

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

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Abstract

Question: How do soils and topography influence Amazonian tree diversity, a region with generally nutrient-starved soils but some of the biologically richest tree communities on Earth?

Location: Central Amazonia, near Manaus, Brazil.

Methods: We evaluated the influence of 14 soil and topographic features on species diversity of rain forest trees (≥ 10 cm diameter at breast height), using data from 63 1-ha plots scattered over an area of ~ 400 km².

Results: An ordination analysis identified three major edaphic gradients: (1) flatter areas had generally higher nutrient soils (higher clay content, carbon, nitrogen, phosphorus, pH and exchangeable bases, and lower aluminium 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 α values), with diversity increasing with higher soil fertility and water availability. Gradient 2 was also the best predictor of the number of rare (singleton) species, which accounted on average for over half (56%) of all species in each plot.

Conclusions: Although our plots invariably supported diverse tree communities (≥ 225 species ha⁻¹), the most species-rich sites (up to 310 species ha⁻¹) 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: Density dependence; Distributional ecology; Fisher's α ; Permanent plots; Rare species; Soil chemistry; Soil texture; Soil water; Species diversity; Species richness; Topography; Tropical trees.

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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 & Luizao 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 (Prance 1977; Gentry 1990; Terborgh & Andresen 1998; Oliveira & Daly 1999; ter Steege et al. 2000; Oliveira & Nelson 2001; Pitman et al. 2002), fewer have focused on variation at smaller landscape scales (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 β -diversity, but did not consider factors affecting tree species diversity at local scales (α -diversity). Related work in this same study area has evaluated the influence of soils on tree (Laurance et al. 1999) and liana biomass.

Here we assess the effects of soils, topography and tree size (stem diameter) on tree diversity and abundance in a central Amazonian landscape spanning ~ 400 km². Like much of the Amazon, the soils in our study area are generally heavily weathered and nutrient-poor (Sombroek 1984, 2000), and we hypothesize that species richness of trees will be higher in sites that are less nutrient-starved, in line with some current theories on the determinants of tropical plant diversity (Gentry 1988; Givnish 1999). We also hypothesize that plots with many large trees (which are ecologically dominant and may reduce the local density of other trees) will have lower tree species richness simply because they will have fewer trees overall.

Our analysis is based on 63 1-ha plots in which nearly all trees [≥ 10 cm diameter at breast height (dbh)] have been identified to species or morpho-species level, and in which detailed data on soil chemistry, texture and topography were collected. 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 north of Manaus, Brazil (2°30'S, 60°W). Today, this area is a partially fragmented landscape spanning $\sim 1,000$ km² (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 January 1981 to January 1987. Rain forests in the study area are evergreen and terra-firme (not seasonally flooded), and range from 50 to 100 m elevation. The climate is tropically hot, with total rainfall from 1900 to 3500 mm. Monthly rainfall averages > 100 mm even in the dry season (June-October), but conditions can become unusually dry during occasional El Niño years. During a strong 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 plateaux dissected by many stream and river gullies. Flat areas tend to have high clay (45-75%) and organic carbon (0.8-3.3%) content, 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, or yellow latosols using the Brazilian 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 content. Clay particles in ferralsols can form very durable aggregations, giving the soil poor water-holding characteristics, even with a high clay content (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 km². Plots were arrayed using a predetermined system of study grids, irrespective of local topography or soil. Within each plot, all trees (≥ 10 cm dbh) were mapped, marked with a numbered aluminium tag, and measured for dbh at 1.3 m height or above any buttresses. A sterile or fertile voucher specimen was collected for nearly all trees and lodged in the BDFFP Herbarium, Manaus, Brazil (Laurance et al. 1998, 2006). 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 examined relationships between tree size and diversity, by dividing trees into two size classes: large trees (≥ 60 cm) and smaller trees (10-59.9 cm).

We generated five parameters that either measure or potentially influence tree diversity in each plot: (1) number of tree stems; (2) overall species

richness; (3) Fisher's α , a diversity index that is quite insensitive to variation in sample size (Magurran 1988); (4) number of 'rare' (singleton) species, represented by just one individual per plot; and (5) number of 'common' species, having two or more individuals per plot. We used Fisher's α in favour of other indices, such as rarefaction or Simpson's index, because the latter may, by themselves, be sensitive to varying sample size (Rosenzweig 1995).

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 m \times 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 sub-sampled. Composite samples for each quadrat were oven-dried, cleaned by removing stones and charcoal fragments, then passed through 20 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 (0.05-2.00 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, percentage 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 field capacity (moisture content retained in soil under a suction of 0.33 atmospheres) and wilting point (moisture content retained at 15 atmospheres), using a pressure membrane apparatus. As is common practice, 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 HNO_3 , HClO_4 and HF, and reaction with ammonium molybdate. Soil phosphate (PO_4^{3-}) was measured in an autoanalyser 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 K^+ , Ca^{2+} , Mg^{2+} , Al^{3+} and H^+ ions. Total exchangeable bases (TEB) were the sum of K^+ , Ca^{2+} , Mg^{2+} and Na^+ . Aluminium 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 K^+ and atomic absorption spectrophotometry to determine Ca^{2+} , Mg^{2+} , Na^+ , Al^{3+} and H^+ . Before analysis samples were digested in HClO_4 , HNO_3 and H_2SO_4 , 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 more 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, and among different tree diversity and abundance variables. Where appropriate, a Bonferroni-corrected α -value 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). Prior to analysis, data transformations were used as needed to improve data normality and reduce outliers (i.e. percentage slope, percentage 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 were transformed.

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 was 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), in the PC-ORD package (McCune & Mefford 1999). 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.

Results

Tree diversity and abundance

Across the 63 plots, species richness ranged from 225 to 310 species ha^{-1} , averaging (\pm SD) 261 ± 18 species a^{-1} . 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 were not significantly correlated ($r = -0.157$, $P = 0.22$; Pearson correlation; see supporting Table S1).

Tree density ranged from 521 to 731 stems per plot, averaging 608 ± 52 stems ha^{-1} . Plots with many large (≥ 60 cm dbh) trees had lower densities of smaller (< 60 cm dbh) trees ($r = -0.497$, $P < 0.0001$), possibly because each large tree displaced many smaller trees, leading to lower stem densities where large trees were abundant (Fig. 1). Plots with many stems tended to have somewhat higher species richness than those with fewer stems, although the relationship was not significant ($r = 0.193$, $P = 0.13$).

Fisher’s α -values were strongly influenced by the number of rare species in each plot ($r = 0.810$, $P < 0.0001$), as expected (i.e. because if species abundances follow a log-series, then Fisher’s α is nearly equal to the number of singletons in the sample; Rosenzweig 1995). Common species, however, had no significant effect on Fisher’s α values ($r = 0.105$, $P = 0.41$; all Pearson correlations).

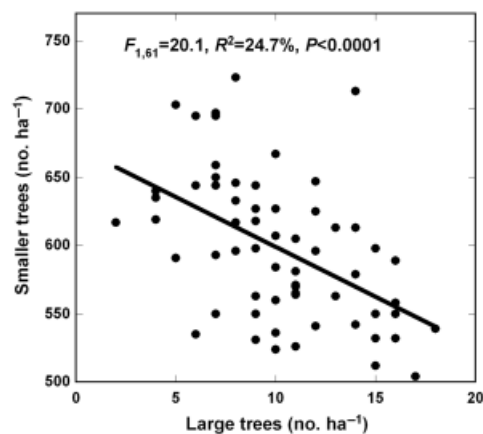


Fig. 1. Relationship between the densities of large (≥ 60 cm dbh) and smaller (10–59.9 cm dbh) trees in central Amazonian forest plots.

Simple correlates of tree diversity

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. 2), which tend to have poorer soils (higher sand content and aluminium 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 significantly with soil water capacity (PAWC) and P. Although only weakly associated with slope, Fisher’s α was positively correlated with many soil fertility variables (lower sand content, aluminium saturation and C:N ratio, and higher TEb, N, P and pH) as well as higher PAWC.

Notably, 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 aluminium 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. Surprisingly, there were proportionally more rare species, and fewer common species, in plots with many large trees (Fig. 3).

Ordination of edaphic gradients

Most of the 14 edaphic variables were significantly intercorrelated with at least one other

Table 1. Pearson correlations between soil or topographic features and five parameters describing Amazonian tree diversity or abundance: tree density, species richness, Fisher's α index and numbers of 'rare' (plot-level singletons) and 'common' (non-singletons) species. ^aBold values are significant using a Bonferroni-corrected α -value ($P \leq 0.011$). ^bSamples sizes: slope, aspect, sand content and soil C, $n = 63$ plots; other attributes, $n = 41$ plots. ^cData arcsine-square-root transformed prior to correlations. ^dData \log_{10} -transformed prior to correlations.

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

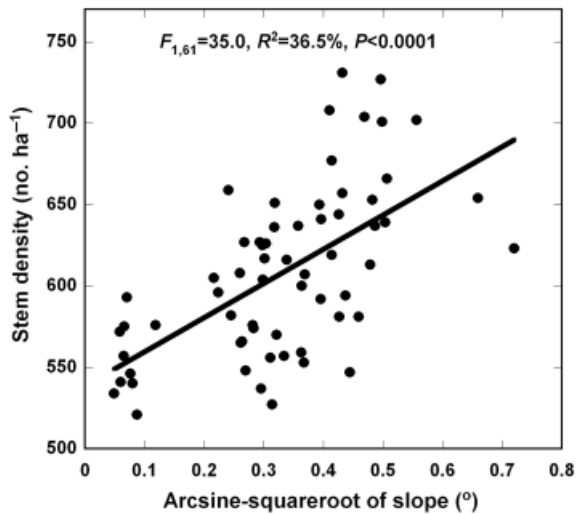


Fig. 2. Relationship between mean slope and density of trees in Amazonian forest plots.

edaphic variable (see Table S2). We therefore used NMS ordination to extract orthogonal axes 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 aluminium 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 aluminium saturation) and sandy sites with the 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.

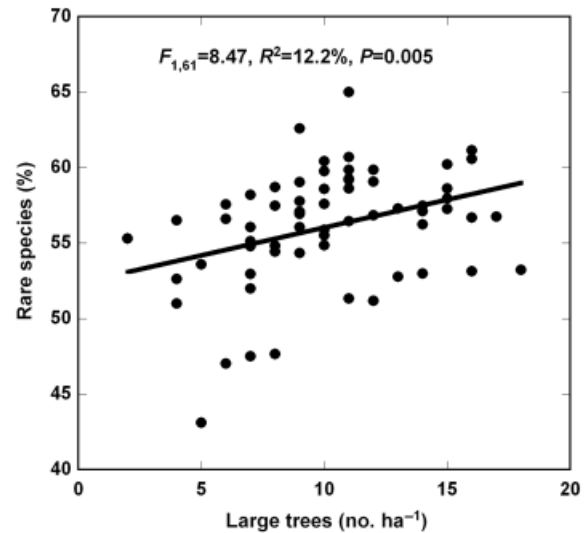


Fig. 3. Relationship between the density of large (≥ 60 cm dbh) trees and percentage of rare (singleton) species in Amazonian forest plots.

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 and low-fertility sites. Species richness, Fisher's α and rare species richness all responded positively to axis 2 (Fig. 4), 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.

Discussion

Edaphic features and tree diversity

Central Amazonia has limited elevational, geological and climatic variability, and hence species turnover across the landscape (β diversity) is modest compared to other, more heterogeneous Neotropical regions (Condit et al. 2002; Bolhman et al. 2008). However, local species richness (α 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 (≥ 225 species ha^{-1}) and some were hyper-diverse, with up to 310 species ha^{-1} .

Local edaphic factors (soils and topography) accounted for at least some of this variability in species diversity, consistent with earlier analyses of tree diversity patterns across the tropics (Ashton & Hall

1992; Wright 1992, 2002; Potts et al. 2002; Leigh et al. 2004; ter Steege et al. 2006). The most species-rich sites in our study area appeared the least constrained by key nutrients such as phosphorus, nitrogen and exchangeable cations (Tables 1 and 3, Fig. 4). This suggests that local species diversity in this region is partly limited 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). Exchangeable cations are also generally scarce in these soils (in part because central Amazonia receives virtually no marine aerosols, which contain mobile cations such as calcium, potassium and magnesium; Chadwick et al. 1999) and may also limit local tree diversity (Table 1). In the most nutrient-poor parts of the Amazon (such as parts of the Rio Negro drainage, Guiana Shield, and especially white sand soils), floras tend to have lower diversity and contain specialized plant families (e.g. Lecythydaceae, Duckeondraceae, Rapateaceae, Rhabdodendraceae, Peridiscaceae) that tolerate highly oligotrophic conditions (Gentry 1990; ter Steege et al. 2000, 2006). In sites where nutrient limitation is less severe, a wider cross-section of the regional flora can apparently 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. 4; 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 forests in Amazonia 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. 2002). The central Amazon is considered a biogeographic crossroad where distinct floras from drier and wetter parts of the basin intermix (Oliveira &

Table 2. Pearson correlations between 14 Amazonian soil and topographic variables versus three ordination axes produced by nonmetric multidimensional scaling. ^aBold values are significant using a Bonferroni-corrected critical value ($P \leq 0.011$). ^b R^2 values for correlations between ordination distances and distances in the original n-dimensional space.

Variable	Axis 1 ^a	Axis 2 ^a	Axis 3 ^a
Slope	0.718	-0.220	-0.069
North aspect	-0.269	-0.381	-0.358
Sand content	0.856	-0.765	-0.168
Plant available water capacity	-0.056	0.739	-0.074
Soil carbon	-0.769	0.524	0.290
C:N ratio	0.106	-0.404	0.250
Cation-exchange capacity	-0.358	0.542	0.495
Aluminium saturation	0.783	-0.471	-0.066
Total exchangeable bases	-0.852	0.560	0.299
Delta pH	-0.020	0.163	0.194
Soil pH	-0.073	0.157	-0.790
Total N	-0.810	0.790	0.118
Total P	-0.248	0.687	-0.570
Phosphate (PO_4^{3-})	0.104	-0.130	-0.267
Variation explained (%) ^b	55.9	25.0	11.5

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>	R^2 (%)	<i>df</i>	<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
	Axis 2	+				
Fisher's α	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	+				

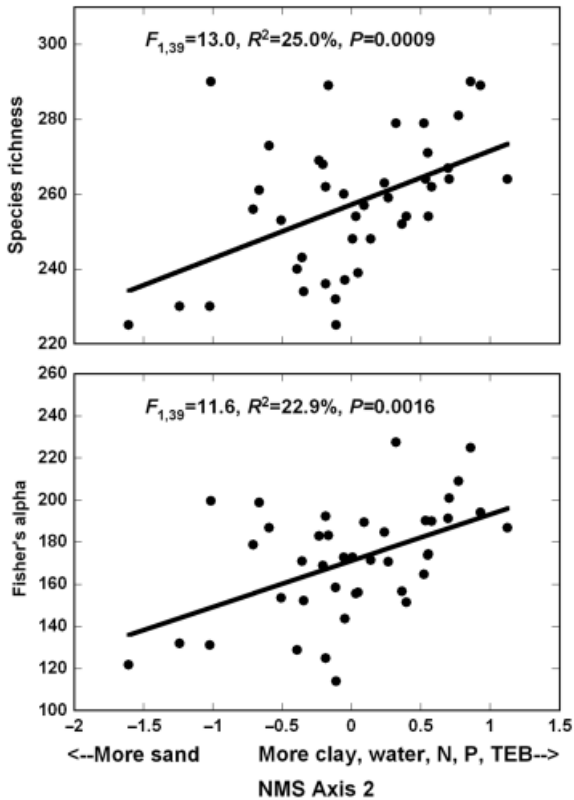


Fig. 4. Relationships between a major gradient in soil fertility and water-storage capacity versus species richness (above) and Fisher's α -values (below) for Amazonian tree communities ('water' is plant available water capacity; 'TEB' is total exchangeable bases).

Daly 1999; Oliveira & Nelson 2001). Notably, like drier areas of the basin, the central Amazon is vulnerable to periodic El Niño droughts, which increase tree mortality (Williamson et al. 2000; Laurance et al. 2002) and might have a strong structuring effect on local tree assemblages. Thus, we believe that variation in local landform and soils provides an underlying mechanism whereby tree species from drier and wetter parts of the Amazon basin can coexist. On sandy, nutrient-starved soils, species tolerant of seasonal drought and oligotrophic conditions are favoured. In less severe conditions, a broader range of species, including drought-sensitive species from wetter parts of the Amazon, can persist.

Local edaphic features influenced tree abundance and size as well as tree diversity. In particular, steeper, sandier and more nutrient-poor sites supported higher tree densities (Fig. 2). The most likely reason for this is that steep sites contain few large (≥ 60 cm dbh) canopy and emergent trees (see also Castilho et al. 2006), which competitively reduce the

abundance of smaller trees (Fig. 1). This is consistent with the observation that steeper, nutrient-poor sites in our study area have high tree densities but low tree biomass (Laurance et al. 1999), as most of the trees present are small. Several factors might explain the paucity of large trees on steep, sandy slopes: (i) scarce soil nutrients in these sites could reduce tree growth; (ii) large trees might be prone to uprooting in steep or sandy sites; or (iii) large trees in sandy soils might be prone to lethal water deficits. Notably, Ashton & Hall (1992) also found fewer large trees on sandy slopes in Sarawak forests, and suggested that large trees in such sites were more susceptible to drought-related mortality.

Diversity of rare and common species

In terms of their environmental correlates, we encountered some surprising differences between rare (singleton) and common (non-singleton) species. First, within each plot, the species richness of rare and common species was not significantly correlated. We had expected these to be positively associated, with both sets of species peaking in diversity under broadly similar environmental conditions. The absence of such an association highlights our limited understanding of how edaphic and biogeochemical heterogeneity affect tropical plant communities (John et al. 2007; Townsend et al. 2008; Turner 2008).

Second, it is intriguing that sites with more large trees supported many locally rare species (Fig. 3). We speculate that such a relationship might arise indirectly – for instance, many rare species might be near the limit of their geographic range or environmental tolerance, and thereby favour sites with less nutrient-starved soils. Alternatively, large canopy and emergent trees, with abundant fruit crops, might be magnets for mobile frugivores (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.

Third, rare and common species responded very differently to edaphic variables. Rare species peaked in diversity on sites with the highest phosphorus and nitrogen availability (low C:N ratio), whereas common species diversity showed no significant association with edaphic variables (Table 1). These findings have some broad similarities to those of Pitman et al. (2002), who found that tree stands in western Amazonia were numerically dominated by a relatively small number of locally common and

widespread ‘oligarch’ species, which tended to show only weak associations with edaphic gradients. Our tree flora in central Amazonia showed a similar oligarch structure (although floristically it overlapped little with the forests of western Amazonia, which occur on more nutrient-rich soils; Bolhman et al. 2008). The results of these two studies are generally consistent with a proposal that locally common species are often widespread edaphic generalists, whereas rare species tend to be edaphically more specialized.

Finally, it must be emphasized that much of the variation in tree diversity encountered was attributable to differing numbers of rare (singleton) species, which comprised from 43% to 65% of the species richness of each plot. Such striking rarity is a conspicuous feature of central Amazonian forests, possibly because of their strong 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 could be especially vulnerable to habitat fragmentation because their many rare species are prone to random demographic events (Melbourne & Hastings 2008) and environmental changes in isolated fragments (Laurance et al. 2002, 2006).

Tree diversity in central Amazonia

In terms of local tree richness, Amazonia and northern Borneo are the two most spectacularly diverse regions in the world (Leigh et al. 2004). The western Amazon, where soil fertility is much higher than in central Amazonia because of inputs of geologically young sediments from the Andes, was once considered the biologically richest part of the Amazon (Gentry 1988). It is now apparent, however, that the zone of peak tree diversity extends well into central Amazonia (Oliveira & Mori 1999; Laurance 2001; ter Steege et al. 2006), with much of this hyper-diverse region overlaying heavily weathered, highly acidic and nutrient-poor soils.

How can nutrient-poor forests sustain such high tree diversity? First, plant species in these forests have evolved highly efficient mechanisms to recycle and scavenge scarce nutrients, especially phosphorus, allowing the forests to maintain relatively high productivity (Herrera et al. 1978; Stark & Jordan 1978). Second, as long as nutrient concentrations exceed a critical threshold, hyper-diverse plant communities can evidently persist on heavily weathered soils – even those that, from a global perspective, would be considered unusually nu-

trient-poor (Huston 1979; Aerts & Chapin 2000). Under such nutrient-limited conditions, plants may invest heavily in a diversity of defensive compounds to reduce tissue loss from herbivores and pathogens (Waterman 1983; Coley et al. 1985). Such diverse chemical defences likely favour specialized over generalized herbivores and pathogens (Waterman 1983; Coley & Barone 1996), which in turn could drive strong density-dependent mortality that helps to maintain local plant diversity (Janzen 1970; Connell 1971; Wills et al. 1997; Harms et al. 2000; but see Givnish 1999). Hence, in our study area, only the most nutrient-starved soils, especially on sandy slopes with limited water storage, have substantially reduced tree diversity. Similar patterns might be evident in species-rich Bornean forests, where tree diversity peaked in soils of intermediate to low fertility, rather than those that were either more fertile or exceptionally nutrient-poor (Potts et al. 2002).

From a regional perspective, we believe a combination of factors, such as the vast Amazonian species pool that enhances local diversity via immigration (Terborgh 1973; Ricklefs 2004), strong density dependence and slow plant growth rates that collectively limit interspecific competition, a mixing of drier- and wetter-adapted regional floras (Whittaker 1977; Oliveira & Daly 1999) and possible mid-domain effects (Colwell & Lees 2000) collectively underlie the very high diversity of central Amazonian forests. On local and landscape scales, soil and topographic features can have quite pronounced effects on local tree diversity, as well as far-reaching influences on community structure (Bolhman et al. 2008) and tree abundance.

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Supporting Information

Table S1. Matrix of Pearson correlations among tree diversity and abundance variables recorded in 63 1-ha plots in central Amazonia. Correlations in bold were significant using a Bonferroni-corrected α -value ($P = 0.015$).

Table S2. Matrix of Pearson correlations among 14 soil and topographic features recorded in Amazonian forest plots. To improve data normality, percentage slope, percentage sand and aspect data were arcsine-square-root transformed, whereas C:N ratios were log-transformed.

Figure S1. A dawn mist rises from the rain forest in central Amazonia (photo by William Laurance). In this issue, Susan and William Laurance and colleagues explore how nutrient-starved soils in Amazonia sustain some of the world's most diverse tree communities.

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