

Dynamics and species richness of tropical rain forests

(mortality/diversity/turnover/disturbance/productivity)

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ABSTRACT We present a worldwide analysis of humid tropical forest dynamics and tree species richness. New tree mortality, recruitment, and species richness data include the most dynamic and diverse mature tropical forests known. Twenty-five sites show a strong tendency for the most species-rich forests to be dynamic and aseasonal. Mean annual tree mortality and recruitment—turnover—is the most predictive factor of species richness, implying that small-scale disturbance helps regulate tropical forest diversity. Turnover rates are also closely related to the amount of basal area turnover in mature tropical forests. Therefore the contribution of small-scale disturbance to maintaining tropical forest diversity may ultimately be driven by ecosystem productivity.

The inverse relationship of species richness with latitude has long attracted ecologists' interest. Some explanations concentrate on the evolutionary origins of high tropical diversity; others focus on its maintenance. High community and regional diversity in the tropics has been linked to available energy (1–3), species-specific predation (4), and delayed competitive exclusion (5–7). Yet, the existence of major differences in species richness among tropical forests, of similar theoretical interest, has only recently been well documented (8–12).

Several hypotheses link tree diversity to disturbance at varying spatial and temporal scales. Frequency- or density-dependent mortality may enhance diversity (13). Locally unpredictable disturbance may counteract the effects of pairwise, predictable competitive displacement (7). Environmental contrasts within and among tree-fall gaps may favor trees with different regeneration requirements (14, 15).

Predictions of each have been examined in specific tropical forests. Thus, Brandini *et al.* (16) showed differential survival among species in different parts of gaps in La Selva, Costa Rica. Condit *et al.* (17) demonstrated density-dependent mortality affecting the most abundant tree species in Barro Colorado Island, Panama. Yet, few coincident data on tropical forest species richness and turnover have been reported, hindering biome-wide evaluation of the dynamics–diversity relationship. In this paper we show that variation in tree species richness among tropical forests not subject to large-scale natural disturbances is related to their dynamism, defined as the mean rate of mortality and recruitment, which in turn is related to productivity. We hypothesize that productivity ultimately drives long-term ecosystem dynamics in mature tropical forests, since the faster a forest grows the more rapid stem turnover must be, as long as total biomass is capped by constraining factors. Therefore, high productivity may help maintain exceptional species richness through

promoting frequent, spatially unpredictable small-scale disturbance.

METHODS

We investigate dynamics and species richness at 25 mature forests from all major tropical regions. Original data come from Peru and Sarawak, where trees ≥ 10 cm in diameter at breast height (d.b.h.) were identified, with additional data from the literature and colleagues [refs. 18 (AN), 19 (AN), 20 (BE), 21 (BL), 22 (K1-2), 23 (KI), 24 (LS), 25 (MA), 26 (PA), 27 (PA), 28 (QU), 29 (S1), 30 (S2), 31 (SC), 32 (SC), and 33 (SM)]; personal communications: W. Palacios and D. Neill; D. Nicholson; J. Terborgh, R. Foster, and P. Nuñez]. In 1983 A.H.G. and R.V. inventoried ten 1-ha (1 ha = 10,000 m²) square plots in seven floristically distinct forests in Amazonian Peru (8, 9). Eight plots were periodically re-enumerated up to 1993, including one established by G. Hartshorn in 1979. In Sarawak, nine 0.6-ha plots representing three forest types at two localities have been monitored since 1965 by P.H. and colleagues (34, 35). Literature data were limited to physiognomically mature humid forests.## The square or nearly square plots often approach the maximum contiguous samples possible without floristic discontinuities. We tallied tree species richness at the most completely identified census as “species per 500 stems ≥ 10 cm d.b.h.” (Table 1; §§). We use this measure for two reasons. First, it describes species richness as a proportion of stem density, similar to mortality and recruitment computations. Second, it circumvents differences in stand density that affect total species found in fixed-area samples of diverse forests (10).

We developed a measure of stem turnover (Table 1) to dampen the effects of short-term fluctuations in population dynamics, calculated in a three-step process. First, following convention (36), we estimated mortality (λ) as \log_e survivor-

Abbreviations: d.b.h., diameter at breast height; PCA, principal components analysis.

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##Mean temperature, $>20^\circ\text{C}$; mean annual precipitation, >1600 mm, ≤ 4 consecutive months <100 mm; stem density and basal area close to steady state; multi-aged stand with large lianas. Median interval used to calculate turnover = 13.7 yr.

§§Species richness for new sites from the best vouchered year (1983: MI, YA, T2; 1985: ME, L1, L2, JS, T1, T5; 1987: T3, T4). Species number derived from: 500 contiguous stems, species/area curves, or the best estimate available, for trees ≥ 10 cm d.b.h. (sources as for dynamics). Vouchers of Peruvian morpho-species at MO, USM: Gentry 45576–46250, 51064–558, 57535–58155, Vásquez 12081–134. Basal area is the mean of each inventory, except L1, L2, ME, T1 (final), BE, JS (first). Tambopata, Lambir, Sepilok, and Kade forest types classified by edaphic and hydrological factors; calculations per forest type based on total area inventoried.

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Table 1. Site data for trees ≥ 10 cm d.b.h. in mature continental tropical forests

Site	Latitude, longitude	Soil and topography	Rain [dry]	Alt., m	A, ha	Time, yr	M	R	D	BA	SD	BAD	Spp ha ⁻¹	Spp-500
T1: Tambopata, Peru	12°49'S, 69°43'W	Waterlogged swamp; 1	2350 [3]	255	0.6	7	0.702	0.940	0.821	57.9*	713	0.405	60	51
T2: Tambopata, Peru	12°49'S, 69°43'W	Alluvial-clay, upper floodplain; 4	2350 [3]	255	0.95	7.75	1.835	2.827	2.331	33.5	523	0.562	168	166
T3: Tambopata, Peru	12°50'S, 69°43'W	Clay, old floodplain; 3	2350 [3]	255	1.0	7.75	2.845	2.372	2.608	26.9	546	0.835	173	164
T4: Tambopata, Peru	12°49'S, 69°43'W	Clay, upland; 3	2350 [3]	260	1.0	11.67	1.969	1.958	1.964	29.1	575	0.497	172	157
T5: Tambopata, Peru	12°49'S, 69°42'W	Sandy-clay, upland; 2	2350 [3]	270	2.0	7.75	2.691	2.245	2.468	26.8	546	0.633	160	156
MA: Manú, Peru	11°45'S, 71°30'W	Alluvial-clay, upper floodplain; 5	2028 [3]	400	0.94	15.5	2.290	1.807	2.049	35.9	649	—	189	151
MI: Mishana, Peru	3°47'S, 73°30'W	Sandy humult, upland; 1	3500 [0]	140	0.95	7.58	1.620	1.174	1.397	29.0	841	0.458	275	204
YA: Yanamono, Peru	3°16'S, 72°54'S	Alluvial-clay, old floodplain; 4	3500 [0]	140	1.0	9.75	2.806	2.322	2.564	32.7	574	0.834	283	267
JS: Jatun Sacha, Ecuador	1°04'S, 77°40'W	Clay, upland; 3	4000 [0]	450	1.0	5.0	1.461	1.626	1.544	30.5	724	—	246	205
AN: Añangu, Ecuador	0°32'S, 76°26'W	Clay, upland; 3	3244 [0]	370	1.0	4.92	1.886	1.803	1.845	23.1	734	0.531	153	125
SC: San Carlos, Venezuela	1°56'N, 67°03'W	Sandy, upland; 2	3500 [0]	119	1.0	10.33	1.143	1.432	1.288	23.0	744	—	83	69
BE: Belém, Brazil	1°30'S, 47°59'W	Clay, upland; 3	2760 [2]	30	2.0	15	1.841 [†]	0.809 [†]	1.325 [†]	27.7 [†]	572 [†]	0.489 [†]	118 [†]	107 [†]
LS: La Selva, Costa Rica	10°26'N, 83°59'W	Various; 4	3994 [0]	44	12.4	13	2.030	2.014	2.022	30.1	444	0.525	96	103
K1: Kade, Ghana	6°09'N, 0°55'W	Clay, upland; 3	1640 [3]	137	1.0	12	1.440	1.581	1.511	29.2	562	—	86	82
K2: Kade, Ghana	6°09'N, 0°55'W	Clay, colluvium; 3	1640 [3]	130	1.0	12	2.100	1.909	2.005	32.5	541	—	92	89
KI: Kibale, Uganda	0°27'N, 30°25'E	Sandy-clay, upland; 3	1700 [3]	1440	49.8	1.67	0.678 [‡]	—	0.678 [‡]	—	752	—	56	50
SM: Sungei Menyala, Malaysia	2°28'N, 101°55'E	Granite-derived alluvium; 4	2376 [1]	30	1.6	38	2.046	1.959	2.003	32.4	496	—	163	164
BL: Bukit Lagong, Malaysia	3°12'N, 101°42'E	Granite-derived, hill ridge; 2	2650 [0]	505	2.0	36	1.404	1.150	1.277	43.3	515	—	168	156
PA: Pasoh, Malaysia	2°55'N, 102°18'E	Granitic alluvium, and shale; 4	2000 [1]	90	8.0	13	2.069	1.710	1.889	29.1	530	—	210	201
S1: Sepilok, Sabah	5°10'N, 117°56'E	Sandy-clay, upland; 2	3150 [0]	40	1.81	6	1.106	1.418	1.262	42.1	655	—	156	138
S2: Sepilok, Sabah	5°10'N, 117°56'E	Alluvial; 4	3150 [0]	15	1.0	9.16	1.920	1.525	1.723	38.5	435	—	117	130
ME: Mersing, Sarawak	2°33'N, 113°04'E	Clay, basalt-derived, upland; 4	3905 [0]	264	3.0	22	1.246	1.434	1.340	43.6	438	0.584	100	134
L1: Lambir, Sarawak	4°11'N, 114°E	Clay udult, upland; 4	2874 [0]	114	0.6	20	2.337	1.938	2.137	43.4	462	0.768	212	235
L2: Lambir, Sarawak	4°11'N, 114°E	Sandy humult, upland; 1	2874 [0]	114	1.8	20	1.191	1.017	1.104	53.0	739	0.583	240	195
QU: Queensland Australia	17°02'S, 145°37'E	Granite-derived, hilly; 2	1800 [4]	730	0.41	32.2	0.671	0.397	0.534	69.6	957	0.423	108	84

Units are as follows: soil class, no.; rain, mm yr⁻¹; [dry], consecutive months <100 mm; mortality, recruitment, dynamism, % yr⁻¹; basal area (BA), m² ha⁻¹; stem density, trees ha⁻¹; BA dynamism, m² ha⁻¹ yr⁻¹. Alt., altitude; A, area; M, mortality; R, recruitment; D, dynamism; SD, stem density; BAD, BA dynamism; Spp ha⁻¹, species ha⁻¹; Spp-500, species per 500 trees.

*Approximate: diameters were inflated by high buttress roots; value given represents 75% of measured value in 1990.

[†]Stems ≥ 9.7 cm d.b.h.

[‡]Stems ≥ 13 cm d.b.h.

Table 2. Variables used for analysis

Variable	Description, units
Spp500	Species per 500 trees
Dynamism	Mean (annual mortality and recruitment), %
Trbasal	Transformed basal area ha ⁻¹ [-(basal ^{-0.5})]
Stem	Tree stems ha ⁻¹
Soil	Soil quality, 1-5
Rain	Mean annual rainfall, mm
Dry	Consecutive months <100 mm mean rainfall
Lat	Latitude, degrees and decimal fraction
Tralt	Transformed altitude, m amsl [ln(alt)]
Badyn	Basal area turnover, log _e model, m ² ha ⁻¹ yr ⁻¹
Climate	Climate factor (PCA factor 1)
Structure	Structure factor (PCA factor 2)
Zresidual	Spp500 minus predicted species richness, standardized (mean = 0, SD = 1)

PCA, principal components analysis; amsl, above mean sea level.

ship vs. time. Second, we developed an analogous logarithmic model to estimate annual recruitment (μ) into the 10-cm d.b.h. class, based on final recruitment and annual mortality of stems ≥ 10 cm d.b.h.¶¶ Third, we averaged mortality and recruitment rates. Averaging measured mortality and recruitment dampens noise inherent in the data. In using this mean value we assume that the community is close to steady state in terms of stem density (35, 37).¶¶¶

Precipitation data come from site (JS, K1-2, KI, LS, MA, SC, T1-5) or closest available sources (plot references and refs. 38-40). We used a simple index to code rainfall seasonality—"consecutive months with mean rainfall <100 mm." Available soil data are not easily comparable, being based on a variety of sampling and analytical methods. Therefore prior to our analysis we estimated forests' soil quality for sustaining plant growth on a scale of 1-5 (climate references). The poorest soils (1) are permanently anaerobic or very acid with low nutrient status and cation-exchange capacity, potential aluminum toxicity, and surface humus accumulation; poor sandy soils (2) have less pronounced humus accumulation and are well-drained. Intermediate (3) are leached clay soils, mostly derived from Tertiary or Quaternary sediments typical of large areas of moist forest. Richer soils (4) are derived from basalt, shale, volcanic ash, or recent alluvium; the richest (5) are periodically replenished by alluvium eroded from young mountains.

¶¶ Estimated annual recruitment, μ , is

$$\mu = \ln [(N_f)/(N_s)]/t$$

equivalent to solving for μ in:

$$N_f = N_o[e^{(\mu-\lambda)t}] - N_o(e^{-\lambda t}),$$

where for trees ≥ 10 cm d.b.h., $N_f = N_o - N_d + N_r$. N_o = original stems; N_f = final stems; N_d = original stems dying between inventories; N_r = recruited stems at final inventory; N_s = original stems surviving to final inventory; t = years between inventories; μ incorporates estimated unobserved mortality between inventories. We use total mortality as a proxy for mortality of stems recruited into the 10-cm d.b.h. class. {For comparable sites [YA, MI, T1-5, MA, Kade (combined), SM], annual mortality in the 10- to 20-cm d.b.h. class averaged 2.02% \pm 0.69% equal to total stem mortality (2.03% \pm 0.59%) ($t = 0.16$, $P = 0.88$).} Strictly, recruitment estimates should also incorporate a term based on the few trees that fall below 10 cm d.b.h. during the inventory period without dying; this phenomenon is rarely reported so we exclude it from the model.

¶¶¶ This assumption is *a priori* invalid for forests with evidence of major demographic changes caused by severe cyclones, flooding, drought, or other large disturbance (e.g., Barro Colorado Island, Panama, where mortality was much higher during and after the extreme 1982-1983 drought than before; R. Condit, personal communication).

Eight variables were available to describe species richness (Table 2). A PCA was performed to identify uncorrelated factors and reduce the number of independent variables. Multiple regression and partial correlation analysis were used to describe variance in species richness (Fig. 1). Finally, an ANOVA was performed on the variables, PCA factors, and regression model residuals in order to test for differences among phylogeographic regions.

RESULTS AND DISCUSSION

Three Amazonian forests have higher annual mortality (YA, T3, T5), and four (YA, T2-3, T5) higher recruitment, than any known mature tropical forest measured over a comparable time scale. Most new Peruvian forests have even higher mortality when liana and strangler stems ≥ 10 cm diameter are included [e.g., YA annual mortality is 2.81% for trees, 3.98% for lianas, 2.89% combined—with a half-life (36) of only 24 yr].

Several variables significantly correlated with species richness also covary with one another (Table 3). To reduce the number of variables and account for collinearity a PCA using orthogonal factor rotation was performed. Dynamism was left out of the PCA because we wished to test explicitly its relationship to species richness. Two factors resulted from the PCA. Rainfall was highly negatively correlated, and latitude and dry months were highly positively correlated with factor 1 (the

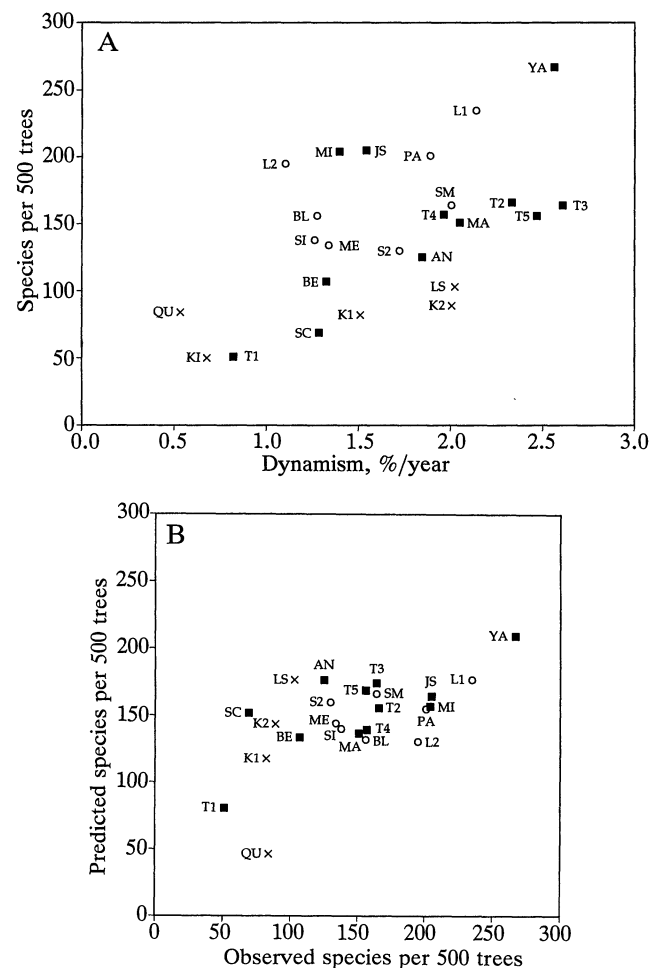


FIG. 1. (A) Tree species richness vs. dynamism (mean of annual mortality and recruitment). (B) Tree species richness predicted by multivariate regression model vs. observed tree species richness. \circ , Sites in South-East Asia; \blacksquare , sites in Amazonia; \times , sites in "Other" phylogeographical regions (Africa, Australia, and Central America). See Table 1 for complete site descriptions, Table 4 for multivariate model.

Table 3. Pearson correlation coefficients of all pairs of variables

	Dynamism	Trbasal	Stem	Soil	Rain	Dry	Lat	Tralt	Badyn	Climate	Structure
Spp500	0.55**	-0.05	-0.22	0.29	0.33	-0.45*	-0.17	0.13	0.72**	-0.29	-0.16
Dynamism		-0.54**	-0.61**	0.61**	0.07	-0.02	0.16	-0.23	0.75**	0.15	-0.67**
Trbasal			0.17	-0.21	-0.16	0.09	0.31	0.14	-0.24	0.23	0.35
Stem	(0.54**)			-0.65***	-0.09	0.17	0.07	0.47*	-0.52	-0.01	0.89***
Soil	(0.50**)				0.05	-0.06	-0.02	-0.25	0.49	0.12	-0.85***
Rain						-0.82***	-0.39	-0.28	0.14	-0.85***	0.01
Dry							0.68***	0.41	-0.25	0.95***	0.07
Lat								0.21	-0.18	0.83***	0.14
Tralt	(0.54**)								-0.08	0.36	0.54**
Badyn										-0.12	-0.51
Climate	(0.56**)										-0.04
Structure	(0.52**)										

$N = 24$ for all correlations except for Badyn ($N = 14$). PCA factors Climate and Structure were built from seven variables. First-order partial correlation coefficients of Dynamism with Spp500, controlling for the effect of each variable significantly correlated with Structure, and for each PCA factor, are given in parentheses in the Dynamism column. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Climate factor). Hence, sites with low Climate scores have high rainfall and little seasonality and are equatorial. Stem density and altitude were positively correlated, and soil and dynamics were negatively correlated with factor 2 (the Structure factor). This factor describes the observed coincidence of poor soils and higher altitudes with high-density forests.

Regression was performed to identify variables that best describe pantropical species richness. The explanatory power of Dynamism, Climate, and Structure was assessed by the change in r^2 due to each variable's addition to the model, after accounting for the effect of the other two variables (Table 4). The final model explains 38% of the variation in species richness for 24 pantropical sites (after removing KI, which has no basal area data). Dynamism explains the most variance in species richness, Climate explains about half as much; Structure describes 7% of the remaining variance, not a significant contribution to the overall model. Dynamism is correlated with Structure but this covariation is independent of the correlation between Dynamism and species richness, as shown in three ways. Structure and species richness are uncorrelated (Table 3). Model r^2 increases even after accounting for Structure and Climate. Finally, there are significant first-order partial correlations for Dynamism with species richness controlling for the effect of each variable that is well described by Structure and for the Structure factor itself. These partial correlations are of similar magnitude to the direct correlation of Dynamism with species richness.

There were few differences among phytogeographical regions for each of the measured variables (Table 5). (Regions were defined as Amazonia, South-East Asia, and Other for sites from Africa, Central America, and Australia.) The regions differ in the number of dry months (seasonality is least in South-East Asia) and basal area (forests are smallest in Amazonia). While there were no significant differences among regions in model residuals, Asian sites tended to have higher

species richness than expected from the recorded values of Dynamism and Climate, and Other sites had negative residuals—perhaps reflecting a historical effect of the relatively depauperate African and Central American floras (41, 42).

The least dynamic plots (KI, QU, T1) are among the least diverse, the most dynamic Asian plot (L1) is the most species-rich Asian forest in the dataset, and one of the two most dynamic plots (YA) represents the most species-rich forest reported in the world (9). But, clearly, there must be upper limits to the association between turnover and species richness: catastrophic disturbance can favor a few pioneer species at the expense of numerous more shade-tolerant species (43, 44).

As well as explaining variation in species richness, stem dynamics are likely a good substitute variable for forest productivity. In a dataset where net primary productivity and dynamics data are both known, they covary (45). Moreover, in our dataset basal area dynamism closely correlates with stem dynamics (Table 3). While we have no complete productivity data, basal area dynamism is a more direct measure of site productivity than regionally averaged factors such as actual evapotranspiration. Given the strong correlation of species richness with basal area dynamism (Table 3) this suggests that species richness is related to forest productivity.

In summary, there is a strong tendency for the richest forests to be aseasonal and subject to high stem turnover and basal area turnover rates (e.g., YA, L1) and for the least species rich to have seasonal climates and be less productive (e.g., T1, QU). Intermediate species richness, by the standards of humid tropical forests, is found on low-turnover aseasonal sites (e.g., L2, MI) and on high-turnover seasonal sites (e.g., MA, T2-3). Plot dynamics may be a better indicator of species richness than are any of the environmental factors that have been shown to correlate with tropical forest diversity. Annual precipitation, seasonality, and soil are all related to species richness on the 0.1-ha scale for Gentry's larger dataset (8, 12, 46), but in our analysis none of these factors is as closely related to species richness as turnover. Gentry's data come from single inventories—turnover rates were not obtained—so some of his correlations could be mediated through the effects of environmental factors on forest productivity and in turn on dynamics.

SYNTHESIS

Detailed investigations reveal different processes operating locally to maintain tropical forest diversity (15–17). Our approach complements these studies by addressing broad patterns in tropical forest diversity. More variance in species richness is explained by forest dynamics than by any other factor, indicating that small-scale disturbance is functionally related to community species richness. We suggest that these results can

Table 4. Regression analysis

Variable	F	P	Change in r^2
Dynamism	11.99	0.003	0.33
Climate	5.61	0.028	0.16
Structure	2.50	0.130	0.07
Variable	F	P	r^2
Final model	6.39	0.007	0.38
Dynamism	9.80	0.005	
Climate	4.70	0.04	

F, P, and r^2 change due to the addition of the stated variable after accounting for the effect of the other two variables given for Dynamism, Climate, and Structure. F, P, regression coefficients, and partial F for each variable in the final model are given. Model coefficients: Spp500 = 54.23 + 54.14(Dynamism) - 20.01(Climate).

Table 5. ANOVA of species-richness variables by region

Variable	F	P	Amazonia (12)	South-East Asia (8)	Other (5)
Spp500	5.51	0.01	151.8 + 59.5	169.1 + 37.7	81.6 + 19.5
Dynamism	1.54	0.24	1.85 + 0.58	1.59 + 0.39	1.35 + 0.71
Mortality	1.43	0.26	1.92 + 0.66	1.66 + 0.48	1.38 + 0.70
Recruitment	0.71	0.51	1.78 + 0.62 (12)	1.52 + 0.34 (8)	1.48 + 0.74 (4)
Trbasal	3.38	0.05	29.9, 26.1 (12)	39.8, 34.0 (8)	36.4, 21.7 (4)
Stem	2.10	0.15	645 + 103	534 + 109	651 + 204
Soil	0.19	0.83	2.8 + 1.2	3.1 + 1.3	2.8 + 0.8
Rain	1.97	0.16	2856 + 652	2872 + 570	2155 + 1030
Lat	1.72	0.20	4.06 + 5.56	3.59 + 1.18	7.94 + 6.19
Tralt	2.24	0.13	204, 127	85, 32	241, 42
Dry	5.80	0.01	1.67 + 1.50	0.25 + 0.46	2.60 + 1.52
Badyn	0.87	0.45	0.58 + 0.16 (9)	0.65 + 0.11 (3)	0.47 + 0.07 (2)
Climate	2.41	0.11	0.03 + 1.18	-0.50 + 0.35	0.78 + 1.03
Structure	0.61	0.56	0.14 + 0.80	-0.36 + 1.01	-0.03 + 1.47
Zresidual	2.05	0.15	-0.05 + 0.94	0.42 + 0.78	-0.71 + 1.10

F, P, and mean + standard deviation of the mean are given for each region for all variables and model residuals. Back-transformed means and lower 95% confidence interval are given for basal area and altitude. Badyn was only measured for 14 sites, Recruitment and Trbasal for 24 sites; regional sample sizes are given after the mean. N for all other ANOVAs is given at each region's column head.

be used to integrate some supposedly competing hypotheses of tropical diversity. In physiognomically mature forests, which therefore have constant biomass, we hypothesize that long-term turnover rates are a function of primary productivity. Thus, the ever-moist continuously warm climate that induces high forest productivity at richer soil equatorial sites leads to high turnover. In the more rapidly growing forests, numerous variously sized tree and branch falls contribute to a structurally complex environment with a wide range of available regeneration niches (14). Moreover, the frequent, spatially unpredictable nature of these small-scale disturbances reduces the potential importance of direct competitive interactions, allowing sympatric existence of ecologically equivalent species (7). In addition, edaphic specialization combined with habitat heterogeneity caused by river-induced large-scale disturbance results in high regional diversity in upper Amazonia (47). In concert with rapid turnover rates that delay local extinctions, regional diversity subsidizes local species richness in mature forests (48). Together, these factors allow maintenance of exceptional species richness.

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