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Supporting Online Material for

Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest

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Supplementary materials

Functional Traits Reveal Niche-Based Community Assembly in an Amazonian Forest

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Materials and Methods

Site

The Yasuní Forest Dynamics Plot (FDP) is a permanent forest census plot in the Center for Tropical Forest Science network located in a mature, Western Amazonian terra firme forest in Ecuador (0° 41'S, 76° 24'W) with an aseasonal climate (*S1, S2*). Our analysis is based on the first recensus of the western 25 ha (*S3*).

Trait collection

Leaf material was collected from randomly selected, censused individuals within the FDP; however, established criteria (*S4*) were used to reject individuals that showed heavy impact of herbivores, epiphylls, or that lacked sufficient recently produced, fully expanded and hardened leaves. We targeted outer canopy leaves of trees in the 1-5 cm dbh size class growing under closed canopy (see below) that were readily accessed from the ground. Two to five leaves were sampled from 1- 20 individuals from 1,089 species (*S5*). In many cases, the extreme rarity of species precluded more extensive within-species sampling. Restrictions on plot impacts precluded the sampling of entire leaves from large compound leaved species (e.g. *Guarea*), thus we collected and report measurements from the minimum photosynthetic unit (i.e. leaflets in compound-leaved species) present on the plant.

SLA was measured using leaf punches, which correlated very well with whole leaf SLA measurements (*S4*) in our preliminary dataset (r^2=0.92, N=409). Leaf size for entire leaves was estimated using Area= Length*Width*0.70, which correlated very well in our preliminary data (r^2= 0.98, N=742) with photographic area estimates using ImageJ (*S6*), as others have previously reported for tropical leaves (*S7*). For lobed leaves, leaf size was calculated exclusively from photographs (*S4, S6*). Leaf nitrogen concentrations (on a mass basis) were analyzed from bulked and ground species samples on a Carlo Erba NC 2500 Soil Elemental Analyzer at the University of California, Berkeley, using acetanilide (10.36% N and 71.09% C) as a reference standard. Height estimation was complicated in Yasuní by a very dense canopy, therefore we used maximum diameter at breast height (dbh), which is allometrically related to height (*S7, S8*), as a proxy. When estimating maximum size, it is often preferable to average the three largest individuals, though this procedure tends to underestimate the maximum size of rare species (*S9*). Therefore, we followed King *et al.* (*S9*) and averaged the largest three dbh values for common species (500+ individuals), the largest two for less common (100-500 individuals), and the largest observation for rare species (<100 individuals). Using the single largest individual or the average of the three largest for all species (when available) did not significantly alter the outcome of our analyses. Dried masses of seeds collected from traps and underneath fruiting trees in the FDP were kindly provided by S.J. Wright and N. Garwood (*S10*). Trait coverage is shown in Table 1, and correlations are shown in Table S5. We followed prior studies utilizing trait-community methods (*S11-14*) by normalizing species trait values via log transformation when necessary.

Trait metrics

All data analysis was performed in the R statistical programming language (*S15*). The FDP was divided into 625 20 x 20 m quadrats (mean richness 129.5, mean stem density 233.5), and for each quadrat, species trait means were matched to the species present in the quadrat to calculate the distribution of trait values. In each quadrat, metrics of trait dispersion were compared to a null expectation. We used community trait range and mean as measures sensitive to habitat filtering (*S14*) and the standard deviation of nearest neighbor distance (as defined by trait distances along univariate trait axes, not physical distance) and kurtosis as measures sensitive to niche differentiation (*S11, S13, S16*). Each trait was considered independently as they were largely orthogonal in our dataset, with the exception of SLA and nitrogen concentrations (Table S5). Species without a given trait value were excluded from that particular analysis. Rarefaction of the SLA dataset (which has close to full species coverage, Table 1) suggests that missing species values do not artificially inflate the proportion of significant results (see below).

Null models

Null distributions of our trait metrics were generated by creating 999 null communities of equal richness to the sample quadrat by drawing species at random from our entire trait database, weighted by plot-wide occurrence (the number of quadrats in which each species is found). We also considered an abundance-weighted null (Table S2) and a presence-absence null (Table S3). We report the occurrence-weighted null in the main text as it produced the most conservative results. We discuss a fourth null, a modification of the occurrence-weighted null that preserves the spatial pattern of species occurrences, below.

As a point of clarification, while Neutral Theory shares some characteristics with ecological null models (*S17*), there are compelling arguments to view it instead as a process-based mechanistic model of species coexistence (*S18*).

Assessing significance

Our primary means of assessing the significance of each metric comes from a plot-wide Wilcoxon signed rank test with a null hypothesis that the observed values of each metric for the 625 quadrats, relative to their respective null distributions, were evenly distributed about the null expectation (Figs. 1C, 1D, S2, S3) (*S13*), summarized in Table 1. We also report a second test in which individual quadrats were judged significantly non-random if the observed metric fell into the extreme 5% of the null distribution, summarized in Table 2. In all analyses, two-tailed tests were used for trait means, while one-tailed tests were used for all other metrics based on a priori predictions of habitat filtering and niche differentiation. The trait means exhibited spatial autocorrelation, which we corrected for in the Wilcoxon test p-values (see below and Table 1).

Sapling and adult comparisons

For the sapling and adult comparison (Table 3), tests of each size class were repeated with an adjusted null pool and recalculated plot occurrences. We compared rankings of the small and large size class in each quadrat in their respective null, and tested if the trait metrics become increasingly non-random in the adult class using a Wilcoxon sign rank test. We removed shrubs and small trees whose maximum observed dbh in the plot was <10 cm from the analyses, as we would be unable to distinguish saplings and adults. However, leaving these smaller species in the analyses did not significantly alter the outcome of the analysis.

Spatial patterns

Limited dispersal plays a key role in Neutral Theory where, among other things, it modulates the strength of ecological drift within local communities. In real communities, limited dispersal can result in a clumped or spatially aggregated distribution of individuals within species. While this clumping of individuals should have no influence on the species-level trait patterns of the sort that we test for, it is a feature of Neutral Theory that is not captured in the occurrence-weighted null presented in the main text.

To explore this effect we ran a fourth null model that kept the spatial arrangement of species quadrat-level occurrences constant. In each application of the null model, the spatial arrangement of the occurrence patterns of each species were randomly rotated and moved across the landscape using a modification of the torus translation (*S19*). Thus, a species with clumped pattern of occurrences retains that clumped distribution and a species with widespread distribution retains its widespread distribution, but both are randomized relative to the landscape and other species. In tests with this algorithm we find similar results to the other null models - that is- evidence for both filtering and niche differentiation from all of the traits with strong statistical support in many trait/ test combinations. However, under this null model it is impossible to maintain constant diversity in the randomized quadrats, and for this reason we prefer the non-spatial occurrence-weighted null as out primary basis for significance testing.

Spatial autocorrelation may alter the outcome of the Wilcoxon signed rank test, as the significance level is influenced by sample size. Using semivariograms, we detected spatial structure in quadrat-level trait means in the main analyses (Figs. 1A and S1). To account for this, we subsampled all possible combinations of quadrats using a regular grid, with samples separated by at a distance where samples could be considered independent (the range parameter of the semivariogram). If any of those subsampled sets produced a Wilcoxon test $p > .05$, the mean test for that trait is reported as nonsignificant (n.s.) in Table 1.

Shade versus sun leaves

Leaves grown in full sun tend to show physiological differences as compared to their shade-grown counterparts and are preferred (*S4*) for trait measurement when available. However, because of practical constraints (lack of tower access, difficulty in accessing canopies of trees in a dense, tall tropical forest), we sampled individuals 1-10 cm dbh growing in shade. At Yasuní, individuals of this size class are predominantly located underneath a closed canopy (*S1, S2*). Many of the woody species in the plot are understory shrub and tree species that will never or rarely be exposed to full sun. Our sampling of sun leaves of 69 common canopy species growing in both sun and shade indicate that species relative rankings are relatively consistent between shade and sun (spearman's rho = 0.59). For these reasons, we use shade-grown leaf measurements as an indicator of light acquisition strategy for all species. A more conservative test of community patterns in the forest is to restrict our analysis to the smaller size class that we sampled from, ignoring larger individuals. We present this analysis for completeness, though it yields similar, if not stronger, conclusions (Table S7).

Intraspecific variation

Many community trait analyses treat intraspecific variation in traits as negligible, as the chosen traits typically vary far more between than within species (*S4, S20*). However, a high degree of intraspecific variation in functional traits could reduce our power to detect nonrandom trait patterns. In our SLA dataset, over 81% of the variation is due to species differences; individuals within species and leaves within individuals account for only 13% and 5% of the variation respectively. Some of this intraspecific variation may be driven by habitat effects, although our intensive sampling of 11 common and widespread species (Table S6) within the plot across the two major habitat types defined by Valencia et al. (*S2*) failed to detect an effect of habitat on SLA (Table S8). While the analysis did find a weakly significant effect of habitat on leaf size, (Table S8, $p= .05262$, sum of squares= 0.346) that effect was dwarfed by the effect of species ($p<.0001$, sum of squares=75.707), which explained greater than 200-fold more of the variation in the data than habitat. This suggests that in the case of leaf traits, species differences, not habitat-specific intraspecific plasticity, is the main source of variation.

Trait Coverage

Our trait database, while one of the largest amassed for a single plant community, does have substantial gaps, particularly for seed size and wood density (Table 1). While over 6 years of intensive seed trap collection have yielded substantial data from the FDP, seed masses for many species remain unknown. Likewise, wood density cores are not permitted inside the FDP, and so we are relying on estimates collected in other locations. These gaps make multivariate trait analyses (*S11, S14*) impractical, though we argue that the univariate analyses that we perform are more interpretable. We explored the effect of incomplete datasets on our analyses by rarifying our SLA dataset (which in total provides coverage for 98% of species and 99.95% of individuals within the plot) to 50 replicates of 100, 250, and 500 species subsamples, and then rerunning our null model analyses on the subsampled data. The percentage of significant plots either decreased or remained constant with decreasing species coverage, and the plot-wide Wilcoxon signed rank test did not return more significant results with rarified data. These results suggest that our main findings are robust to gaps in the trait data. Nevertheless, we urge caution in interpreting the results of seed mass and wood density tests until more complete trait data can be obtained.

As noted in the main text, analysis of additional traits for which data were not available at the time of publication may provide further insights into the processes occurring within plot. Because of this, some caution should be used in interpreting plots where observed trait patterns matched the null expectation as evidence for neutral processes, as convergence or divergence may have occurred along unmeasured axes.

Figure S1 Rank of average quadrat trait values in the null distribution for 5 traits in our analysis. SLA is shown in Figure 1A. Contours indicate topography within the plot (interval= 2 m). See main text for more information.

Figure S2 *First column*: histograms of the distribution of each trait in our database. All traits except wood density are log transformed. *Second column:* Results of null model tests of trait range. Points indicate the observed range of each trait (all are log transformed except wood density) in each quadrat as a function of quadrat richness, black line indicates the range value predicted by the null model, dashed line indicates the 5% confidence interval of the null distribution. See Tables 1 and 2 for statistical tests. *Third column:* Same format as second column, except for the standard deviation nearest neighbor distance.

Figure S3 Continuation of Figure S2 for trait mean, kurtosis and variance. Dashed lines in trait mean panels (first column) correspond to 2.5% and 97.5% confidence interval as two tailed tests were used; dashed lines in all other panels correspond to 5% confidence intervals as one-tails tests were used. See Tables 1 and 2 for associated statistical tests.

Figure S1

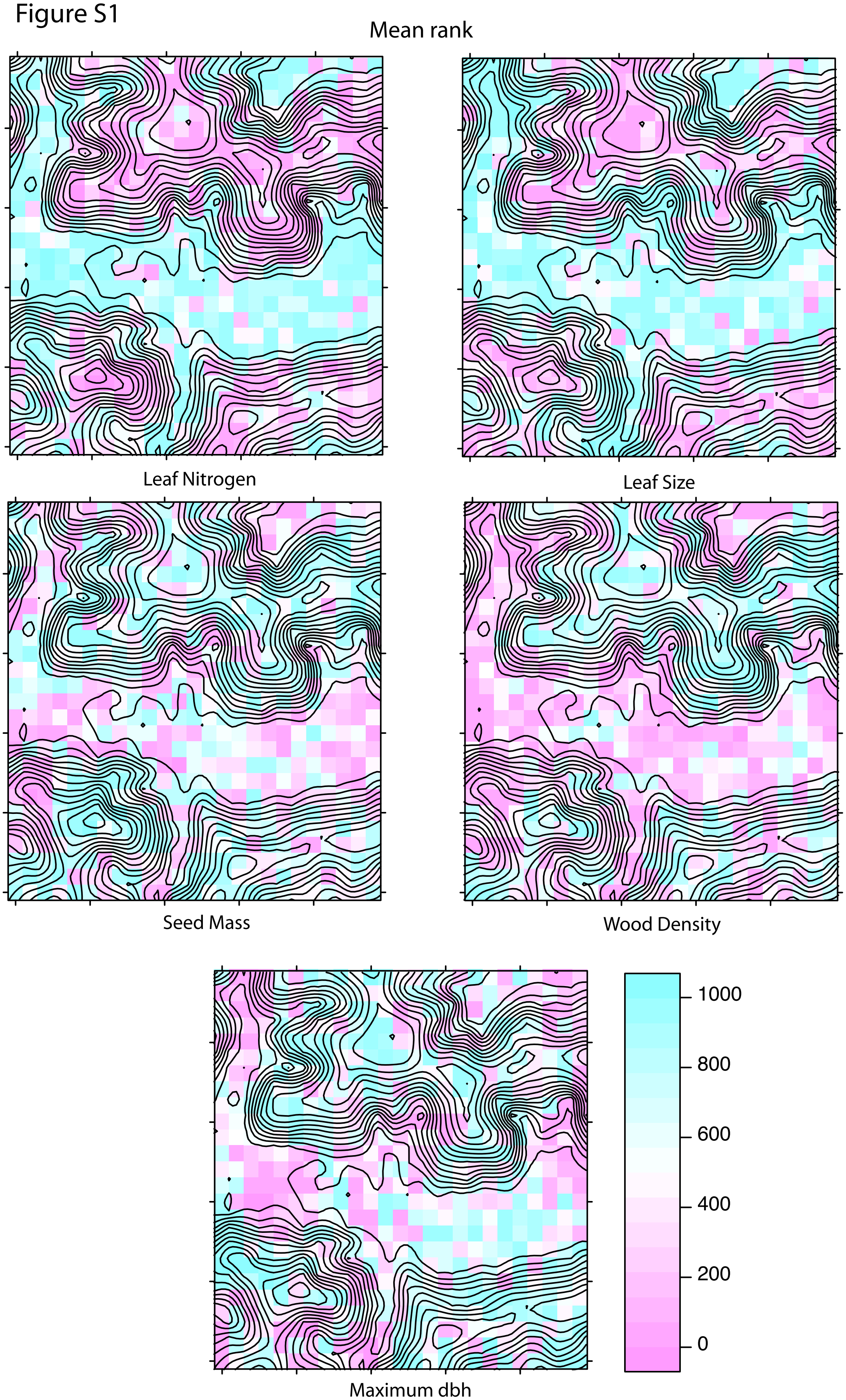
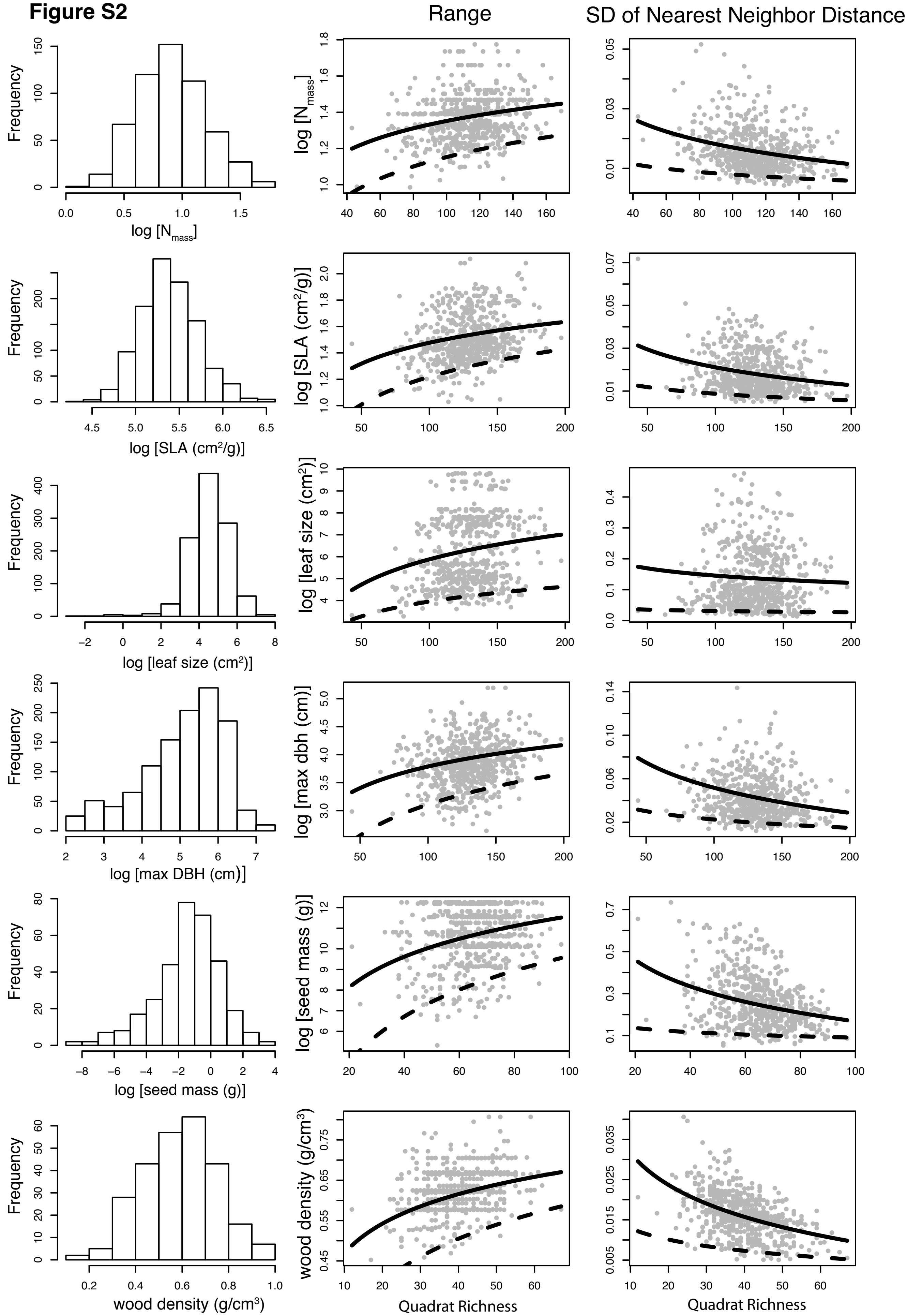

Mean rank
Leaf Nitrogen
Leaf Size
Seed Mass
Wood Density
Maximum dbh
1000
800
600
400
200
0

Figure S2



Range
SD of Nearest Neighbor Distance
Frequency
log [N_mass]
log [SLA (cm²/g)]
log [leaf size (cm²)]
log [max DBH (cm)]
log [max dbh (cm)]
log [seed mass (g)]
wood density (g/cm³)
Quadrat Richness
Quadrat Richness

Figure S3

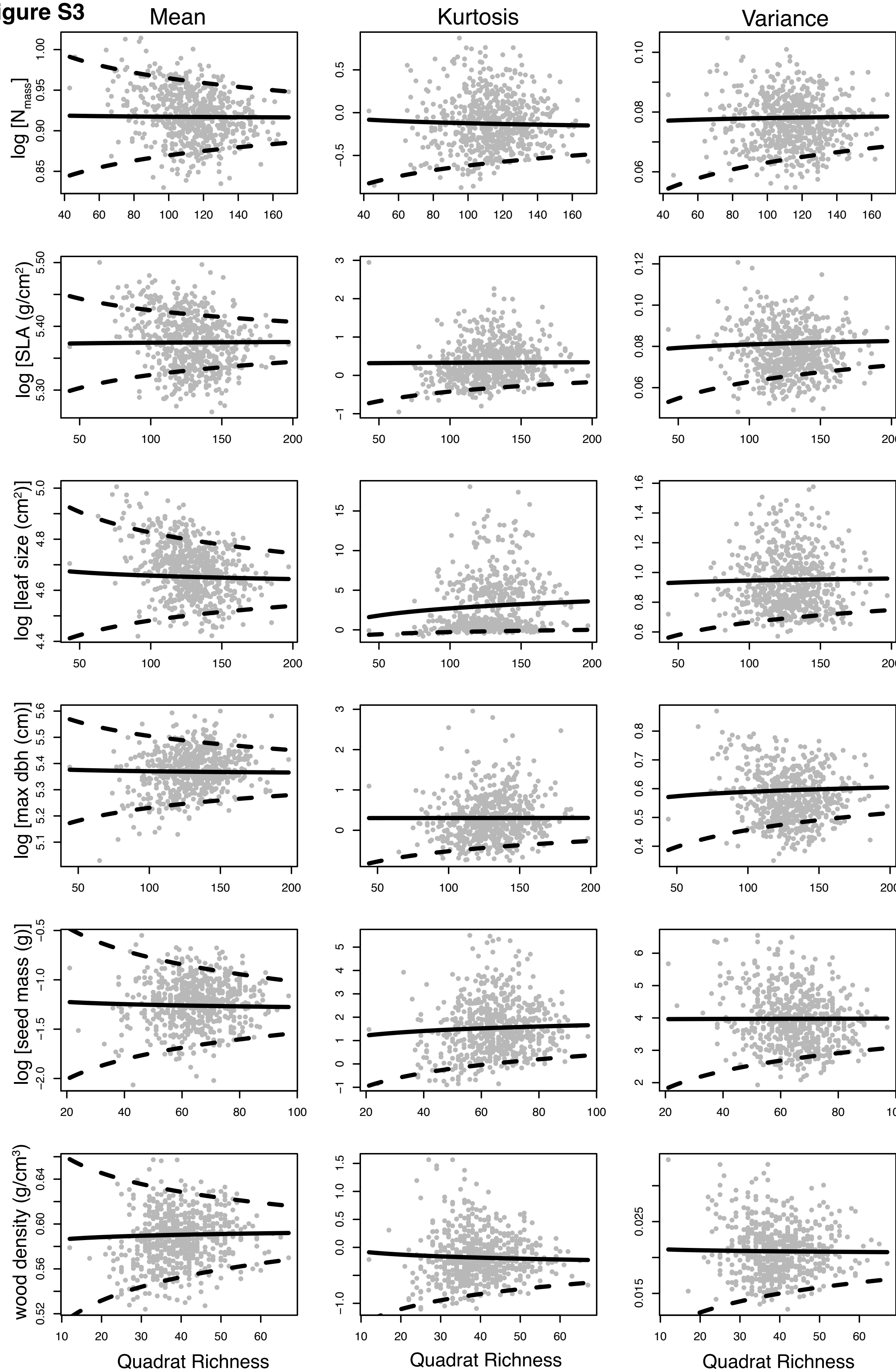

Mean
Kurtosis
Variance
log [N_{mass}]
log [SLA (g/cm²)]
log [leaf size (cm²)]
log [max dbh (cm)]
log [seed mass (g)]
wood density (g/cm³)
Quadrat Richness
Quadrat Richness
Quadrat Richness

Table S1: Average effect size (± 1 SE) of occurrence-weighted null model tests (observed – expected / null SD). As the test of the mean was two-tailed, we report the absolute value of the effect size.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	1.867 ± 0.050	-0.213± 0.050	0.003 ± 0.048	-0.019 ± 0.048	-0.458 ± 0.054
Leaf Nitrogen Concentration	1.307 ± 0.038	-0.107 ± 0.044	-0.036 ± 0.047	0.067 ± 0.046	-0.243 ± 0.047
Leaf Size	1.342 ± 0.038	-0.161 ± 0.048	-0.138 ± 0.050	-0.118 ± 0.050	-0.131 ± 0.048
Seed Mass	1.122 ± 0.034	-0.051 ± 0.051	0.108 ± 0.050	-0.027 ± 0.052	-0.030 ± 0.052
Wood Density	1.137 ± 0.034	0.149 ± 0.039	0.050 ± 0.040	0.044 ± 0.042	0.043± 0.043
Maximum dbh	1.168 ± 0.037	-0.272 ± 0.050	-0.096 ± 0.050	-0.009 ± 0.052	-0.398 ± 0.055

Table S2A: Wilcoxon signed rank test of Abundance-Weighted null model results

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	.11	.08	.21	.90	.06
Leaf Nitrogen Concentration	**<.0001**	.16	. **<.0001**	**.001**	.99
Leaf Size	.56	**<.0001**	**.0001**	**.004**	**<.0001**
Seed Mass	**<.0001**	**<.0001**	.99	.99	**<.0001**
Wood Density	**<.0001**	**.002**	.99	**.001**	**<.0001**
Maximum dbh	**<.0001**	.35	**<.0001**	.84	.67

Table S2B: Percentage of quadrats in Yasuní deviating from Abundance-Weighted null model. The mean test was two-tailed; all other tests were one-tailed.

Trait	Mean	Range	SD of NN	Kurtosis	Variance
SLA	**38.9%**	**5.6%**	**5.4%**	4.5%	**11.4%**
Leaf Nitrogen Concentration	**19.1%**	4.8%	**7.4%**	**7.2%**	**5.4%**
Leaf Size	**18.1%**	**26.1%**	**22.4%**	**19.4%**	**14.7%**
Seed Mass	**15.7%**	**17.6%**	**8.7%**	**9.0%**	**28.9%**
Wood Density	**12.7%**	**7.9%**	4.0%	**5.3%**	**5.6%**
Maximum dbh	**16.2%**	**6.9%**	**6.2%**	**5.4%**	**9.5%**

Table S2C: Average effect size (± 1 SE) of Abundance-Weighted null model tests (observed – expected / null SD). As the test of the mean was two-tailed, we report the absolute value of the effect size.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	2.002 ± 0.054	0.032 ± 0.051	0.088 ± 0.050	0.170 ± 0.050	-0.075 ± 0.058
Leaf Nitrogen Concentration	1.471 ± 0.044	0.003 ± 0.048	-0.037 ± 0.051	-0.100 ± 0.048	0.168 ± 0.051
Leaf Size	1.411 ± 0.041	-0.185 ± 0.064	-0.095 ± 0.068	0.024 ± 0.062	-0.244 ± 0.053
Seed Mass	1.335 ± 0.039	-0.489 ± 0.070	0.709 ± 0.081	0.658 ± 0.079	-1.116 ± 0.054
Wood Density	1.242 ± 0.038	-0.135 ± 0.051	0.116 ± 0.044	-0.067 ± 0.047	-0.162 ± 0.046
Maximum dbh	1.335 ± 0.042	-0.015 ± 0.050	-0.077 ± 0.050	0.175 ± 0.056	-0.059 ± 0.061

Table S3A: Wilcoxon test of Presence-Absence null model.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	. **<.0001**	**<.0001**	**<.0001**	.31	**<.0001**
Leaf Nitrogen Concentration	**<.0001**	**<.0001**	**<.0001**	.99	**<.0001**
Leaf Size	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**
Seed Mass	**<.0001**	.99	.99	.99	**<.0001**
Wood Density	**<.0001**	**<.0001**	**<.0001**	.99	**<.0001**
Maximum dbh	**<.0001**	**<.0001**	.99	.99	**<.0001**

Table S3B: Percentage of quadrats deviating from Presence-Absence null model. The mean test was two-tailed; all other tests were one-tailed.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	**23.1%**	**38.1%**	**9.0%**	3.7%	**75.8%**
Leaf Nitrogen Concentration	**11.4%**	**10.1%**	4.0%	1.6%	**24.7%**
Leaf Size	**46.3%**	**17.3%**	**13.3%**	**7.2%**	**24.5%**
Seed Mass	**12.8%**	**7.1%**	3.2%	**5.4%**	**11.7%**
Wood Density	4.0%	2.9%	2.6%	0.2%	**13.9%**
Maximum dbh	**90.5%**	**89.3%**	**11.3%**	2.7%	**99.8%**

Table S3C: Average effect size (± 1 SE) of Presence-Absence null model tests (observed – expected / null SD). As the test of the mean was two-tailed, we report the absolute value of the effect size.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	1.572 ± 0.043	-1.483 ± 0.041	-0.465 ± 0.046	0.079 ± 0.050	-2.575 ± 0.041
Leaf Nitrogen Concentration	1.226 ± 0.035	-0.541 ± 0.038	-0.248 ± 0.041	0.317 ± 0.045	-1.167 ± 0.042
Leaf Size	2.227 ± 0.050	-0.758 ± 0.049	-0.252 ± 0.054	-0.342 ± 0.054	-0.984 ± 0.039
Seed Mass	1.277 ± 0.035	0.285 ± 0.056	0.936 ± 0.068	0.726 ± 0.068	-0.429 ± 0.049
Wood Density	0.947 ± 0.028	-0.456 ± 0.030	-0.157 ± 0.030	0.256 ± 0.039	-0.918 ± 0.034
Maximum dbh	3.851 ± 0.045	-4.323 ± 0.076	0.523 ± 0.078	1.247 ± 0.081	-5.281 ± 0.038

Table S4: Effect of reducing the null model species pool from the entire plot to a habitat-specific pool. Wilcox signed-rank test p-value reported for each of four statistics, split by two habitats.

	Range effect weakened		Variance effect weakened		SD NN effect strengthened		Kurtosis effect strengthened	
Trait	Ridge	Valley	Ridge	Valley	Ridge	Valley	Ridge	Valley
SLA	**<.0001**	**<.0001**	**<.0001**	>.5	>.5	>.5	**<.0001**	>.5
Leaf Nitrogen Concentration	**<.0001**	.0539	**.0030**	>.5	>.5	**.0018**	>.5	>.5
Leaf Size	>.5	**<.0001**	**<.0001**	>.5	**<.0001**	>.5	**<.0001**	>.5
Seed Mass	**<.0001**	>.5	**<.0001**	>.5	**.0098**	**<.0001**	**<.0001**	**<.0001**
Wood Density	.226	**<.0001**	>.5	**<.0001**	>.5	>.5	>.5	>.5
Maximum dbh	**<.0001**	>.5	**<.0001**	>.5	**<.0001**	>.5	**<.0001**	>.5

Table S5: Trait correlations (Spearman's rho).

Trait	Leaf [N]	Leaf Size	Seed Mass	Wood Density	Max. dbh
SLA	.59	-.05	-.31	-.13	-.05
Leaf Nitrogen Concentration		-.08	-.11	-.15	.02
Leaf Size			.09	-.16	-.01
Seed Mass				.30	.23
Wood Density					-.07
Maximum dbh					

Table S6: Species targeted for intensive sampling across habitats

Genus	Species	Family	Plotwide abundance
Brownea	*grandiceps*	Fabaceae	2,164
Eschweilera	*coriacea*	Lecythidaceae	1,345
Eugenia	*florida*	Myrtaceae	712
Guarea	*silvatica*	Meliaceae	472
Inga	*umbratica*	Fabaceae	615
Iryanthera	*hostmanniana*	Myristicaceae	877
Miconia	‘tipica’	Melastomataceae	835
Nectandra	*viburnoides*	Lauraceae	666
Perebea	*xanthochyma*	Moraceae	689
Protium	*nodulosum*	Burseraceae	764
Unonopsis	*veneficiorum*	Annonaceae	1,069

Table S7A: Wilcoxon test of occurrence-weighted null model restricted to 1-10 cm dbh individuals.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	>.5	**<.0001**	**.0005**	**<.0001**	**<.0001**
Leaf Nitrogen Concentration	**.0083**	**.0015**	**.0014**	.3948	**<.0001**
Leaf Size	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**
Seed Mass	**.0070**	>.5	>.5	**.0072**	.3452
Wood Density	**.0090**	.0696	**.0006**	**.0016**	**.0163**
Maximum dbh	>.5	**<.0001**	**<.0001**	**.0081**	**<.0001**

Table S7B: **Percentage of quadrats in Yasuní deviating from null model restricted to 1-10 cm dbh individuals. The mean test was two-tailed; all other tests were one-tailed.**

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	**32.7%**	**8.0%**	**6.4%**	**7.9%**	**16.5%**
Leaf Nitrogen Concentration	**13.5%**	**5.1%**	**5.3%**	4.3%	**6.9%**
Leaf Size	**14.9%**	**6.4%**	**7.2%**	**5.3%**	**6.1%**
Seed Mass	**8.5%**	4.3%	4.5%	**5.3%**	**5.1%**
Wood Density	**8.7%**	4.3%	4.2%	4.5%	5.0%
Maximum dbh	**12.3%**	**10.6%**	**7.1%**	**6.4%**	**14.9%**

Table S7C: Average effect size (± 1 SE) of null model tests (observed – expected / null SD) restricted to 1-10 cm dbh individuals. As the test of the mean was two-tailed, we report the absolute value of the effect size.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	1.824 ± 0.050	-0.272 ± 0.049	-0.044 ± 0.046	-0.091 ± 0.048	-0.463 ± 0.056
Leaf Nitrogen Concentration	1.252 ± 0.036	-0.085 ± 0.045	-0.002 ± 0.048	0.051 ± 0.047	-0.206 ± 0.048
Leaf Size	1.347 ± 0.039	-0.149 ± 0.049	-0.138 ± 0.048	-0.097 ± 0.053	-0.141 ± 0.048
Seed Mass	1.087 ± 0.033	-0.002 ± 0.049	0.100 ± 0.047	-0.033 ± 0.052	0.005 ± 0.051
Wood Density	1.089 ± 0.032	-0.064 ± 0.045	-0.094 ± 0.045	-0.039 ± 0.045	-0.067 ± 0.046
Maximum dbh	1.230± 0.039	-0.299 ± 0.050	-1.131 ± 0.050	-0.001 ± 0.053	-0.412 ± 0.055

Table S8: Results of intensive sampling of 11 species across habitats.

2 Way ANOVA- Log(SLA)

	DF	Sum of Squares	Mean Squared	F Value	Prob (>F)
Species	10	6.2743	0.6274	33.3634	**<.0001**
Habitat	1	0.0161	0.0161	0.8667	.3558
Species*habitat	10	0.3131	0.0313	1.6650	.0911
Residuals	200	3.7612	0.0188		

2 Way ANOVA- Log(Leaf Size)

	DF	Sum of Squares	Mean Squared	F Value	Prob (>F)
Species	10	75.707	7.571	83.0837	**<.0001**
Habitat	1	0.346	0.346	3.8011	.05262
Species*habitat	10	0.864	0.086	0.9485	.48994
Residuals	200	18.224	0.091		

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S3. Census data for the Yasuni 25-ha forest plot is available by formal request to Renato Valencia (lrvalencia@puce.edu.ec), followed by acceptance of a data use agreement.

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