microscopic analyses (*15*) is shown in Fig. 4. Although much remains to be learned about the molecular architecture of the midbody and the precise stereochemistry of cytokinesis, the results and model presented here provide one foothold for furthering such an understanding.

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

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It is debated whether species-level differences in ecological strategy, which play a key role in much of coexistence theory, are important in structuring highly diverse communities. We examined the co-occurrence patterns of over 1100 tree species in a 25-hectare Amazonian forest plot in relation to field-measured functional traits. Using a null model approach, we show that co-occurring trees are often less ecologically similar than a niche-free (neutral) model predicts. Furthermore, we find evidence for processes that simultaneously drive convergence and divergence in key aspects of plant strategy, suggesting that at least two distinct niche-based processes are occurring. Our results show that strategy differentiation among species contributes to the maintenance of diversity in one of the most diverse tropical forests in the world.

Explaining the high species diversity of moist tropical forests has proved an enduring challenge to ecologists and has inspired many theories of species coexistence and much debate (*1–3*). Current coexistence theories can be divided into two categories: those that invoke a role for meaningful differences in the ecological strategy (niche) of co-occurring species (*2–5*), and those that rely on dispersal and stochastic demographic processes that explicitly assume the equivalent per capita fitness of species (*1*). The latter, termed neutral theory, was initially developed to explain coexistence in diverse tropical forests (*1*), where it seemed implausible that each tree species occupied a unique niche, although it can be applied to a range of communities.

Few large-scale tests of coexistence theories in tropical forests have explicitly examined the ecological strategy of co-occurring species, in part because of difficulties in identifying more than a few discrete plant strategies (such as shade-tolerant, light-demanding pioneer, etc.) (*6*). Recent advances in functional ecology now permit a more precise quantification of woody plant strategy along a number of continuous, often orthogonal, axes of variation related to resource acquisition strategy, regeneration niche, environmental tolerance, and life history (*7–10*), opening the door for previously intractable analyses.

Here we present a critical test of neutral and niche-based coexistence theories in one of the most diverse tropical forest plots in the world. The stochastic processes associated with neutral theory assume the equivalence of all individuals, and therefore species, with the result that species co-occurrence patterns should be random with respect to ecological strategy (*1, 11*). We tested for two niche-based alternatives: (i) that co-occurring species converge in strategy because of establishment and/or survival barriers imposed by the abiotic environment ("environmental filtering") (*4, 12, 13*); and (ii) that co-occurring species diverge in strategy as predicted by classic coexistence theory ("niche differentiation") (*5, 14*). The latter pattern may occur as a result of competition or of enemy-mediated density dependence (*15*) if plant susceptibility (*16*) and overall plant strategy are phylogenetically conserved. A strength of our approach is that we are able to test for both processes (*17*), because environmental filtering should limit the range of strategies found in a community (*12, 17*), whereas niche differentiation should spread individuals evenly along strategy axes (*14, 17*). These two features of community-trait distributions can be assessed sequentially.

We tested these predictions in the Yasuní Forest Dynamics Plot (FDP) in eastern Ecuador, a 25-ha plot containing over 150,000 mapped trees ≥1 cm in diameter at breast height (dbh) from over 1100 species (*18*). The ecological strategy for each species was quantified with field-measured estimates of specific leaf area (SLA, leaf area divided by dry mass), leaf nitrogen concentration, leaf size, seed mass, and maximum dbh (used here as a proxy for maximum height), as well as published estimates of wood density (*19, 20*). We combined this trait information with species co-occurrence data to develop estimates of the community-trait distribution at the 20-by-20–m ("quadrat") scale. Metrics of community-trait structure sensitive to environmental filtering and niche differentiation were compared to a null expectation. We generated our null expectation by creating random communities of equal richness by drawing species from the entire plot weighted by their plot-wide occurrence, irrespective of trait values (*20*).

We predict that if habitat filtering is occurring at the quadrat scale, the range of observed trait

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values will be smaller than the null expectation (*12*). The variance may also be reduced by habitat filtering, although this is a more difficult metric to interpret, as it may also be affected by niche differentiation (*17*). Habitat filtering may shift the mean of the quadrat trait distribution relative to the null expectation, although filtering can occur without this effect. Likewise, if niche differentiation is occurring, we predict that the standard deviation (SD) of nearest-neighbor distances (measured along trait axes) will be lower (species spaced more evenly), and the kurtosis of the distribution of trait values will be smaller (fat-tailed distribution) as compared to the null expectation (*14*, *17*).

Trait-based community analysis requires the selection of traits that are critical to the community processes of interest. Our selection of traits (Table 1) connected to the leaves, seeds, wood, and overall life form of each species covers a range of traits frequently deemed essential to woody plant strategy (*8–10*). Logistical concerns related to the extremely high diversity of the system limited us to these practical traits that are established proxies for plant strategy, although additional traits such as rooting depth, leaf secondary chemistry, and seedling relative growth rate would be of great interest, if and when data become available.

Our analyses found strong evidence for niche-based processes throughout the FDP (Fig. 1, Tables 1 and 2, and table S1). Across the entire plot, mean trait values varied more among quadrats (Table 2, Fig. 1A, and fig. S1), and trait ranges were significantly smaller within quadrats (Table 1, Fig. 1C, and fig. S2), as compared to expectations from our null model. These patterns are consistent with a role for habitat filtering. The Yasuní FDP contains two principal topographically defined habitats: ridgetops and valley bottoms (Fig. 1A). Prior analyses of species distributions in Yasuní have shown that many species show associations with topographic habitat (*18*) and soil nutrients (*21*), results that agree with our trait-based analysis. Our analyses highlight the fact that the topographic habitats support communities with divergent strategies, in addition to contrasting species identities, despite close physical proximity between the two habitat types. Ridgetops tend to be composed of species with lower average SLA, smaller leaves, heavier seeds, and denser wood as compared to valley communities (Fig. 1A and fig. S1). Comparing our initial results to a null model restricted to topographic habitat reduces the habitat filtering effect in many cases (table S4), suggesting that the two topographic habitats explain some, but not all, of the habitat filtering effect we observe in the plot. Habitat or microsite variation that does not correspond with topographic habitats may be responsible for the remainder.

Against this background of habitat filtering, all traits with the exception of wood density were more evenly distributed than predicted (Table 1), as measured either by the SD of nearest-neighbor

Table 1. Trait coverage, an example of the ecological significance of each trait, and Wilcoxon signed-rank test of plot-wide null model results. The mean test was two-tailed; all other tests were one-tailed. n.s., not significant; NN, nearest neighbor.

| Trait	Species sampled (% of plot stems)	Strategy correlation	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	1088 (99.9%)	Leaf economics–resource capture (*29*)	n.s.	<0.0001	0.012	0.007	<0.0001
Leaf nitrogen concentration	559 (90.5%)	Leaf economics–resource capture (*29*)	n.s.	0.0001	<0.0001	0.604	<0.0001
Leaf size	1084 (99.8%)	Disturbance and nutrient stress strategy (*7*)	n.s.	<0.0001	<0.0001	<0.0001	<0.0001
Seed mass	321 (58%)	Regeneration strategy (*9*)	n.s.	0.825	0.761	0.014	0.186
Wood density	265 (29%)	Allocation to growth versus strength/pathogen resistance (*19*)	n.s.	0.998	0.913	0.233	0.533
Maximum dbh	1123 (100%)	Light capture strategy (*30*)	n.s.	<0.0001	<0.0001	0.011	<0.0001
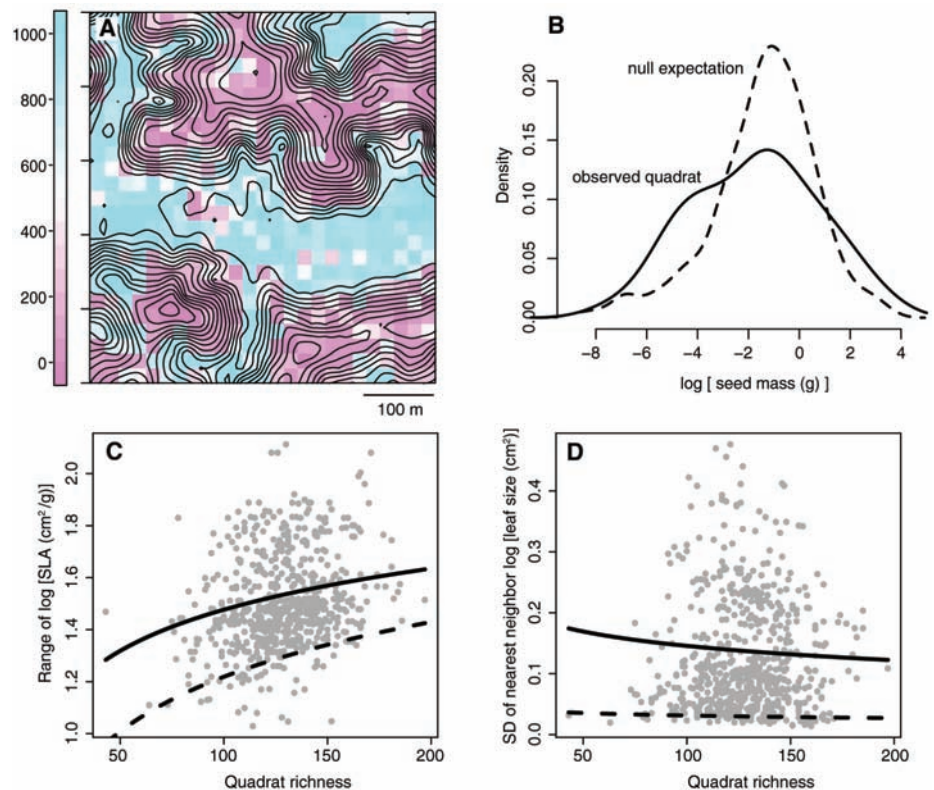
Fig. 1. Examples of community trait patterns at Yasuní. See figs. S1 to S3 for complete results. (**A**) The rank of observed mean SLA in the null distribution for all 625 quadrats. Contours indicate topography within the plot (interval = 2 m); thus, ridgetops have lower than expected SLA and valleys have higher. (**B**) Observed (solid line) and expected (dashed line) distribution of seed masses in one quadrat with significantly low kurtosis. (**C**) Points indicate the observed range of SLA (log-transformed) in each quadrat as a function of quadrat richness. The solid line indicates the expected range value predicted by the null model, and the dashed line indicates the 5% confidence interval of the null distribution used to assess significance in Table 2. Only one interval is indicated because the test is one-tailed. The distribution of observed points is significantly shifted below the null expectation (Table 1), suggesting that in aggregate, quadrat-level SLA ranges are smaller than expected across the forest. (**D**) Same plot for the SD of nearest-neighbor distances for leaf size (log-transformed). The distribution of observed points is significantly shifted below the null expectation (Table 1), indicating that in aggregate, quadrat-level leaf size distributions are more evenly spread than expected.

Table 2. Percentage of individual quadrats in Yasuní significantly deviating from the null model. The mean test was two-tailed; all other tests were one-tailed.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	33.5%	8.2%	5.1%	6.1%	14.1%
Leaf nitrogen concentration	14.6%	5.3%	5.1%	3.8%	7.9%
Leaf size	15.9%	6.1%	6.9%	5.9%	7.2%
Seed mass	9.8%	6.1%	5.0%	6.4%	6.9%
Wood density	10.1%	1.8%	2.7%	3.5%	2.1%
Maximum dbh	10.9%	9.0%	6.9%	6.4%	13.9%

Table 3. Wilcoxon signed-rank test of sapling and adult comparisons. Significant values reflect a shift toward greater departures from the null expectation in adults, relative to saplings. The mean test was two-tailed; all other tests were one-tailed.

Trait	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	0.007	>0.5	>0.5	0.188	>0.5
Leaf nitrogen concentration	<0.0001	<0.0001	0.0037	0.0524	<0.0001
Leaf size	<0.0001	>0.5	>0.5	>0.5	>0.5
Seed mass	<0.0001	>0.5	<0.0001	<0.0001	>0.5
Wood density	<0.0001	>0.5	>0.5	>0.5	>0.5
Maximum dbh	<0.0001	>0.5	>0.5	>0.5	<0.0001

distances (Fig. 1D and fig. S2) or by kurtosis (fig. S3), a pattern we attribute to niche differentiation. In ecological terms, a platykurtic distribution (Fig. 1B) indicates that species with a broad distribution of trait values (such as small, medium, and large seeds, or shrub, midcanopy, and emergent growth forms) co-occur more often than predicted, whereas a low SD of nearest-neighbor distances (Fig. 1D) suggests that, on average, co-occurring species are more evenly spaced along the trait axis than predicted. In many cases, these effects were strengthened when habitat-specific species pools were used (table S4). Although many individual quadrats are indistinguishable from the null expectation (Table 2), the presence of detectable, significant, plot-wide niche differentiation effects (Table 1) in such a diverse community is surprising evidence against a purely neutral explanation of species coexistence.

Dispersal, seedling establishment, or postestablishment mortality that is nonrandom with respect to trait values may have produced the patterns we observed. As plants only enter the FDP census once they reach 1 cm in dbh, we cannot test for trait effects at the earliest life stages. On the other hand, we can indirectly examine mortality that occurs during the transition from sapling to adult. We tested the hypothesis that trait patterns became increasingly nonrandom in adults in the community by repeating our analyses for restricted cohorts of co-occurring individuals 1 to 10 cm in dbh (saplings) or >10 cm in dbh (adults) and comparing the sapling assemblage in each quadrat to the adult assemblage in each quadrat (20). In many cases, adults in each quadrat exhibited stronger nonrandom patterns than saplings (Table 3), despite a reduction in power to detect nonrandom patterns in the adults that arises

in the analysis because of smaller community sizes (22). Thus, it appears that at least some of the community-wide pattern is due to post-sapling mortality that is nonrandom with respect to traits.

The evenly distributed trait patterns that we observed may be produced by direct competition (14) or by other density-dependent processes. For example, previous studies have shown that density-dependent attack by specialist herbivores or pathogens may be pervasive in tropical forests (23) and that the probability of attack by natural enemies for plants has a strong phylogenetic component (24). In general, studies have shown that closely related plants have similar ecological strategies (19, 25), including qualitative defenses (26). Thus, our results may reflect nonrandom mortality inflicted by natural enemies.

Using a functional trait approach, we have found evidence for niche-based processes known to have stabilizing effects on diversity (27) in one of the most species-rich tropical forest assemblages on the planet. Although the magnitude of these processes still needs to be quantified (28), their existence indicates that forces included in neutral theory (such as demographic stochasticity and dispersal limitation) may not be sufficient to explain species distributions and the maintenance of diversity in this forest, even though they are occurring. Taken together, our results support a niche-based view of tropical forest dynamics in which subtle but pervasive habitat specialization and strategy differentiation contribute to species coexistence.

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