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Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest

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Abstract. Despite a long history of the study of tropical forests, uncertainty about the importance of different ecological processes in shaping tropical tree species distributions persists. Trait- and phylogenetic-based tests of community assembly provide a powerful way to detect community assembly processes but have seldom been applied to the same community. Both methods are well suited to testing how the relative importance of different ecological processes changes with spatial scale. Here we apply both methods to the Yasuní Forest Dynamics Plot, a 25-ha Amazonian forest with >1100 tree species. We found evidence for habitat filtering from both trait and phylogenetic methods from small (25 m^2) to intermediate (10 000 m^2) spatial scales. Trait-based methods detected even spacing of strategies, a pattern consistent with niche partitioning or enemy-mediated density dependence, at smaller spatial scales (25–400 m^2). Simulation modeling of community assembly processes suggests that low statistical power to detect even spacing of traits at larger spatial scales may contribute to the observed patterns. Trait and phylogenetic methods tended to identify the same areas of the forest as being subject to habitat filtering. Phylogenetic community tests, which are far less data-intensive than trait-based methods, captured much of the same filtering patterns detected by trait-based methods but often failed to detect even-spacing patterns apparent in trait data. Taken together, it appears that both habitat associations and niche differentiation shape species co-occurrence patterns in one of the most diverse forests in the world at a range of small and intermediate spatial scales.

Key words: coexistence theory; functional equivalence; functional traits; habitat filtering; neutral theory; null models; phylogenetic community structure; power analysis; simulation modeling; Yasuní Forest Dynamics Plot, Ecuador.

Introduction

Despite a long history of the study of tropical forest diversity (reviewed by Connell 1978, Wright 2002, Leigh et al. 2004), uncertainty persists regarding the importance of different ecological processes in shaping tropical tree species distributions. Recently two related sets of methods have been developed that offer new insights into community structure and assembly processes based on observational data. One set of methods is based on quantifying the ecological similarities and differences among co-occurring species using functional traits (Ricklefs and Travis 1980, Weiher et al. 1998, Stubbs and Wilson 2004, Cornwell et al. 2006, Kraft et al. 2008, Cornwell and Ackerly 2009), while the other draws on patterns of phylogenetic relatedness (Webb 2000, Cavender-Bares et al. 2004, 2009, Kraft et al. 2007, Vamosi et al. 2009).

These approaches are particularly suited to address the role that species differences in ecological strategy play in shaping tropical forests (Hubbell 2005, Kembel and Hubbell 2006, Kraft et al. 2008, Swenson and Enquist 2009). One advantage of these methods is that they should have more power to detect strategy-based ecological processes than analyses that simply place species into functional groups (see examples in Turner 2001) or that divide a forest into conspecifics and heterospecifics (e.g., Janzen 1970). For example, many ecological strategy differences among plant species are best described as continuous axes or as a manifold (Hubbell and Foster 1992, Reich et al. 1997, Westoby et al. 2002). Arbitrarily grouping species at different positions along these axes into functional groups (e.g., Turner 2001) is convenient and may capture gross differences between taxa, but discards information about within-group strategy differentiation, thereby implicitly imposing within-group functional equivalence (Hubbell 2005, Purves and Pacala 2005) and biasing the analyses against detection of nonrandom assembly processes such as niche differentiation. Similar arguments can be made for the benefits of treating evolutionary relatedness as a continuous measurement (e.g., Webb 2000, Webb et al. 2006).

Both trait and phylogenetic community methods share the same conceptual approach in which the observed distribution of either traits or phylogenetic distances within a local community is compared to a null

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TABLE 1. Conceptual framework for interpreting patterns of trait and phylogenetic community structure for the ecological processes of interest in this analysis (after Cavender-Bares et al. 2004, Kraft et al. 2007).

Process	Trait pattern	Phylogenetic pattern	
		Traits conserved	Traits convergent
Habitat filtering (community sample includes one habitat)	resource use and/or environmental tolerance traits clustered	clustered	evenly dispersed
Habitat filtering (community sample includes >1 habitat)	random or resource use and/or environmental tolerance traits evenly dispersed	random or evenly dispersed	random
Competitive exclusion/niche differentiation	resource use strategy traits evenly dispersed	evenly dispersed	random
Enemy-mediated negative density dependence	physical and/or chemical defense traits evenly dispersed	evenly dispersed	random
Dispersal assembly (e.g., neutral theory, lottery models)	random	random	random

expectation generated by drawing species at random from a regional pool of potential colonists (Webb 2000, Cornwell et al. 2006). Deviations from the null expectation can be used as evidence for the action of a number of ecological processes in the assembly of the local community (see Table 1). Any spatial and taxonomic scale can be used to define the "community" and the "pool" in the analysis (Cavender-Bares et al. 2006, Swenson et al. 2006), but the interpretation of the results depends critically on the scales chosen for both (Kraft et al. 2007, Vamosi et al. 2009). Phylogenetic-based methods have been broadly applied to many communities, including many tropical forests (see review in Vamosi et al. 2009), but relatively few studies have applied both methods to the same community (e.g., Cavender-Bares et al. 2004, Ingram and Shurin 2009). Recently, Swenson and Enquist (2009) applied both approaches to a Neotropical dry forest and found that far more insight into the processes structuring the community could be drawn from a combined approach than from phylogenetic methods alone.

The flexibility of trait and phylogenetic analyses to quantify patterns at multiple spatial scales makes them ideally suited to address the issue of scale dependency in community ecology (e.g., Cavender-Bares et al. 2006, Swenson et al. 2006). Different forces are known to shape the distribution and abundance of organisms at different spatial and temporal scales (e.g., Shmida and Wilson 1985, Ricklefs and Schluter 1993, Emerson and Gillespie 2008), so interpretations of trait and phylogenetic analyses must consider scale. However, one challenge for interpretation of phylogenetic-based tests across spatial scales is that the statistical power of the methods has been shown to vary with the richness of the community and the species pool (Kraft et al. 2007). Trait-based methods are likely to suffer from similar issues (Kraft et al. 2008, Swenson and Enquist 2009) as the underlying mechanics of the statistical tests are the same, although this has yet to be investigated.

In this paper we have three goals: (1) to connect hypotheses about ecological dynamics in tropical forests to predicted outcomes of trait- and phylogenetic-based tests; (2) to apply the tests across four nested spatial scales in the Yasuní Forest Dynamics Plot, one of the most diverse tropical forests in the world (Losos and Leigh 2004); and (3) to use an ecological simulation modeling approach (Colwell and Winkler 1984, Kraft et al. 2007) to account for the effects of the varying statistical power of trait-based tests at different spatial scales. These methodological issues are essential to address in order to connect the outcome of the tests to ecological processes.

Framing ecological hypotheses in the context of trait and phylogenetic analyses

An important first step to applying trait and phylogenetic community analyses is to translate the predictions of existing tropical forest diversity hypotheses into a set of predictions for trait- and phylogenetic-based tests (Table 1). Several stabilizing mechanisms (processes that give a species an advantage when rare; Chesson 2000) are known to occur in tropical forests (reviewed in Wright 2002). The most familiar is the hypothesis of niche partitioning in relation to heterogeneous light environments inside and outside treefall gaps (Grubb 1977, Orians 1982, Turner 2001), to different canopy strata (Terborgh 1985, Kohyama 1993, Falster and Westoby 2003), and to habitat or microtopographic specialization (e.g., Svenning 1999, Harms et al. 2001, Valencia et al. 2004*b*). The predicted outcomes of these processes in a trait-based context are dependent on the scale of environmental heterogeneity, the traits chosen for study, and the scale of analysis. Within a habitat, light environment, or canopy strata, this process is predicted to result in co-occurring species that share a similar set of adaptations to the environment, reflected by a shared set of resource use traits ("habitat filtering"; van der Valk 1981, Weiher and Keddy 1995, Cornwell et al. 2006). To the extent that these traits exhibit phylogenetic signal (meaning close relatives share similar trait values), this filtering should result in co-occurrences of closely related species (Webb et al. 2002, Kraft et al. 2007). On the other hand, a regular or even dispersion of strategies is the predicted outcome of the classic con-

cepts of competitive exclusion or niche partitioning (Ricklefs and Travis 1980, Stubbs and Wilson 2004, Kraft et al. 2008, Cornwell and Ackerly 2009). If resource partitioning occurs at small spatial scales relative to the scale of analysis (such as sampling across canopy strata or microtopographic environments), one might expect co-occurring species to exhibit an even dispersion or spread of strategies related to resource use, reflecting the range of environments within the sample (Tilman 2004, Schwilk and Ackerly 2005). In communities with patterns of even trait dispersion, if traits are phylogenetically conserved (i.e., a high phylogenetic signal), co-occurring species are predicted to be less related than expected, while if the traits are convergent (i.e., a low signal), random phylogenetic patterns are expected (Webb et al. 2002, Kraft et al. 2007).

Another important stabilizing mechanism in tropical forests is reduced performance or recruitment near conspecifics (or close relatives) as a result of the facilitation of host-specific natural enemies (Gillet 1962, Janzen 1970, Connell 1971, Condit et al. 1992, Wills 1996, Webb et al. 2006). This mechanism was originally formulated in the context of species-specific enemies (Janzen 1970, Connell 1971). Since then, we have learned that natural enemies may target a range of closely related hosts (Coley and Barone 1996, Gilbert and Webb 2007; but see Coley et al. 2005). This process leads to the prediction that co-occurring species will tend to differ in enemy susceptibility, reflected by distinct physical and chemical defenses. Given the diversity and complexity of plant defenses in the tropics (Rosenthal and Janzen 1979, Coley and Aide 1991) and the challenges in characterizing the relevant traits for all species in a community-based tropical forest analysis, it may be some time before community-wide tests of defense traits can be performed in tropical forests (see Beccera [2004] for a clade-level approach). However, if phylogenetic relatedness is a good proxy for enemy susceptibility, then co-occurring species should be distantly related.

Other deterministic processes are known to shape species distributions in tropical forests, though many of them do not lead to clear trait and phylogenetic test predictions. First, in addition to the effects of natural enemies, negative density dependence is often observed in abundant species (Harms et al. 2000, Wright 2002, Peters 2003, Wills et al. 2006) and may be caused by a combination of intraspecific competition, allelopathy, or other factors. Second, most tropical forest stabilizing mechanisms are not mutually exclusive (Wright 2002) and may have interactive effects (e.g., Fine et al. 2004). The presence of multiple processes can create a challenge for trait and phylogenetic analyses, as particular combinations of ecological processes may erase each other's signatures in some circumstances, resulting in random or otherwise altered trait and phylogenetic patterns (Colwell and Winkler 1984, Kraft et al. 2007). For example, Swenson and Enquist (2009) suggest that the simultaneous clustering of some functional traits and even dispersion of others in a Neotropical dry forest community may contribute to the random phylogenetic community structure detected in an earlier analysis (Swenson et al. 2007).

Equalizing mechanisms (sensu Chesson 2000; factors that reduce average interspecific fitness differences) have also been hypothesized to play an important role in species coexistence in tropical forests. Perhaps the most notable example is Hubbell's neutral theory (Hubbell 1997, 2001), which draws on three distinct components: dispersal limitation, demographic stochasticity, and demographic equivalence of all individuals. Neutral theory is therefore a model with fully equalized species without any stabilizing mechanisms (Adler et al. 2007). There are several arguments that have been put forth for adopting a fully equalized view of tree species in tropical forests. Many of these arguments have focused on the inability of a single stabilizing mechanism to account for the observed diversity of a forest. For example, most of the diversity in the Barro Colorado Island forest, Panama, and probably in most tropical forests, is in shade-tolerant species (Hubbell and Foster 1992); thus, specialization to different light environments in and out of treefall gaps is insufficient, on its own, to explain high levels of diversity. Topographic gradients provide an additional resource, but micro-topographic gradients (e.g., ridges and valley bottoms) within tropical forests tend to be partitioned into a small number of identifiable groups (such as "high" and "low" topographic relief specialists; Wright 2002, Valencia et al. 2004*b*), with many species generalizing across the gradient. Another argument for an equalized view of tropical trees is that the low relative abundances of many species, dispersal limitation, and high species richness all conspire to reduce pairwise species interactions, which reduces the power of natural selection to drive niche partitioning between co-occurring species (Dayton and Hessler 1972, Goldberg and Werner 1983, Hubbell 2005). Instead, some have argued that most species live and evolve against an averaged competitive environment of all species within the community, which should lead to evolutionary convergence on similar strategies (Hubbell 2006).

The observed variation in traits within communities can be reconciled with the equalized view by hypothesizing that there are strong fitness trade-offs between different traits such that all species in a community have roughly equal fitness (Hubbell 2001, Purves and Pacala 2005). While fitness-equalizing trade-offs between strategies have been demonstrated to evolve in detailed simulations of plant evolution (Niklas 1994, Marks and Lechowicz 2006), evidence for them at the community scale is scarce. It is also worth noting that equalizing trade-offs do not necessarily lead to neutral dynamics (Turnbull et al. 2008) and that all mechanisms of stable coexistence in saturated communities by definition lead to equivalence of long-term growth rates (i.e., $dN/dt = 0$). In the context of this paper, what is important is that

neutral dispersal assembly models lead to the prediction of random patterns in the functional and phylogenetic identities of co-occurring species.

Ecological dynamics in the Yasuní Forest Dynamics Plot

Here we apply both trait- and phylogenetic-based tests of community assembly in the Yasuní Forest Dynamics Plot (FDP), a 25-ha plot of mature Amazonian terra firme forest with >1100 freestanding woody plant species (Valencia et al. 2004*b*). In previous work, we used trait-based methods to detect evidence for habitat associations as well as even spacing of species along some trait axes at the 20 × 20 m spatial scale (Kraft et al. 2008, Kraft and Ackerly 2009). We combine both trait and phylogenetic tests in the Yasuní FDP at four nested spatial scales to determine whether the importance of different assembly processes changes with scale. We predict that processes generating even trait spacing of species will be most important at small spatial scales because it is the scale at which neighbors interact and compete for resources, as well as the scale at which enemy-mediated density dependence is likely to have the greatest impact on species co-occurrence (Janzen 1970, Condit et al. 1992, Gilbert and Webb 2007). We predict that habitat filtering will be important at larger spatial scales because topographic environments, which are an important habitat feature within the plot (Valencia et al. 2004*b*), occur as large contiguous patches within the FDP spanning several hectares. We use simulation models of community assembly and rarefaction analyses to account for changing statistical power to detect nonrandom assembly across spatial scales. Finally, we test whether phylogenetic- and trait-based tests of community assembly identify analogous nonrandom patterns in the same locations within the plot. If phylogenetic approaches capture differences in the same ecological strategies that the trait-based tests measure, then the two methods should produce congruent results in the plot overall and within individual patches as well.

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°2′ W; Fig. 1, Plate 1) with an aseasonal climate (Valencia et al. 2004*a*). Our analysis is based on the second census of the western 25 ha (Valencia et al. 2004*b*).

Trait sampling

Six plant functional traits were used in the analysis: specific leaf area (SLA, in square centimeters of fresh leaf area per gram of dry leaf mass), leaf nitrogen concentration (on a mass basis), leaf size (in square centimeters), wood density (in grams per square centimeter), seed mass (in grams), and maximum height estimated from tree diameter distributions. Previous work details the ecological significance of each trait (e.g., Westoby et al. 2002, Cornelissen et al. 2003, Wright et al. 2004, Falster and Westoby 2005, Chave et al. 2006) and the collection methods used within the Yasuní FDP (Kraft et al. 2008). Briefly, foliar material was collected from haphazardly selected, censused individuals within the FDP, rejecting individuals that showed heavy impact of herbivores, epiphylls, or that lacked sufficient recently produced, fully expanded and hardened leaves (Cornelissen et al. 2003). We targeted outer canopy leaves of trees in the 1–5 cm dbh size class (measured, usually, at 1.3 m above the ground surface [Valencia et al. 2004*b*]) growing under closed canopy that were readily accessed from the ground. Two to five leaves were sampled from 1–20 individuals from 1083 species (the extreme rarity of many species precluded more extensive within-species sampling). Restrictions on plot impacts precluded the sampling of entire leaves from large compound-leaved species; in these cases, we collected and report measurements from the minimum photosynthetic unit (i.e., leaflets in compound-leaved species) present on the plant. Dried masses of seeds collected from traps and underneath fruiting trees in the FDP were kindly provided by S. J. Wright and N. Garwood, and wood density was taken from published compilations (Chave et al. 2006).

We expand on the data set presented in our earlier analysis with leaf nitrogen data from an additional 524 taxa, for a combined total of 1083 species-level leaf nitrogen estimates. Leaf nitrogen concentrations (on a mass basis) were analyzed from bulked and ground species samples on a soil elemental analyzer (NC 2500 Carlo-Erba, Milan, Italy) at the University of California, Berkeley, using acetanilide (10.36% N and 71.09% C) as a reference standard. In addition, we used whole-leaf specific leaf area calculated from photographs (Cornelissen et al. 2003) in place of punch-based estimates used in our earlier analysis. To calculate SLA and leaf area, leaves were flattened between Plexiglas and a white background with scale bars and photographed using a digital SLR camera. Leaf area was then calculated from the images using the program ImageJ (Abramoff et al. 2004). Whole-leaf and punch-based SLA estimates are highly correlated ($r = 0.95$, Appendix K) and yielded similar conclusions in all analyses (results not shown), so we report results based on whole-leaf SLA. Leaf nitrogen and SLA are correlated ($r = 0.56$) and part of a well-recognized suite of leaf economics traits (Wright et al. 2004), but are presented separately here for clarity. We replaced earlier leaf size estimates largely based on leaf dimensions (see Kraft et al. 2008) with area estimates from photographs. Finally, maximum height estimation is complicated at Yasuní by a very dense canopy; therefore we used maximum dbh, which is allometrically related to height (Thomas and Ickes 1995, Chave et al. 2003), as a proxy. We improved on our earlier estimates of maximum height of species that used a simple average of the maximum diameters of each species (maximum

FIG. 1. View from the forest canopy in Yasuní National Park, Ecuador, close to the research plot used in this study.

dbh in Kraft et al. [2008]; see method in King et al. [2006*b*]) with a more reliable estimate derived from the 95th quantile of the diameter distribution of all trees $\geq$0.1 of the maximum diameter observed for the species, known as $D95_{0.1}$ (King et al. 2006*a*). This method cannot be used reliably on rare species with fewer than 20 individuals, so both maximum dbh from our earlier analyses and $D95_{0.1}$ are presented for comparison. Traits were normalized via $\log_{10}$ transformation when needed. The revised leaf trait data set is available in Supplement 1, and the entire trait data set is summarized in Appendix A. Additional discussion of the features and limitations of the trait data set, including the sampling of leaf traits from shade-grown trees and the role of intraspecific trait variation, can be found in earlier publications (Kraft et al. 2008, Kraft and Ackerly 2009).

Phylogeny construction

We constructed a phylogenetic tree for the taxa in Yasuní FDP using the software program Phylomatic (Webb and Donoghue 2005), which matches a taxon list against a background phylogeny of plant family and genus-level relationships and returns a trimmed phylogeny for the group. For this analysis we used the most recent phylogenetic hypothesis available at the time of analysis (tree R20081027; *available online*).[2] Unresolved relationships between genera and all species within genera were treated as polytomies. We used the BLADJ algorithm in the program Phylocom (Webb et al. 2008) to adjust the branch lengths of the phylogeny using known ages of plant fossils (Wikström et al. 2001). The "ape" library was then used to import and manipulate the phylogeny as needed in R (Paradis 2006, R Development Core Team 2009).

The Yasuní FDP includes three species of locally rare tree ferns, which are distantly related to the angiosperms that constitute the remaining 1121 freestanding woody species in the plot. The long phylogenetic branches associated with the tree ferns tend to overwhelm any other phylogenetic patterns present in tropical forest plots by virtue of their length (Kembel and Hubbell 2006), and therefore we chose to restrict the analyses to the angiosperms.

[2] ⟨http://svn.phylodiversity.net/tot/megatrees/⟩

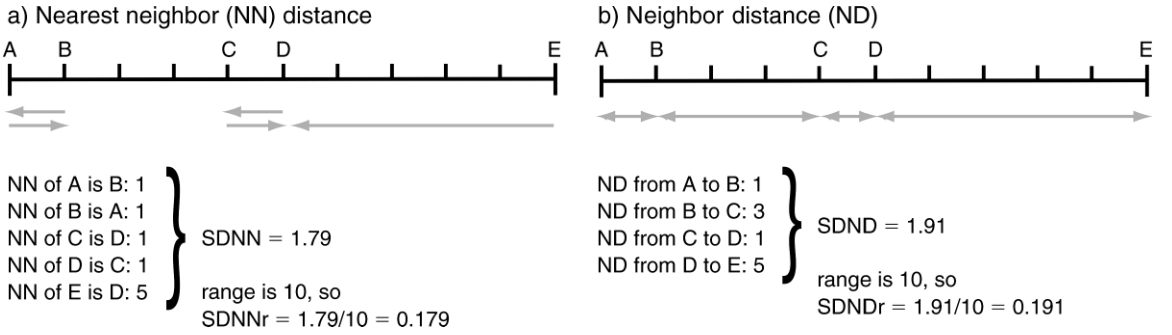

FIG. 2. An illustration of the three metrics of even trait spacing used in this study for five species (A–E) placed along an arbitrary trait axis. (a) Nearest-neighbor (NN) distance-based metrics measure the distance from each species to its nearest neighbor. Thus, some distances between species (such as the distance between species B and C) are not included. Our first metric, SDNN, is the standard deviation of these distances. (b) Neighbor distance (ND)-based metrics instead measure the distances separating each species along the trait axis and always sum to the total range of the trait within the community. The standard deviation of these distances, SDND, is an index of how regularly spaced species are across a trait axis. SDNN and SDND can be divided by the total range to partially correct for effects of habitat filtering, producing SDNNr and SDNDr, our second and third even-spacing metrics. We do not consider uncorrected SDND here as it is directly related to range.

Measuring trait conservatism

The degree of phylogenetic signal in each trait was quantified using the K statistic (Blomberg et al. 2003) implemented in the "picante" package (Kembel et al. 2009) in the R programming language (R Development Core Team 2009). Phylogenetic signal with the K statistic is assessed using a Brownian motion-like model of trait evolution. K values of 1.0 indicate that the trait distribution on the phylogeny perfectly matches a Brownian motion expectation of trait evolution on the phylogeny, while $K < 1$ indicates greater convergence in values than expected under a Brownian trait evolution model, and $K > 1$ indicates a higher degree of phylogenetic signal (i.e., trait similarity of related taxa) than Brownian motion. Significance was assessed by comparing the observed value of K to the distribution of K values obtained by shuffling the traits across the tips of the phylogeny 999 times (note that this null model of random trait distributions corresponds to no phylogenetic signal, with $K_{\text{null}} \ll 1$). Traits were significantly conserved (relative to the random-tip-shuffling model) if the observed K was in the upper 2.5% of the null distribution. We also tested to see whether there was phylogenetic signal in species abundances within the FDP, as this can create misleading signatures of nonrandom community structure in phylogenetic analyses (Kembel 2009).

Constructing sampling units

We divided the FDP into adjacent, nonoverlapping square sample quadrats that were 5, 20, 50, and 100 m on a side (25, 400, 2500, and 10 000 m^2, respectively). The average number of species and individuals at each scale is as follows: 5 m, 12.9 species, 14.6 individuals; 20 m, 129.6 species, 233.5 individuals; 50 m, 408.6 species, 1619.2 individuals; 100 m, 661.4 species, 5829 individuals. As the overall plot is 25 ha, the number of quadrats declined with increasing quadrat size: 10 000, 625, 100, and 25, respectively. The 20 × 20 m sampling scale corresponds to earlier analyses (Kraft et al. 2008).

Trait-based community tests

In each quadrat, species trait means were matched to the species present in the quadrat to calculate the distribution of trait values. Several metrics of trait dispersion sensitive to environmental filtering and niche differentiation were compared to a null expectation. We used community trait range and variance as measures sensitive to habitat filtering (Cornwell et al. 2006, Kraft et al. 2008) and the standard deviation of nearest neighbor distance along trait axes (henceforth SDNN, as defined by trait distances along univariate trait axes, not physical distance) and kurtosis as measures sensitive to niche differentiation (Ricklefs and Travis 1980, Stubbs and Wilson 2004, Kraft et al. 2008, Cornwell and Ackerly 2009). In addition to these metrics used in the previous analysis of the FDP, we used two new metrics designed to detect patterns of even spacing against a background of habitat filtering (Cornwell and Ackerly 2009). First, we divided the SDNN by the observed trait range within a quadrat (henceforth SDNNr) (Stubbs and Wilson 2004, Kraft and Ackerly 2009). Both SDNN and SDNNr are calculated by identifying the most similar co-occurring species to each successive species in the community (Fig. 2) and are therefore conceptually linked to the classic concept of limiting similarity (a finite limit to how similar two co-occurring species can be; MacArthur and Levins 1967, Weiher et al. 1998, Stubbs and Wilson 2004). Theoretical work has shown that there may be no absolute limit to similarity required to promote coexistence (Abrams 1983, 1996). Rather, competitive interactions combined with stochastic population dynamics may lead to regular or even spacing among successive species along niche or trait axes (Chesson 2000, Tilman 2004, Schwilk and Ackerly 2005). To address even

spacing we used the standard deviation of successive neighbor distances along trait axes (Fig. 2), divided by range (henceforth SDNDr) (Ingram and Shurin 2009). This metric shifts the focus from testing for minimum spacing to a focus on how regularly spaced species are across a given range of trait values. We used community assembly simulations to compare the performance of these three even-spacing metrics (SDNN, SDNNr, and SDNDr; Fig. 2) under known conditions.

In each quadrat, the observed metrics were compared to a null expectation generated by creating 999 random communities of equal richness by drawing species from the entire plot weighted by their plot-wide frequency of occurrence (the fraction of quadrats at the scale of analysis in which each species is found), irrespective of trait values (see Kraft et al. 2008). The primary means of assessing the significance of each metric comes from a plot-wide Wilcoxon signed-ranks test with a null hypothesis that the observed values of each metric across all quadrats, relative to their respective null distributions, were evenly distributed about the null expectation (Kraft et al. 2008, Cornwell and Ackerly 2009). We also report a second analysis in which individual quadrats were judged significantly nonrandom if the observed metric fell into the extreme 5% of the null distribution for the quadrat. The results of this approach are summarized as the percentage of quadrats at each spatial scale that would be judged significant if considered alone. This percentage itself is not used as a test statistic. One-tailed tests were used based on a priori predictions of habitat filtering (reduced range and variance) and niche differentiation (reduced SDNN, SDNNr, SDNDr, and kurtosis).

Phylogenetic community structure tests

We estimated two indices of phylogenetic community structure for each quadrat, net relatedness index (NRI) and nearest taxon index (NTI; Webb 2000, Kraft et al. 2007), in an analogous manner to the trait-based tests.

NRI focuses on mean pairwise phylogenetic distances (MPD) between co-occurring taxa, where distances are measured in millions of years down to the common ancestor of two species and back up to the other tip, while NTI is based on the phylogenetic distance to the most closely related co-occurring taxon (mean nearest taxon distance, MNTD). The significance of NRI for an individual quadrat is assessed by comparing the observed MPD to a null distribution of MPD measured on 999 null communities. Null communities for a quadrat were created by randomly drawing an equal number of species from the plot-wide phylogeny. NRI then represents the standardized effect size of MPD (observed − expected/standard deviation of expected) multiplied by −1 (Kraft et al. 2007). NTI is calculated in the same way from MNTD. Positive values of NRI and NTI indicate that taxa are more related than expected (phylogenetically clustered), while negative values indicate that taxa are less related than expected (phylogenetically evenly dispersed).

PLATE 1. Interior of the forest near the Yasuní Forest Dynamics Plot, Ecuador. Photo credit: N. J. B. Kraft.

As with the trait tests, significance was assessed in two ways. At the whole-plot level, a two-tailed Wilcoxon signed-ranks test was used to test the hypothesis that the observed ranks of quadrat level MPD/MNTD was equally distributed about the null expectation. At the quadrat level, the proportion of all quadrats with significantly low or high MPD/MNTD (observed ranked in either 2.5% extreme of the null distribution) was calculated at each spatial scale as an estimate of quadrat-by-quadrat phylogenetic structure. Tests were two-tailed because each metric is used to detect phylogenetic clustering and even dispersion, patterns that drive the metrics in opposing directions (Webb 2000, Kraft et al. 2007).

The choice of null models in testing the significance of NRI and NTI has important implications for type I and II error rates (Kembel and Hubbell 2006, Hardy 2008, Kembel 2009). We use two null models, a simple one in which all taxa on the phylogeny have the same probability of being selected (Webb 2000; analogous to the presence/absence trait null model in Kraft et al. [2008]) and an occurrence-weighted null in which taxa are selected weighted by the fraction of quadrats in which they occur at the scale of analysis (functionally

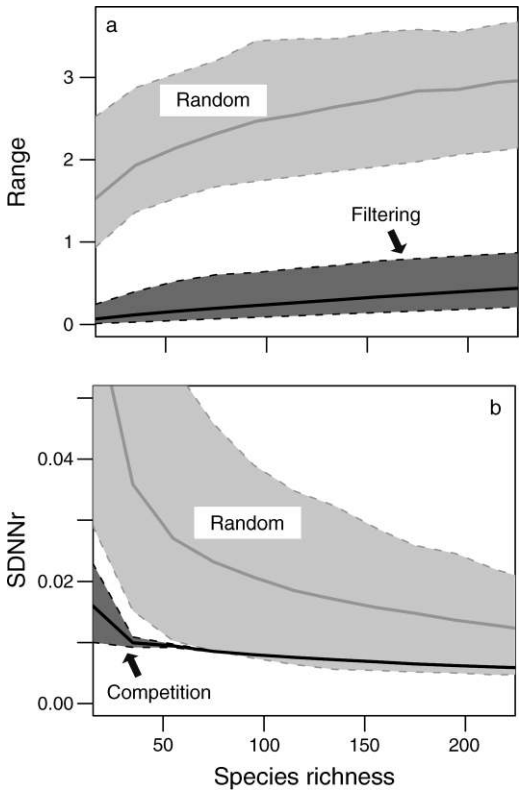

FIG. 3. An example of how power estimation was performed by community assembly simulation. (a) The range of leaf size ($\log_{10}$-transformed, originally measured in cm^2) expected in a 20×20 m quadrat under the random-assembly and habitat-filtering models as a function of species richness within a quadrat. Range is a single number calculated as the maximum minus the minimum. Solid lines indicate the median; shaded areas enclose the area between the 5% and 95% quantiles of the distributions. Both the medians and the extreme 5% quantiles do not overlap, so the range metric has adequate plot- and quadrat-level statistical power to detect filtering in leaf size at the 20-m scale. (b) The SDNNr values (see Fig. 2) expected for leaf size under the random assembly and competition models. In this case, the upper 95% quantile of the competition and the lower 5% quantile of the random model overlap for more than half of the richness levels observed in the forest dynamics plot (in this case, $N = 47$–197), so SDNNr has insufficient quadrat-level power. However, the median of the competition model is always lower than the median of the random distribution, so SDNNr has adequate plot-level power. See *Methods* for additional explanation.

identical to the independent swap of Gotelli and Graves [1996] and Kembel and Hubbell [2006], identical to the occurrence-weighted trait null in Kraft et al. [2008]). The occurrence-weighted null is known to be more conservative (Kembel and Hubbell 2006) and is important to use if there is a phylogenetic signal to species occurrence frequencies (Kembel 2009).

Trait-based community assembly simulations

Previous work has shown than the power of randomization-based phylogenetic tests varies with the size of the pool and the community and with the particular metrics being used (Kraft et al. 2007). In order to determine whether trait-based tests are subject to the same limitations, we performed a set of computer simulations to generate an expectation of how each trait metric should change with species richness in quadrats of varying sizes under three simple models of community assembly. In the random assembly model, identical to the occurrence-weighted null used in the trait tests, a specified number of species was selected from the plot list weighted by their plot-wide occurrence, irrespective of trait values. For nonrandom assembly, we first used a competition model that examined the trait similarity of all species in the pool, selected the most similar pair, and randomly removed one of them (Colwell and Winkler 1984, Kraft et al. 2007). The process was repeated until a specified richness level was reached. Second, we used a habitat filtering model in which we randomly selected a "trait optimum" within the observed range of trait values and systematically removed taxa that were farthest in trait space from that optimum (Kraft et al. 2007). The competition and habitat filtering models are not intended to reproduce the dynamics of real communities, but rather are intended to caricature the distribution of traits under the most deterministic form of the two processes that trait metrics are designed to detect. We ran all of the models on each trait individually, setting final species richness levels from the maximum richness for a given trait to a minimum of 10 taxa, in 10-taxa increments. We ran the competition and habitat filtering models 99 times on each trait, and the random assembly model 999 times for each of the four sets of species occurrence data corresponding to each spatial scale of analysis.

To estimate the statistical power of the trait-based test to detect nonrandom assembly processes, we compared the distribution of a given trait metric produced by the random assembly model at a given richness to the distribution produced by the nonrandom assembly model that the metric was designed to test. For example, we compared the distribution of SLA range produced by the random model to the distribution produced by the habitat-filtering model, as trait range is used as a test for habitat filtering (Fig. 3). We estimated statistical power from this comparison in two ways. First, if the lower 5% quantile of the random model did not overlap the upper 95% quantile of the nonrandom model over more than half of the range of richness levels observed in the community at a given spatial scale, we heuristically designated the metric as having adequate quadrat-level power. If the median of the random distribution was larger than the median of the nonrandom distribution over at least half of the richness levels, we designated the metric as having adequate plot-level power. Both of these designations are arbitrary, but the upper/lower 5% confidence level limit is relevant to the way that individual quadrat-level significance is typically measured in a community (Kraft et al. 2007), and the median overlap is relevant to the way that plot-wide significance is tested using a

Wilcoxon signed-ranks test and related tests in a meta-analytic framework (Kraft et al. 2008, Cornwell and Ackerly 2009, Ingram and Shurin 2009).

Early in the simulation process it became clear that the habitat filtering assembly model produced ranges of traits that were drastically smaller than the random assembly model, so we decided to explore how much the filtering effect could be reduced and still be distinguished from purely random assembly. We did this by combining deterministic species loss through habitat filtering with random species loss as in the random model. We explored weak filtering models with 50%, 25%, and 10% of the species loss due to habitat filtering, with the remaining percentage of species selected in the same manner as the random assembly model.

Finally, we used the assembly models to assess the ability of our even-spacing metrics (SDNN, SDNNr, and SDNDr; Fig. 2) to distinguish patterns produced by habitat filtering from patterns of differentiation, as expected under a competition-based process (Appendix D). We also explored the effect of combining the habitat filtering and competition assembly models in equal proportion. Previous work has suggested that a combination of assembly forces in this way could lead to patterns that appear random (Colwell and Winkler 1984, Kraft et al. 2007). All community assembly simulations were performed in R (R Development Core Team 2009), and sample code for each of the models is available in Supplement 2.

Comparing effect sizes across scales via rarefaction

Comparisons of effects across spatial scales are complicated by the fact that, for a fixed area like the Yasuní FDP, more quadrats are available at smaller spatial scales. This gives additional statistical power to the plot-wide tests when the forest is divided into smaller, more numerous quadrats. In order to test whether there were differences in the strength of effects at different scales despite changes in power, we randomly selected 25 quadrats from each spatial scale (except at the largest scale, where only 25 quadrats were available) and used one-way ANOVA to test whether the distribution of the standard effect sizes for each metric (calculated as the difference between the observed and expected value divided by the standard deviation of the null model) differed between spatial scales.

Congruence in trait and phylogenetic patterns

In order to determine whether trait and phylogenetic tests tended to identify the same individual quadrats as exhibiting nonrandom structure, we scored each quadrat for, respectively, the presence of at least one trait-based test supporting habitat filtering, at least one trait-based test supporting even spacing, one phylogenetic test showing clustering, and one phylogenetic test showing even dispersion. We then used a chi-square test to determine whether quadrats that had a trait-based signal of filtering also had a phylogenetic signal of clustering. Likewise, we tested whether quadrats that had a trait signal of even spacing also had a phylogenetic signal of even dispersion. Separate tests were performed at each spatial scale of analysis.

TABLE 2. Results of trait conservatism tests using the K statistic.

Trait	K	P
SLA	0.32	**<0.001**
Leaf nitrogen	0.44	**<0.001**
Leaf size	0.28	**<0.001**
Seed mass	0.57	**0.004**
Wood density	0.51	**0.004**
Maximum dbh	0.44	**<0.001**
$D95_{0.1}$	0.41	**<0.001**
Abundance	0.23	0.064

Notes: Values of 1 indicate that the observed trait distribution matches a Brownian motion model of trait evolution across the phylogeny. Values <1 indicate greater convergence than a Brownian model; values >1 indicate more conservatism (phylogenetic signal) than expected. P values refer to the results comparing the observed K to a null distribution of K values obtained by shuffling the traits across the tips of the phylogeny 999 times. The P values were calculated by dividing the number of all null K values greater than the observed K by 999. The abbreviation $D95_{0.1}$ stands for the 95th quantile of the diameter distribution of all trees ≥0.1 of the maximum diameter observed for the species. SLA is specific leaf area. Boldface type indicates $P < 0.05$.

RESULTS

Trait conservatism

All of the traits measured exhibited intermediate levels of trait conservatism, with K values ranging from 0.28 for leaf size to 0.57 for seed mass, indicating that all traits were more phylogenetically convergent than a Brownian motion model of trait evolution would predict (all trait K values < 1; Table 2) but more conserved than would be predicted by a random association between traits and the phylogeny (all trait P values < 0.05; Table 2). Leaf morphological traits (SLA and leaf size) were the most evolutionarily labile, while seed mass and wood density were the most conserved. These results indicate moderate trait conservatism. There was no significant phylogenetic signal to species abundances ($P = 0.064$; Table 2), though the marginal nature of the result does suggest a trend. Accordingly, we focus our discussion on analyses that account for differences in abundance in the null model as a precaution.

Trait-based community structure

Nonrandom patterns of even spacing of species along functional trait axes previously reported at the 20-m spatial scale (Kraft et al. 2008) were also found at the 5-m scale (Table 3, Fig. 4). However, plot-wide tests at larger scales did not detect nonrandom patterns except for SDNN for wood density at the 50-m scale.

Plot-wide trait ranges and variances were significantly reduced relative to the null expectation at the 20-m scale, as previously reported (Kraft et al. 2008), and also for

TABLE 3. Results of plot-level trait-based tests of community assembly at four nested spatial scales.

Trait and scale (m)	Habitat filtering		Even spacing			
	Range	Variance	SDNN	SDNNr	SDNDr	Kurtosis
SLA						
5	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
20	**<0.001**	**<0.001**	**0.001**	0.217	0.351	**0.002**
50	**0.004**	**<0.001**	0.159	0.350	0.330	0.665
100	0.447	**<0.001**	0.994	0.995	0.984	0.406
Leaf [N]						
5	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
20	**<0.001**	**<0.001**	**0.001**	**0.044**	**0.029**	0.580
50	0.392	**<0.001**	0.573	0.681	0.098	0.909
100	0.962	**0.001**	0.988	0.991	0.879	0.386
Leaf size						
5	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
20	**0.019**	**0.001**	**<0.001**	**0.001**	**0.001**	**<0.001**
50	**0.050**	**<0.001**	0.272	0.513	0.846	0.106
100	0.787	**0.012**	0.573	0.521	0.755	0.468
Seed mass						
5	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**
20	0.828	0.207	0.750	0.855	0.086	**0.012**
50	0.995	**0.029**	0.534	0.595	0.860	1.000
100	1.000	**0.005**	0.802	0.635	0.563	1.000
Wood density						
5	**<0.001**	**<0.001**	**<0.001**	0.604	0.109	0.983
20	1.000	0.540	0.897	0.899	**0.001**	0.202
50	**0.001**	**<0.001**	**0.034**	0.081	0.664	0.394
100	**0.015**	**0.007**	0.205	0.326	0.308	0.336
Maximum dbh						
5	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
20	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.011**
50	**0.001**	**<0.001**	0.237	0.360	0.508	0.353
100	0.245	**<0.001**	0.965	0.979	0.987	0.895
$D95_{0.1}$						
5	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
20	**0.003**	**<0.001**	**0.023**	0.115	**0.005**	0.427
50	**0.023**	**<0.001**	0.139	0.260	0.106	0.450
100	0.063	**0.001**	0.237	0.346	0.105	0.779

Notes: *P* values are reported for a Wilcoxon signed-ranks test of the hypothesis that the observed distribution of observed trait metrics is less than the null expectation. Scale refers to the length of the sides of a square quadrat. Abbreviations are: SLA, specific leaf area; $D95_{0.1}$, the 95th quantile of the diameter distribution of all trees $\geq$0.1 of the maximum diameter observed for the species (see *Methods: Trait-based community tests*). Boldface type indicates $P < 0.05$. See Fig. 2 for explanations of SDNN, SDNNr, and SDNDr. See Table 4 and Appendix C for additional results.

all traits at the 5-m scale and most traits at the 50-m scale. At the 100-m scale, trait range was reduced for wood density and trait variance was reduced for all traits (Table 3, Fig. 4). While many plot-wide trait tests were statistically significant, mean standard effect sizes were small in many cases (Table 4) and relatively few quadrats were detectably nonrandom when considered individually (Appendix C).

Phylogenetic community structure

Using the more conservative occurrence-weighted null model, plot-wide tests revealed phylogenetic clustering at all spatial scales of analysis, indicating that co-occurring taxa tended to be more related than expected (Table 5, Fig. 4). At the 20-, 50-, and 100-m scales the distribution of observed MNTDs was significantly shifted above the null expectation (Wilcoxon $P \leq 0.001$ at each scale; Table 5) and mean NTI (effect size for MNTD) ranged from 0.20 at the 20-m scale to 0.81 at the 100-m scale. At the 5-m scale, the distribution of observed MPDs was significantly shifted above the null expectation (Wilcoxon $P < 0.0001$), though the average effect size (NRI) was very small (0.01). The more lenient null model (which does not account for species abundance differences) revealed patterns that were qualitatively similar to the occurrence-weighted null model but considerably more nonrandom (Appendix B).

Trait-based assembly simulations

A representative set of simulations for one trait (SLA) at one spatial scale (20 m) is shown in Fig. 5; other trait results are shown for the 20-m scale in Appendices E–J. Across most spatial scales and traits the distributions of

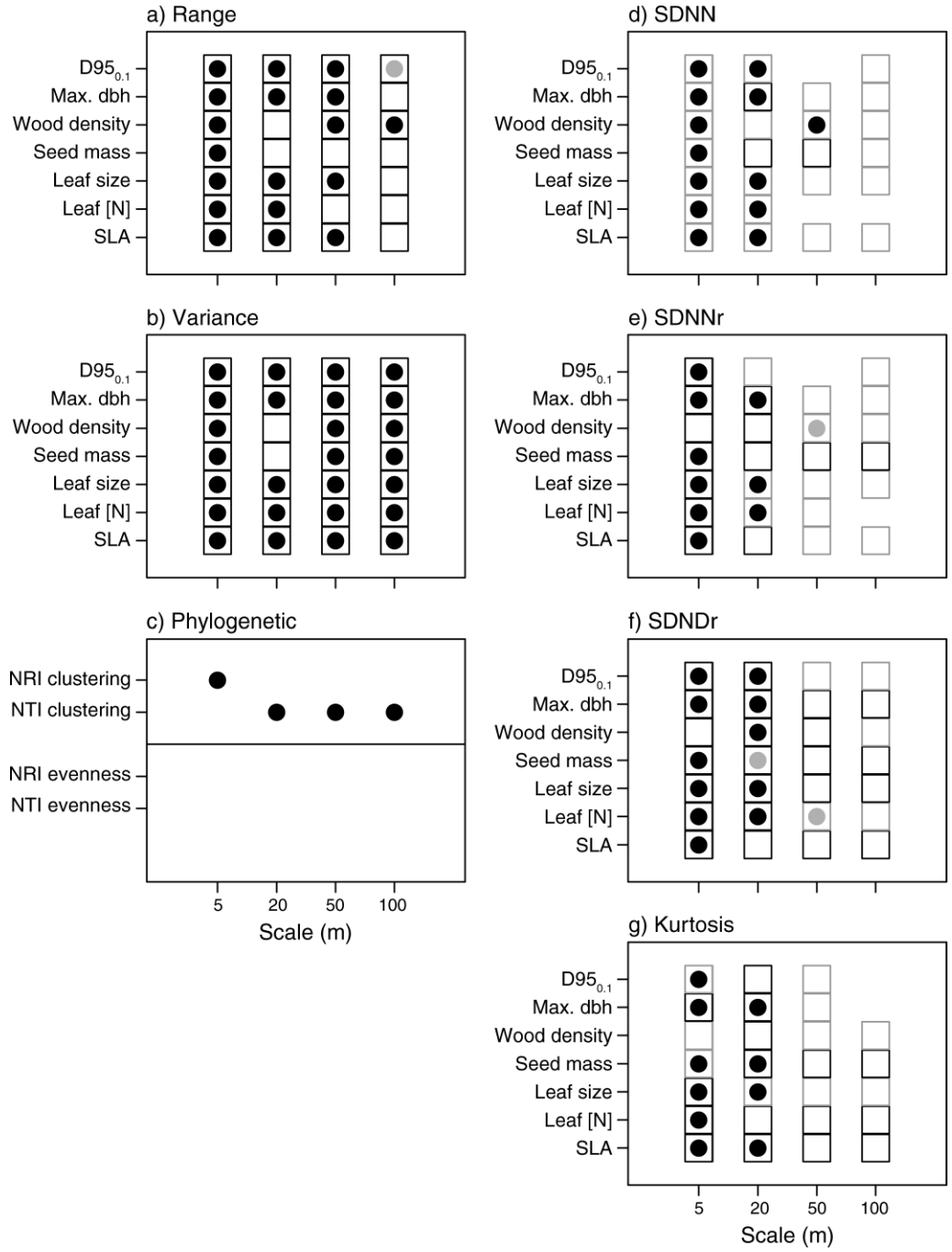

FIG. 4. Summary of trait and phylogenetic tests at the plot level compared with statistical power as determined by community assembly simulations: (a, b) tests for habitat filtering; (d–g) tests for even spacing. Black circles indicate a plot-level test (Tables 3 and 5) in which the Wilcoxon P value was <0.05; gray circles show $P < 0.10$. Black squares indicate that the assembly simulations found adequate plot- and quadrat-level power; gray squares indicate that there was adequate plot-level power but insufficient quadrat-level power. Power is not shown for the phylogenetic tests (panel c); see Kraft et al. (2007) for discussion of the power of phylogenetic tests. See Table 6 for explanations of abbreviations. Scale refers to the length of the sides of a square quadrat.

the range and variance of trait values produced by the habitat filtering assembly simulation was noticeably lower and well separated from the distributions produced by the random assembly null models, indicating that trait range and variance tended to have adequate quadrat- and plot-level power to detect patterns produced by a simple model of habitat filtering (summarized at all spatial scales in Fig. 4). Overlap of the distributions

TABLE 4. Standard effect sizes (mean ± SE) for plot-wide trait-based tests of community assembly at four nested spatial scales.

Trait and scale (m)	Habitat filtering		Even spacing			
	Range	Variance	SDNN	SDNNr	SDNDr	Kurtosis
SLA						
5	−0.02 ± 0.01	−0.02 ± 0.01	−0.02 ± 0.01	−0.01 ± 0.01	0 ± 0.01	0 ± 0.01
20	−0.16 ± 0.04	−0.31 ± 0.04	−0.01 ± 0.04	0.04 ± 0.04	0.06 ± 0.04	0 ± 0.04
50	−0.3 ± 0.1	−0.74 ± 0.11	−0.08 ± 0.11	−0.03 ± 0.11	0 ± 0.11	0.1 ± 0.1
100	−0.11 ± 0.21	−0.84 ± 0.24	0.56 ± 0.22	0.63 ± 0.23	0.51 ± 0.22	−0.04 ± 0.23
Leaf [N]						
5	−0.03 ± 0.01	−0.03 ± 0.01	−0.03 ± 0.01	−0.02 ± 0.01	0 ± 0.01	−0.02 ± 0.01
20	−0.11 ± 0.04	−0.23 ± 0.04	−0.02 ± 0.04	0.01 ± 0.04	0.02 ± 0.04	0.04 ± 0.04
50	−0.08 ± 0.11	−0.44 ± 0.09	0.01 ± 0.1	0.03 ± 0.09	−0.11 ± 0.09	0.11 ± 0.1
100	0.04 ± 0.17	−0.65 ± 0.19	0.23 ± 0.16	0.25 ± 0.16	0.03 ± 0.15	0.04 ± 0.21
Leaf size						
5	0 ± 0.01	0 ± 0.01	0.01 ± 0.01	0 ± 0.01	0.02 ± 0.01	0.01 ± 0.01
20	−0.1 ± 0.04	−0.08 ± 0.04	−0.11 ± 0.04	−0.1 ± 0.04	−0.09 ± 0.04	−0.03 ± 0.04
50	−0.23 ± 0.12	−0.41 ± 0.1	0 ± 0.12	0.07 ± 0.12	0.14 ± 0.12	−0.14 ± 0.12
100	−0.06 ± 0.24	−0.54 ± 0.21	0.16 ± 0.25	0.17 ± 0.24	0.26 ± 0.22	−0.08 ± 0.23
Seed mass						
5	−0.01 ± 0.01	−0.01 ± 0.01	0 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	−0.01 ± 0.01
20	−0.03 ± 0.04	−0.02 ± 0.04	0.09 ± 0.04	0.11 ± 0.04	0.04 ± 0.04	−0.03 ± 0.04
50	0.06 ± 0.12	−0.27 ± 0.12	0.09 ± 0.1	0.09 ± 0.1	0.18 ± 0.11	0.31 ± 0.11
100	0.39 ± 0.01	−0.55 ± 0.19	0.14 ± 0.15	0.1 ± 0.15	0.13 ± 0.16	0.83 ± 0.18
Wood density						
5	−0.04 ± 0.01	−0.04 ± 0.01	0 ± 0.01	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
20	0.12 ± 0.03	0.03 ± 0.04	0.04 ± 0.03	0.02 ± 0.03	−0.07 ± 0.03	0.03 ± 0.03
50	−0.27 ± 0.09	−0.33 ± 0.09	−0.19 ± 0.1	−0.16 ± 0.11	0.06 ± 0.1	0.02 ± 0.09
100	−0.58 ± 0.24	−0.6 ± 0.21	−0.28 ± 0.23	−0.21 ± 0.24	0.02 ± 0.26	−0.08 ± 0.2
Maximum dbh						
5	−0.05 ± 0.01	−0.05 ± 0.01	−0.04 ± 0.01	−0.02 ± 0.01	−0.01 ± 0.01	−0.02 ± 0.01
20	−0.23 ± 0.04	−0.33 ± 0.05	−0.08 ± 0.04	−0.04 ± 0.04	−0.04 ± 0.04	0 ± 0.04
50	−0.38 ± 0.12	−1.01 ± 0.12	−0.05 ± 0.12	0 ± 0.12	0.09 ± 0.12	−0.02 ± 0.12
100	−0.36 ± 0.26	−2.13 ± 0.18	0.47 ± 0.25	0.54 ± 0.24	0.64 ± 0.26	0.3 ± 0.26
$D95_{0.1}$						
5	−0.03 ± 0.01	−0.04 ± 0.01	−0.03 ± 0.01	−0.01 ± 0.01	0.01 ± 0.01	0 ± 0.01
20	−0.09 ± 0.04	−0.22 ± 0.04	−0.02 ± 0.04	0 ± 0.04	−0.03 ± 0.04	0.07 ± 0.05
50	−0.22 ± 0.11	−0.38 ± 0.11	−0.05 ± 0.1	−0.02 ± 0.1	−0.03 ± 0.1	0 ± 0.12
100	−0.39 ± 0.2	−0.68 ± 0.19	−0.18 ± 0.19	−0.14 ± 0.18	−0.24 ± 0.19	0.14 ± 0.2

Notes: Scale refers to the length of the sides of a square quadrat. Abbreviations are: SLA, specific leaf area; $D95_{0.1}$, the 95th quantile of the diameter distribution of all trees ≥0.1 of the maximum diameter observed for the species (see *Methods: Trait-based community tests*). See Fig. 2 for explanations of SDNN, SDNNr, and SDNDr.

TABLE 5. Summary of plot- and quadrat-level tests of phylogenetic community structure at four nested spatial scales using an occurrence-weighted null model.

Scale (m)	Net relatedness index (NRI)					Nearest taxon index (NTI)				
		Quadrats					Quadrats			
	Mean	Nonrandom (%)	Clustered (%)	Evenly dispersed (%)	*P*	Mean	Nonrandom (%)	Clustered (%)	Evenly dispersed (%)	*P*
5	0.01	6.12	3.29	2.84	**<0.001**	0.02	6.03	3.18	2.86	0.173
20	0.04	7.21	4.17	3.04	0.832	0.20	6.89	5.13	1.76	**<0.001**
50	0.05	5.56	3.33	2.22	0.844	0.69	8.89	8.89	0.00	**<0.001**
100	0.00	0.00	0.00	0.00	0.895	0.81	12.00	12.00	0.00	**0.001**

Notes: Positive values of NRI and NTI indicate phylogenetic clustering, while negative values indicate phylogenetically even dispersion. *P* values refer to a plot-wide Wilcoxon signed-ranks test of the null hypothesis that the observed distribution of phylogenetic distances across all quadrats was distributed evenly about the null expectation. Percentages refer to the fraction of all quadrats in which the observed phylogenetic metric was in the upper or lower extreme 2.5% of the null distribution, corresponding to significant even dispersion or clustering, respectively. Scale refers to the length of the sides of a square quadrat. Boldface type indicates $P < 0.05$. See Appendix B for an alternative analysis using a presence/absence null model.

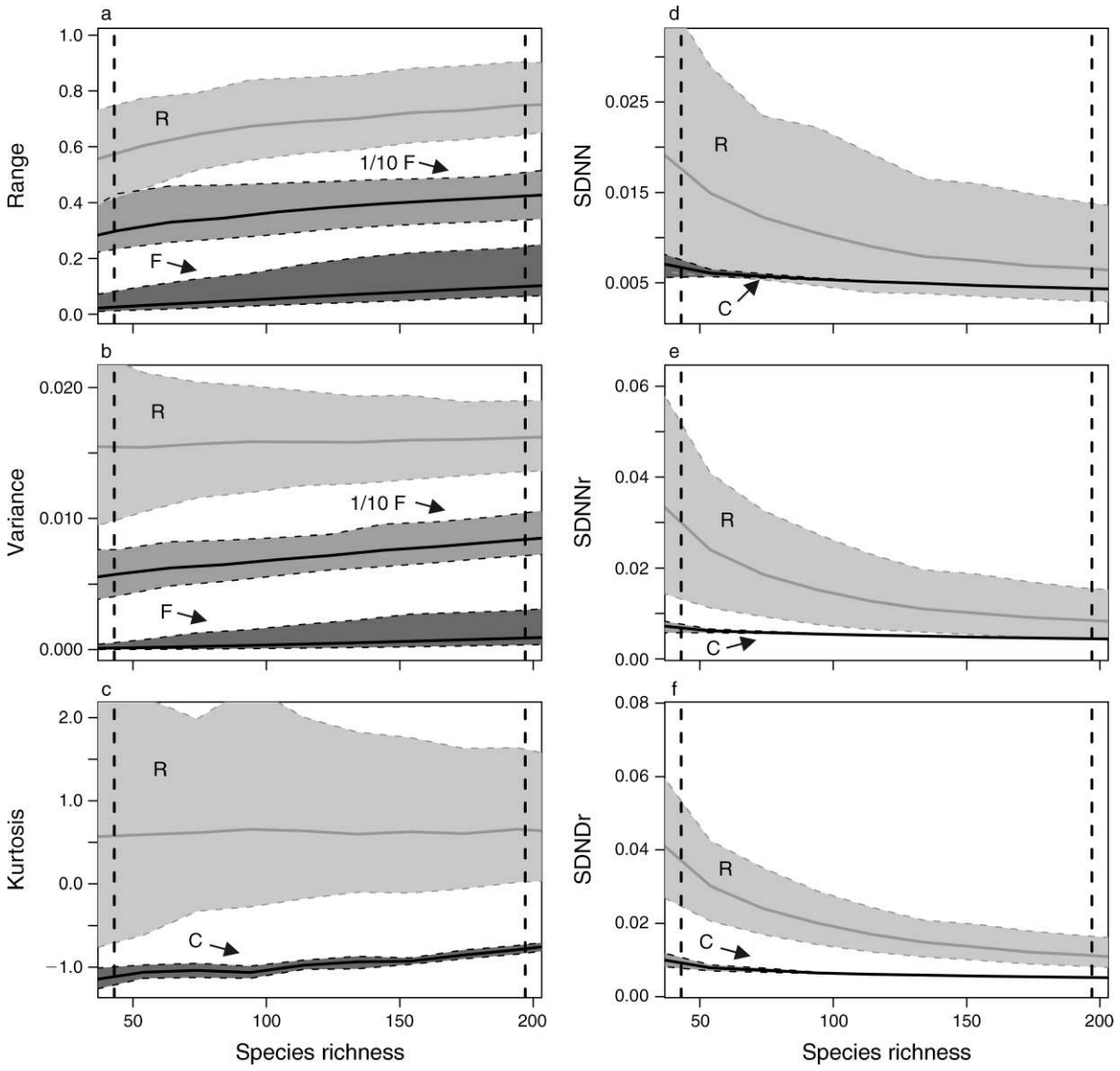

FIG. 5. Distribution of values of six trait metrics for specific leaf area, SLA ($\log_{10}$-transformed, originally measured in cm^2/g) produced by four assembly models for 20×20 m size quadrats plotted as a function of species richness. Shaded distributions indicate the area enclosed by the 5% and 95% quantile of each distribution, while the solid line through each distribution indicates the median. Predictions of the random assembly model are labeled "R," predictions of the habitat filtering model are labeled "F" in panels (a) and (b), and predictions of the competition model are labeled "C" in panels (c)–(f). Predictions of a filtering model in which 10% of species mortality is due to filtering and 90% is random is labeled "1/10 F" in panels (a) and (b). Observed species richness in quadrats at this spatial scale ranges from 47 to 197, as indicated by the vertical dashed lines in each panel. See Appendices E–J for additional traits and Fig. 2 for explanations of trait metric abbreviations.

of the random and habitat filtering models was observed in some cases, but outside of the range of richness levels observed at the corresponding spatial scale (e.g., maximum dbh variance at high richness levels).

Power was often lower for the metrics designed to detect even spacing. While the spacing metrics have adequate plot-level power across most traits and spatial scales, quadrat-level power was inadequate in many instances (Fig. 4), particularly at larger spatial scales where more species are present within quadrats. Kurtosis and SDNDr tended to be the most powerful of the statistics used to detect even spacing, while nearest-neighbor-based metrics (SDNN and SDNNr) were the least powerful. Of the three even-spacing metrics, SDNDr was also the most resistant to producing nonrandom values when analyzing simulated communities produced by the habitat-filtering model (see example and discussion in Appendix D).

The weak filtering assembly models produced distributions of traits that were still distinguishable from random

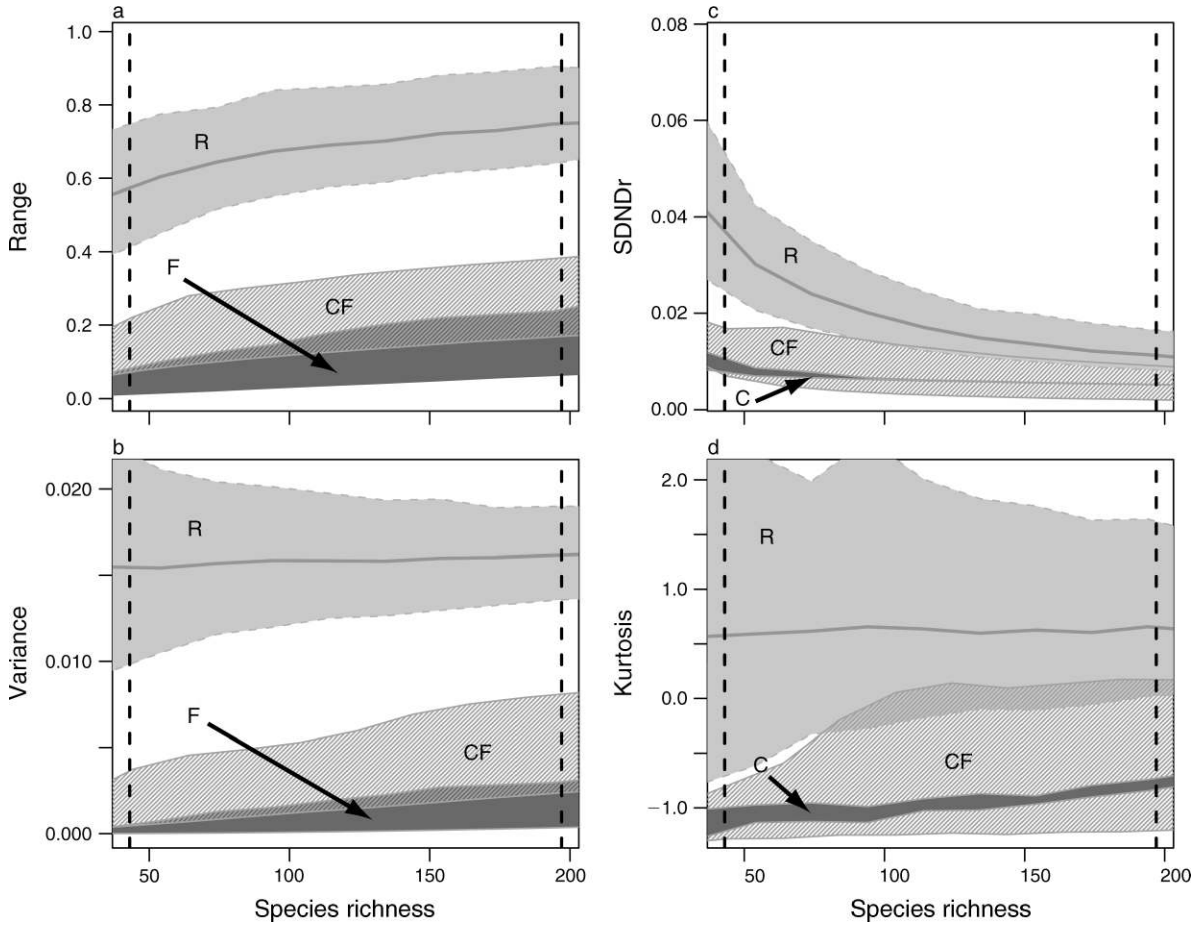

FIG. 6. Example of effect of combining habitat filtering and competition assembly models overlaid with panels (a), (b), (c), and (f) from Fig. 3. The four metrics shown are generally able to distinguish a mixture of competition and habitat filtering (labeled "CF") from the random assembly model (labeled "R"), as indicated by the low overlap between the two distributions in each panel. The combined model produces trait range and variance values [panels (a) and (b)] that are moderately shifted toward random relative to a pure habitat-filtering model (labeled "F") and a broader distribution of SDNDr and kurtosis values [panels (c) and (d)] relative to a pure competition model (labeled "C"). See Fig. 2 for an explanation of SDNDr.

assembly when 50% and 25% of species were removed from the community by deterministic filtering and the remainder removed at random (results not shown). When only 10% of the species where removed by filtering we began to observe overlap between the extreme 5% range quantiles of the random and weak filtering models for some traits (e.g., Appendices G and H).

Most metrics were generally able to distinguish the combined habitat filtering and competition assembly model from the random model (Fig. 6). Trait range and variance values produced by the combined model tended to be shifted toward random relative to the simple habitat-filtering model, while SDNDr and kurtosis values from the combined model tended to produce median values similar to the simple competition model but with a broader distribution. Thus, competition did not erase the signature of habitat filtering and vice versa; the signal of both assembly processes could be detected in the simulated data.

Effect size comparisons across spatial scales

Our rarefaction analyses did not find many significant differences in effect sizes across spatial scales (Table 6). The effect sizes at different scales for the variance in maximum dbh were most distinct from one another, while the remaining significant results tended to indicate that the largest spatial scale (100 m) was distinct from one smaller scale. NTI, a phylogenetic metric, also differed significantly between the biggest (100 m) and smallest spatial scales (5 m and 20 m).

Congruence in patterns

Trait and phylogenetic tests tended to identify the same quadrats as having nonrandom patterns associated with habitat filtering at the 5-m ($\chi^2 = 33.83$, $P < 0.0001$) and 20-m ($\chi^2 = 4.54$, $P = 0.032$) scales. There was no detectable congruence between the quadrats identified as

TABLE 6. Summary of effect size comparisons across four spatial scales (5, 20, 50, and 100 m), using rarefaction and ANOVA.

Metric and trait	df	Residual df	SS	Residual SS	F	P	Tukey hsd contrasts
Range							
SLA	4	96	7.48	88.61	2.03	0.097	
Leaf [N]	4	96	1.67	88.03	0.46	0.769	
Leaf size	4	96	2.79	115.60	0.58	0.679	
Seed mass	4	96	2.25	78.97	0.68	0.605	
Wood density	4	96	10.97	93.87	2.80	**0.030**	20 vs. 100
Maximum dbh	4	96	3.50	124.49	0.67	0.612	
$D95_{0.1}$	4	96	8.32	92.68	2.15	0.080	
Variance							
SLA	4	96	13.65	109.89	2.98	**0.023**	5 vs. 100
Leaf [N]	4	96	8.49	94.60	2.16	0.080	
Leaf size	4	96	11.23	89.53	3.01	**0.022**	
Seed mass	4	96	8.60	103.41	2.00	0.101	
Wood density	4	96	11.99	82.23	3.50	**0.010**	20 vs. 100
Maximum dbh	4	96	81.44	101.46	19.26	**>0.001**	5 vs. 50, 5 vs. 100, 20 vs. 50, 20 vs. 100, 50 vs. 100
$D95_{0.1}$	4	96	17.10	103.37	3.97	**0.005**	5 vs. 50, 5 vs. 100
SDNN							
SLA	4	96	5.97	84.69	1.69	0.158	
Leaf [N]	4	96	5.66	56.17	2.42	0.054	
Leaf size	4	96	7.91	118.70	1.60	0.181	
Seed mass	4	96	2.85	70.21	0.98	0.425	
Wood density	4	96	2.24	98.13	0.55	0.701	
Maximum dbh	4	96	6.54	115.04	1.36	0.252	
$D95_{0.1}$	4	96	1.49	80.45	0.45	0.775	
SDNNr							
SLA	4	96	8.51	93.29	2.19	0.076	
Leaf [N]	4	96	5.11	82.26	1.49	0.211	
Leaf size	4	96	5.13	112.92	1.09	0.366	
Seed mass	4	96	7.01	79.73	2.11	0.085	
Wood density	4	96	4.65	104.96	1.06	0.379	
Maximum dbh	4	96	7.17	116.00	1.48	0.213	
$D95_{0.1}$	4	96	2.94	79.33	0.89	0.473	
SDNDr							
SLA	4	96	7.61	94.31	1.94	0.110	
Leaf [N]	4	96	2.51	62.48	0.96	0.432	
Leaf size	4	96	1.04	145.57	0.17	0.953	
Seed mass	4	96	12.47	124.48	2.40	0.055	5 vs. 20
Wood density	4	96	3.64	87.16	1.00	0.410	
Maximum dbh	4	96	12.79	104.97	2.92	**0.025**	50 vs. 100
$D95_{0.1}$	4	96	1.88	89.77	0.50	0.734	
Kurtosis							
SLA	4	96	2.99	133.08	0.54	0.707	
Leaf [N]	4	96	4.70	81.90	1.38	0.248	
Leaf size	4	96	2.51	108.38	0.56	0.696	
Seed mass	4	96	13.12	83.79	3.76	**0.007**	5 vs. 100, 20 vs. 100
Wood density	4	96	3.81	93.31	0.98	0.423	
Max. dbh	4	96	4.19	141.66	0.71	0.587	
$D95_{0.1}$	4	96	2.54	117.34	0.52	0.721	
NRI							
Phylogenetic	4	96	0.24	114.31	0.07	0.977	
NTI							
Phylogenetic	4	96	17.53	96.26	5.83	**0.001**	5 vs. 50, 5 vs. 100

Notes: We randomly chose 25 quadrats at each spatial scale (except at the 100-m spatial scale, where all 25 quadrats, representing the entire forest dynamics program plot, were used). Scale refers to the length of the sides of a square quadrat. For each test and each trait, the effect sizes from the selected quadrats were compared using scale as a categorical variable in a one-way ANOVA. Scales that differed significantly from one another using Tukey's hsd are summarized in the final column. Abbreviations are: SLA, specific leaf area; $D95_{0.1}$, the 95th quantile of the diameter distribution of all trees ≥ 0.1 of the maximum diameter observed for the species; NRI, net relatedness index; NTI, nearest taxon index. See Fig. 2 for an explanation of SDNN, SDNNr, and SDNDr. Boldface type indicates $P < 0.05$.

TABLE 7. Congruence between quadrat-level trait- and phylogenetic-based tests of community assembly at five nested spatial scales.

Scale (m)	Filtering		Even spacing	
	P	χ^2	P	χ^2
5	**<0.001**	33.83	0.814	0.06
20	**0.032**	4.54	0.882	0.02
50	0.291	1.11	0.792	0.07
100	0.878	0.02	0.841	0.04

Notes: Individual quadrats were scored for the presence of at least one trait-based test consistent with habitat filtering and at least one phylogenetic-based test indicating phylogenetic clustering. A χ^2 test (df = 1) was used to test the hypothesis that both kinds of tests identified the same quadrats. The process was repeated for trait-based tests indicating even spacing and phylogenetic tests indicating even dispersion. Scale refers to the length of the sides of a square quadrat. Boldface type indicates $P < 0.05$.

nonrandom with respect to even trait spacing and even phylogenetic dispersion (Table 7).

DISCUSSION

Methodological concerns and the statistical power of trait-based tests

The trait-based community assembly simulations indicate that trait range and trait variance, coupled with an occurrence-weighted null model, are statistically powerful means of detecting habitat filtering. The distribution of trait range and trait variance values produced by the habitat-filtering model were always well separated from the distributions produced by the random assembly model over the range of richness levels observed in the Yasuní FDP (Fig. 4). Furthermore, the effect of habitat filtering could be diluted by random mortality as much as 90% and still produce trait range distributions that were distinct from the randomly generated distributions (e.g., Fig. 5).

The competition assembly model, on the other hand, frequently produced distributions of trait metrics (SDNN, SDNNr, SDNDr, and kurtosis) that overlapped the distributions produced by the random assembly model, suggesting that these metrics have less power to detect even spacing, particularly as species richness increases (Fig. 4). This is in strong contrast to the high power we found with tests to detect habitat filtering. For example, at the 20-m spatial scale, at the mean community richness of our SLA analyses (130 species), the habitat-filtering model produced an average effect size of −8.29 using SLA range, meaning it produced SLA range values that were >8 SD smaller than the random model. This is in contrast to the competition model at the same scale and richness level, in which the best performing metric measured a mean effect size less than one-third as large (−2.64, using SDNDr) and the worst metric was 1/18th as large (−0.45, using SDNN).

Put simply, it is much easier for trait-based approaches outlined here to detect habitat filtering than it is for them to detect an even spacing pattern as might be produced by niche differentiation or competitive exclusion, particularly as species richness within a community increases. As the strongly deterministic competition and filtering simulation models likely produce more structured patterns of trait distributions than those produced by ecological processes in real communities, caution should be used in interpreting lack of results of even trait spacing or low effect sizes in empirical tests as a true absence of process. The low power of trait-based tests to detect even spacing, particularly in species-rich communities, strongly parallels the poor performance of phylogenetic metrics in the same circumstances (Kraft et al. 2007).

The simulation models also revealed that statistical approaches that account for any reduction in trait range within a community when testing for even spacing (such as SDNNr and SDNDr) have better ability to distinguish patterns produced by habitat filtering from patterns produced by even-spacing processes than those that do not account for range (such as SDNN) (Appendix D), as others have previously suggested (Cornwell and Ackerly 2009). However, even the most robust of the even-spacing metrics in the study (SDNDr) was moderately influenced by habitat filtering (Appendix D), suggesting that improved approaches may be needed. One alternative that may be appropriate in some communities is to restrict the species pool to only include species that are known to be able to establish within the community, effectively imposing habitat filtering on the species pool before testing for even trait spacing (Cornwell and Ackerly 2009). However, this approach requires the investigator to determine the trait thresholds for establishment within the community and may be inappropriate in analyses of communities with only a moderate degree of habitat filtering (Kraft and Ackerly 2009).

The results of the combined filtering and competition model suggest that the operation of multiple ecological processes simultaneously within a community does not necessarily undermine the power of trait-based tests, which were generally able to distinguish the combined model from the random assembly model (Fig. 6). The only caveats are that habitat-filtering patterns tend to be shifted slightly toward random relative to a simple habitat-filtering model (Fig. 6a, b), and even-spacing patterns tend to be more variable relative to a simple competition model (Fig. 6c, d).

As a final caveat to the simulation portion of our analysis, it should be noted that we evaluated the performance of the metrics here using the actual trait values and species abundances from our study. This gives us more insight into the power of these approaches in our community, but decreases our ability to generalize to other communities. For one, the Yasuní FDP is very species-rich, and analyses of communities with fewer

species are likely to find differences. We suspect analyses of less species-rich communities may have higher statistical power to detect even spacing, as power of the associated metrics tended to decline with increasing richness in most of our analyses (e.g., Fig. 5). Second, most of our trait distributions were approximately normally (or log-normally) distributed (Kraft et al. 2008); the behavior of the tests used here may differ in communities with other trait distributions.

Phylogenetic community structure of the Yasuní FDP

Across the entire Yasuní FDP species tend to be more phylogenetically related at every spatial scale than either a presence/absence or an occurrence-weighted random assembly model predicts (Table 5, Appendix B). This pattern was most evident when measuring the phylogenetic distance to the most closely related co-occurring species (MNTD, NTI) at the largest spatial scales. As key functional traits related to ecological strategy all showed significant conservatism (Table 2), this indicates a role for habitat filtering (Table 1; Webb 2000, Kraft et al. 2007). The effect of phylogenetic clustering is stronger at larger spatial scales, with the effect sizes associated with the significant tests increasing monotonically at larger spatial scales (Table 5), a trend that was largely supported by rarefaction analysis (Table 6).

While it is tempting to make inferences about the changing importance of habitat filtering at different spatial scales and about the relative strength of phylogenetic tip-level (NTI) and clade-level (NRI) clustering based on these results, it is important to remember that statistical power to detect habitat filtering differs between NTI and NRI and that the power of both metrics shifts as the size of the community sample changes relative to the size of the source pool. Previous simulation modeling work (Kraft et al. 2007) has shown that NTI tends to have higher overall power to detect filtering than NRI and also that when the species pool is large the power of both metrics is greatest when the richness of the community is approximately half the size of the regional pool. The most nonrandom phylogenetic structure at Yasuní was detected at the largest spatial scales with NTI (Tables 5 and 6), which corresponds to a mean community richness of approximately half of the pool (mean richness at 50 m = 409, mean richness at 100 m = 661, pool richness = 1121), precisely where statistical power is highest to detect filtering. The random or close-to-random structure observed at 5 m and the lack of significant NRI clustering at larger scales could be due to a lack of habitat filtering at those spatial and phylogenetic scales or it could be due to lower power; there is no easy way to distinguish the alternatives from the phylogenetic patterns alone. Similarly, both NRI and NTI have very low power to detect phylogenetically even dispersion in communities as species-rich as Yasuní (Kraft et al. 2007), which may contribute to the low percentage of quadrats that were evenly dispersed (Table 5).

Trait-based patterns within the Yasuní FDP

The analyses presented here suggest that at least two distinct stabilizing mechanisms are occurring at Yasuní. First, we observed reduced ranges and variances (relative to a dispersal assembly model) of key functional traits across the forest, a pattern that is best explained by habitat associations (Table 1; Cornwell et al. 2006). The trait-based tests detected patterns consistent with habitat filtering from the 5–50 m scale (trait range, with one significant result from wood density at 100 m) or from the 5–100 m scale (trait variance; Fig. 4). As the simulation modeling results indicate that there was statistical power to detect nonrandom filtering patterns at the largest spatial scale, it is possible that filtering shapes species co-occurrence patterns up to the 50–100 m spatial scale. Rarefaction analysis suggests that the effect of filtering is relatively constant across spatial scales, with wood density and maximum dbh being the only traits with significant difference in effect sizes across scales (Table 6). It is likely that species associations with either ridgetops or valley bottoms within the plot (Valencia et al. 2004*b*) are the primary mechanism of these patterns. Prior analyses (Kraft et al. 2008) have shown that restricting the scope of the analysis to areas within one topographic habitat removed the significant filtering effect in many cases and that trait averages within quadrats at the 20-m scale shift across habitat types, suggesting that differences in strategy are favored in the two environments. Topographic habitats within the Yasuní FDP tend to occur in patches up to approximately 100 × 100 m (Valencia et al. 2004*b*), further suggesting a role for habitat filtering up to this spatial scale.

In addition to habitat filtering, we found consistent patterns of even trait spacing in many traits at the 5- and 20-m scales, but only one at larger spatial scales (SDNN of wood density at 50 m; Fig. 4). Patterns of even spacing indicate that co-occurring species are more dissimilar from one another than a dispersal assembly model would predict. Ecologically, given the traits we included, this means that quadrats tended to have a broad distribution of adult heights, light acquisition strategies, and regeneration strategies (Cornelissen et al. 2003), a pattern consistent with niche differentiation into areas of different age since disturbance and heights within the canopy. The scale at which the patterns were found (5–20 m) is consistent with these processes: nonrandom patterns were detected at spatial scales where trees could conceivably be interacting; at larger scales (50 m and up) it may be that there is enough space for species to co-occur without being negatively impacted by growing near functionally similar species. However, as statistical power also tended to decline at larger scales (Fig. 4), it is difficult to say whether this drop in significance at 20 m is due to low power or a change in the underlying ecological dynamics. Rarefaction analyses generally did not detect differences in the effect size

of even-spacing tests across scales, except for seed size and maximum dbh (Table 6).

Does phylogenetic relatedness capture the same information as functional traits?

Phylogenetic tests of community assembly are considerably less data intensive than trait-based methods, particularly in plant communities for which tools exist for rapidly creating site-specific phylogenies (e.g., Phylomatic; Webb and Donoghue 2005). This study demonstrates that phylogenetic community methods capture at least some of the story that trait-based methods offer. Both methods report patterns consistent with habitat filtering at the plot-wide level at the same range of spatial scales (Fig. 4), and both methods tended to identify nonrandom patterns consistent with filtering in the same individual quadrats at smaller spatial scales (Table 7). This suggests that phylogenetic relatedness may integrate important ecological similarities between species that our functional trait measurements also capture.

Keeping in mind the low power of the tests in this analysis to detect even phylogenetic spacing (Kraft et al. 2007), one intriguing result of this study is that trait and phylogenetic tests tended to detect even spacing (of traits or phylogenetic distances) in different areas of the forest (Table 7). This could be due to the small number of quadrats that were evenly dispersed phylogenetically (Table 5). It could also be that different mechanisms may be contributing to the patterns. For example, an even dispersion of traits within plots could capture the fact that species with a broader array of resource use strategies tend to co-occur more than a dispersal assembly model would predict, while an even phylogenetic dispersion could indicate an even spread along unmeasured ecological dimensions such as rooting depth. Perhaps more likely, the phylogenetic tests may capture the impact of enemy-meditated density dependence if enemy susceptibility is phylogenetically conserved (e.g., Gilbert and Webb 2007). Enemy-mediated density dependence, as it is typically hypothesized to occur in tropical forests, is essentially niche differentiation along numerous niche axes corresponding to susceptibility to each type of specialized natural enemy (Gillet 1962, Chase and Leibold 2003). To the best of our knowledge these axes are not strongly correlated with the suite of morphological traits measured on the species in this study (though low SLA can be correlated with increased structural defenses against generalist herbivores). In this latter example, phylogenetic relationships may capture important axes of ecological similarity that the functional traits measured in this study do not capture. It will take a more detailed understanding of shared natural enemy susceptibilities within tropical forests at a community scale to know for certain.

Another limitation of phylogenetic metrics used in this study is that they are sensitive both to filtering and to patterns that create even spacing, and the two processes tend to drive the metric in opposite directions. In quadrats or communities in which both processes are present, phylogenetic methods may be reduced to revealing a weak signal of whichever process is strongest or to detecting random patterns (Colwell and Winkler 1984, Kraft et al. 2007). Simulations in this study have shown that trait-based metrics are less sensitive to this issue (e.g., Fig. 6).

Conclusions

Assembly processes across spatial scale in the Yasuní FDP

Taken together, these results indicate that stabilizing processes influence species occurrence patterns at Yasuní. Habitat associations drive species co-occurrence patterns at small to intermediate scales (5–100 m) and some combination of strategy differentiation and/or enemy-mediated density dependence shapes species occurrence patterns at smaller scales (5–20 m). These results are difficult to reconcile with the species (and individual) equivalence component of neutral theory. Patterns consistent with stabilizing forces (which are absent from neutral theory) are evident across the plot, and a key corollary of fitness-equalizing trade-offs, which is that species should be distributed randomly with respect to traits, was not supported.

However, it is also unlikely that a traditional niche-based view of the forest is sufficient to explain patterns of distribution and abundance at Yasuní. Many individual quadrats were indistinguishable from predictions of dispersal assembly (Appendix C), and the evidence for stabilizing forces, while pervasive (Table 3), typically was accompanied by low effect sizes (Table 4). There may be several explanations for the low trait-based effect sizes that we observed. The first is simply that the processes that produce the patterns we detected are in fact quite weak. The second has to do with the low power of the even-spacing trait-based metrics that we used (see *Discussion: Methodological concerns* ...). A third explanation has to do with the traits we measured. Our traits, which capture important information about growth and resource use strategy differences across woody plants, are nevertheless only proxies for the more detailed physiological and demographic traits that influence population dynamics. Particularly lacking, though by no means easy to remedy, are belowground traits and data on plant defenses. Finally, it is likely that a multivariate approach to trait-based tests (e.g., Cornwell et al. 2006), which could offer an integrated measure of the ecological similarities of co-occurring species, would have more power to detect nonrandom patterns. This is consistent with the fact that the phylogenetic tests, which may be acting as an integrator of ecological similarity, had among the largest effect sizes in our analysis (Tables 4 and 5). While our trait database is among the most extensive collected for a single community, it does have gaps, particularly in wood density and seed size, which precluded a full multivariate

analysis of the community (Appendix A). Likewise, sampling limitations prevented us from fully considering the role of intraspecific variation (but see discussion in Kraft et al. 2008, Kraft and Ackerly 2009). It will be valuable to revisit these analyses as more trait data become available.

These concerns aside, if the nonrandom processes we detected are in fact subtle, an integrated view of communities that incorporates both dispersal assembly and niche assembly processes will likely be the most applicable to understanding the dynamics of the forest in Yasuní (Chesson 2000, Purves and Pacala 2005, Schwilk and Ackerly 2005, Gotelli and McGill 2006, Adler et al. 2007). For example, it may be that tree species fitnesses are close to equalized and that the patterns that we found are evidence for relatively weak but pervasive stabilization across the forest by niche differences and natural enemies. While the difference between this view of the forest and a purely neutral view may sound negligible on the surface, the contrast between the two is important on large temporal scales (e.g., McGill et al. 2005), in relation to ecosystem structure and function (Purves and Pacala 2005), and in the species dynamics at the spatial scales investigated in this study.

Finally, while improved trait databases, better resolved phylogenies, and improved methods for detecting even spacing of species in trait and phylogenetic space may sharpen our perception of the patterns we have detected, it will take new conceptual and demographic approaches to connect nonrandom trait and phylogenetic patterns to formal coexistence theory. For example, the regular spacing of species along a niche or trait axis is one potential outcome of niche differentiation, but by no means the only one. In particular, approaches that allow the estimation of the relative contribution of stabilizing and equalizing processes to community dynamics (e.g., Chesson 2000, Adler et al. 2007, Levine and HilleRisLambers 2009) may be particularly useful. In the meantime, we are left with striking patterns that suggest that habitat associations, strategy differentiation among species, and natural enemies shape patterns of species co-occurrence in one of the most diverse forests in the world.

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APPENDIX A

Summary of the functional trait database used in the study (*Ecological Archives* M080-013-A1).

APPENDIX B

Alternative phylogenetic community structure analysis using a presence/absence null model (*Ecological Archives* M080-013-A2).

APPENDIX C

Percentage of quadrats where the observed trait metrics were significantly different from the null expectation (*Ecological Archives* M080-013-A3).

APPENDIX D

Comparison of the ability of three different metrics of even trait spacing to distinguish between alternative models of community assembly (*Ecological Archives* M080-013-A4).

APPENDIX E

Distributions of six trait metrics for leaf nitrogen produced by four community assembly simulation models (*Ecological Archives* M080-013-A5).

APPENDIX F

Distributions of six trait metrics for leaf size produced by four community assembly simulation models (*Ecological Archives* M080-013-A6).

APPENDIX G

Distributions of six trait metrics for seed size produced by four community assembly simulation models (*Ecological Archives* M080-013-A7).

APPENDIX H

Distributions of six trait metrics for wood density produced by four community assembly simulation models (*Ecological Archives* M080-013-A8).

APPENDIX I

Distributions of six trait metrics for maximum dbh produced by four community assembly simulation models (*Ecological Archives* M080-013-A9).

APPENDIX J

Distributions of six trait metrics for the 95th quantile of the diameter distribution of all trees ≥ 0.1 of the maximum diameter observed for the species, $D95_{0.1}$, produced by four community assembly simulation models (*Ecological Archives* M080-013-A10).

APPENDIX K

Relationship between specific leaf area (SLA) estimated from leaf punches and SLA estimated from whole leaves (*Ecological Archives* M080-013-A11).

SUPPLEMENT 1

Leaf trait data set from the Yasuní Forest Dynamics Plot, Ecuador (*Ecological Archives* M080-013-S1).

SUPPLEMENT 2

Community assembly simulation code for use in the R programming language (*Ecological Archives* M080-013-S2).