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DOMINANCE AND DISTRIBUTION OF TREE SPECIES IN UPPER AMAZONIAN TERRA FIRME FORESTS

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Abstract. Amazonian forests are the largest and most diverse in the tropics, and much of the mystery surrounding their ecology can be traced to attempts to understand them through tiny local inventories. In this paper we bring together a large number of such inventories scattered across immense areas of western Amazonia in order to address simple questions about the distribution and abundance of tropical tree species in lowland terra firme forests there. The goal is to describe patterns of commonness and rarity at local (1 ha), landscape ($\sim10^4$ km^2), and regional ($>10^6$ km^2) scales, and to fuse the results into a more complete picture of how tropical tree communities are structured. We present estimates of landscape-scale densities for ~1400 taxa, based on data from tree plots scattered over large tracts of terra firme forest in eastern Ecuador and southeastern Peru. A database of morphological, ecological, and other traits of >1000 of these species compiled from the taxonomic literature is then used to explore how species that are common in the inventories differ from species that are rare.

Although most species show landscape-scale densities of <1 individual/ha, most trees in both forests belong to a small set of ubiquitous common species. These common species combine high frequency with high local abundance, forming predictable oligarchies that dominate several thousand square kilometers of forest at each site.

The common species comprising these oligarchies are a nonrandom subset of the two floras. At both sites a disproportionate number of common species are concentrated in the families Arecaceae, Moraceae, Myristicaceae, and Violaceae, and large-statured tree species are more likely to be common than small ones. Nearly a third of the 150 most common tree species in the Ecuadorean forest are also found among the 150 most common tree species in the Peruvian forest. For the 254 tree species shared by the two data sets, abundance in Ecuador is positively and significantly correlated with abundance ~1400 km away in Peru.

These findings challenge popular depictions of Amazonian vegetation as a small-scale mosaic of unpredictable composition and structure. Instead, they provide additional evidence that tropical tree communities are not qualitatively different from their temperate counterparts, where a few common species concentrated in a few higher taxa can dominate immense areas of forest. We hypothesize that most Amazonian forests are dominated at large scales by oligarchies similar in nature to the ones observed in Ecuador and Peru, and we argue that the patterns are more indicative of regulation of relative abundances by ecological factors than of nonequilibrium chance-based dynamics. The paper concludes with a discussion of the practical applications of predictable oligarchies over large areas of unexplored forest.

Key words: Amazon basin; Ecuador; environmental heterogeneity; Manu National Park (Peru); Peru; rarity; tree oligarchies; tropical forests; tropical trees; Yasuní National Park (Ecuador).

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INTRODUCTION

Ask a long-term inhabitant of a tropical forest whether some tree species there are more common than others, and they will look at you with astonishment. The obvious answer is ''Yes.'' Ask an ecologist the same question, and the reply will be much more tentative. It may even be ''No.''

The ecologist has good reason to be wary, given the confusing accounts in the ecological literature. While all tropical forest plots are dominated by a few common species (e.g., Campbell 1994), many inventories report that the single most common tree species in a given patch of woods is rare or absent in others nearby (Balslev et al. 1987, Gentry 1988, Campbell 1994, Duivenvoorden and Lips 1995, Ruokolainen and Tuomisto 1998, this study), and some stochastic models of forest dynamics suggest that this unpredictability in community composition and structure is an inescapable aspect of diverse ecosystems (Hubbell and Foster 1986*a*, Chesson 1991, Hubbell 1995; but see Hubbell 1997).

Complicating the picture are field reports demonstrating that even the most abundant species in tropical tree inventories are not very abundant in absolute terms, while rare species are immeasurably rare (Black et al. 1950, Richards 1996). The single most common species in diverse South American tree plots accounts for only 3–12% of all stems, and rarely exceeds a density of 90 adults/ha (Faber-Langendoen and Gentry 1991, Valencia et al. 1994, this study [Ecuadorean plots]). The same inventories typically find ~50% of the species in a hectare represented by a single adult, and ecologists are not yet able to estimate the landscape-scale densities of these rare species to within an order of magnitude.

Finally, attempts to understand how common plant species differ from rare ones have uncovered surprisingly few, and in some cases contradictory, patterns (Gaston 1994, Gaston and Kunin 1997). Even in forests dominated by a single very common species it has been difficult to pinpoint attributes responsible for their success, relative to rare species in the same community (Hartshorn 1983, Connell and Lowman 1989, Hart et al. 1989, Richards 1996). That difficulty has provided tacit support for the radical suggestion that most common species in tropical tree communities are ecologically indistinguishable from rare ones (Hubbell and Foster 1986*a*).

Faced with this perplexing landscape, we set out to answer simple questions about the commonness and rarity of tropical tree species, in the light of new data from large-scale forest inventories in eastern Ecuador and southeastern Peru. We focus on describing and interpreting abundance patterns at local (~1 ha), landscape (~10^4 km^2), and regional (>10^6 km^2) scales, with special emphasis on landscape-scale patterns. As in earlier contributions from these data sets (Terborgh et al. 1996, Terborgh and Andresen 1998, Pitman et al. 1999), a key aim is to draw inferences about the huge expanses of unexplored forest that surround the handful of scattered research sites in western Amazonia.

Our approach is modeled on Hubbell and Foster's (1986*b*) paper reporting the relative abundances of woody plants in a 50-ha tree plot in Panamanian forest. The key difference is one of scale. While their large inventory afforded an intensive look at community patterns on a single forested plateau in central Panama, our scattered smaller inventories allow a more fleeting glimpse of community patterns across forests nearly as large as Panama itself. In addition, our inventories contain >50% of the tree species known from each region we studied, rather than the ~11% at the Panamanian site. A 50-ha survey underway at the Ecuadorean site (Romoleroux et al. 1997) and new plot networks surrounding the original 50-ha plot in Panama (R. Condit, K. Harms, and J. Wright, *personal communications*) will soon provide ample opportunities to test the generality of the observations set forth here.

STUDY SITES

Field work was carried out in two forests at the westernmost margin of the Amazon basin—in and around Manu National Park, Peru (~12° S, 71° W; Terborgh 1983, 1990), and in and around Yasuní National Park, Ecuador (~01° S 76° W; see Pitman [2000] for a detailed description). This is lowland forest on rolling or sometimes sharply dissected terrain at the base of the Andes, with all elevations <500 m. More than 80% of both landscapes is upland or terra firme forest, this crisscrossed with rivers and narrow bands of associated riparian, swamp, and successional vegetation.

Plots span the range of topographic and edaphic conditions in each region, with topography ranging from perfectly flat to steeply dissected and the proportion of sand in surface soil samples varying from 11 to 51% in Ecuador and from 27 to 85% in Peru. Soils at the two sites are tentatively classified as Ultisols and Inceptisols, derived in both cases from geologically young deposits of Andean alluvium. Soils are significantly sandier at Manu, but the two sites are otherwise similar edaphically, particularly in concentrations of micro- and macro-nutrients (Pitman 2000; N. Pitman, *unpublished data*). Annual rainfall at the Peruvian site is ~2300 mm, generally recorded outside of a three- to four-month dry season, while eastern Ecuador's ~3200 mm fall year-round, with two less pronounced peaks and troughs. Both sites are warm, with mean shade temperatures ~23°C at the Peruvian study site and only slightly higher in Ecuador. During occasional cold snaps, temperatures in southeastern Peru can drop low enough to cause chilling damage in some plants—4.5°C—while eastern Ecuador never sees temperatures below the critical level of 10°C (Pitman 2000).

The floras of eastern Ecuador and southeastern Peru are among the best studied in Amazonia. Large-scale collection efforts preceding our inventories provided a strong specimen base for sterile-character taxonomic identifications (Foster 1990; D. A. Neill, *unpublished report* for Maxus Ecuador), and both sites have recent floristic checklists (Brako and Zarucchi 1993, Jørgensen and León-Yánez 1999; R. Foster, *unpublished data*).

METHODS

Field work

At both sites inventory data were collected from a network of small plots scattered over large areas of terra firme forest. The Peruvian network is composed of nine plots ranging in size from 0.875 to 2 ha and totalling 13.875 ha. The Ecuadorean network is composed of 15 1-ha plots. The Peruvian plots are generally square or rectangular, while seven of the Ecuadorean plots are long, thin transects and eight are square (see Appendix A). Between-plot distances vary from ~100 m to 171 km, averaging >30 km in Ecuador and >70 km in Peru, with most plots at each site covered by a square area of 10 000 km^2. Plots span a range of edaphic and topographic conditions in each region, as inferred from satellite and aerial photos.

In every plot a full inventory was made of all free-standing trees ≥10 cm in diameter at breast height (dbh). Trees were marked with a numbered aluminum tag, measured for diameter at breast height (avoiding trunk irregularities), and identified to species or morphospecies, or vouchered if field identification was not possible. Voucher specimens were distributed to taxonomic specialists or matched to specialist-identified material before being deposited in the long-term collections of Peruvian, Ecuadorean, and American herbaria (see Appendix B for herbaria locations and detailed voucher information).

Many of these plots and transects were initially established by different people for different reasons (see the *Acknowledgments*). More than 80% of the trees in Ecuador were identified by N. Pitman and the same proportion in Peru identified by P. Núñez and J. Terborgh, and all trees were revisited and/or their vouchers examined by a single person over the last three years at each site (N. Pitman in Ecuador and P. Núñez in Peru). Though we are confident that taxonomy is standard from one plot to another at each site, standardization of morphospecies between the two sites is not yet complete. Morphospecies were excluded from all analyses asking how many species were shared by the two tree communities.

Some of the inventory data presented here have been published elsewhere, and may differ in some respects due to new identifications (Phillips et al. 1994, Terborgh et al. 1996, Cerón and Montalvo 1997, DiFiore 1997, Palacios 1997, Pitman et al. 1999). Where plots were established several years ago, we used the most recent recensus for analyses.

Distinguishing common species from rare species

Because the abundance of organisms is a continuous variable measurable at a variety of spatial scales, distinguishing common species from rare ones requires setting arbitrary thresholds (see Rabinowitz 1981, Hubbell and Foster 1986*b*, Gaston 1994, Pitman et al. 1999). To minimize confusion, we only set a threshold for species densities at the landscape scale, i.e., the estimated densities of species over large areas of terra firme at each site. These estimates were arrived at by combining all plots for a single site and then calculating the total number of individuals per hectare for each species. The threshold density decided on for common species was ≥1 individual/ha. Because there are 15 ha in the Ecuadorean plot network and 13.875 in the Peruvian network, species represented by at least 15 trees in Ecuador and at least 14 trees in Peru qualified as common at the landscape scale, while species with fewer stems were considered rare. Where it was desirable to isolate a smaller subset of rare species, we used the species that were represented by a single tree in either Ecuador or Peru.

Species attributes analyses

We combed the taxonomic literature and various Neotropical florulas (Croat 1978, Spichiger et al. 1989, 1990, Killeen et al. 1993, Vásquez-Martínez 1997) for morphological, ecological, and other information on the 1039 named species recorded to date in the Ecuadorean and Peruvian inventories. The resulting database contains information on 36 different attributes, ranging from the date a species was described by taxonomists to the color of its flowers to the latitudinal span of its geographic range. For some well-reported attributes, like maximum leaf length or reproductive system, we were able to locate information for nearly every species. For most attributes, however, information was found for only a subset of species. A few categories, like the specific gravity of a species's wood, or the identity of its pollinators, are empty but for a few scattered records. At the time the analyses for this paper were carried out, 55% of the cells in the species × character matrix contained information.

Nineteen continuous and two categorical variables were tested for correlations with landscape-scale abundance, once each for Peru and Ecuador. We tested for associations between continuous variables (e.g., seed mass vs. abundance) with a nonparametric rank correlation test (Spearman's rho, r_S). Associations between abundance and categorical variables (e.g., abundance vs. deciduousness) were analyzed with two-tailed t tests. To test whether the distribution of common and rare species was random among families, we first calculated the number of common and rare species expected per family under the null hypothesis that those taxa were distributed with equal probability among families. For instance, 150 (14.7%) of the 1017 species in our Ecuadorean data set are common according to our definition (≥1 stem/ha), while 274 (26.9%) are represented by a single stem in the total 15 ha. Then the expected number of common and rare species in a family in Ecuador was calculated as the total number of species in that family multiplied by these proportions, and expected and observed values compared with a chi-square statistic. Patterns were also tested for individual families with chi-square.

Because many species attributes are correlated with phylogeny, we made an attempt to take these relationships into account when searching for correlates of rarity and commonness (Harvey and Pagel 1991, Kelly and Woodward 1996, Cotgreave and Pagel 1997). When significant correlations were found with ''uncorrected'' data, we double-checked that they remained significant when phylogeny was taken into account. The phylogenetic tree used for these analyses was based on hypotheses of Chase et al. (1993), though we made some modifications to include families not treated by those authors, e.g., Thymelaeaceae and Lecythidaceae. We treated all clades below the family level (i.e., genera within families and species within genera) as polytomies. Analyses were carried out with the program CAIC, under the assumption of equal branch lengths (Purvis and Rambaut 1995). Phylogenetic correction was only carried out for trees at the Peruvian site.

Biogeographic null models

To test whether Hubbell's (Hubbell and Foster 1986*a*, Hubbell 1997) non-equilibrium null model could produce the abundance patterns we observed in Ecuador and Peru, we calculated the probability that the 150 most abundant species at one site would share *k* species with the 150 most abundant species at the other site, if all selecting and ranking of species were performed at random. This is a simplification but not a caricature of the non-equilibrium model, based on the assumption that the two communities are far enough apart for the spatial autocorrelation of their composition and structure (due to dispersal) to be ~0. This assumption is supported by empirical data showing that community similarity declines steeply and exponentially with distance in a Panamanian tree plot (Hubbell 1995: Fig. III-3.14). Fitting a negative exponential curve to those data and solving for 1400 km gives a spatial autocorrelation coefficient of <0.01 (1 for identical samples, 0 for uncorrelated samples). Thus if stochastic processes determine which species are common in Ecuadorean and Peruvian forests, they do so independently at each site. This makes it simple to calculate the probability that such processes are responsible for the patterns we observed.

Current estimates of regional tree species diversity in the Peruvian department of Madre de Dios and lowland eastern Ecuador are 1004 and 1356 species, respectively (Brako and Zarucchi 1993, Jørgensen and León-Yánez 1999; R. Foster, *unpublished data*; count limited to species known or likely to exceed 10 cm dbh). Based on the known distribution patterns of those taxa identified to species, we estimated the number of all tree species shared by the two regions as 700 species. Then the expected number of 150 common Ecuadorean species occurring in Madre de Dios if all Ecuadorean species have the same probability of doing so is $150 \times (700/1356) = 77$. Then a randomly selected sample of 150 species in Madre de Dios will be expected to contain $77 \times (150/1004) = 11.5$ common Ecuadorean species. The distribution around this mean is Poisson, so the standard deviation around the expectation should be the square root of 11.5, or 3.4. Then the probability of observing a certain number *k* of shared common species can be calculated with simple statistics. An identical calculation was carried out for the Ecuadorean site.

FIELD RESULTS

Overview

The Peruvian plots contained 8291 trees ≥10 cm dbh belonging to 67 families, 269 genera, 547 named species, and 146 morphospecies (693 total species-level taxa). Average stem density was 598 trees/ha (range = 465–724 trees/ha), average basal area was 29.2 m^2/ha, and average local diversity was 174 species/ha (range = 126–217 species/ha). The Ecuadorean plots contained 9809 trees ≥10 cm dbh belonging to 72 families, 303 genera, 651 named species and 366 morphospecies (1017 total species-level taxa). Average stem density was 654 trees/ha (range = 542–790 trees/ha), average basal area was 30.2 m^2/ha, and local diversity averaged 239 species/ha (range = 188–295 species/ha). Further details of plot attributes are given in Appendix A.

Common species

In both the Ecuadorean and Peruvian inventories, 150 species had landscape-scale densities of ≥1 individual/ha (Fig. 1). The 150 common Ecuadorean taxa accounted for 15% of all species, 56% of total basal area, and 63% of all stems inventoried in Ecuador, and the 150 common Peruvian taxa for 22% of all species, 68% of total basal area, and 73% of all stems inventoried in Peru. At each site, these 150 common species represented 55–83% of all stems in a hectare plot (Ecuadorean mean = 63%, range = 55–68%; Peruvian mean = 73%, range = 62–83%; see Appendix A).

Most of the common species at a site were also frequent, i.e., most species with landscape-scale densities ≥1 individual/ha were found in a majority of plots, rather than occurring as isolated clumps in a few plots (Fig. 2). Species that were locally abundant in one plot also tended to be encountered in many plots. There was a strong positive correlation between the average local

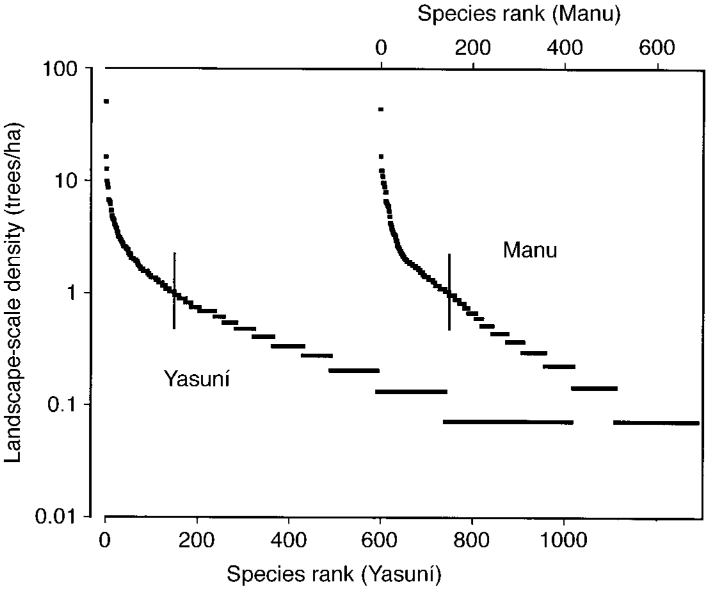

FIG. 1. Distributions of landscape-scale densities of all tree species recorded in the Ecuadorean (Yasuní) and Peruvian (Manu) inventories. The vertical line intercepting each distribution marks the threshold density of 1 individual/ha, at and above which species were considered to be common. Note that the two study sites have precisely the same number of common species, while Ecuador has more rare species. The most abundant species in both Ecuador and Peru is the palm *Iriartea deltoidea.*

density of a species and its frequency in the plot network (Ecuadorean Spearman's rho, r_S, = 0.53, $P <$ 0.0001; Peruvian r_S = 0.53, $P <$ 0.0001). The average common species in Ecuador occurred in 9.1 of the 15 1-ha plots, among which it was a ''singleton'' (represented by a single individual) in 2.6 plots. The average common species in Peru occurred in 7.8 of the 14 plots (when 2-ha plots are treated as adjacent 1-ha samples), among which it was a singleton in 2.2 plots.

The most common tree at both sites was the palm *Iriartea deltoidea,* and its mean landscape-scale density in Peru was statistically indistinguishable from its mean landscape-scale density in Ecuador (45 ± 28 individuals/ha [mean ± 1 SD] in Peru, 49 ± 22 ind./ha in Ecuador, t test $P >$ 0.65). *Iriartea* was the most abundant species in 73% of the plots in Ecuador, and in 56% of the plots in Peru. Apart from *Iriartea,* 41 other species qualify as common in both Peru and Ecuador (Table 1). Six additional species are probably also shared, but lingering doubts as to their taxonomy prevent certainty. For example, a very similar alternate-leaved treelet in the genus *Rinorea* (Violaceae) forms dense stands in both our Ecuadorean and Peruvian forests. In southern Peru it has traditionally been identified as *R. guianensis* (Dallmeier et al. 1993; R. Foster, *personal communication*), while Ecuadorean material has all been assigned to *R. apiculata* (Jørgensen and León-Yánez 1999). A small number of the species currently identified only to morphospecies may also prove to be shared by both sites.

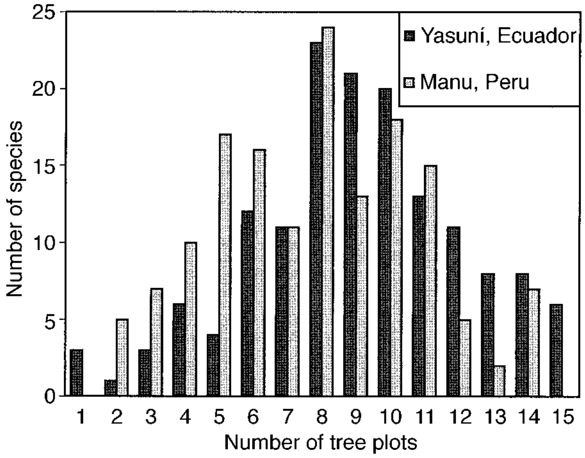

FIG. 2. Distributions of the frequencies of the 150 most common species in the two plot networks. There are 15 plots in Ecuador and 9 plots in Peru. In this figure the nine Peruvian plots are separated into 13 1-ha samples plus one 0.875-ha sample. At both sites, a majority of the common species occur in a majority of samples, and very few occur in <5 samples.

For the 254 species recorded in both the Ecuadorean and Peruvian inventories, abundance at one site was positively correlated with abundance at the other (r_S = 0.4025, $P <$ 0.0001; see Fig. 3). Because this is a nonparametric test, the high abundance of *Iriartea deltoidea* at both sites has no disproportionate effect on the correlation. Linear regression indicated a slope significantly <1 when plotted as in Fig. 3 (slope: 0.83 ± 0.03, $P <$ 0.05; overall r^2 of regression = 0.7, $P <$ 0.0001). When the outlier *Iriartea deltoidea* was removed, the slope declined dramatically to 0.34 ± 0.04 but the P value remained the same. Thus for every individual of a species recorded in Ecuador, nearly three individuals of that species were recorded in Peru.

Given what is known about the regional diversities of each site and their floristic overlap, the probability of finding the same 42 species among the most abundant 150 species at both sites under non-equilibrium community drift conditions was calculated as $<10^{-10}$.

TABLE 1. Species common in both the Ecuadorian and the Peruvian forest-plot networks.

Family	Species
Arecaceae	*Astrocaryum murumuru*
	Euterpe precatoria
	Iriartea deltoidea
	Oenocarpus bataua
Bombacaceae	*Matisia cordata*
Caricaceae	*Jacaratia digitata*
Cecropiaceae	*Cecropia sciadophylla*
	Pourouma cecropiifolia aff.
	Pourouma minor ssp. *minor* cf.
Euphorbiaceae	*Drypetes amazonica* cf.
	Mabea maynensis aff.
	Pausandra trianae
Fabaceae	*Inga coruscans* aff.
	Inga thibaudiana ssp. *thibaudiana*
Flacourtiaceae	*Lindackeria paludosa*
Lauraceae	*Ocotea javitensis* cf.
Lecythidaceae	*Eschweilera coriacea* cf.
	Gustavia hexapetala
Meliaceae	*Guarea gomma*
	Guarea kunthiana
	Guarea pterorhachis
	Trichilia solitudinis
Monimiaceae	*Siparuna cuspidata*
	Siparuna decipiens
Moraceae	*Helicostylis tomentosa*
	Naucleopsis krukovii
	Perebea xanthochyma
	Pseudolmedia laevigata
	Pseudolmedia laevis
	Pseudolmedia macrophylla
	Pseudolmedia rigida
Myristicaceae	*Iryanthera juruensis*
	Otoba parvifolia
Olacaceae	*Minquartia guianensis*
Rubiaceae	*Warscewiczia coccinea*
Sapotaceae	*Micropholis venulosa*
Sterculiaceae	*Theobroma speciosum*
Tiliaceae	*Apeiba aspera*
Ulmaceae	*Ampelocera edentula*
	Celtis schippii
Violaceae	*Leonia glycicarpa* cf.
	Rinorea viridifolia cf.

Note: The suffixes ''cf.'' and ''aff.'' denote a low and high level of uncertainty, respectively, regarding the identification.

Very rare species

In Ecuador 274 species and in Peru 176 species were represented by a single tree. In both Ecuador and Peru the rarest quarter of the tree species accounted for only 2–3% of all stems in the inventory. On average, Peruvian hectares contained 81 species represented by a single stem (47% of all species in the hectare), and Ecuador hectares 128 species (54%). Only 14–17% of the singletons in any hectare were also singletons in the entire data set. A species represented by a single tree in some hectare was more likely to be common at the landscape scale than to be a singleton in the combined Peruvian or Ecuadorean plots.

SPECIES-ATTRIBUTES RESULTS

Taxonomic patterns

Common species were disproportionately concentrated in certain families in Ecuador, χ^2 (df 72, n = 1017 species) = 194, $P \approx 0$, but there was no pattern to their distribution with regard to family in Peru, χ^2 (df 66, n = 693 species) = 68, $P = 0.41$. The rarest species were not disproportionately concentrated in particular families at either national park (Ecuadorean $\chi^2 = 50$, $P = 0.97$, Peruvian $\chi^2 = 65$, $P = 0.48$). Most families with exceptional numbers of common species at one site also had exceptional numbers of common species at the other site, whereas families showing exceptional numbers of rare species at one site never followed the same trend at the other site (Table 2). In five cases families appear in opposite categories at the two sites (e.g., there are too few rare Rubiaceae in Peru but too many in Ecuador).

There was a weakly significant negative correlation at both sites between the abundance of a species and its number of congeners worldwide (see Table 3; Ecuadorean $r_S = -0.2246$, $P < 0.0001$, Peruvian $r_S = -0.1837$, $P < 0.0001$). In Ecuador but not Peru, there was a slight but significant tendency for abundant species to occur in species-poor families ($r_S = -0.082$, $P = 0.04$).

Occurrence in other habitats

Species that were common in terra firme were more likely to be found growing in other habitats than species that were rare. Three quarters of the landscape-scale common species in Ecuadorean terra firme were also found in floodplain plots (5 ha sampled) or swamp plots (5 ha sampled) in the region, while only a quarter of the rarest terra firme species were found in these other habitats. In Peru, too, at least 63% of the 150 most common species in terra firme also occur in successional forest (10.5 ha sampled), floodplain forest (11.5 ha sampled), or swamps (5.5 ha sampled) in the area, while fewer than half of the rarest terra firme species have been recorded in these other forest types.

Other attributes

Most attributes were not correlated with landscape-scale abundance. Only one morphological attribute, the maximum height attained by a species, showed a correlation at both sites (Table 3). In tests of independent contrasts (phylogenetically corrected values), one of the significant associations in Table 3 became nonsignificant (wet seed mass).

Deciduous species did not differ in abundance from evergreen species, and species with compound leaves did not differ in abundance from species with simple leaves (t tests, $P > 0.2$). Monoecious species had significantly higher mean abundances than both dioecious and hermaphroditic species at both sites ($P < 0.05$), chiefly due to the high abundances of monoecious palms. Eight of the ten most abundant monoecious tree species in the Peruvian plots are palms. Dioecious and hermaphroditic species were equally abundant at both sites.

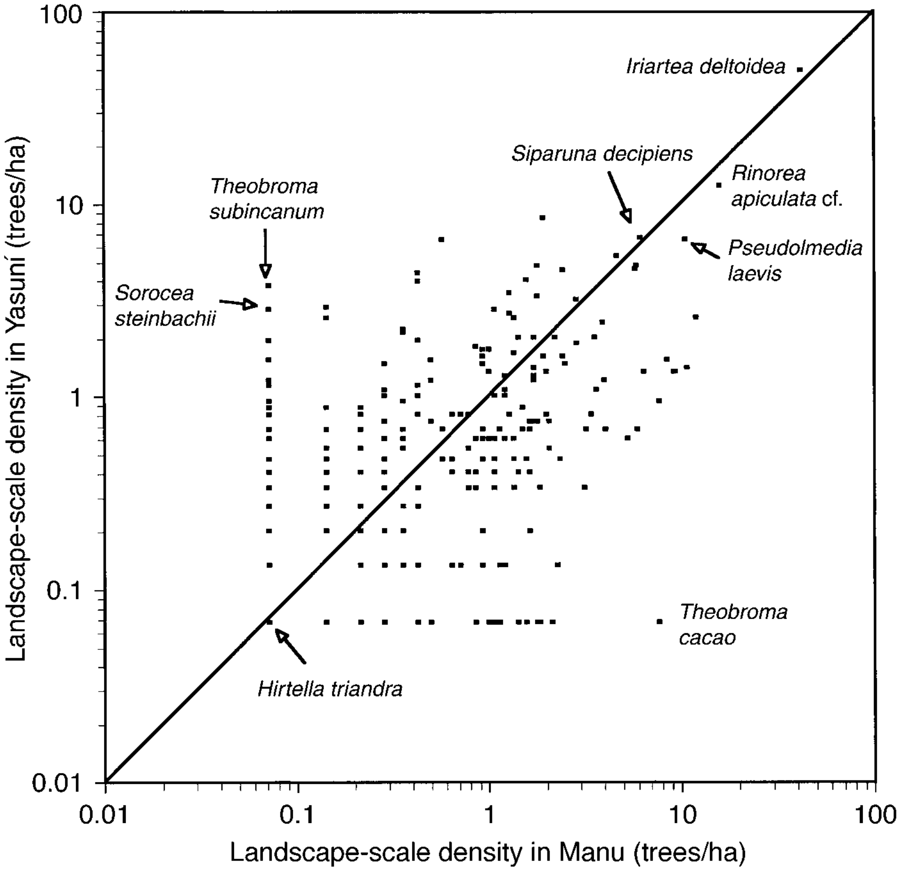

FIG. 3. A scatterplot of the landscape-scale densities of 254 species shared by plot networks in Manu National Park, Peru, and Yasuní National Park, Ecuador. Both parametric and nonparametric tests of association reveal a highly significant correlation. The diagonal line $y = x$ represents the null hypothesis that densities are identical at the two sites. The null hypothesis was rejected: the actual slope is 0.83 with *Iriartea deltoidea,* and 0.34 without it. Thus for every individual of a given species recorded in Ecuador, an average of three individuals of that species was recorded in Peru. (For *Rinorea apiculata* cf. see explanation in *Field results: Common species.*)

DISCUSSION

Overview

Ecologists have long suspected that most tree species in Amazonian forests grow at densities <1 individual/ha (Black et al. 1950), and that suggestion is confirmed for the forests we studied. What has not been widely appreciated is that this majority of rare species accounts for a minority of the individual trees in the landscapes they occupy. In both Peru and Ecuador, it is a small proportion of common species that dominates the tree community, accounting for >50% of the trees at all scales. These common species combine high local densities with high frequencies, forming a predictable oligarchic matrix over immense tracts of forest (Fig. 4).

In practical terms, this means that a hectare established anywhere in the thousands of square kilometers of terra firme forest around our tree plots in Ecuador is not only virtually assured of containing *Iriartea deltoidea, Matisia ochrocalyx sensu latu, Brownea grandiceps,* and dozens of other common species—it is also more likely than not to contain them at densities of >1 individual/ha. Similarly, a hectare established in the Peruvian terra firme forests we studied can be predicted with high confidence to contain >1 individual of *Iriartea deltoidea, Leonia glycicarpa,* and *Pseudolmedia laevis,* and dozens of other common species.

Extrapolating from our tiny inventories to vast areas of unexplored forest is a risky exercise, but we believe the data are sufficient to challenge Amazonia's reputation as a forest ecosystem of dizzying patchiness and unpredictability. Forests in Peru and Ecuador are undeniably complex, but because so much of their diversity is concentrated in scattered, rare species, most individual trees encountered in these forests belong to a fairly predictable set of families, genera, and species. The result, as foresters have long recognized, is that a person capable of recognizing 100 tree species can identify a large proportion of the standing timber in Amazonian forests—even when those forests contain more than ten times as many species (G. Guerra, *unpublished manuscript*). More specifically, our results

TABLE 2. Families with exceptional numbers of common or rare species, at Manu National Park, Peru, and Yasuní National Park, Ecuador.

Direction of excess	Rare (<0.07 individuals/ha)		Common (≥1 individual/ha)	
	Manu	Yasuní	Manu	Yasuní
Too many	Sapotaceae (5) Polygonaceae (4*) Myrtaceae (3) Nyctaginaceae (2) Annonaceae (2) Verbenaceae (2) Humiriaceae (2)	Chrysobalanaceae (6*) Rubiaceae (5) Euphorbiaceae (3) Lauraceae (3) Fabaceae (2) Clusiaceae (2) Moraceae (2) Rutaceae (2) Ebenaceae (2) Flacourtiaceae (2)	**Arecaceae** (6*) **Moraceae** (6*) Euphorbiaceae (4) **Myristicaceae** (4*) Sapotaceae (4) **Violaceae** (3*) Rubiaceae (2)	Lecythidaceae (7*) **Myristicaceae** (7*) Cecropiaceae (6*) Bombacaceae (5*) Meliaceae (5) **Arecaceae** (5*) Sterculiaceae (58) **Moraceae** (4) Burseraceae (4) **Violaceae** (3*) Tiliaceae (2*) Flacourtiaceae (2)
Too few	Moraceae (6) Rubiaceae (5*) Cecropiaceae (3) Apocynaceae (2)	Meliaceae (6) Sapindaceae (4) Myrtaceae (4) Melastomataceae (3) Burseraceae (3) Bombacaceae (3) Sterculiaceae (2) Lecythidaceae (2)	**Lauraceae** (6) **Annonaceae** (5) **Myrtaceae** (5*) **Sapindaceae** (3) **Melastomataceae** (3) **Chrysobalanaceae** (2) Boraginaceae (2)	**Lauraceae** (8*) **Myrtaceae** (8*) Sapotaceae (6*) **Annonaceae** (4) **Melastomataceae** (4) **Chrysobalanaceae** (4) Rubiaceae (3) Elaeocarpaceae (3) **Sapindaceae** (2) Clusiaceae (2)

Note: Numbers in parentheses indicate the number of species in each category; boldface identifies families found in the same category at both sites.

* $P < 0.05$ in chi-square analysis.

TABLE 3. Strengths of correlations between tree species abundances and a variety of attributes, at Manu National Park, Peru, and Yasuní National Park, Ecuador.

	Manu		Yasuní	
Attribute	n	r_S	n	r_S
Geographic range size				
Latitudinal range	138	0.134	190	0.051
Longitudinal range	138	0.037	189	−0.006
Maximum elevation collected in Neotropics	206	0.058	252	0.094
Morphology				
Maximum height attained*	436*	0.179*	546*	0.183*
Maximum flower dimension	384	0.014	471	−0.004
Minimum fruit length	403	−0.007	477	0.006
Maximum fruit length	414	0.033	490	0.020
Minimum fruit width	375	0.071	456	0.068
Maximum fruit width	387	0.093	468	0.069
Minimum seed length	134	0.017	154	0.009
Maximum seed length	138	0.062	159	0.010
Minimum seed width	75	0.028	89	−0.014
Maximum seed width	78	0.127	92	0.002
Wet seed mass†	78†	0.414†	60	−0.024
Maximum leaf(let) length (palms excluded)*	404	0.036	506*	0.143*
Abundance and diversity				
Abundance at other site*	254*	0.388*	254*	0.388*
Number of species in family worldwide*	509	−0.037	620*	−0.082*
Number of species in genus worldwide*	518*	−0.184*	580*	−0.225*
Date of species description	397	0.013	470	−0.061

Notes: In the column headings, n = no. of species; r_S = value of Spearman's rank correlation test. Positive values indicate positive correlations, and negative values indicate negative correlations.

* $P < 0.05$.

† Correlation found to be nonsignificant when phylogeny was taken into account.

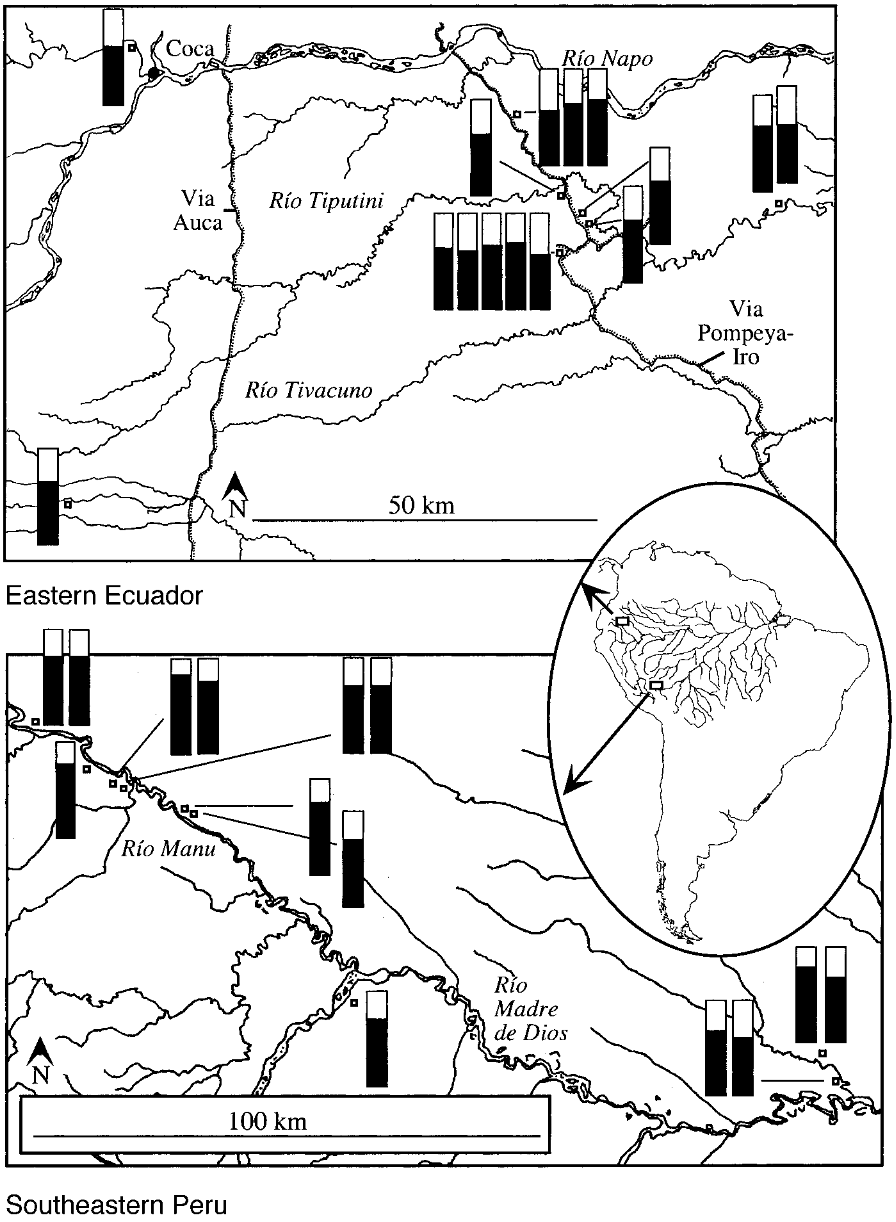

FIG. 4. A map of the study sites, with small squares indicating the locations of tree plots discussed in this paper. The black portion of the vertical bars shows the proportion of stems in each 1-ha sample that belong to 150 common species. There are 693 species in the Peruvian plot network and 1014 in the Ecuadorean network. In the Peruvian map, double bars represent adjacent hectares of 2-ha plots.

substantiate earlier suggestions that oligarchies at local scales may also extend over large areas of primary forest (Balée and Campbell 1990, Campbell 1994), and not just in places where they form monodominant stands (Peters et al. 1989).

The data presented here are the product of a wide-ranging and so far fruitless search for an upland tree community in southeastern Peru or eastern Ecuador that is sufficiently distinct from other forests in those regions to justify the common perception of tropical forests as complex floristic mosaics. Instead, the impression given by our scattered inventories is one of widespread familiarity and sameness. Recently, two of the authors made an expedition to the easternmost border of Madre de Dios to establish a tree plot in what they suspected would be a refreshingly different forest growing along the Río Acre, >100 km from any of the Peruvian plots discussed in this paper—only to find that two thirds of the trees there belonged to the same suite of 150 oligarchic species that dominate forests throughout the department (J. Terborgh and P. Nuñez *unpublished data*). Even if the remaining third of the trees in the plot had belonged to previously unrecorded species, it would still be difficult to argue that the Río Acre tree community represented a remarkable departure from other forests in Madre de Dios.

The idea of predictable oligarchies dominating huge tracts of tropical forest is at odds with most current depictions of tropical tree communities, in part because ecologists have chosen to emphasize rarity and heterogeneity over commonness and stasis. We suspect that the picture uppermost in most ecologists' minds when they think of tropical tree distributions derives from a classic thumbnail sketch of Wallace (1878). That widely cited anecdote about searching in vain for two trees of the same species in a Malaysian forest is an enduring illustration of tropical rarity, but it is a poor example of the patterns in the Ecuadorean and Peruvian forests we studied. It is true that in some Ecuadorean tree plots the probability that the next tree examined will belong to the same species as the last tree examined is ~2%. But if one selects a tree at random in an Ecuadorean hectare, the probability that another adult of the same species will be found growing in the same hectare exceeds 80%. When the search is extended to smaller trees and to adjacent hectares, the probability approaches 100%. A modern-day Wallace wandering around our two forests might more accurately complain that wherever he went he encountered the same species over and over.

This should come as no real surprise to ecologists, given that the same pattern is a prominent feature of well-studied forests around the world. What we observe at our South American sites is not qualitatively different from the situation in North America, where immense areas of upland forest are dominated by a few consistently common tree species belonging to a handful of higher-level taxa (e.g., *Juniperus*, *Pinus, Quercus;* Barbour and Major 1977, Barbour and Billings 1988). The difference is that rather than a few common species, tropical forests have dozens. And because tropical forests are so diverse, common trees there are not as abundant in absolute terms or as immediately obvious as common trees in temperate forests.

The remainder of this discussion is devoted to exploring how far these patterns in Ecuador and Peru might apply to tropical forests in general, what they imply about forest dynamics, and how they originate in nature. We begin by asking why our results run contrary to the many recent reports emphasizing heterogeneity in tropical vegetation, and how far the patterns at our study sites might be extrapolated to tropical forests elsewhere. The discussion then reviews the traits shared by common species, in an effort to identify the processes that produce large-scale oligarchies. We close with a discussion of the practical implications of the findings.

Environmental heterogeneity and community homogeneity

The predictability of tree communities over large areas in Amazonian Ecuador and Peru is especially interesting because the environmental conditions in our tree plots are anything but uniform. Some of the forests we inventoried grow on flat, high plateaus; others on sandy, knife-edged ridges; and others on rolling clay hills intersected by streams. They include forests choked with stands of bamboo or *Heliconia*, forests punctuated with large sunlit treefall gaps, and forests with closed canopies and deeply shaded understories. A growing number of studies have demonstrated that many tropical plant species are distributed nonrandomly with respect to this sort of variation, and the consensus is that these patterns reflect species-specific habitat preferences or life-history variation (Davis and Richards 1933, ter Steege et al. 1993, Tuomisto and Ruokolainen 1994, Clark et al. 1995, 1998, 1999, Malo and Olano 1997, Ruokolainen and Tuomisto 1998, Pitman et al. 1999, Svenning 1999, Terborgh and Mathews 1999). Thus a major challenge is to reconcile these reports with our observation that the same small group of species dominates our forests everywhere.

The first step is to recognize that the two patterns are not mutually exclusive. The large-scale oligarchy in Ecuador comprises only 15% of the species inventoried there, which means that the remaining 85% could be strict habitat specialists without having any effect on the widespread homogeneity we report. It is possible that a majority of tree species at our sites are highly sensitive to environmental heterogeneity, while the minority of common species comprising the large-scale oligarchies are largely indifferent to it (and perhaps common for that reason; see Brown 1984, 1995, and Hubbell and Foster 1986*b*). This conjecture is supported by the fact that most common terra firme species can also be found in inventories of nearby riparian and swamp forests (Pitman et al. 1999; N. Pitman, C. Cerón, H. Mogollón, and R. Burnham, *unpublished data*).

It is also true that, despite the homogeneity emphasized in this paper, there are striking compositional and structural differences from plot to plot in the Ecuadorean and Peruvian data sets. Some of this variation may indeed reflect species responses to between- and within-plot differences in soil characters, topography, successional stage, and other environmental factors, but a large proportion of it reflects nothing more than the inevitable sampling error when sampling very diverse communities with small tree plots. For example, an average 1-ha sample of Peruvian terra firme forest contains 83 of the region's 150 oligarchic species, or 55% ($n = 15$ plots), while an average 2-ha rectangle contains 107 of them, or 72% ($n = 5$ plots). The implication is that if one were to compare independent 5- or 10-ha samples of these forests, they would be very likely to contain relatively large populations of all 150 of these common species.

How much of the noise at the 1-ha scale is due to sampling effects and how much due to environmental preferences should be discernible via null models on the one hand and multivariate ordinations with environmental data on the other. For the time being, the key conclusion is that even if small-scale environmental conditions do prove to be important determinants of the distributions of Amazonian trees, those rules may only apply to a minority of the trees on Amazonian landscapes.

Extrapolations to other regions

It is not clear to what extent the high predictability in the tree communities we studied extends to other forests in Amazonia, or to large tracts of tropical forest elsewhere. It is sobering to observe that the common species in the forests we studied are almost entirely absent from other well-known sites in the western portion of the Amazon basin. For instance, not one of the 42 common species shared by our sites (Table 1) is listed among the common species found in an inventory of terra firme forests in the Caquetá river basin of Colombia, just ~400 km east of our Ecuadorean site (Duivenvoorden and Lips 1995:183). Indeed, very few of the tree species common in Caquetá are even *present* in our data sets. The same problem is evident when we compare our species lists to those from forests near Iquitos, Peru, or Manaus, Brazil (Ruokolainen and Tuomisto 1998, De Oliveira and Mori 1999).

These comparisons suggest that the particular suite of common species we observe in eastern Ecuador and southeastern Peru may only be characteristic of a narrow crescent of forests at the eastern base of the Andes. More generally, the pattern may be that upper Amazonian forests change much more rapidly along an east–west axis than along a north–south axis (Ducke and Black 1953). If true, this is probably due to the gross similarity of edaphic and climatic conditions obtaining up and down the Andean piedmont, relative to the differences that accumulate as one moves eastward (Terborgh and Andresen 1998, Pitman et al. 1999).

Whatever the particular floristic composition of an Amazonian forest, we propose that an oligarchy of common species dominates it at large spatial scales. Even in regions where the tree flora is utterly distinct from those of eastern Ecuador and southeastern Peru, we predict that a small proportion of taxa will be found to occur with high frequency and at high local abundances across the landscape. Where environmental heterogeneity is low, or perceived as low by tree species, the areas dominated by these predictable oligarchies may measure thousands of square kilometers in extent. Where environmental heterogeneity is high—for example, among the patchy edaphic conditions at Iquitos, Peru—the areas dominated by predictable oligarchies may be much smaller (Ruokolainen and Tuomisto 1998). Thus the oligarchic taxa will vary from region to region, and in cases of environmental heterogeneity from patch to patch, but the patches themselves may be largely homogeneous in composition and structure.

This proposition is based on an extrapolation of the traditional Hutchinsonian niche model (Hutchinson 1957) to larger spatial scales, as outlined by Brown (1984, 1995). The basic argument is that locally common species are common because their niche requirements overlap with local environmental conditions to a greater extent than do those of rare species. To the extent that environmental conditions are spatially autocorrelated, species that are locally common will also tend to be frequent and abundant across the surrounding landscape.

One pattern not explained by this line of argument is the observation that the 254 species shared by the two sites tend to be three times more abundant in Peru than they are in Ecuador. This is probably nothing more than a necessary consequence of the higher local and regional tree diversity in Ecuador.

Implications for forest dynamics

The large-scale homogeneity of western Amazonian forests provides a new perspective on how these communities may behave over time, via a space-for-time substitution (Pickett 1989). The observation that a large number of diverse seedling communities growing under a variety of environmental conditions and separated by great distances consistently converges on a similar adult community structure strongly suggests that seedling communities at any time in the past or in the future would also tend to converge on the same oligarchies reported here, given similar climatic conditions. The implication, which should soon be testable at our sites with pollen records (Athens and Ward 1999), is that the species common today are likely to have dominated these forests for several thousands of years—at least since the arrival of modern-day climates.

Again, these ideas run contrary to recent depictions of tropical forest landscapes, which emphasize their patchiness or unpredictability (Denslow 1987, Gentry and Ortiz 1993, Clark et al. 1995, 1998), their exposure to a constant battery of disturbances large and small (Colinvaux 1987, Salo and Räsänen 1989), and their shifting composition and structure under postulated non-equilibrium dynamics (Hubbell 1995; but again see Hubbell 1997). As with environmental preferences, reconciling ideas of stability and homogeneity with widespread evidence of temporal and spatial heterogeneity of tropical environments is not as problematic as it appears. Ecologists have too often implied that the unpredictable regime of treefalls, storms, rainfall, temperature, disease outbreaks, and other environmental factors in tropical forests should result in highly heterogeneous plant communities there (Mabberley 1992, Whitmore 1998, and many others). This is no more true in tropical forests than it is in temperate forests. All that is required for a homogeneous community to dominate a spatially and temporally heterogeneous landscape is that some species be better adapted to heterogeneous conditions than others.

What the data presented here establish beyond a doubt is that western Amazonian forests are not non-equilibrium systems sensu Hubbell and Foster (1986*a*). There are too many compositional and structural similarities between our Ecuadorean and Peruvian forests—as far apart from each other as the North American cities of Boston and Chicago—to accept the proposition that they share nothing but membership in the same enormous, chance-driven meta-community. Chance-based models may be capable of producing stable biological oligarchies over very large areas (Hubbell 1997), but they cannot explain why the oligarchies in natural communities are nonrandom assemblages of the larger species pool. Even if a chance-driven process were to reproduce a situation under which a single species dominated two very distant communities at identical densities—as the palm *Iriartea deltoidea* does in Ecuador and Peru—the likelihood that the model would select a species belonging to a family that also dominated the community composition and structure of many other putatively chance-driven tropical forests around the world (and a family that appears to have been an important component of South American tree communities since the Cretaceous) is incontestably minute (Romero 1993). The probability that the chance-based model would also select most of the other palm species at our sites to be common there is similarly close to nil. There is clearly something about palms, and something about *Iriartea deltoidea* in particular, that predisposes them toward success in the forests we studied, and in many others in the wet tropics (Gentry 1988, Richards 1996, Terborgh and Andresen 1998).

Traits associated with commonness and rarity

It is not yet clear what that something is. As the scarcity of significant correlations between species attributes and abundance suggests (Table 3), there are no magical traits that confer numerical success upon an Amazonian tree species, or predestine it to rarity. As in temperate forests, physiological and life-history trade-offs mean that there are several very different constellations of traits that might lead to abundance or rarity under a given set of environmental conditions. Thus it makes sense that particular genera and families should reappear again and again in oligarchies. It means that the constellations of traits that systematists have traditionally used to delineate these families overlap with the constellations of traits that predispose a tree to abundance under wet tropical forest conditions (i.e., Gentry's [1988] family-level niches).

Again, it is not clear what those constellations of traits are. In general, our expectation is that common tropical tree species lack the sorts of attributes correlated with rarity throughout the natural world (Gaston and Kunin 1997). Thus the species and families dominating tropical forests at large scales should tend to combine high reproductive investment and success, long-distance dispersal abilities, and a tolerance of a broad range of environmental conditions. Perhaps most importantly, a species' abundance at local and large scales may be a simple function of its ability to recruit in close proximity with conspecific adults (Janzen 1970, Connell 1971).

There are two patterns that we were surprised not to find, given that they have been well documented at other sites. Species abundances tend to be positively correlated with geographic range sizes (McNaughton and Wolf 1970, Hanski 1982, Brown 1984, 1995, Gaston and Lawton 1990.), but no such result was found in these analyses. This may be because range-size estimates were only available for 20% of the species at each site, or because range-size estimates of tropical species are still error prone. It was also a surprise that monoecious species are more abundant in our forests than species with other reproductive systems. At both La Selva, Costa Rica, and Barro Colorado Island, Panama, dioecious species are more common than hermaphroditic or monoecious species (Hubbell and Foster 1986*b*, Lieberman and Lieberman 1994). These are intuitively satisfying results, because, other factors being equal, a dioecious species should have a minimum viable density twice that of a self-compatible bisexual species. It is not clear why the pattern is switched in western Amazonia.

Rarity

Most of the insight emerging from these inventories concerns the most common species, and we can do little more than reiterate how little is known about the very large number of species that are rare. The rarest species in our inventories occurred at a density of 1 out of every 9809 trees, and so locating these taxa is very much akin to finding a needle in a haystack. For now, there is no way to know how accurately the lowest landscape-scale density we were able to record reflects the lowest density found in nature. If long-range pollination allows some tree species to routinely exist at extremely low densities—for instance, 1 adult/km^2—then it is possible that there is a significant component of the tree floras at our sites that remains invisible to our sampling methods (Chase et al. 1996, Nason et al. 1996). Put another way, if the rarest tropical trees are as rare as harpy eagles or jaguars, botanists will never find them. If this is the case, then the figures now in use for regional diversities in western Amazonia may be significant underestimates (Vásquez-Martínez 1997, Jørgensen and León-Yánez 1999).

Practical considerations

The news that important components of tropical forests are homogeneous over immense areas clears the way for predictive models that can forecast the composition and structure of unvisited tropical tree communities with a minimum of parameters (Pitman 2000; N. Pitman, *unpublished manuscript*). As Appendix A makes clear, simple models based on the oligarchies we describe in this paper have the potential to predict 34–59% of the species present in unvisited terra firme forest plots at our study sites, as well as the species identities of 55–83% of the stems in those plots. Designing and field testing these models, incorporating finer-scale information on environmental variation and species-habitat preferences, and wedding the result to satellite mapping projects in Amazonia should be a high priority. Armed with such a model, conservationists and ecologists could potentially sketch in vast areas of terra incognita that presently occupy the vegetation map of tropical South America.

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APPENDIX A

Distinguishing characteristics of tree plots in Yasuní National Park, Ecuador, and Manu National Park, Peru.

Tree plot	Coordinates	Plot Area (ha)	 Shape (m × m)	No. stems ≥ 10 cm dbh
Ecuador				
Bogi				
1	00°41.911′ S, 76°28.931′ W	1	10 × 1000	542
2	00°41.875′ S, 76°28.428′ W	1	10 × 1000	589
3	00°41.559′ S, 76°28.199′ W	1	10 × 1000	557
4	00°41.799′ S, 76°28.373′ W	1	10 × 1000	679
5	00°42.024′ S, 76°28.620′ W	1	10 × 1000	586
6	00°40.160′ S, 76°27.482′ W	1	100 × 100	727
Capiron	00°37.591′ S, 76°27.866′ W	1	100 × 100	790
Payamino	00°27′ S, 77°02′ W	1	100 × 100	645
Piraña	00°39.379′ S, 76°26.883′ W	1	§	669
Shipati				
1	00°31.086′ S, 76°32.412′ W	1	100 × 100	653
2	00°30.875′ S, 76°32.258′ W	1	100 × 100	731
3	00°31.346′ S, 76°32.145′ W	1	100 × 100	656
Shiripuno	01°01.217′ S, 76°58.567′ W	1	100 × 100	628
Tiputini				
2	00°37.681′ S, 76°08.693′ W	1	§	623
5	00°38.267′ S, 76°08.615′ W	1	100 × 100	734
Totals		15		9809
Averages (per hectare)				654
Peru				
Amigos downriver				
1	12°32′ S, 70°05′ W	1	100 × 100	515
2	12°32′ S, 70°05′ W	1	100 × 100	465
Amigos upriver				
1	12°30′ S, 70°06′ W	1	100 × 100	565
2	12°30′ S, 70°06′ W	1	100 × 100	601
Barranco	11°53′ S, 71°23′ W	0.875	irregular‖	525
Diamante	12°19′ S, 70°56′ W	1	100 × 100	586
Maizal				
1	11°48′ S, 71°28′ W	1	100 × 100	622
2	11°48′ S, 71°28′ W	1	100 × 100	688
Pakitza				
1	11°58′ S, 71°13′ W	1	100 × 100	612
3	11°58′ S, 71°13′ W	1	100 × 100	565
Trans-Manu ravine				
1	11°53′ S, 71°21′ W	1	100 × 100	564
2	11°53′ S, 71°21′ W	1	100 × 100	643
Trans-Manu terrace				
1	11°53′ S, 71°21′ W	1	100 × 100	616
2	11°53′ S, 71°21′ W	1	100 × 100	724
Totals		13.875		8291
Averages¶				598

† The palm *Iriartea deltoidea* is the most common species overall.

‡ Common species are those 150 species with landscape-scale densities of ≥1 tree/ha. Overall there are 1014 species in the Ecuadorian plot network and 693 species in the Peruvian plot network.

§ Ten parallel transects of 10 × 100 m, transects separated by 100 m.

‖ Roughly square.

¶ Averages are per hectare except for Barranco, which are per 0.875 ha.

APPENDIX B

Voucher information for the Ecuadorean specimens deposited in the long-term collections of five herbaria—the National Herbarium of Ecuador (QCNE; Quito, Ecuador), the Catholic University of Ecuador Herbarium (QCA; Quito, Ecuador), the Missouri Botanical Garden (MO; Saint Louis, Missouri, USA), the Alfredo Paredes Herbarium, Central University of Ecuador (QAP; Quito, Ecuador), and the Herbarium of the Universidad San Francisco de Quito (USFQ; Quito, Ecuador)—is available in ESA's Electronic Data Archive: *Ecological Archives* E082-021-A1.

APPENDIX C

A phylogeny of Amazonian tree families, based on the hypotheses of Chase et al. (1993), is available in ESA's Electronic Data Archive: *Ecological Archives* E082-021-A2.

APPENDIX A. Extended.

Percentage of stems belonging to common species†	No. individuals		No. species	No. common spp.‡	No. singletons	Basal area (m^2)		
	Single commonest sp.	*Iriartea deltoidea*†				All spp.	Common spp.‡	Single commonest sp.
62	39	39	226	86	132	30.3	14.7	1.1
60	51	51	237	86	137	23.8	14.5	1.6
65	53	53	220	91	115	28.7	14.6	1.5
67	53	53	243	99	130	37.3	20.7	1.6
56	24	24	218	77	112	18.9	10.3	0.7
63	57	40	217	89	108			
65	84	84	295	100	165	35.3	20.3	2.2
63	27	26	211	83	104	29.6	17.8	1.1
63	42	40	249	100	134	37.8	21.9	1.1
55	44	44	273	92	142	26.1	13.3	1.2
61	87	87	279	94	165	34.0	17.2	2.5
67	80	80	235	85	133	38.5	20.7	1.8
66	29	29	188	82	80	22.9	14.4	0.8
57	20	20	248	100	128			
68	81	67	248	96	131	29.6	18.3	1.5
		737	1017	150				
63	51	49	239	91	128	30.2	16.8	1.4
69	21	3	166	81	80	25.8	16.7	0.4
62	32	5	147	70	65	22.9	13.9	2.1
76	48	48	174	92	86	27.9	19.3	2.5
70	39	39	205	94	100	25.3	17.3	1.7
78	43	4	153	76	81	28.8	21.8	1.1
72	29	29	151	70	65	35.2	21.4	1.2
71	85	85	185	93	91	30.1	20.9	4
69	42	42	203	86	96	32.6	20.2	2
78	179	62	150	72	77	30.3	21.1	5.7
72	28	7	126	59	53	19.9	15.8	0.5
74	67	67	180	87	87	32.8	19.1	2.6
71	42	42	217	103	113	33.8	18.2	1.4
83	81	81	158	93	66	31.7	25.6	3.8
78	73	73	185	91	80	31.2	25.3	2.7
		587	693	150				
73	58	42	171	83	81	29.2	19.8	2.3