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- Brako, L. & Zarucchi, J.L. (1993) Catalog of the flowering plants and Gymnosperms of Peru. *Monographs in Systematic Botany from the Missouri Botanical Garden*, **45**, 1–1286.
- Clark, D.B., Palmer, M.W. & Clark, D.A. (1999) Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology*, **80**, 2662–2675.
- Condit, R. (1998) *Tropical Forest Census Plots. Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer-Verlag, Berlin.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Hua Seng, L., Itoh, A., LaFrankie, J.V., Losos, E., Manokaran, N., Sukumar, R. & Yamakura, T. (2000) Spatial patterns in the distribution of tropical tree species. *Science*, **288**, 1414–1418.
- Condit, R., Foster, R.B., Hubbell, S.P., Sukumar, R., Leigh, E.G., Manokaran, N. *et al.* (1998) Assessing forest diversity on small plots: calibration using species-individual curves from 50 ha plots. *Forest Biodiversity: Research, Monitoring, and Modeling* (eds F. Dallmeier & J.A. Comiskey), pp. 247–268. UNESCO, Paris.
- Condit, R., Hubbell, S.P., LaFrankie, J.V., Sukumar, R., Manokaran, N., Foster, R.B. *et al.* (1996) Species-area and species-individual relationships for tropical trees: a comparison of three 50 ha plots. *Journal of Ecology*, **84**, 549–562.
- Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B. *et al.* (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666–669.
- Croat, T.R. (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California.
- Dewdney, A.K. (1997) A dynamical model of abundances in natural communities. *Coenoses*, **12**, 67–76.
- Duque, A., Sánchez, M., Cavelier, J. & Duivenvoorden, J. (2002) Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. *Journal of Tropical Ecology*, **18**, 499–525.

- Gartlan, J.S., Newbery, D.M., Thomas, D.W. & Waterman, P.G. (1986) The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve Cameroon. *Vegetatio*, **65**, 131–148.
- Gentry, A.H. (1982) Patterns of neotropical plant species diversity. *Evolutionary Biology*, **15**, 1–84.
- Gentry, A.H. (1992) Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos*, **63**, 19–28.
- Grubb, P.J. (1986) Problems posed by sparse and patchily distributed species in species-rich plant communities. *Community Ecology* (eds J. Diamond & T.J. Case), pp. 207–225. Harper & Row, New York.
- Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a neotropical forest. *Journal of Ecology*, **89**, 947–959.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey.
- Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R.B. (2001) Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research*, **16**, 859–875.
- Hubbell, S.P. & Foster, R.B. (1986) Biology, chance, and history and the structure of tropical rain forest tree communities. *Community ecology* (eds J. Diamond & T.J. Case), pp. 314–329. Harper and Row, New York.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & Loo de Lao, S. (1999) Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.
- Hurttt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.
- Kahn, F. (1987) The distribution of palms as a function of local topography in Amazonian terra-firme forests. *Experientia*, **43**, 251–259.
- Kohyama, T. (1993) Size-structured tree populations in gap-dynamic forest – the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology*, **81**, 131–143.
- Kohyama, T. (1996) The role of architecture in enhancing plant species diversity. *Biodiversity: an Ecological Perspective* (eds T. Abe, S.A. Levin & M. Higashi), pp. 21–33. Springer-Verlag, Berlin.
- Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T. & Kubo, T. (2003) Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *Journal of Ecology*, **91**, 797–806.
- Korning, J., Thomsen, K., Dalsgaard, K. & Nornberg, P. (1994) Characters of three adults and their relevance to the composition and structure of virgin rain forest of amazonian Ecuador. *Geoderma*, **63**, 145–164.
- Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659–1673.
- Lieberman, M., Lieberman, D., Hartshorn, G.S. & Peralta, R. (1985) Small-scale altitudinal variation in lowland tropical forest vegetation. *Journal of Ecology*, **73**, 505–516.
- Malo, G. & Arguello, C. (1984) *Proyecto Oriente, Mapa de Compilación Geológica de la Provincia Del Napo*. Departamento de Geología, Instituto Ecuatoriano de Minería, Ministerio de Energía y Minas, Quito.
- Netherly, P. (1997) Loma y ribera: patrones de asentamiento prehistórico en la Amazonía ecuatoriana. *Fronteras de la Ciencia*, **1**, 33–54.
- Pacala, S.W. & Rees, M. (1998) Models suggesting field experiments to test two hypotheses explaining successional diversity. *American Naturalist*, **152**, 729–737.
- Pennington, T.D. (1990) Sapotaceae. *Flora Neotropica*, **52**, 1–770.
- Pennington, T.D., Terence, D. & Styles, B.T. (1981) Meliaceae. *Flora Neotropica*, **28**, 1–470.
- Phillips, O.L., Hall, P., Gentry, A.H., Check, S.S.A. & Vásquez, R. (1994) Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences*, **91**, 2805–2809.
- Phillips, O.L., Vargas, P.N., Monteagudo, A.L., Cruz, A.P., Zans, M.-E.C., Sánchez, W.G. et al. (2003) Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology*, **91**, 757–775.
- Pitman, N.C.A., Terborgh, J., Silman, M.R. & Núñez, V.P. (1999) Tree species distributions in an upper Amazonian forest. *Ecology*, **80**, 2651–2661.
- Pitman, N.C.A., Terborgh, J., Silman, M.R., Núñez, V.P., Neill, D.A., Palacios, W.A. et al. (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, **82**, 2101–2117.
- Prance, G.T. (1979) Chrysobalanaceae. *Flora of Ecuador*, **10**, 1–24.
- Rees, M., Condit, R., Crawley, M., Pacala, S. & Tilman, D. (2001) Long-term studies of vegetation dynamics. *Science*, **293**, 650–655.
- Rohwer, J.G. (1993) Lauraceae. *Nectandra. Flora Neotropica*, **60**, 1–332.
- Romero-Saltos, H., Valencia, R. & Macía, M.J. (2001) Patrones de diversidad, distribución y rareza de plantas leñosas en el Parque Nacional Yasuní y la Reserva Étnica Huaorani, Amazonía ecuatoriana. *Evaluación de Recursos Vegetales No Maderables En la Amazonía Noroccidental* (eds J.F. Duivenvoorden, H. Balslev, J. Cavelier, C. Grandez, H. Tuomisto & R. Valencia), pp. 131–162. IBED, Universiteit van Amsterdam, Amsterdam.
- Romoleroux, K., Foster, R., Valencia, R., Condit, R., Balslev, H. & Losos, E. (1997) Especies leñosas (dap \geq 1 cm) encontradas en dos hectáreas de un bosque de la Amazonía ecuatoriana. *Estudios Sobre Diversidad Y Ecología de Plantas* (eds R. Valencia & H. Balslev), pp. 189–215. Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Ruokolainen, K., Linna, A. & Tuomisto, H. (1997) Use of Melastomataceae and pteridophytes for revealing phytogeographical patterns in Amazonian rain forests. *Journal of Tropical Ecology*, **13**, 243–256.
- Sierra, R., Cerón, C., Palacios, W. & Valencia, R. (1999) El mapa de vegetación del Ecuador continental. *Propuesta Preliminar de un Sistema de Clasificación de Vegetación Para El Ecuador Continental* (ed. R. Sierra), pp. 120–139. Proyecto INEFAN/GEF-BIRF y EcoCiencia, Quito, Ecuador.
- Silman, M.R. (1996) *Regeneration from seed in a Neotropical rain forest*. PhD thesis, Duke University, Durham, North Carolina.
- Sleumer, H.O. (1980) Flacourtiaceae. *Flora Neotropica*, **22**, 1–499.
- Svenning, J.-C. (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology*, **87**, 55–65.
- Svenning, J.-C. (2000) Small canopy gaps influence plant distributions in the rain forest understorey. *Biotropica*, **32**, 252–261.
- Svenning, J.-C. (2001a) Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rain forest (Maquipucuna, Ecuador). *Journal of Tropical Ecology*, **17**, 97–113.
- Svenning, J.-C. (2001b) On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). *Botanical Review*, **67**, 1–53.
- Ter Steege, H., Sabatier, D., Castellanos, H., Van Andel, T., Duivenvoorden, J., De Oliveira, A.A. et al. (2000) An

- analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology*, **16**, 801–828.
- Terborgh, J., Foster, R.B. & Núñez, V.P. (1996) Tropical tree communities: a test of the nonequilibrium hypothesis. *Ecology*, **77**, 561–567.
- Tuomisto, H., Poulsen, A.D., Ruokolainen, K., Moran, R.C., Quintana, C., Celi, J. *et al.* (2003a) Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications*, **13**, 352–371.
- Tuomisto, H. & Ruokolainen, K. (1994) Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *Journal of Vegetation Science*, **5**, 25–34.
- Tuomisto, H., Ruokolainen, K., Aguilar, M. & Sarmiento, A. (2003b) Floristic patterns along a 43-km long transect in an Amazonian rainforest. *Journal of Ecology*, **91**, 743–756.
- Tuomisto, H., Ruokolainen, K., Kalliola, R., Linna, A., Danjoy, W. & Rodríguez, Z. (1995) Dissecting Amazonian biodiversity. *Science*, **269**, 63–66.
- Valencia, R., Balslev, H. & Paz y Miño, G. (1994) High tree alpha-diversity in Amazonian Ecuador. *Biodiversity and Conservation*, **3**, 21–28.
- Van der Maarel, E. & Sykes, M.T. (1993) Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science*, **4**, 179–188.
- Vásquez, R. (1997) *Flórula de Las Reservas Biológicas de Iquitos, Perú*. The Missouri Botanical Garden Press, St Louis.
- Weaver, P.L. (1991) Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. *Interciencia*, **16**, 142–151.
- Webb, C.O. (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, **88**, 464–478.
- Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.

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