A COMPARISON OF TREE SPECIES DIVERSITY IN TWO UPPER AMAZONIAN FORESTS

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Abstract. We inventoried two Amazonian tree communities separated by ~1400 km of continuous lowland tropical forest, in an effort to understand why one was more diverse than the other. Yasuní National Park, near the equator in eastern Ecuador, has one of the most diverse tree communities in the world. Manu National Park, at 12° S in Peru's Madre de Dios region, is only moderately diverse by upper Amazonian standards. Following the field inventories, a database of morphological, ecological, and other traits was compiled from the taxonomic literature for 1039 species from the plots. Our goals were (1) to describe how terra firme tree communities at the two sites differed in composition, diversity, and structure; (2) to characterize the ''extra'' species responsible for the higher diversity at Yasuní; and (3) to assess, in the light of those observations, some explanations for why forests near the equator are so diverse.

Yasuní has ~1.4 times as many tree species as Manu at all three spatial scales we examined: local (1 ha), landscape (<10 000 km²), and regional (<100 000 km²). Yasuní samples contain more families and genera, more individual trees per unit area, and a larger proportion of small trees. Tree species at Yasuní have smaller stature, larger leaves, larger seeds, and smaller geographic and altitudinal ranges than those at Manu, and disproportionate increases in species diversity are observed within the Myrtaceae, Lauraceae, Melastomataceae, and several other families. Community structures were strikingly similar, with the same species (*Iriartea deltoidea*, a palm) dominating both sites at identical densities. Common species at Yasuní occur at the same densities as equally ranked species at Manu, but there are substantially more very rare species at Yasuní. The poorer tree flora is not a nested subset of the richer tree flora, though a majority of species in each inventory do occur at the other site.

Several models that offer explanations for geographic variation in tropical tree species diversity are assessed in light of these data. Most do a poor job of accounting for the patterns revealed by the inventories. We speculate that the most important factor in producing the higher diversity in Yasuní is its rainier, aseasonal climate, and we discuss two specific rainfall-related mechanisms that appear to be supported by the data: (1) year-round water availability allowing more species to persist in the understory at Yasuní and (2) a newly described ''mixing effect'' related to the higher stem density there.

Key words: Amazon basin; Ecuador; Manu National Park, Peru; Peru; species diversity; tropical forests; tropical trees; Yasuní National Park, Ecuador.

INTRODUCTION

Tree species diversity in the tropics varies dramatically from place to place. Some 1-ha plots in South America contain nearly as many tree species as the moist temperate forests of North America (Latham and Ricklefs 1993, Vásquez-Martínez and Phillips 2000). Others are less diverse than equivalent plots in temperate forests. Even within the Amazon basin, Fisher's alpha of trees in 1-ha plots ranges from 222 to 6 (ter Steege et al. 2000).

Most attempts to explain this geographical variation in tropical tree diversity have taken the form of multivariate regression analyses that combine data from different sites to look for correlations between diversity and environmental variables like rainfall or soil fertility (Whitmore 1975, Hall and Swaine 1981, Gentry 1988, O'Brien 1993, 1998, Phillips et al. 1994, Clinebell et al. 1995, Givnish 1999, Leigh 1999, ter Steege et al. 2000). But these studies can do little to pinpoint the specific processes that regulate diversity. For example, a positive relationship between diversity and rainfall

is consistent with several very different mechanistic hypotheses.

In this paper we come at the problem from a different angle, by describing how one of the most diverse tree communities in the Amazon basin differs in composition, structure, and species attributes from a moderately diverse tree community in the same region. The idea behind the approach is that comparing the traits of tree communities and species at two sites may reduce the broad question of why one site is more diverse than the other to the more focused question of why one site favors higher richness of certain kinds of species than the other (see Latham and Ricklefs 1993, Ricklefs and Latham 1993, Qian and Ricklefs 1999).

Of particular interest is identifying species guilds that contribute disproportionately to the difference in diversity between the sites. For example, is the richer site disproportionately rich in understory tree species? Is the poorer site especially poor in Lauraceae? In formal terms, we examine the null hypothesis that the two communities are distinguishable only by their difference in diversity. Characters found to deviate from the null hypothesis are then pursued and their contribution to the diversity differences assessed.

We use the same approach to test several existing explanations for why some tropical forests are more diverse than others. For five published models, we derive testable predictions about how a very diverse community should differ from a less diverse community, apart from the fact that it has more species. We also describe and test a previously unpublished explanation for geographic variation in diversity. Thus our aim in the paper is first a detailed bookkeeping of how the more diverse tree community differs from the less diverse tree community, and second, a testing of mechanistic models that explain their difference in diversity.

Study Sites

Trees were inventoried in and around Yasuní National Park, Ecuador ($\sim$01° S, 76° W) and in and around Manu National Park, Peru ($\sim$12° S, 71° W). Both forests are located at the westernmost margin of the Amazon river basin, <100 km from the Andean foothills. The two sites are separated by $\sim$1400 km and 11 degrees of latitude and the intervening landscape is unbroken closed-canopy tropical moist forest. Detailed descriptions of the Peruvian site are given in Terborgh (1983, 1990) and Terborgh and Petren (1991). The Ecuadorean site is described in Pitman (2000) and Herrera-MacBryde and Neill (1997).

Both sites are dominated by rolling or sometimes sharply dissected uplands that cover 80–90% of the landscape. Elevation does not exceed 500 m at either locale. The Peruvian site receives $\sim$2300 mm of precipitation per year and has a 3-mo dry season, while the Ecuadorean site receives $\sim$3200 mm and has no dry season. Mean shade temperature is $\sim$23°C at the Peruvian site and 24–27°C at the Ecuadorean site, and

absolute minima are $\sim$6°C and $\sim$15°C, respectively (Pitman 2000).

Both sites are underlain by geologically young deposits eroded from the Andes. Soils were collected at 19 of 24 plots from immediately beneath the organic layer and analyzed for texture, pH, percentage of organic matter, total nitrogen, and concentrations of four macronutrients and four micronutrients at an Ecuadorean Ministry of Agriculture soils laboratory (INIAP: Instituto Nacional Autonomo de Investigaciones Agropecuarias). Samples were acidic, low in most cations but rich in aluminum and iron, and lacked rocks and pebbles (Kapos et al. 1990, Korning et al. 1994, Woodward 1996; N. Pitman, *unpublished data*). The proportion of sand in samples ranged from 11% to 51% in Yasuní and from 27% to 85% in Manu. On average, Manu samples contained more than twice as much sand as Yasuní samples (*t* test, $P < 0.01$), as well as less organic matter, more total nitrogen, and less magnesium. All other means (pH, concentrations of P, K, Ca, Fe, Mn, Cu, and Zn, and pooled nutrient concentrations) were statistically indistinguishable between the two sites.

Methods

Data collection

At both sites we established a network of small plots scattered over large areas of terra firme (unflooded) forest. Nine plots ranging in size from 0.875 to 2 ha and totaling 13.875 ha were established in Manu; 15 1-ha plots were established in Yasuní. Plots are mostly square or rectangular, but seven of the Yasuní plots are long, narrow transects. Five of the Manu plots are 2-ha rectangles, and in analyses these were treated as two 1-ha samples. Interplot distances average >30 km in Yasuní and >50 km in Manu, with the most distant plots at both sites >100 km apart. The nonrandom placement of individual plots across these landscapes reflects our attempt to sample a broad range of soil and topographic conditions. Additional information on the plot network, including a map of the study sites, plot coordinates, and plot dimensions, is given in Pitman et al. (2001).

In each plot all free-standing trees $\geq$10 cm dbh (measured at $\sim$1.3 m above the ground surface) were measured for circumference and either identified or collected. Collected specimens were subsequently identified to species or sorted to morphospecies (morphologically similar species-level taxa) by comparing them with mounted material in the National Herbarium of Ecuador. Voucher specimens were subsequently sent to taxonomic specialists for additional identification and are currently deposited in Peruvian, Ecuadorean, and North American herbaria. Detailed voucher information for the Yasuní inventory is available in ESA's Electronic Data Archive: *Ecological Archives* E082-021-A1 (Pitman et al. 2001).

At the time of the inventories 2.8% of the trees in Yasuní plots and 2% of the trees in Manu plots were leafless, dying, or otherwise unassignable to species or morphospecies. These unidentified individuals were lumped together into a single category of unknowns and were not included in species counts. They were included when tabulating stem densities and basal area measurements. Thus alpha diversities reported in this paper underestimate to a small extent the true number of species in a plot.

Some of these plots and transects were not established by the authors (see Pitman et al. 2001), but we have standardized taxonomic identifications through recensusing old plots and reidentifying previously vouchered material. All identifications in the Manu plots were made by P. Núñez and J. W. Terborgh. All identifications in 12 of the 15 Yasuní plots were made by N. C. A. Pitman; those in the remaining three were initially made by C. E. Cerón, D. A. Neill, W. A. Palacios, and M. Aulestia, and later confirmed by N. C. A. Pitman. The >4000 voucher specimens collected in the Yasuní inventory have not yet been compared with the Manu vouchers, so the two data sets are not standardized in their morphospecies taxonomy. Some of the data presented in this paper have appeared elsewhere in different forms (Phillips et al. 1994, Cerón and Montalvo 1997, Palacios 1997, Terborgh and Andresen 1998, Pitman et al. 1999, 2001, Condit et al. 2002).

Both study sites have been the focus of long-term inventory efforts by the Missouri Botanical Garden, and species concepts in our data sets are based on checklists maintained by that museum. Taxonomy in the Peruvian data set follows Brako and Zarucchi (1993), while taxonomy in the Yasuní data set reflects the state of Missouri's TROPICOS database in the years 1997–1999 (i.e., it predates Jørgensen and León-Yánez [1999]).

Measuring diversity

Local diversity was defined as the number of species and morphospecies found in a hectare. Landscape diversity is the total number of species and morphospecies recorded in each plot network and thus an incomplete list of the tree flora in the <10 000 km² areas containing the plots in each country. Regional diversity was derived independently of our plot data, via checklists that summarize historical plant collections in the study regions. We used Jørgensen and León-Yánez's (1999) estimate of the number of tree species occurring in the ~67 000 km² Amazonian lowlands of Ecuador and Brako and Zarucchi's (1993) checklist, updated with our own unpublished data, to estimate the number of tree species occurring in the ~78 000 km² department of Madre de Dios, Peru. Because these checklists include species growing in non-terra firme forest and may be significant underestimates of regional diversity

(Pitman et al. 2001), only the landscape-scale data were used for analyses involving large-scale diversity.

The beta diversities of these communities are not treated here, but analyses of compositional turnover with distance and between habitats have been published elsewhere (Pitman et al. 1999, Pitman 2000, Condit et al. 2002). Pairwise comparisons of Yasuní hectares average 0.37 on the Sørenson similarity index (i.e., hectares share ~37% of their species on average); the comparable number for Manu is 0.33 (R. Condit and N. C. A. Pitman, *unpublished data*).

Forest structure and community structure

Mean basal area per hectare and stem density were compared between sites via *t* tests. Differences in size-class distributions were assessed by comparing an 8152-tree sample from Manu with a 9206-tree sample from Yasuní.

We compared the local community structures of the two sites by comparing mean abundance attributes of 1-ha plots at each site with *t* tests. These attributes included the mean number of species in a hectare that were represented by one individual (the mean number of singletons), the mean number of species represented by two individuals, and likewise up to the mean number of species represented by seven individuals. We also calculated the mean number of individuals belonging to the most abundant species in each hectare, the mean number of individuals belonging to the second-most abundant species in each hectare, and likewise up to the mean number of individuals belonging to the 13th-most abundant species in each hectare. To compare local community structure graphically, we plotted these mean abundance attributes in the form of rank-abundance distributions that illustrate typical abundance patterns for 1-ha plots in Yasuní and Manu (Fig. 3).

Species attributes

We searched the taxonomic literature for morphological, ecological, and other attributes of the identified species at the two sites (sources include Flora of Ecuador, Flora Neotropica, Croat 1978, Spichiger et al. 1989, 1990, Killeen et al. 1993, Mabberley 1997, Vásquez-Martínez 1997). The resulting matrix includes information on 36 different traits for 1039 species, though not all information has been located for every species. None of these trait data represent our own measurements of the trees at our study sites; rather, they are published measurements of herbarium specimens collected at one or more locations in each species' range.

For 20 attributes with sufficiently large sample sizes, we examined the null hypothesis that species assemblages did not differ between the two sites. Nine of these attributes are listed in Table 1. The other 11 were: maximum corolla dimension, maximum leaf length, minimum and maximum seed width, minimum and maximum seed length, minimum and maximum fruit

TABLE 1.   Mean values of nine morphological and ecological attributes for five subsets of named species in tree inventories in Yasuní National Park, Ecuador, and Manu National Park, Peru.

| Subset | Mean values | | | | | | Percentage | | Mean date described |
	Latitudinal range(°)	Longitudinal range (°)	Range size†	Maximum elevation in range (m)	Maximum tree height (m)	Minimum leaf length (cm)	Dioe-cious‡	Com-pound leaves§	
Manu plot network	25.4[A] [152]	30.9[A] [151]	953[A] [151]	1013[BC] [236]	24.6[ABD] [520]	9.0[AB] [482]	27	28	1876[A] [473]
In Manu plots and not in eastern Ecuador	16.7[B] [29]	19.8[BD] [29]	538[BD] [29]	716[A] [49]	23.6[CDE] [128]	8.4[BC] [118]	23	27	1890[B] [135]
Shared by both plot networks	27.4[A] [97]	33.6[A] [96]	1061[A] [96]	1078[CD] [144]	26.1[B] [298]	9.5[ACD] [276]	32	31	1871[A] [246]
In Yasuní plots and not in Madre de Dios	11.8 [92]	16.6[D] [92]	275[D] [92]	803[A] [100]	21.3[E] [247]	11.1 [226]	24	27	1914 [226]
Yasuní plot network	20.4[B] [213]	25.8[B] [212]	690[B] [212]	979[BD] [275]	23.6[AC] [619]	10.1[D] [570]	27	29	1891[B] [534]

Notes: Sample sizes are given below the means, in brackets. Within a column, means not followed by the same letter are significantly different at the $P = 0.05$ level.
† Product of latitudinal and longitudinal ranges.
‡ Percentage of dioecious species.
§ Percentage of species with compound leaves.

length, minimum and maximum fruit width, and presence in Central America. Five subsets of species were scrutinized separately: (1) all species occurring in the Yasuní plots, (2) all species occurring in the Manu plots, (3) species shared by both plot networks, (4) species occurring in the Manu plots and not known to occur in eastern Ecuador, and (5) species occurring in the Yasuní plots and not known to occur in the department of Madre de Dios. All 10 pairwise comparisons for each species character were assessed via *t* tests, using Tukey's honestly significant differences correction for multiple comparisons.

Assessing the contribution of community attributes to diversity

To estimate how many species were lost from a Yasuní hectare when a given number of stems was removed, we applied rarefaction (Sanders 1968, Hurlbert 1971) to the typical abundance distribution of a 1-ha plot (see Fig. 3). Linear relationships between the stem number and species number of full hectares were used to estimate how many species were gained by a plot when a given number of stems was added. A linear relationship is a reasonable approximation in this case because the relatively large sample sizes and short extrapolation distances mean that the relevant segment of the species-individual curve is approximately straight.

Algebra and contingency tables (chi-squared tests) were used to assess the relative contributions of particular attributes to the observed differences in local and landscape diversity. For instance, we used the proportion of Manu tree species belonging to the family Rubiaceae to calculate an expected number of Rubiaceae species in Yasuní by assuming the same proportional representation. Because chi-squared tests showed the number of Rubiaceae species observed in Yasuní to be significantly higher than the expected number, we then divided the number of "excess" Rubiaceae species by the number of "excess" Yasuní species at the landscape scale to estimate the proportion of the greater landscape diversity in Yasuní attributable to a higher diversity of Rubiaceae. Estimates calculated for a single spatial scale were converted using the ratio of local species diversity to landscape species diversity in Yasuní (239:1017). In other words, a process that contributed 100 extra species at the landscape scale was estimated to contribute 24 species at the hectare scale, and vice versa.

A strict partitioning of the "extra" diversity was not undertaken, because explanatory variables overlapped. For example, some proportion of the higher diversity in Yasuní is due to a higher number of endemic species and some proportion is due to a higher number of understory tree species, but several of the endemic species are understory trees. Here the proportions are reported independently, with the understanding that the partitioning is not exclusive.

RESULTS

Overview

Upland forests in Yasuní are more diverse at all spatial scales and all taxonomic levels than their counterparts in Manu (Appendix, Fig. 1). The challenge is to explain an additional 65 species/ha at the local scale in Yasuní, an additional 324 species at the landscape scale, and an additional 352 species at the regional scale.
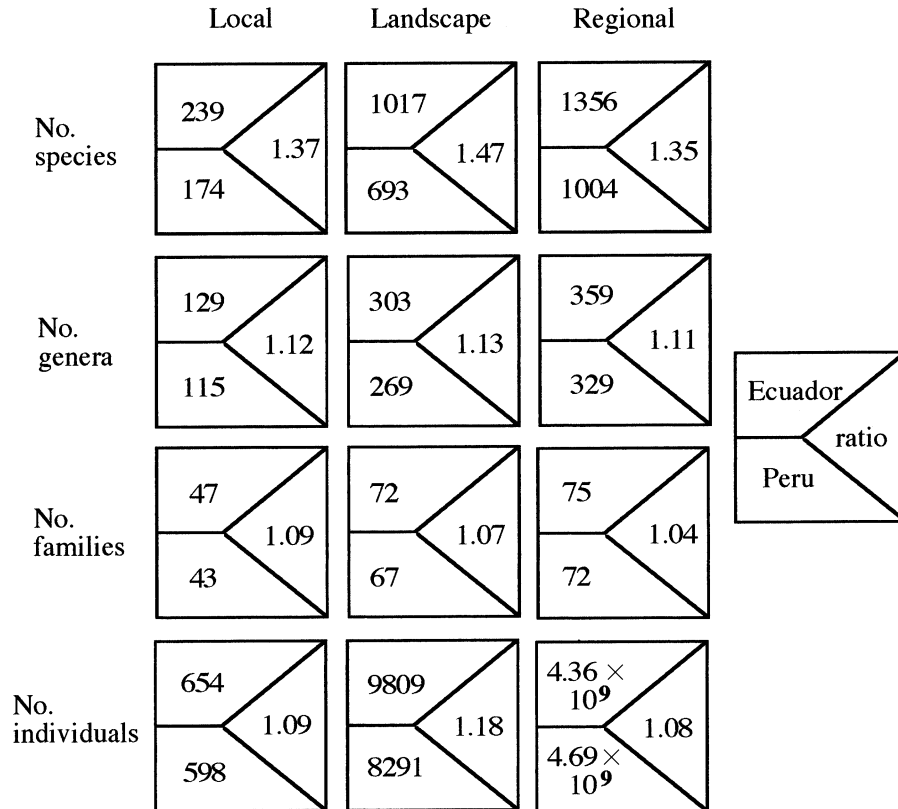
FIG. 1. Tree diversity and stem density at three spatial scales and three taxonomic levels for the two sites. Values at the local scale are means for 1 ha. Values at the landscape scale are from the combined data sets for each site (15 ha in Yasuní, Ecuador, and 13.875 ha in Manu, Peru). Values at the regional scale are for the ~78 000 km² department of Madre de Dios in Peru and for the ~67 000 km² eastern lowlands of Ecuador. See *Methods: Measuring diversity* for further explanation.

The Manu plots contained 8291 trees ≥ 10 cm dbh belonging to 67 families, 269 genera, and 693 species-level taxa. Mean stem density was 598 trees/ha (range = 465–724), mean basal area was 29.2 m²/ha, and mean local diversity was 174 species/ha (range = 126–217). The Yasuní plots contained 9809 trees ≥ 10 cm dbh belonging to 72 families, 303 genera, and 1017 total species-level taxa. Mean stem density was 654 trees/ha (range = 542–790), mean basal area was 30.2 m²/ha, and local diversity averaged 239 species/ha (range = 188–295). The total number of identified species (not including morphospecies) in the two plot networks is 1039. Morphospecies (taxa sorted to species level but not yet identified) account for 36% of all taxa in Yasuní and 22% of all taxa in Manu. Data for individual plots are given in the Appendix.

Forest structure

Forests in Yasuní terra firme average 9% more trees ≥ 10 cm dbh per unit area (a difference of 56 trees/ha) than those in Manu, but the difference is only marginally significant due to high within-site variation (*t* test, $P < 0.06$). Yasuní forests also show a higher proportion of small stems and a lower proportion of very large stems (Fig. 2) and contain on average two fewer big trees (dbh > 50 cm) per ha. Because most of the higher stem density in Yasuní is contributed by small trees, basal area per hectare and thus total biomass per hectare are not significantly different between the sites (*t* test, $P = 0.64$).

Rarefying 56 trees from the mean abundance distribution of a 1-ha plot in Yasuní (see Fig. 3) resulted in a loss of 12 species. Adding 56 trees to a Manu hectare resulted in a gain of 10 species. Thus 11/65 = 17% of the difference in local diversity between the two sites can be attributed to unequal sampling intensity related to the difference in stem density. Assuming that these additional species scale up to the landscape at the same ratio in the same proportion as species number (239/1017), then higher stem density gives 47 "extra" species at the landscape level in Yasuní, accounting for 15% of the difference at that scale (Fig. 4).

Community structure

The same species was most common in both forests and at the same density (the palm *Iriartea deltoidea*:
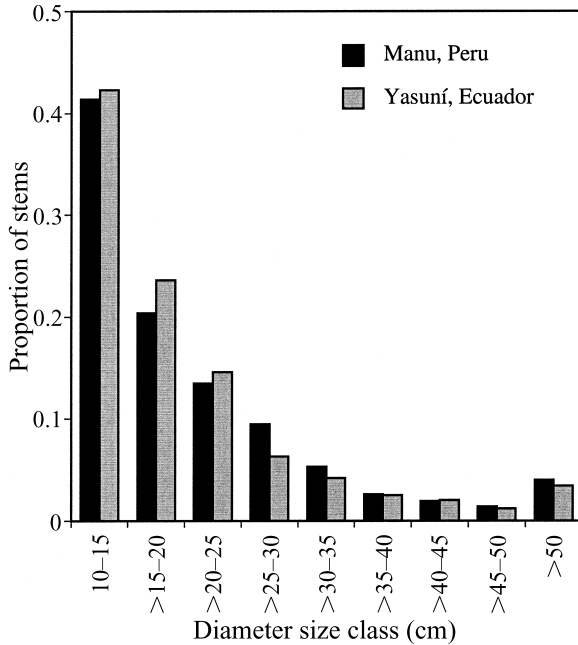
FIG. 2. Diameter size-class distributions (measured in centimeters of diameter at breast height) in tree plots in Yasuní, Ecuador, and Manu, Peru. Proportions are based on a 8152-tree sample for Manu and a 9206-tree sample for Yasuní. Note that there are proportionally more small trees in Yasuní and proportionally fewer large trees.
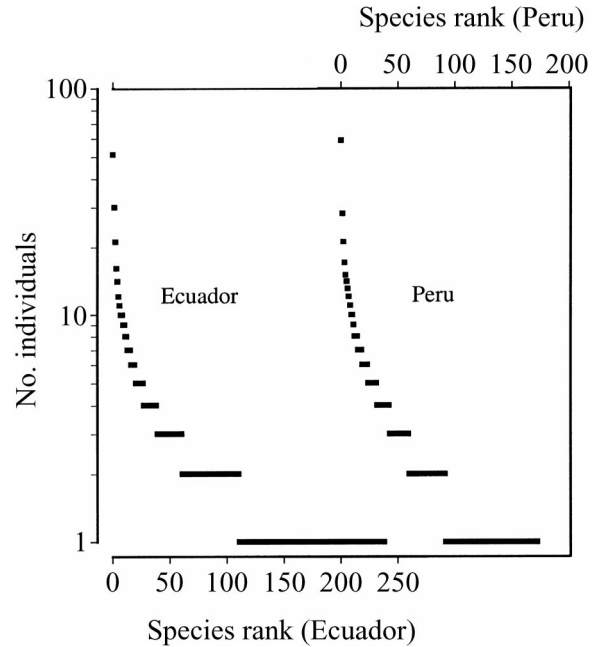

FIG. 3. Rank-abundance diagrams showing mean abundance attributes of 1-ha samples of tree communities in Yasuní, Ecuador, and Manu, Peru. The only significant difference between the distributions is the longer "tail" of rare species in the Ecuadorean community. See *Methods: Forest structure and community structure* for explanation.

Yasuní mean = 49 individuals/ha, Manu mean = 42 individuals/ha, t test, $P = 0.50$). Most attributes of local community structure at the two sites are statistically indistinguishable (Fig. 3). There is no difference in the mean number of individuals belonging to the most abundant species in hectares of the two forests ($P > 0.55$), nor in the mean numbers of individuals belonging to the 2nd through the 13th most abundant species. In the middle of the distribution, there is no significant difference in the number of species represented by four, five, six, or seven individuals (all P values > 0.05).

The only significant differences between the two curves are in the tails (rank ~40 and below). There are more species represented by one, two, or three individuals in a hectare of Yasuní forest than in a hectare of Manu forest (all P values ≤ 0.01). Yasuní hectares average 47 more singletons than Manu hectares, as well as 18 more doubletons, and five more tripletons. Taken together, these 70 "extra" rare taxa account for most or all of the difference in diversity at the three spatial scales examined (Fig. 4).

Taxonomy

At the landscape scale, the Yasuní inventory recorded nearly 10% more families than the Manu inventory (Fig. 1). This has a negligible effect on species diversity, however, since the additional families are obscure and species-poor in lowland Amazonia (e.g., Symplocaceae, Oleaceae, Santalaceae, all with a single species

in the Ecuadorean plots). Higher family-level diversity contributes only five species at the landscape scale in Yasuní and one species at the hectare scale, for ~1.5% of the higher species diversity at both scales (Fig. 4).

Generic diversity is also higher in Yasuní. For every genus recorded in the Manu data set there are 1.13 in the Yasuní data set. This ratio is lower than the cor-
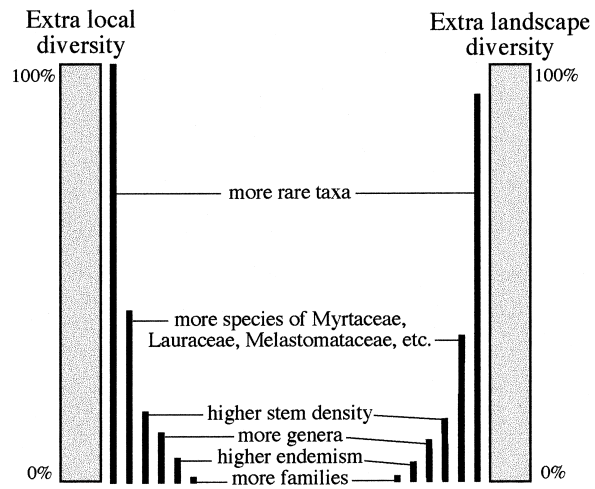

FIG. 4. Proportions of the "extra" local and regional diversity in Yasuní (Ecuador) accounted for by various factors. Factors sum to more than 100% because they are not mutually exclusive.
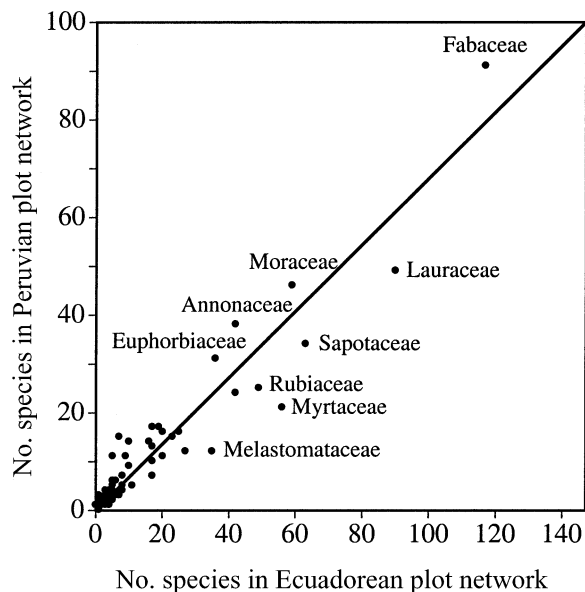
FIG. 5. Species diversity of families in plot networks in Yasuní, Ecuador, and Manu, Peru. The diagonal line marks the null hypothesis that a family's Peru:Ecuador ratio in species diversity is equal to the overall Peru:Ecuador ratio in species diversity for the entire data set, 1.47. Families below the line are more diverse than expected in Yasuní; those above the line are less diverse than expected in Yasuní.

responding value for species diversity (1.47), indicating that higher species diversity in Ecuador is due more to an increase in the number of species per genus than to an increase in the number of genera. The species/genus ratio in the Manu data set is 2.6, compared with 3.0 for Yasuní.

The most diverse families at both sites are the large, cosmopolitan families that dominate forests throughout the lowland tropics (Ricklefs and Renner 1994). The number of species belonging to a family in one data set is a good predictor of the number of species belonging to the family in the other (Fig. 5; Spearman's rho, $P < 0.0001$). In several families the ratio of Yasuní/Manu diversity diverges significantly from the overall ratio of 1.47 (chi-squared tests, df = 1, $P < 0.05$). Families with significantly more species than expected in Yasuní include Myrtaceae (26 more species), Lauraceae (20), Melastomataceae (17), Burseraceae (10), and Elaeocarpaceae (6). Sapotaceae, Rubiaceae, and Meliaceae have 14, 13, and 7 more species than expected in Yasuní, respectively, but these increases are only marginally significant ($P < 0.10$). Together, these families contribute 113 "extra" species to the Yasuní landscape. This translates to nearly 35% and 42% of the "extra" diversity at landscape and local scales, respectively.

Only three families show significantly lower-than-expected species diversity in Yasuní: Apocynaceae (15 species fewer than expected), Rutaceae (11), and Ster-

culiaceae (11). Other families with large but nonsignificant shortfalls in Yasuní include Fabaceae (13), Annonaceae (12), Euphorbiaceae (9), Arecaceae (7), and Moraceae (7).

Biogeography

Of the 1039 identified species in the two plot networks, 30% occur in both networks, and roughly half are known to occur in both geographic areas. At least 68% of the identified species in the Manu plots are known to occur in eastern Ecuador, while at least 55% of the identified species in the Yasuní plots are known to occur in the department of Madre de Dios. At least 300 tree species in the Yasuní plots have never been collected in southeastern Peru, but these are counterbalanced by at least 200 species in the Manu plots that have never been collected in Ecuador.

Seventeen of the 1017 species in the Yasuní plots (1.7%) have never been collected outside of eastern Ecuador, while only one of those in the Manu plots is thought to be endemic to the department of Madre de Dios (the recently described *Klarobelia candida*; see Chatrou 1998, Pitman et al. 1999). Higher endemism sensu Gentry (1986, 1992, i.e., geographical restriction at the 50–75 000 km² scale) therefore accounts for ~5% of the difference in landscape diversities and a correspondingly tiny fraction of excess local diversity (Fig. 4). The 20–60 apparently undescribed taxa among our Yasuní morphospecies may prove to be geographically restricted at some scale, but their addition to the tally of endemics will probably be counterbalanced by range extensions of other species currently believed to be endemic (Pitman et al. 1999).

At a larger spatial scale, 28% of the Yasuní species not known to occur in southeastern Peru, and for which range size data are available, have geographic ranges that do not exceed 6° in either latitude or longitude (for ranges of <500 000 km²). These species, while not endemics by Gentry's definition, may be restricted to a large patch of equatorial western Amazonia characterized by rather homogeneous geology and aseasonal climate (Pitman 2000).

At least 45 genera found in the Yasuní plots have never been collected in southeastern Peru, and these genera account for 67 species or 20.7% of the "extra" species at the landscape scale in our Yasuní data set. Since each of those 67 species has a 23.5% chance of occurring in a Yasuní hectare (i.e., 239/1017), we expect to find 16 species belonging to these genera at the local scale, equivalent to almost a quarter of the "extra" diversity there. However, there are also 26 genera in the Manu plots that have never been collected in eastern Ecuador. About half of the gain in species diversity in Yasuní due to higher generic diversity there is offset by a loss of species in genera that do not reach the region.

Fourteen families believed to have immigrated into South America as part of the biotic interchange that

followed the continent's collision with Central America (Raven and Axelrod 1974, Gentry 1982) were recorded in the Yasuní inventory, while 10 were found in the Manu inventory. As the proportion of Laurasian species is the same at both sites (~3.5%), remnant historical effects from the biotic interchange play no role in producing the observed differences in diversity.

Species attributes

Tree species in Yasuní show trends towards shorter stature, smaller geographic ranges, larger leaves, and larger seeds than trees in Manu (Table 1). Identified species in the Yasuní plots had smaller mean latitudinal and longitudinal ranges than those in the Manu plots, with species in Yasuní ranging an average of five fewer degrees both latitudinally and longitudinally. Species occurring in the Yasuní plots and not known to occur in the Peruvian department of Madre de Dios had significantly smaller geographic and altitudinal ranges, larger leaves, smaller maximum heights, and longer (but not wider) seeds than all species occurring in the Yasuní plots. They were also more recently described by taxonomists and less likely to be dioecious. We found no significant differences between any subsets for flower size (generally corolla length) and fruit size (minimum and maximum fruit length and width).

Discussion

Overview

Forests in Yasuní have ~40% more tree species than forests in Manu, at each of the three spatial scales examined. The higher diversity at Yasuní seems to derive from a greater abundance of rare species, geographically restricted species, and smaller-statured tree species, and these tend to belong to a few large families. These trends are superimposed on contrasts in the physical structure of the tree communities, with denser, smaller, larger-leaved forests growing at Yasuní. At the same time, there are some marked similarities between the Ecuadorean and Peruvian forests, which share more than half their species and are dominated by equally dense populations of the palm *Iriartea deltoidea*.

These are complex patterns open to many interpretations, and they point to no single explanation for why the Ecuadorean forest contains so many more tree species than the Peruvian one. We begin this discussion by reviewing four published theories proposed to explain variation in tropical tree species diversity that do not appear to be supported by our data. It should be noted that these ideas are tested strictly in the context of the Yasuní–Manu comparison, i.e., their rejection here does not necessarily undermine their validity in other cases or at other spatial scales.

Two more promising ideas are then presented, and methods for disproving them discussed. The first idea focuses on the physiological benefits for understory plants of growing in a wetter, more stable climate. The second describes how higher stem density may increase local species diversity, above and beyond the obvious recognition that larger samples contain more species. The paper concludes with a brief inventory of other unmeasured factors and untested mechanisms that may also be playing important roles in producing Yasuní's higher diversity.

Because local and regional diversity tend to be strongly correlated (Cornell and Lawton 1992, Holt 1993, Caley and Schluter 1997), the most parsimonious approach to understanding the difference in diversity between Yasuní and Manu might be to assume that the patterns we observed are the consequence of a process operating at a single scale. For example, one might argue that the question of why hectares in Yasuní are more diverse than hectares in Manu is a trivial footnote to the question of why eastern Ecuador as a whole is more diverse than southeastern Peru (Hubbell and Foster 1986), or vice versa (Balslev et al. 1998). That approach is supported to some degree by our finding that average hectares in both Yasuní and Manu contain the same proportion of their respective regional floras (17.6% in Yasuní, 17.3% in Manu; Fig. 1). However, we have outlined our misgivings with this approach elsewhere (Pitman 2000), and the discussion that follows reflects our expectation that a satisfying explanation for why one hectare of tropical forest has more tree species than another will need to explain how three factors intersect—regional diversity, stem density, and the degree to which common species dominate local communities.

Unsupported models

The congeneric diversity hypothesis.—It has been suggested that the species richness of diverse tree communities may be the result of conditions allowing the coexistence of numerous species in hyperdiverse genera like *Inga* and *Pouteria*, or, alternatively, explosive speciation in these groups (Rogstad 1989, Rankin de Merona et al. 1992, Valencia et al. 1994, De Oliveira and Mori 1999, Wright 1999). We tested the idea by counting the number of species in large genera (those containing five or more species) in the Manu data set and comparing the corresponding numbers for Yasuní. Of the 23 large genera in Manu, the majority showed a *smaller* increase than one would expect if species diversity had increased in these genera at the average rate of 1.47. Only 6 of the 23 large genera (26%) had more species in Yasuní than expected, and together these contributed only 17 additional species. We repeated the test for the same genera by counting the number of species known from eastern Ecuador and the department of Madre de Dios, according to recent checklists of the areas (Brako and Zarucchi 1993, Jørgensen and León-Yánez 1999). Again, no evidence was found for a larger-than-expected increase in the diversity of large genera, leading us to reject the congeneric diversity hypothesis. Disproportionate richness

in a few higher taxa is not unique to diverse communities like Yasuní, but a common attribute of biological communities worldwide (Willis 1922, Dial and Marzluff 1989).

The biodiversity crossroads hypothesis.—This model proposes that some forests are especially rich in tree species because they stand at the intersection of different phytogeographic regions (see Mori 1990, Prance 1994, De Oliveira and Daly 1999, De Oliveira and Mori 1999). The idea is intriguing, but it has not yet been stated in a testable fashion, and it relies on the poorly defined boundaries of South American phytogeography. It is also somewhat circular, in that a flora with two species will tend to have more diverse geographic range patterns than a flora with one. Thus it is difficult to assess the value of this idea from our perspective, i.e., to determine to what degree the Ecuadorean site has a richer flora than the Peruvian site simply because of its geographic location in South America.

The data, however, suggest that the ''extra'' tree species in Yasuní are not visitors from neighboring phytogeographic regions, e.g., spillover from the nearby lower montane forests of the Andes. Though many of the excess species in Yasuní belong to families typical of Andean forests (Myrtaceae, Lauraceae, Melastomataceae, etc.), they have lower elevational maxima and smaller geographic ranges than the Manu flora (Table 1). The standard error of geographic range size is also lower for Yasuní species than for Manu species. Indeed, it is the poorer Manu flora whose diversity is boosted by an infusion of species from another phytogeographic region: wind-dispersed genera like *Gallesia*, *Pterygota*, and *Physocalymna* characteristic of the nearby dry forests of Bolivia and absent from Yasuní.

Given that null models predict the centers of artificial continents to harbor more diversity than the edges when species distributions are scattered at random (Colwell and Hurtt 1994, Colwell and Lees 2000), the crossroads explanation may be valid for the place it was proposed for, centrally located Manaus. But it does not work as a general explanation for geographical variation in tropical plant diversity. The Chocó region of Colombia and Brazil's Atlantic Forest provide good counterexamples of high local tree species diversity within single, well-defined phytogeographic regions on the margins of the South American continent (Faber-Langendoen and Gentry 1991, Herrera-MacBryde et al. 1997). Alternatively, a site may lie at the intersection of many floristically different forests, but if none of those forests are very diverse it will remain poor in species. This returns us to the original question: Why are some forests more diverse than others?

The Janzen-Connell hypothesis.—Density-dependent mortality of young plants caused by pathogens, herbivores, and seed predators is well documented in tropical forests (Janzen 1970, Connell 1971, Condit et al. 1994, Gilbert et al. 1994; other examples reviewed

in Leigh 1999). Givnish (1999:195) has recently proposed that the strength of these processes might vary geographically with climate, since wetter, aseasonal forests should support larger communities of ''insects. . . , fungi, nematodes, or other small-bodied, desiccation-intolerant natural enemies'' (also see Wright 1999). In this model, stronger density-dependent mortality in rainier Yasuní would tend to lower the densities of tree species there, creating more space in the community for rare species and thereby increasing diversity.

This is not what happens. There are many more rare species in Yasuní than in Manu, but not because common species occupy any less space there. Common species in Yasuní occur at the same densities as correspondingly ranked species in Manu (see Fig. 3). *Iriartea deltoidea*, the most common tree species at both sites, occurs in Yasuní and Manu at the same mean density. These patterns challenge assumptions that species in more diverse forests must necessarily grow at lower densities (see for example Givnish 1999). The reason that Yasuní can be more diverse than Manu without its species becoming rarer is that the increase in the number of tree species in a hectare of Yasuní forest is matched by an almost identical increase in the number of trees, and most of the additional species are singletons. So while frequency-dependent mortality probably does play an integral role in maintaining the diversity of these communities by limiting the densities of common species (Terborgh et al. 2002; but see Wright 1999), we reject the idea that the higher diversity in Yasuní is the result of geographic variation in the strength of that mechanism.

The intermediate disturbance hypothesis.—Connell (1978) has hypothesized that an intermediate regime of disturbance might favor the development of a diverse tree community (see also Horn 1975, Hubbell 1979, Tilman and Pacala 1993, Huston 1994, Phillips et al. 1994, Wright 1999), by allowing a mix of species guilds that could not persist under very extreme or very mild disturbance regimes. An explanation based on unequal disturbance rates is supported by structural differences between our two communities. The Yasuní forest has more stems, smaller stems, and fewer massive trees than the Manu forest (see Fig. 2), and a more active disturbance regime in Yasuní would be a satisfying explanation for these patterns. Rainier sites tend to have more violent storms, more lightning strikes, heavier epiphyte communities, shallower roots, more erosion, and mechanically weaker, more waterlogged soils than drier sites and thus can be expected to have a more active tree-fall regime (Huston 1994, Givnish 1999, and others). Rainier forests in Brazilian Amazonia are also subject to a higher frequency of large blowdowns (Nelson et al. 1994). Seen from this perspective, the Yasuní forest may have more tree species than Manu because a more active disturbance regime

there allows for a larger contingent of early- and mid-successional species.

Though the idea is attractive, the data do not provide strong support for it. The density of trees in the family Cecropiaceae, which typically require gaps to germinate, is lower in Yasuní than in Manu, contrary to the expectation if there were a more active disturbance regime in Yasuní. Cecropiaceae accounts for a mean of 3.4% of trees in Yasuní but 4.5% of trees in Manu (22 and 27 individuals/ha, respectively). The guild of early successional tree species is not significantly more diverse in the Yasuní plots, either, with only three more species and morphospecies of Cecropiaceae there than in Manu. And published turnover rates for Ecuadorean plots are *lower* than those from southeastern Peru, though data are sparse (mean annual turnover rate for Manu = 2.16%, $n = 3$; for Yasuní = 1.65%, $n = 3$; data from Phillips et al. [1994] and Palacios [1997]).

Promising models

The modern climate/understory diversity hypothesis.—The most striking environmental differences between our Peruvian and Ecuadorean forests are climatic, and it is tempting to link the higher diversity in Yasuní to a more hospitable climate for plant growth there. Manu's seasonal drought (five continuous months averaging <120 mm of rain) and cold (as low as 8°C at Cocha Cashu and 4.5°C at nearby Puerto Maldonado) present plants there with much more severe physiological challenges than the aseasonal climate in Yasuní, where no month averages below 100 mm of rain and absolute temperature minima reach only ~15°C (Pitman 2000). Thus one mechanism reducing diversity in Manu may be a simple climatic filter, in which drought or cold prevents the establishment or persistence of species adapted to wet and warm conditions (Gentry and Ortiz 1993).

But even were such a filter confirmed experimentally, it would not be a satisfying explanation for the difference in diversity between Yasuní and Manu. The reason is that there is also a climatic filter working the other way; i.e., there are a large number of taxa adapted to dry forest that occur in Manu but not in Yasuní. So while climatic factors probably do restrict certain species to only one of our sites, assessing the effect of those filters on the difference in diversity will require an understanding of why more species are adapted to wet environments than dry.

Wright (1999) and Givnish (1999) have recently reviewed other mechanisms by which higher rainfall might lead to higher woody plant diversity. Two of these, higher disturbance rates and higher pest pressure, are not strongly supported by our data (see *Unsupported models: The Janzen-Connell hypothesis* and *The intermediate disturbance hypothesis,* above). A third explanation is that higher water availability in rainier sites may allow more species to survive and regenerate under the physiological constraints imposed by low
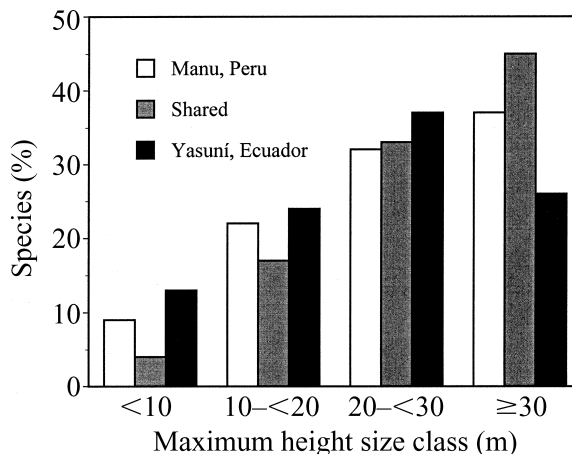

FIG. 6. Proportion of species that are understory trees, mid-story trees, and canopy trees in three subsets of identified species in the data set. "Manu" bars show data for 112 species in the Peruvian plot network that are not known to occur in eastern Ecuador; "shared" bars show data for 298 species shared by the Ecuadorean and Peruvian plot networks; "Yasuní" bars show data for 240 species in the Ecuadorean plot network that are not known to occur in southeastern Peru.

light levels in the understory (Gentry 1982, Gentry and Emmons 1987, Smith and Huston 1989, Wright 1992, Huston 1994, Givnish 1999). This notion suggests that the "extra" diversity in wetter sites should be concentrated in smaller-statured species that spend most of their life in the shade.

Our data appear to support the idea. The subset of species unique to Yasuní has the smallest average stature in our data set (Table 1), and a disproportionate increase in diversity is observed in families characterized by small trees (e.g., Myrtaceae, Melastomataceae). A similar trend towards elevated diversity of smaller taxa in richer sites is found when Yasuní's woody plant community is compared to that of Barro Colorado Island, Panama (R. Valencia, *personal communication*).

But the model comes with a number of caveats. First, the proportion of very small tree species is only slightly higher in Yasuní than in Manu (Fig. 6), and there is a similarly large contribution to Yasuní's higher diversity from canopy trees (20–30 m tall). Second, it is conceivable that *any* mechanism that enhanced tree diversity overall might concentrate species in the understory, because the canopy will become saturated with species much more rapidly than smaller size classes, due to its necessarily lower stem density (Fig. 2). Third, forests at Manaus, Brazil, receive only slightly more rain than those in Manu (Laurance 2001), but have higher local tree diversity than Yasuní (Ferreira and Rankin-de-Mérona 1998, De Oliveira and Mori 1999).

This last observation points to a simple test of the understory diversity idea. If the diverse forest in Manaus also has a rich sub-canopy flora, then higher water

availability is unlikely to be the only source of the higher understory diversity in Yasuní. Alternatively, greenhouse or transplant experiments can test whether the combined physiological stress of low light and periodic drought might prevent some Yasuní species from persisting in seasonal forests. Finally, the hypothesis makes the testable prediction that the geographic ranges of many of Yasuní's ''extra'' sub-canopy species should be largely predictable from rainfall and seasonality maps of the Amazon basin.

The mixing hypothesis.—A hectare of forest in Yasuní contains 56 more trees ≥ 10 cm dbh, on average, than a hectare of forest in Manu. Traditionally, ecologists have treated such density differences as little more than a sampling nuisance that must be corrected before proceeding on to a careful comparison of diversities. For example, one might typically (as we did) use rarefaction to remove 56 randomly selected trees from a typical Yasuní hectare, record the average of 12 species lost in the process as the amount of excess diversity attributable to Yasuní's higher density, and then proceed on to other explanations for the excess species that remain after the correction (Sanders 1968, Gotelli and Graves 1996).

But a diversity-enhancing effect of density may persist in these corrected data. The reason is that vacant sites in denser forests, all else being equal, will be within the effective dispersal range of more adult trees and will therefore receive propagules of more species than vacant sites in sparser forests. If competitive interactions among colonizing seedlings are weak (i.e., if the winning species is selected more by chance than by competitive superiority), then models show that the more diverse seed rain in denser forests will translate, over time, into lower levels of conspecific clumping and a larger number of species for a given number of stems.

We call this idea the mixing effect, though it is just a previously unappreciated facet of dispersal limitation. Dispersal limitation has been mostly invoked to demonstrate how competitively inferior species can resist extinction indefinitely in plant communities (Hurtt and Pacala 1995, Hubbell 2001). We suggest that the mechanism is also a promising explanation for large-scale variation in plant diversity, and, more specifically, for the Yasuní-Manu difference in tree diversity. The key observation is that dispersal limitation is inherently weaker in denser plant communities than in sparser plant communities, because the distances that plants must disperse their seeds to colonize a vacant site shrink as plants grow closer together. If the outcome of colonization lotteries is determined by chance, then the more diverse seed rain in denser forests will lead to a broader array of outcomes and lower the probability that adjacent vacant sites are occupied by individuals of the same species.

The mixing effect differs from most other diversity-enhancing mechanisms in that it neither accelerates speciation nor slows extinction. Instead, its contribution is to mix a landscape's existing diversity more evenly in space, leading to higher concentrations of species for a given number of contiguous stems. The mixing effect is not the ''density effect'' (Denslow 1995). Several generations are required for the mechanism to generate higher diversity, which means that it is only pertinent for cases in which the stem densities of the communities being compared are at or near equilibrium. It has no relevance to temporary variation in plant density, e.g., as a result of disturbance or succession.

The mechanism is easily demonstrated in computer simulations. We used a simple, standard null model of forest dynamics developed by C. Webb and D. Peart (2001; see also Hubbell [1979], Chesson and Warner [1981]), in which cells on a grid are occupied by individual trees that suffer random mortality and are replaced by a lottery among seeds contributed by trees in the cells surrounding a vacancy. In the model, two forests initially identical in everything but density showed significantly different numbers of species in the same number of contiguous stems after 1000 generations (N. C. A. Pitman and C. Webb, *unpublished data*).

Similar results have been obtained in recent papers examining the effect of different dispersal rates in modelled communities (Hubbell 2001, Chave et al. 2002, Condit et al. 2002). In a typical example, Hubbell (2001:215) showed that higher dispersal rates (lower dispersal limitation) between metacommunities lead to higher local diversity, because the dominance of locally common species is reduced by increased competition with immigrating species. Hubbell's analysis also shows that dispersal can theoretically regulate diversity at a variety of spatial scales, not just locally. Our contribution here is to observe that significant variation in the strength of dispersal limitation should be expected at large spatial scales in the Neotropics, even between communities whose species have identical dispersal capabilities, because the strength of dispersal limitation can vary with the equilibrium stem densities of those communities.

The mixing effect is a promising explanation for the Yasuní/Manu difference in diversity because it predicts two key features of the comparison. First, it predicts that most of the ''extra'' diversity at a richer site will derive from very rare species (Hubbell 2001, Chave et al. 2002). Second, it predicts that conspecific trees will be more clumped in space in Manu than in Yasuní. That appears to be true, because simulated hectares of stems selected at random with replacement from the combined Manu data set, and thus free of conspecific clumping, average 45% more species than actual Manu hectares, compared with only 30% in Yasuní.

But this model, too, comes with several caveats. Some tropical forests are both very dense and very poor in species, which suggests that the diversity-enhancing

effect of better dispersal is easily swamped by diversity-depressing mechanisms. In addition, the mechanism only works if the winners of colonization lotteries are picked by chance. If certain species are competitively superior, then high dispersal rates will depress diversity quickly, as all sites are colonized by those species. Finally, the model's most obvious prediction, that conspecific individuals should be more clumped at less diverse sites, is not supported by a comparative study of tree distributions in three other tropical forests (Condit et al. 2000).

History and other models

There are many other unexplored factors that could potentially lead to the higher diversity observed in Yasuní (see Rohde 1992, Schluter 1993). In an earlier analysis (Pitman 2000), we found little support for the habitat diversity hypothesis (MacArthur 1964, Shmida and Wilson 1985) and the endozoochory hypothesis (Givnish 1999), though we were not able to test those ideas rigorously. No attention has been given here to soil nutrients (because the data suggest the sites are edaphically similar), nor to light, mycorrhizal associations, or interactions between the >2000 tree species in these forests and their uncountable animal associates. Perhaps the most tractable of these missing pieces of the puzzle is light. Forests at different latitudes show differences in the quantity, quality, color, intensity, and angle of illumination they receive (Terborgh 1985, Endler 1993), and local tree species diversity in Amazonia shows a strong latitudinal gradient, with the most diverse samples located within five degrees of the equator (ter Steege et al. 2000).

We have also avoided discussing historical effects on diversity. This is mostly because clear predictions about plant diversity have yet to emerge from the debate on Amazonian paleoclimatic history. Though we concur that history can be an important source of variation in diversity (Ricklefs and Schluter 1993, Ricklefs et al. 1999), we suspect that its role in this case is minor, having been largely erased by dispersal. There do not appear to have ever been geographical barriers isolating the Ecuadorean site from the Peruvian site, meaning that species in western Amazonia have been free since their origins to migrate from one site to the other. If the Peruvian site experienced much more severe drying during the last glacial maximum, then it is conceivable that some species driven locally extinct in southern Peru during the Pleistocene but capable of surviving there now have not yet returned due to slow migration rates. However, climatic models explain 86% of the regional-scale variation in North American tree species diversity (Currie and Paquin 1986) and 79% of the variation in South African woody plant species diversity (O'Brien 1993, 1998), and we see no reason why tree species in Amazonia, with their much less dramatic climatic history, should be any less at equilibrium with climate than tree species elsewhere.

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APPENDIX

A table presenting the distinguishing characteristics of 24 tree plots in Yasuní National Park, Ecuador, and Manu National Park, Peru, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-059-A1.