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# **Influence of soils and topography on Amazonian tree diversity: a landscape-scale study**

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## **ABSTRACT**

We evaluated the influence of 14 soil and topographic features on species diversity of rainforest trees ( $\geq 10$  cm diameter-at-breast height) in central Amazonia, a region with nutrient-starved soils but some of the biologically richest tree communities on earth. Our study was based on a network of 63 1-ha plots scattered over an area of  $\sim 400$  km<sup>2</sup>. An ordination analysis identified three major edaphic gradients: (1) flatter areas had better soils (higher clay content, carbon, nitrogen, phosphorus, pH, and exchangeable bases, and lower aluminum saturation) than did slopes and gullies; (2) sandier soils had lower water storage (plant-available-water capacity), phosphorus, and nitrogen; and (3) soil pH varied among sites. Gradient 2 was the

strongest predictor of tree diversity (species richness and Fisher's alpha values), with diversity increasing with higher soil fertility and water availability. Gradient 2 also was the best predictor of the number of rare (singleton) species, which accounted for over half (56%) of all species in each plot on average. We conclude that, although our plots invariably supported diverse tree communities ( $\geq 225$  species  $\bullet$  ha<sup>-1</sup>), the most species-rich sites (up to 310 species  $\bullet$  ha<sup>-1</sup>) were least constrained by soil water and phosphorus availability. Intriguingly, the numbers of rare and common species were not significantly correlated in our plots, and they responded differently to major soil and topographic gradients. For unknown reasons rare species were significantly more frequent in plots with many large trees.

### **Keywords**

Amazon, density dependence, Fisher's alpha, permanent plots, rare species, species diversity, species richness, soil chemistry, soil texture, soil water, topography, tropical trees.

### **INTRODUCTION**

Central Amazonia sustains some of the biologically richest tree communities on earth (Oliveira & Mori, 1999; Leigh *et al.*, 2004) and faces escalating pressures from forest colonization, logging, and infrastructure expansion (Fearnside & Graça, 2006; Laurance & Luizão, 2007). Understanding the factors that influence Amazonian tree diversity at varying spatial scales is important for effective conservation planning and for assessing the potential threats from imminent forest conversion on species survival (Laurance *et al.*, 2001; Hubbell *et al.*, 2008).

Although a number of studies have evaluated tree-community composition and diversity at broad geographic scales in Amazonia (e.g. Prance, 1977; Gentry, 1990; Terborgh & Andresen, 1998; ter Steege *et al.*, 2000, 2006; Oliveira & Nelson, 2001; Pitman *et al.*, 2002),

fewer have focused on variation at smaller landscape scales (e.g. Phillips *et al.*, 2003; Tuomisto *et al.*, 2003; Valencia *et al.*, 2004). Working in our same central-Amazonian study area, Bohlman *et al.* (2008) recently assessed the influence of soils, topography, and geographic distance on tree-community composition and  $\beta$  diversity, but did not consider factors affecting tree diversity. Related work in this same study area has evaluated the influence of soils on tree (Laurance *et al.*, 1999) and liana (Laurance *et al.*, 2001) biomass.

Here we assess the effects of soils and topography on tree diversity and abundance in a central Amazonian landscape spanning about 400 km<sup>2</sup>. Our analysis is based on 63 1-ha plots in which nearly all trees ( $\geq 10$  cm diameter-at-breast-height) have been identified to species or morphospecies level, and in which detailed data on soil chemistry, texture, and topography were collected. Our study area, like much of the Amazon basin, overlays heavily weathered, nutrient-starved soils (Sombroek, 1984, 2000; Richter & Babbar, 1991). Our findings provide insights into how local edaphic features influence tree diversity in one of the world's most hyper-diverse forests.

## **METHODS**

### **Study area**

The study area is located 80 km N of Manaus, Brazil (2° 30' S, 60° W). Today, this area is a partially fragmented landscape spanning ~1,000 km<sup>2</sup> (Lovejoy *et al.*, 1986; Laurance *et al.*, 2002), but the soil and floristic data reported here were collected before or during initial forest clearing, from Jan. 1981-Jan. 1987. Rainforests in the study area are evergreen and terra-firme (not seasonally flooded), and range from 50-100 m elevation. The climate is tropically hot with total rainfall ranging from 1,900-3,500 mm. Monthly rainfall averages >100 mm even in the dry season (June-October) although conditions can become unusually dry during occasional

El Niño years. During a severe drought in 1997, for example, dry-season rainfall was less than a third of normal (Laurance, 2001).

The topography of the study area consists of undulating plateaus dissected by many stream and river gullies. Flat areas tend to have high clay (45-75%) and organic-carbon (0.8-3.3%) contents, which are associated with relatively high (although still very modest) concentrations of important nutrients such as nitrogen (N) and exchangeable bases (Laurance *et al.*, 1999; Luizão *et al.*, 2004; Castilho *et al.*, 2006). On sloping terrain, however, a ‘podzolization’ process occurs over time because lateral water movement results in the gradual destruction of clay-rich upper soil horizons. This ultimately leads to the creation of dendritic valley systems with increasing sand on lower slopes and valley bottoms (Chauvel *et al.*, 1987; Bravard & Righi, 1989).

The soils in the study area are mostly classified as xanthic ferralsols (using the FAO/UNESCO system; Beinroth, 1975). Ferralsols are widespread in the Amazon Basin, heavily weathered, and usually have a low base saturation. They often are well aggregated, porous, and friable, with variable clay contents. Clay particles in ferralsols can form very durable aggregations, giving the soil poor water-holding characteristics, even with high clay contents (Richter & Babbar, 1991). Xanthic ferralsols in the Manaus area are derived from Tertiary deposits and are typically acidic and very poor in nutrients such as phosphorus (P), calcium (Ca), and potassium (K) (Chauvel *et al.*, 1987; Fearnside & Leal-Filho, 2001).

### **Tree communities**

For this study we used data from 63 square, 1-ha plots scattered over an area of ~400 km<sup>2</sup>. Plots were arrayed using a predetermined system of study grids, irrespective of local topography or soils. Within each plot all trees ( $\geq 10$  cm diameter-at-breast-height [dbh]) were

mapped, marked with a numbered aluminum tag, and measured for dbh. A sterile or fertile voucher specimen was collected for nearly all trees and lodged in the BDFFP Herbarium, Manaus, Brazil (see Laurance *et al.*, 1998, 2006 for details). On average, 97.6% of the trees in each plot were identified to species (or genus and morphospecies) level (range: 94.1-99.7%). Non-identified trees were excluded from analyses.

We generated five parameters to assess tree diversity in each plot: (1) number of tree stems; (2) overall species richness; (3) Fisher's alpha, a diversity index that is quite insensitive to variation in sample size (Magurran, 1988); (4) the number of 'rare' (singleton) species, represented by just one individual per plot; and (5) the number of 'common' species, having two or more individuals per plot.

### **Edaphic features**

For each plot we derived 12 soil parameters from soil-surface samples (0-20 cm), using field and laboratory methods detailed in Fearnside & Leal-Filho (2001) and briefly summarized here. Although we did not sample deeper soil strata, surface soils tend to integrate the nutrient cycle in the forest and thus represent local site characteristics, and also are the zone where tree seedlings develop and obtain nutrients and water (Belknap *et al.*, 2003).

Each 1-ha plot was divided into 25 quadrats of 20 X 20 m each. Within each plot, 9-13 quadrats were selected for sampling, using an alternating pattern to provide good coverage of the plot. Within each quadrat, 15 surface samples were collected at haphazard locations using a soil auger, then bulked and subsampled. Composite samples for each quadrat were oven-dried, cleaned by removing stones and charcoal fragments, then passed through 20 mm and 2 mm sieves. In all cases, values for soil parameters were derived separately for each quadrat, and then combined to yield a mean value for each 1-ha plot.

Textural analyses were conducted to separate samples into percentage clay (particles <0.002 mm diameter), silt (0.002-0.05 mm), and sand (0.05-2 mm) components, using the pipette method. Clay and sand, the dominant soil components, were so strongly and negatively associated ( $F_{1,61}=1049.0$ ,  $R^2=94.5\%$ ,  $P<0.0001$ ; linear regression) that the clay-sand gradient could be represented by a single variable, percent sand content.

Plant-available-water capacity (PAWC), a measure of the amount of water the soil can hold in a form extractable by plant roots, was estimated as the difference between the field capacity (moisture content retained in soil under a suction of 0.33 atmospheres) and the wilting point (moisture content retained at 15 atmospheres), using a pressure membrane apparatus. Samples were dried, sieved, and re-wetted before determining available water capacity, making the results only an index of water available to plants in the field.

A pH meter was used to measure soil pH. Total N was determined by Kjeldahl digestion and total organic carbon (C) by dry combustion. Total P was determined by digestion in  $\text{HNO}_3$ ,  $\text{HClO}_4$ , and HF, and reaction with ammonium molybdate. Soil phosphate ( $\text{PO}_4^{3-}$ ) was measured in an autoanalyzer using the molybdenum blue method. Organic (Walkley-Black) carbon to total nitrogen (C:N) ratios were calculated to provide an index of N availability; if  $\text{C/N}>15$ , N tends to be limiting for plant growth.

Cation exchange capacity (CEC) was the sum of  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Al}^{3+}$ , and  $\text{H}^+$  ions. Total exchangeable bases (TEB) was the sum of  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and  $\text{Na}^+$ . Aluminum saturation was  $((\text{Al}^{3+} + \text{H}^+)/\text{CEC}) \times 100$ . Cation concentrations were derived at the Brazilian Center for Nuclear Energy and Agriculture (CENA), Piracicaba, São Paulo, using atomic emission spectroscopy to assess  $\text{K}^+$  and atomic absorption spectrophotometry to determine  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$ ,  $\text{Al}^{3+}$ , and  $\text{H}^+$ . Before analysis samples were digested in  $\text{HClO}_4$ ,  $\text{HNO}_3$ , and

H<sub>2</sub>SO<sub>4</sub>, with extracts buffered to pH 7.0.

For each plot, slope was the average of the maximum slope (determined with a clinometer) for each of the 25 quadrats. Plot aspect (percentage of quadrats with northern aspects, facing 1-45° or 315-360°) was determined with a compass. Because our study area is in the southern hemisphere, northern aspects receive greater direct insolation over the year than do other aspects.

### **Data analysis**

We used two strategies for data analysis. First, Pearson correlations were used to search for associations between the edaphic and tree-diversity variables. This involved a substantial number of tests, so a Bonferroni-corrected alpha value ( $P=0.011$ ) was employed to reduce the likelihood of spurious correlations, using an experiment-wise error rate of 0.15 to limit Type II statistical errors (Chandler, 1995).

Second, we used an ordination analysis to identify major gradients in the edaphic data, and then tested the effects of these gradients on tree diversity using multiple linear regressions. This approach ensures that multiple regressions do not suffer from collinearity effects because the ordination axes are statistically independent, and minimizes the chances of spurious associations because only a few axes are tested. Best-subsets regressions were used to select the predictors. Performance of the final regression models were assessed by comparing the standardized residuals to the fitted values and to each significant predictor (Crawley, 1993).

We used a robust ordination method, nonmetric multidimensional scaling (NMS), on the PC-ORD package (McCune & Mefford, 1995). All variables were weighted equally prior to analysis with the standardization by maximum method (Noy-Meir *et al.*, 1975).

Randomization tests ( $n=250$ ) were used to determine the number of ordination axes that



explained significantly more variation than expected by chance.

For the predictor variables, data transformations were used as needed to reduce outliers (i.e. percent slope, percent sand, and aspect data were arcsine-square-root transformed, whereas C:N ratios were log-transformed). None of the five tree-community variables departed significantly from normality ( $P > 0.10$  in all cases; Wilk-Shapiro tests), so none was transformed.

## RESULTS

### Tree diversity and abundance

Across the 63 plots, species richness ranged from 225 to 310 species  $\bullet$  ha<sup>-1</sup>, averaging ( $\pm$ SD) 261 $\pm$ 18 species  $\bullet$  ha<sup>-1</sup>. On average, 56% of the species in each plot (range 43-65%) were classified as ‘rare’ (singletons), with the remainder being ‘common’ (>1 stem per plot). Notably, the numbers of rare and common species in each plot (Fig. 1) were not significantly correlated ( $r = -0.205$ ,  $P = 0.11$ ; Pearson correlation).

Tree density ranged from 521 to 731 stems per plot, averaging 608 $\pm$ 52 stems ha<sup>-1</sup>. Plots with many large ( $\geq 60$  cm dbh) trees had fewer trees overall ( $F_{1,61} = 14.95$ ,  $R^2 = 19.7\%$ ,  $P = 0.0003$ ), evidently because each large tree displaced many smaller trees, leading to lower stem densities where large trees were abundant (Fig. 2). Plots with many stems tended to have somewhat higher species richness than those with fewer stems, although the relationship was not significant ( $F_{1,61} = 2.21$ ,  $R^2 = 3.7\%$ ,  $P = 0.13$ ).

As expected, Fisher’s alpha values were strongly and positively associated with species richness ( $F_{1,61} = 109.37$ ,  $R^2 = 64.2\%$ ,  $P < 0.0001$ ). Fisher’s alpha values were strongly associated with the number of rare species in each plot ( $F_{1,61} = 116.1$ ,  $R^2 = 65.6\%$ ,  $P < 0.0001$ ) but not with the number of common species ( $F_{1,61} = 0.67$ ,  $R^2 = 1.1\%$ ,  $P = 0.41$ ; all linear regressions).

### **Simple correlates of tree diversity**

Simple Pearson correlations revealed a number of significant associations between tree diversity and edaphic features, even with Bonferroni-corrected  $P$  values (Table 1). Stem densities increased in steeper areas (Fig. 3) with poorer soils (higher sand content and aluminum saturation; lower C, N, TEB, and pH), possibly because such sites supported few large, competitively dominant trees (for instance, the density of big trees was strongly and negatively associated with soil sand content;  $F_{1,61}=9.36$ ,  $R^2=13.3\%$ ,  $P=0.003$ ; linear regression). Species richness increased with soil water capacity (PAWC) and P. Although only weakly associated with slope, Fisher's alpha was positively correlated with many soil-fertility variables (lower sand content, aluminum saturation, and C:N ratio, and higher TEB, N, P, and pH) as well as higher PAWC.

Rare and common species had differing associations with edaphic features (Table 1). Rare-species richness increased with higher N (lower C:N ratios) and P availability, and also had positive but weaker associations ( $P<0.067$ ) with other fertility variables (low aluminum saturation; high pH and N) as well as PAWC. Common species were not significantly associated with any edaphic variable, but were weakly and positively correlated ( $P=0.04$ ) with PAWC. Notably, there were proportionally more rare species, and fewer common species, in plots with many large trees (Fig. 4).

### **Ordination of edaphic gradients**

Most of the 14 edaphic variables were significantly intercorrelated with at least one other edaphic variable. We therefore used NMS ordination to extract orthogonal axes from the dataset corresponding to major edaphic gradients in the study area. Three axes were selected, explaining over 92% of the total variation (Table 2). Axis 1, which captured 56% of the

variation, described a soil-fertility gradient between flatter (high C, N, and TEB) and steeper (high sand content and aluminum saturation) sites. Axis 2, capturing 25% of the variation, described a gradient between clay-rich sites with high PAWC and soil fertility (high P, N, C, CEC, and TEB; low aluminum saturation) and sandy sites with opposite attributes. Axis 3 explained 12% of the total variation and distinguished among sites with more-acidic soils with low P, and more-basic soils with higher P.

Best-subsets and multiple regressions revealed that all of the tree-community parameters were influenced by at least one major edaphic gradient (Table 3). Tree density was positively affected by axes 1 and 3, indicating that tree abundance was highest in steep, sandy, low-fertility sites. Species richness, Fisher's alpha, and rare-species richness all responded positively to axis 2 (Fig. 5), indicating that all increased in clay-rich sites with higher PAWC and soil fertility. Common-species richness was significantly affected by all three axes, suggesting that steepness, higher PAWC, and possibly soil infertility contributed to higher species numbers.

The moderate coefficients of determination for the regression models ( $R^2$  values ranging from 13-51%; Table 3) probably reflected the relatively large size of the 1-ha plots relatively to fine-scale edaphic and floristic variation in the study area. In no case did the regression models appear inadequate, based on comparisons of the standardized residuals to fitted values and to each significant predictor.

## **DISCUSSION**

### **Edaphic features and tree diversity**

Central Amazonia has very limited elevational, geological, and climatic variability, and for this reason species turnover across the landscape ( $\beta$  diversity) is modest compared to other, more-

heterogeneous Neotropical regions (Condit *et al.*, 2002; Bohlman *et al.*, 2008). However, local species richness ( $\alpha$  diversity) of central-Amazonian terra-firme forests is among the highest recorded anywhere in the world (Oliveira & Mori, 1999). All of the 63 plots in our study area supported very high tree diversity ( $\geq 225$  species  $\bullet$  ha<sup>-1</sup>), and some were hyper-diverse, with up to 310 species per hectare.

Local edaphic factors (soils and topography) accounted for at least some of this variability in species diversity, consistent with earlier analyses of tropical-forest diversity patterns (e.g. Ashton, 1964; Wright, 1992, 2002; Leigh *et al.*, 2004; ter Steege *et al.*, 2006). The most species-rich sites appeared least limited by key nutrients such as phosphorus, nitrogen, and exchangeable bases (Tables 1 and 3, Fig. 5). This suggests local species diversity in this region is partly constrained by soil nutrients—especially, we believe, by phosphorus availability, which tends to be critically limiting to plant growth in geologically old, heavily weathered soils (Sollins, 1998; Vitousek, 2004; Lambers *et al.*, 2008; Turner, 2008). The floras of the most nutrient-poor parts of the Amazon Basin are strongly biased toward specialized plant families (e.g. Lecythidaceae, Duckeondraceae, Rapateaceae, Rhabdodendraceae, Peridiscaceae) that tolerate extremely oligotrophic conditions (Gentry, 1990; ter Steege *et al.*, 2000, 2006). In sites where nutrient limitation is less extreme, we suggest, a wider cross-section of the regional flora can become established, and local tree diversity is enhanced.

The water-storage capacity of soils also appears to limit local tree diversity (Tables 1 and 3, Fig. 5; see also Wright, 1992, 2002). In terms of rainfall and dry-season intensity, the central Amazon is intermediate between drier, seasonal forests of eastern and southern Amazonia and hyper-wet forests in western Amazonia. Drier, seasonal forests support much

lower tree diversity than do wetter, aseasonal areas (ter Steege *et al.*, 2006), with trees in drier regions maintaining evergreen canopies only by virtue of having deep root systems (Nepstad *et al.*, 1999). We suggest that sites with poor soil-water-storage capacity will lack drought-sensitive species that characterize wetter parts of the Amazon. Central Amazonia is considered a biogeographic crossroads where distinct floras from drier and wetter parts of the basin intermix (Oliveira & Daly, 1999; Oliveira & Nelson, 2001).

Local edaphic features had additional effects on tree diversity and abundance. Site slope and its correlates had a strong influence on tree stem density, with steeper, sandier, more nutrient-poor sites supporting higher tree densities (Fig. 3). The most plausible explanation, we believe, is that such steep sites have few large ( $\geq 60$  cm dbh) canopy and emergent trees (see also Castilho *et al.*, 2006), which competitively reduce the abundance of smaller trees (Fig. 2). Thus, steeper sites with poorer soils support high tree densities but have low tree biomass (Laurance *et al.*, 1999), because most of the trees present are small. Large trees may be scarce on steep slopes because soil nutrients (nitrogen and exchangeable bases) are critically limiting or because large trees are prone to uprooting on steep or sandy sites.

It is intriguing that sites with many large trees also supported many locally rare species (Fig. 4). We speculate that such a relationship might arise indirectly—for instance, many rare species might be near the limits of their geographic ranges or environmental tolerances, and thereby favor sites with less nutrient-starved soils. Alternatively, large canopy and emergent trees, with their abundant fruit crops, might be magnets for mobile frugivores (e.g. Kwit *et al.*, 2004) that bring in propagules of new tree species from afar. It would be interesting to test the generality of this pattern elsewhere, to see if rare species tend to cluster around large trees in other tropical forests.

Although different tropical tree species often show distinctive associations with soil properties (e.g. John *et al.*, 2007; Turner, 2008), it is puzzling that common tree species in our study area exhibited different associations with edaphic variables than did rare species (Tables 1 and 3). Moreover, within each plot, the numbers of rare and common species were not significantly correlated (Fig. 1). These differences highlight the fact that much of the variation in overall tree diversity among plots was attributable to varying numbers of rare (singleton) species, which comprised 43-65% of the species richness of each plot. Such striking rarity is a conspicuous feature of central Amazonian forests, evidently because of their extreme nutrient limitation (Laurance, 2001) and because the vast regional species pool in Amazonia enhances local biodiversity via continual species colonization (Oliveira & Daly, 1999). Forests such as these are especially vulnerable to habitat fragmentation because their many rare species are prone to random demographic events (cf. Melbourne & Hastings, 2008) and to environmental changes in isolated fragments (Laurance *et al.*, 2002, 2006).

### **Tree diversity in central Amazonia**

In terms of local tree diversity, Amazonia and northern Borneo are the two most spectacularly biodiverse regions in the world (Leigh *et al.*, 2004). The western Amazon, where soil fertility is far higher than central Amazonia because of inputs of geologically young sediments from the Andes, was once considered the biologically richest part of the Amazon Basin (Gentry, 1988). It is now apparent, however, that the zone of peak tree diversity extends from the western Amazon well into central Amazonia (Oliveira & Mori, 1999; ter Steege *et al.*, 2006), with much of this hyper-diverse region overlaying strong weathered, nutrient-poor soils.

How can nutrient-starved forests sustain such high tree diversity? First, it is apparent that plant species in these forests have evolved highly efficient mechanisms to recycle and

scavenge scarce nutrients, especially phosphorus, and the forests thereby maintain relatively high productivity (Herrera *et al.*, 1978; Stark & Jordan, 1978). Second, poor soils might actually help to promote species coexistence. Where nutrients are strongly limiting, plants are likely to invest heavily in defensive compounds to reduce tissue loss from herbivory and pathogens (Waterman, 1983; Coley & Barone, 1996). Givnish (1999) has proposed that, by promoting strong plant defenses, low soil nutrients should reduce—rather than increase—tree diversity because the diversity-enhancing role of density-dependent herbivores and pathogens (Janzen, 1970; Connell, 1971; Wills *et al.*, 1997, 2006; Harms *et al.*, 2000) is lessened. The central Amazon, however, with its remarkably high tree diversity and infertile soils, stands in stark contrast to this hypothesis. We assert the opposite of Givnish (1999), that low soil nutrients may actually promote tree diversity (e.g. Huston, 1979; Aerts & Chapin, 2000) because strong plant defenses (especially diverse chemical defenses) should favor specialized over generalized herbivores and pathogens (Waterman, 1983; Coley & Barone, 1996). It is these specialized enemies that drive density-dependent mortality and thereby help to maintain local tree diversity. In this vein it is notable that, in dipterocarp forests in Borneo, tree diversity peaks on relatively infertile rather than richer soils (Ashton, 1989).

It has also been suggested that high rates of canopy turnover (corrected for rainfall variation) should promote local tree diversity, by promoting a mix of species with different life-history characteristics (Phillips *et al.*, 1994; Clinebell *et al.*, 1995). Again, the features of central Amazonian forests appear to be in opposition to this idea (S. G. Laurance *et al.*, submitted). Rates of tree growth and turnover are considerably lower in central Amazonia than in many other parts of the tropics, with long-term turnover averaging just 1.2% per year (Laurance, 2001). Yet these forests sustain some of the richest tree communities ever

observed.

In our view a combination of factors, such as the vast Amazonian species pool that enhances local diversity via immigration (cf. Terborgh, 1973; Ricklefs, 2004), possible mid-domain effects (Colwell & Lees, 2000), strong density-dependence and slow growth rates that collectively limit interspecific competition, and a mixing of drier- and wetter-adapted regional floras (Oliveira & Daly, 1999), collectively underlay the very high local diversity of central Amazonian forests. It is also apparent that soil and topographic features have pronounced effects on local tree diversity in this region, as well as far-reaching influences on community structure and tree abundance.

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**Table 1.** Pearson correlations between soil or topographic features and five parameters describing Amazonian tree diversity or abundance: tree density, species richness, Fisher's alpha index, and the numbers of 'rare' (plot-level singletons) and 'common' (non-singletons) species.

	Attribute	Stem	Species	Fisher's	Rare	Common
<u>Attribute<sup>a,b</sup></u>	<u>mean±SD</u>	<u>density</u>	<u>richness</u>	<u>alpha</u>	<u>species</u>	<u>species</u>
Slope <sup>c</sup> (°)	12.2±8.8	<b>0.604</b>	0.106	0.274	-0.022	0.221
Northern aspect <sup>c</sup> (%)	20.6±16.9	-0.065	-0.176	-0.137	-0.097	-0.154
Sand content <sup>c</sup> (%)	23.1±16.8	<b>0.483</b>	-0.138	<b>-0.424</b>	-0.157	-0.011
Plant-avail. Water capacity	7.4±1.9	0.074	<b>0.513</b>	<b>0.423</b>	0.345	0.321
Soil C (%)	1.61±0.25	<b>-0.378</b>	-0.095	0.155	-0.105	0.002
C:N ratio <sup>d</sup>	9.8±1.5	0.262	-0.391	<b>-0.479</b>	<b>-0.465</b>	0.074
Cation-exchange capacity	2.49±0.43	0.059	-0.008	-0.038	-0.053	0.070
Aluminum saturation	92.4±1.6	<b>0.488</b>	-0.244	<b>-0.493</b>	-0.337	0.119
Total exchangeable bases	0.196±0.055	<b>-0.406</b>	0.176	<b>0.394</b>	0.245	-0.090
Delta pH	-0.24±0.12	-0.042	0.218	0.229	0.066	0.264
Soil pH	4.16±0.25	<b>-0.516</b>	0.206	<b>0.441</b>	0.313	-0.145
Total N (%)	0.165±0.032	<b>-0.468</b>	0.257	<b>0.497</b>	0.290	-0.023
Total P (ppm)	121.3±40.6	-0.308	<b>0.425</b>	<b>0.527</b>	<b>0.429</b>	0.040
PO <sub>4</sub> <sup>3-</sup> (m.e./100 g dry soil)	0.030±0.006	-0.285	-0.092	0.106	0.011	-0.172

<sup>a</sup>Bold values are significant using a Bonferroni-corrected alpha value ( $P \leq 0.011$ ).

<sup>b</sup>Samples sizes: slope, aspect, sand-content, and soil C, n=63 plots; other attributes, n=41 plots.

<sup>c</sup>Data arcsine-squareroot transformed prior to correlations.

<sup>d</sup>Data log<sub>10</sub>-transformed prior to correlations.

**Table 2.** Pearson correlations between 14 Amazonian soil and topographic variables versus three ordination axes produced by nonmetric multidimensional scaling.

Variable	Axis 1 <sup>a</sup>	Axis 2 <sup>a</sup>	Axis 3 <sup>a</sup>
Slope	<b>0.718</b>	-0.220	-0.069
North-aspect	-0.269	-0.381	-0.358
Sand content	<b>0.856</b>	<b>-0.765</b>	-0.168
Plant-available-water capacity	-0.056	<b>0.739</b>	-0.074
Soil carbon	<b>-0.769</b>	<b>0.524</b>	0.290
C:N ratio	0.106	-0.404	0.250
Cation-exchange capacity	-0.358	<b>0.542</b>	<b>0.495</b>
Aluminum saturation	<b>0.783</b>	<b>-0.471</b>	-0.066
Total exchangeable bases	<b>-0.852</b>	<b>0.560</b>	0.299
Delta pH	-0.020	0.163	0.194
Soil pH	-0.073	0.157	<b>-0.790</b>
Total N	<b>-0.810</b>	<b>0.790</b>	0.118
Total P	-0.248	<b>0.687</b>	<b>-0.570</b>
Phosphate (PO <sub>4</sub> <sup>3-</sup> )	0.104	-0.130	-0.267
Variation explained (%) <sup>b</sup>	55.9	25.0	11.5

<sup>a</sup>Bold values are significant using a Bonferroni-corrected critical value ( $P \leq 0.0036$ ).

<sup>b</sup> $R^2$  values for correlations between ordination distances and distances in the original n-dimensional space.

**Table 3.** Significant predictors of tree stem density and diversity in central Amazonia, using best-subsets and multiple regressions.

Response variable	Predictors	Slope	---Multiple-regression statistics---			
			<i>F</i>	<i>R</i> <sup>2</sup> (%)	d.f.	<i>P</i>
Stem density	Axis 1	+	19.67	50.7	2, 38	<0.0001
	Axis 3	+				
Species richness	Axis 2	+	11.57	22.9	1, 39	0.0016
Fisher's alpha	Axis 2	+	12.98	35.0	1, 39	0.0009
Rare species	Axis 2	+	5.97	13.3	1, 38	0.019
Common species	Axis 1	+	4.10	24.9	3, 37	0.013
	Axis 2	+				
	Axis 3	+				

## FIGURE CAPTIONS

**Figure 1.** Numbers of ‘rare’ (1 stem per plot) versus ‘common’ (>1 stem per plot) tree species within 63 1-ha plots in central Amazonia.

**Figure 2.** Relationship between the densities of large ( $\geq 60$  cm dbh) and smaller (10-59.9 cm dbh) trees in central Amazonian forest plots.

**Figure 3.** Relationship between mean slope and the density of trees in Amazonian forest plots.

**Figure 4.** Relationship between the density of large ( $\geq 60$  cm dbh) trees and percentage of rare (singleton) species in Amazonian forest plots.

**Figure 5.** Relationships between a major gradient in soil fertility and water-storage capacity versus species richness (above) and Fisher’s alpha values (below) for Amazonian tree communities (‘water’ is plant-available-water capacity; ‘TEB’ is total exchangeable bases).

Fig. 1

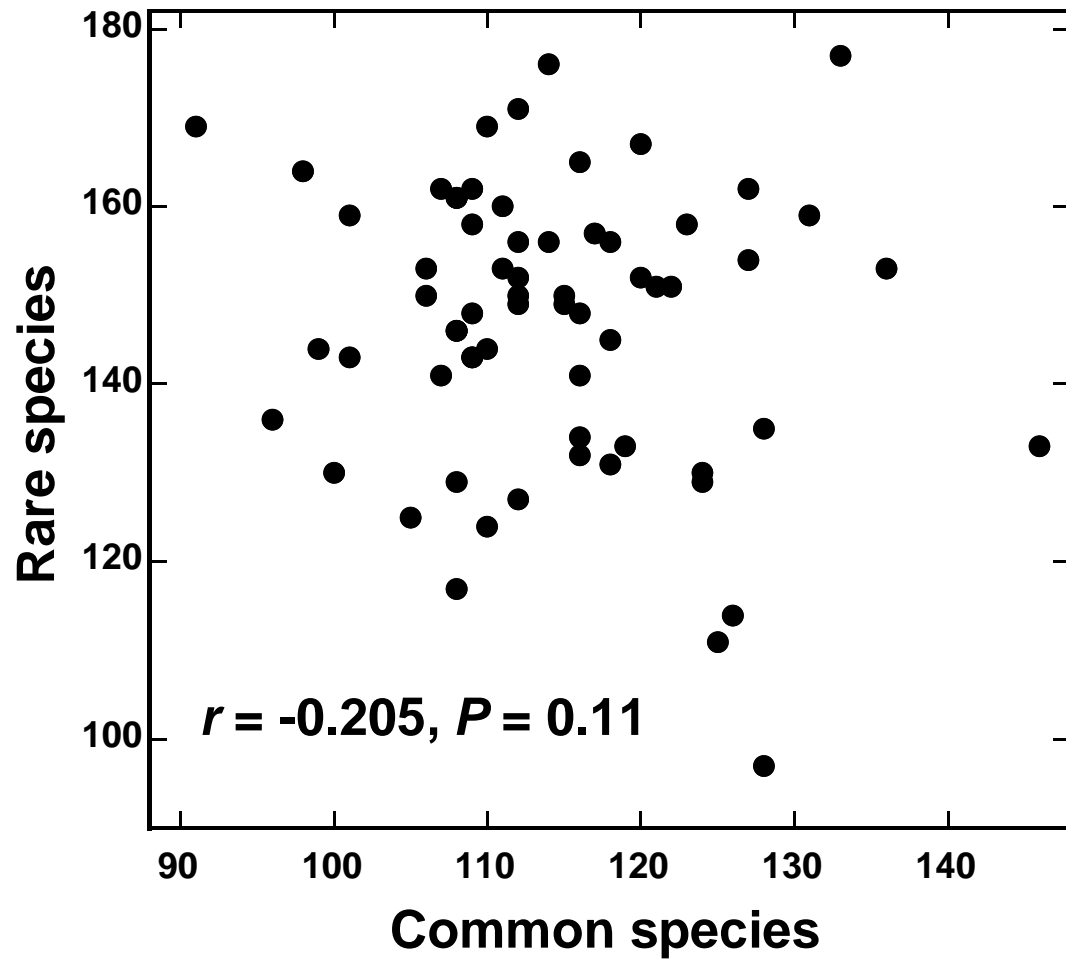


Fig. 2

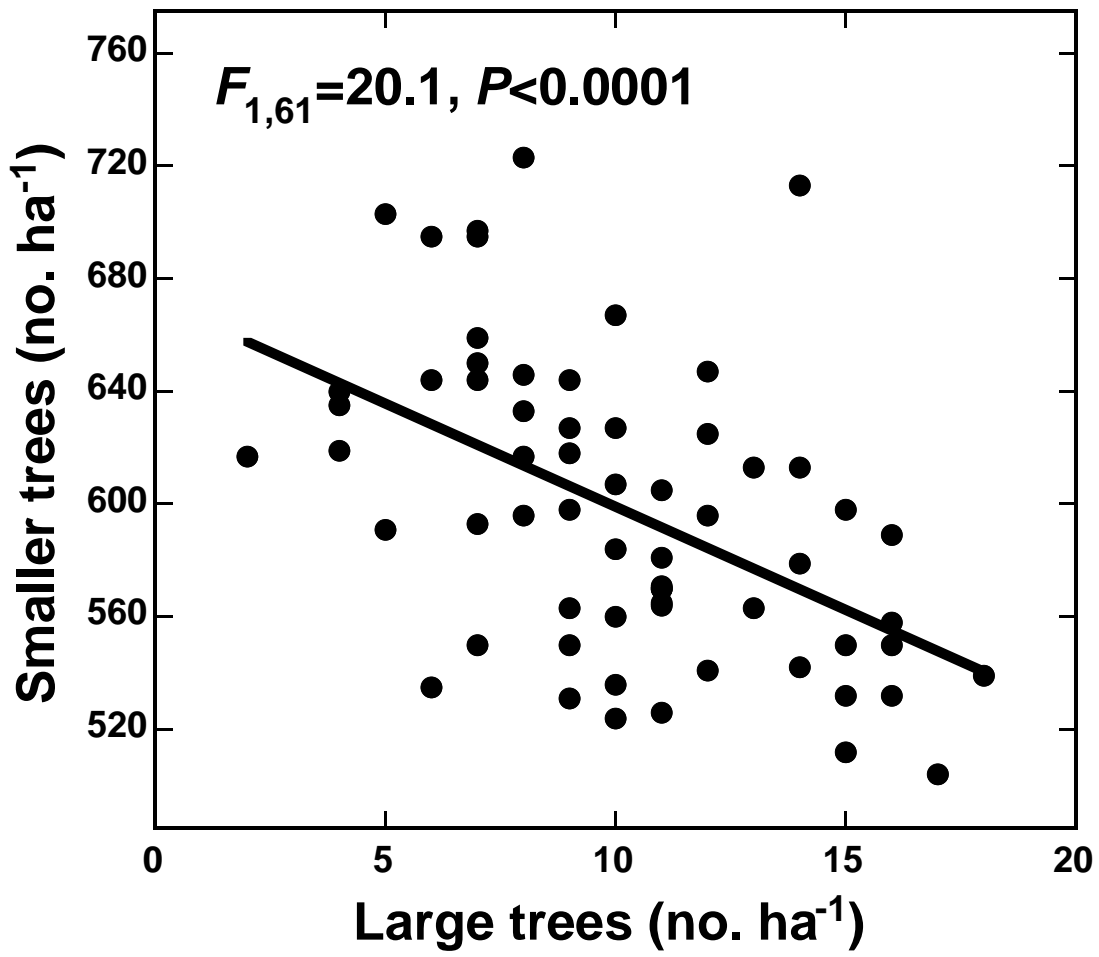


Fig. 3

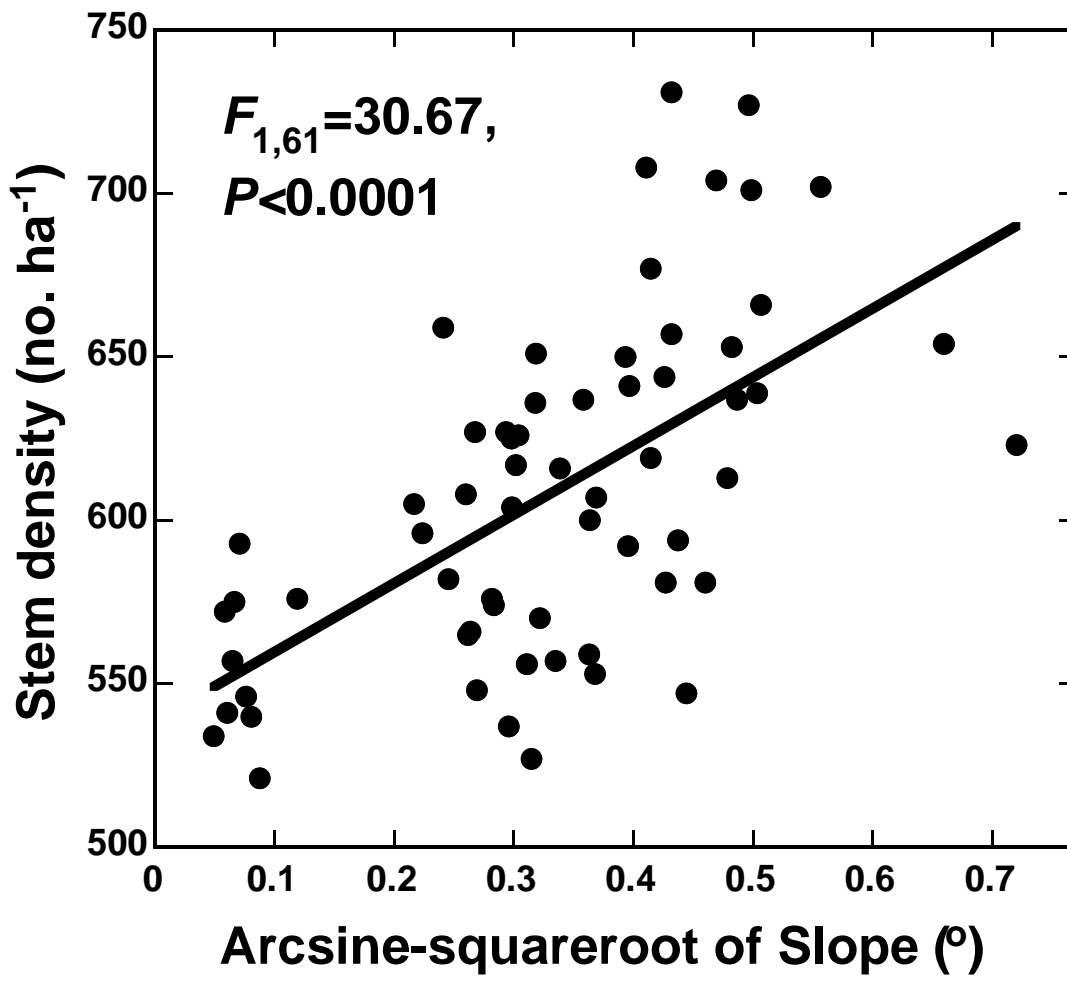


Fig. 4

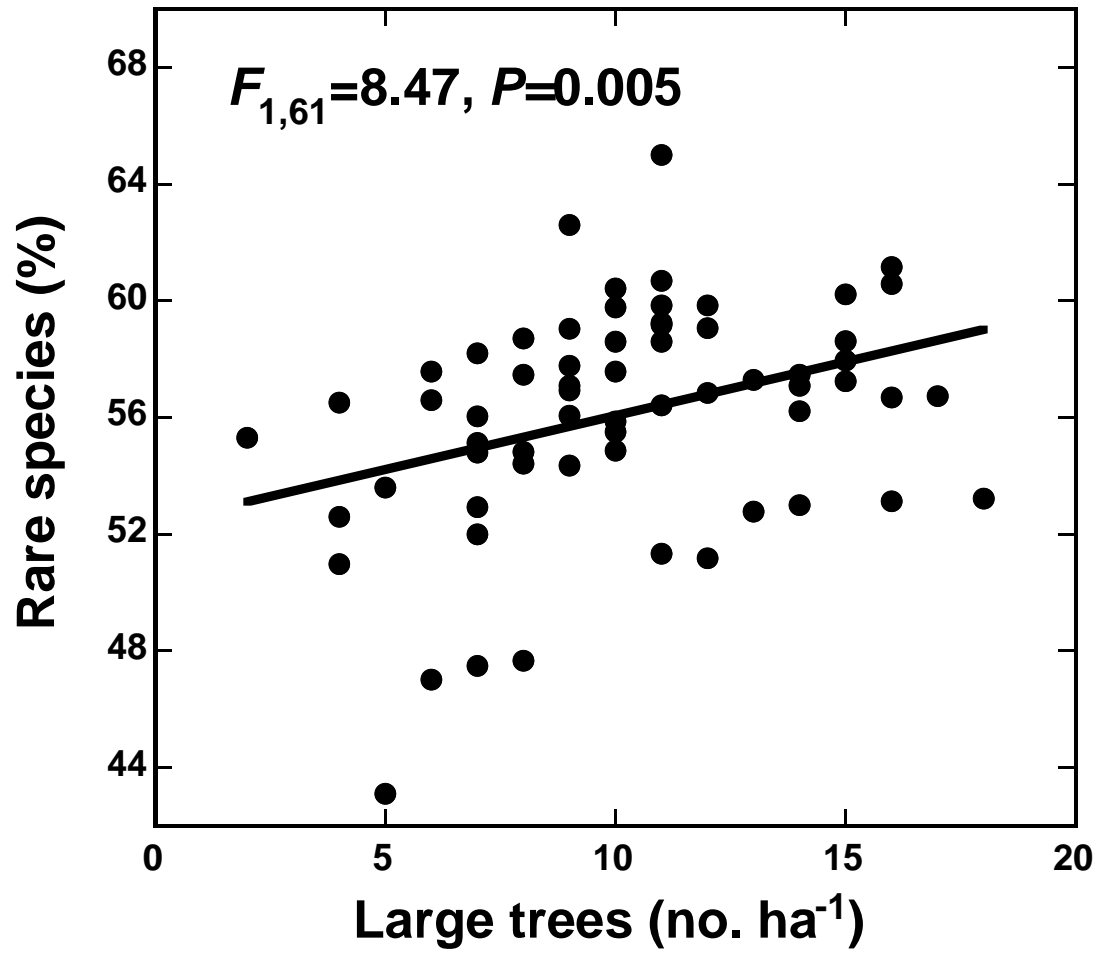




Fig. 5

