

THE INFLUENCE OF SPATIAL AND SIZE SCALE ON PHYLOGENETIC RELATEDNESS IN TROPICAL FOREST COMMUNITIES

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Abstract. The relative importance of biotic, abiotic, and stochastic processes in structuring ecological communities continues to be a central focus in community ecology. In order to assess the role of phylogenetic relatedness on the nature of biodiversity we first quantified the degree of phylogenetic niche conservatism of several plant traits linked to plant form and function. Next we quantified the degree of phylogenetic relatedness across two fundamental scaling dimensions: plant size and neighborhood size. The results show that phylogenetic niche conservatism is likely widespread, indicating that closely related species are more functionally similar than distantly related species. Utilizing this information we show that three of five tropical forest dynamics plots (FDPs) exhibit similar scale-dependent patterns of phylogenetic structuring using only a spatial scaling axis. When spatial- and size-scaling axes were analyzed in concert, phylogenetic overdispersion of co-occurring species was most important at small spatial scales and in four of five FDPs for the largest size class. These results suggest that phylogenetic relatedness is increasingly important: (1) at small spatial scales, where phylogenetic overdispersion is more common, and (2) in large size classes, where phylogenetic overdispersion becomes more common throughout ontogeny. Collectively, our results highlight the critical spatial and size scales at which the degree of phylogenetic relatedness between constituent species influences the structuring of tropical forest diversity.

Key words: *body size; community ecology; phylogenetic trait conservatism; phylogeny; scaling; species pool; specific leaf area; stoichiometry; tropical forest dynamics plot; wood density.*

INTRODUCTION

Since the writings of early naturalists, tropical forests have presented a persistent and challenging problem to biologists (Wallace 1876, Dobzhansky 1950). Specifically, what are the critical ecological and evolutionary forces that generate and maintain patterns of tree species richness in tropical forests? Here we argue that recent applications of phylogenetic information (Losos 1996, Tofts and Silvertown 2000, Webb 2000, Cavender-Bares et al. 2004) and scaling (Menge and Olson 1990, Milne 1992, Enquist and Niklas 2001) in community ecology together offer an analytical framework that provides detailed information that could help elucidate the mechanisms that promote and maintain tropical forest diversity.

The use of phylogenies to assess the relative influence of the forces that structure diversity requires knowledge of whether traits central to resource acquisition and allocation, often referred to as functional traits, display convergence or conservatism in their evolution. In other words, if traits are phylogenetically conserved on a phylogeny, species that are closer to one another on the phylogeny have traits that are more similar than

expected. This has also been referred to as phylogenetic signal (Blomberg et al. 2003). If functional traits are found to be phylogenetically conserved then the level of phylogenetic relatedness between co-occurring species can be used to infer the processes important in structuring the focal community. For example, if functional traits are conserved and co-occurring species are more closely related than expected, phylogenetically clustered, this is suggestive of abiotic filtering (Webb et al. 2002). Conversely, if co-occurring species are less related than expected, phylogenetically overdispersed, this suggests biotic interactions are important in structuring the focal community (Webb et al. 2002). Using the phylogenetic approach outlined above provides a novel framework for testing some of the central mechanisms promoted as being important in structuring ecological communities.

There are three mechanisms that are often invoked to understand the structure of diversity within ecological communities: neutrality, competitive exclusion, and abiotic filtering. The concept of competitive exclusion has been a cornerstone of modern “niche-based” ecological theory and has provided a link between ecological processes and evolutionary theory (Roughgarden 1983), while lately arguments for the importance of abiotic filtering have become more common (e.g., Weiher and Keddy 1999). As a result there is a rich literature assessing the importance of biotic and abiotic

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forces in structuring ecological communities (Gause 1934, Hardin 1966, Janzen 1970, Roughgarden 1983, Pacala and Tilman 1994, Tilman 1994, 2004), yet there are also compelling theoretical arguments against the importance of niches that instead point to the fundamental role of neutral processes (Bell 2001, Hubbell 2001). Each of these three mechanisms makes explicit hypotheses regarding the phylogenetic structure of communities when functional traits are found to be phylogenetically conserved. Below we outline these predictions and show how they are expected to change along various scaling axes.

A neutral model assumes that (1) all taxa are demographically and ecologically equivalent and (2) dispersal limitation plays a prominent role in the structuring of communities (Hubbell 2001). Therefore, a neutral model makes three predictions: (1) phylogenetic relatedness should play no role in determining the co-occurrence of tree species in a community (Hubbell 2001); (2) there will be no difference in phylogenetic relatedness across different size cohorts of trees; and (3) the degree of phylogenetic dispersion should not change with the spatial scale of analysis.

The competitive exclusion model (Hardin 1966, Roughgarden 1983, Tilman 1994) (1) assumes that competitive displacement occurs at the small spatial scale of inter-individual interactions and (2) posits that when species are morphologically (and hence ecologically) similar the superior competitor will drive the other species to local extinction. Thus, a competitive exclusion model yields three predictions for patterns of phylogenetic relatedness, assuming that more closely related species are also more ecologically similar: (1) By limiting similarity, the process of competitive exclusion results in the phylogenetic overdispersion of co-occurring species (i.e., species assemblages will be comprised of taxa that are further apart on a phylogenetic tree than expected from chance). (2) If competitive exclusion is more apparent at small spatial scales (to be expected in sessile organisms such as trees), the degree of phylogenetic overdispersion will increase with decreases in spatial scale. (3) At small spatial scales, because of competitive thinning, the degree of phylogenetic overdispersion will increase with increasing plant size (Enquist et al. 2002). This is hypothesized to occur because as tree cohorts grow in size (saplings to adults) there is a reduction or thinning of individuals because of the steady state (or zero-sum) size distribution (Enquist and Niklas 2001). Therefore there is a strong mortality effect of individuals within cohorts as they grow from saplings to trees (Harms et al. 2000). Under a competitive exclusion model this mortality should be phylogenetically non-random so that as tree cohorts mature they should become more overdispersed as tree size increases.

An abiotic filtering model assumes that the immigrants arriving at a given location will result in a winnowed subset of taxa, or traits, that can survive in that given spatially defined abiotic regime (Weiher and

Keddy 1995, 1999, Webb et al. 2002). Thus, an abiotic filtering model yields three predictions that differ from the competitive exclusion and neutral models: (1) co-occurring species will share similar traits that are necessary to tolerate the given abiotic backdrop (i.e., variability in edaphic or topological conditions), and therefore co-occurring species should be phylogenetically clustered; (2) phylogenetic clustering should be most apparent at medium to large spatial scales, because of edaphic and topological variation on medium spatial scales and biogeographic and evolutionary time scale processes (i.e., speciation or diversification within regional clades; Webb et al. 2002) occurring at large spatial scales; and (3) as trees grow in size from seedlings to adults, filtering of traits will continue through differential mortality, so neighboring trees should become more phylogenetically clustered (Silvertown et al. 2006).

A study using spatial scaling and phylogenetic methods has recently been conducted using the tropical forest dynamics plot (FDP) on Barro Colorado Island (BCI), Panama (Kembel and Hubbell 2006). This study found a slightly clustered to random signal across spatial scales ranging from 100 m² to 1 ha. Other recent work using phylogenies to analyze communities has found that at spatial scales finer than 100 m² phylogenetic overdispersion is more evident in Floridian oak communities and in the Cape Floristic Region (Cavender-Bares et al. 2006, Slingsby and Verboom 2006). Both of these studies argue for the importance of competition in structuring plant communities at fine scales. Therefore it is presently unknown whether at spatial scales finer than 100 m² tropical forest communities are phylogenetically structured. Furthermore, the relative role of the phylogenetic relatedness of species within different size classes and cohorts in structuring tropical tree communities has remained completely unexplored. As the above three models make predictions regarding phylogenetic relatedness of species in space and make predictions of the relatedness of species in time, it is important that we now also analyze the combined effects of spatial and size scales in communities.

Here we first test for, and provide evidence of, phylogenetic conservatism in ecologically important traits in tropical trees. Second, we expand upon previous work that addresses spatial scale and relatedness in tropical forests (Kembel and Hubbell 2006) by analyzing smaller spatial scales across multiple different tropical forest communities. Third, we provide the first analysis of the combined influence of size and spatial scales on phylogenetic relatedness across multiple different forest communities. We argue that by incorporating a size axis into community phylogenetic analyses, along with more finely delineating the neighborhood size, one's ability to detect a nonrandom phylogenetic structure in a local assemblage increases. Finally, we discuss the general importance of scaling axes presented in the present work

along with axes presented elsewhere on the phylogenetic relatedness of co-occurring species.

MATERIALS AND METHODS

Plot descriptions

A total of five tropical forest dynamics plots (FDPs) were utilized for the study. With the exception of San Emilio, for which we used census data from 1996, for all other FDPs we used the 1995 census data. The FDPs included: Barro Colorado Island (BCI), a 50-ha FDP characterized as tropical lowland moist forest and located in Lake Gatun, Panama (Hubbell and Foster 1983, Condit et al. 1996); San Emilio FDP (16 ha), a seasonally dry forest in northwestern Costa Rica (Enquist et al. 1999); Luquillo FDP (16 ha), a pre-montane moist forest located in the Luquillo Experimental Forest in Puerto Rico, part of the National Science Foundation Long-Term Ecological Research Program (Thompson et al. 2002, 2004, Brokaw et al. 2004); Sherman FDP (6 ha), a lowland moist forest located on the Atlantic coast of Panama; and Cocoli FDP (4 ha), a semi-deciduous plot located on the Pacific coast of Panama (Condit et al. 2004). Each FDP census includes all freestanding woody stems ≥ 1 cm (3 cm or greater at San Emilio) measured at 1.3 m from the ground (Condit 1998).

Phylogenetic niche conservatism

Phylogenetic analyses of community structure often assume that traits closely associated with plant life history (growth, reproduction strategy, etc.) and ecological interactions are phylogenetically conserved (but see Tofts and Silvertown 2000, Cavender-Bares et al. 2004, 2006). To assess this critical assumption we conducted an analysis of several functional traits associated with tropical-tree life history and growth (including seed size, wood density, specific leaf area, and leaf nitrogen and phosphorus content). Seed size was used as a surrogate for the reproductive strategy of species in each plot as plants can span the gradient of producing few large seeds to many small seeds (Moles et al. 2005a, b). Wood density was used as it is highly correlated with tree radial growth rates and is indicative of the trees' place along the succession continuum (ter Steege and Hammond 2001). Leaf nitrogen and phosphorus are highly correlated with photosynthetic capacities in plants and are central to what has been referred to as the "world-wide leaf economics spectrum" (Wright et al. 2004). We tested for the phylogenetic conservatism of these traits from data collected from the literature for tropical trees from each FDP where available. Although trait data was not available for each species in each FDP, analyses have shown that the degree of phylogenetic trait conservatism generally increases with an increase in sampling (N. G. Swenson, *unpublished data*). Thus the results stemming from these analyses may be conservative estimates of trait conservatism in these forests.

A phylogenetic supertree was constructed for the species from each FDP for which we had a trait value. The trait values were then assigned to the taxa in the supertree for analysis. The supertrees were constructed with Phylomatic and Phylocom (Webb et al. 2004, Webb and Donoghue 2005) as described below and in the Appendices. Using the Analysis of Traits program (Webb et al. 2004) tree-wide trait conservatism was quantified by randomizing trait values across the tips of the phylogenetic supertree 9999 times. Next, the average magnitude of the standard deviation between descendant trait means from each internal node across the whole tree was quantified for each randomization. This process created a null distribution of trait divergences to which we could compare our observed values. Observed values landing in one of the first 500 quantiles were considered phylogenetically conserved. A similar method of permutating trait values across the tips of the phylogeny has been promoted by Blomberg et al. (2003) for quantifying the "phylogenetic signal" in data, which is synonymous with what we term "phylogenetic conservatism."

Plant size and spatial scaling

The raw data from BCI, San Emilio, Cocoli, Luquillo, and Sherman FDPs were managed using the statistical platform "R" (R Development Core Team 2005). Prior to importing, the data from the Luquillo FDP were georeferenced by binning trees into 25-m² quadrats in which they occur in order to attach x , y coordinates to each quadrat for data selection purposes. Each plot was divided into square quadrats with sides ranging, in increments of 5 m per side, from 25 m² to 225 m². During this process the abundance of each species was calculated for each quadrat in each FDP. Because the metrics used to test for phylogenetic structure of communities are based on measures of interspecific dispersion only quadrats that contained two or more species were used. Quadrats containing only one species therefore were omitted because they could not be interpreted. This is because quadrats containing only one species could be seen as a prime example of competitive exclusion of all other species, the ultimate example of abiotic filtering in which only one species can exist in that quadrat, or even an example of dispersal limitation, which is a central component of the neutral model. The numbers of quadrats that contained two or more species, and therefore used for our analyses, can be found in the Appendices.

This above process for generating quadrats was initially performed for all trees and the full range of diameters. For the second analysis the stem diameters were divided into five size classes and the abundance of stems in each diameter size class in each quadrat was calculated in order to perform analyses that could make inferences concerning plant size and community structure. The San Emilio census data only included stem diameters larger than 3 cm so only four size classes were

used for this FDP. The size classes were 1–2.9 cm, 3–4.9 cm, 5–9.9 cm, 10–14.9 cm, and 15 cm and above. For a more refined analysis using plant size as a surrogate for time, each FDP was divided into 25-m² quadrats. Next, a list of tree species that can reach the canopy was compiled for each FDP. For the purposes of this study, we deemed any tree species from an FDP that has an individual reaching ≥ 15 cm diameter as being a species that can reach the canopy. Next all individuals, regardless of size, that were deemed canopy species were extracted from the FDP census data. These individuals were divided into the same five size classes described above for the analysis. The species composition for each separate size class of canopy species was compiled for each of the 25-m² quadrats.

Species pool construction

Phylogenetic supertrees representing species pools were constructed by inputting all of the species in all of the FDPs into the plant phylogeny database Phylomatic (Webb and Donoghue 2005). We used Phylomatic to output a supertree that contained all taxa in all of the plots. The backbone of the supertree was taken from the latest Angiosperm Phylogeny Group classification (APG II 2003; Phylomatic tree version R20031202). This supertree was then assigned branch lengths and was pruned to construct species pools for each plot using the community phylogenetic software Phylocom version 3.21 (Webb et al. 2004). Branch lengths were assigned to the original supertree by applying known molecular and fossil dates (Wikstrom et al. 2001) to nodes on the phylogeny using the BLADJ algorithm (Webb et al. 2004). This algorithm fixes dates to nodes on the supertree evenly between “known” nodes on the phylogeny. This resulted in a phylogeny with branch lengths calibrated in millions of years rather than a cladogram with all branch lengths set to one. Thus, the degree of phylogenetic overdispersion or clustering is quantified by differences in time. It should be noted that “known” molecular and fossil dates applied to the supertrees are only estimates, yet they represent the best and most widely accepted dates currently available to botanists (Moles et al. 2005a, b) and make phylogenetic analyses of communities much more robust when compared to the alternative of using nodal distances (Webb 2000).

A species pool was created for each FDP as a whole and for each FDP size class by pruning the original calibrated supertree. Finally, the list of canopy species compiled using the method described above was used to generate a species pool for each FDP from which a supertree could be constructed. In sum a total of 48 species pools (10 for each FDP except for San Emilio, where $n = 8$) were utilized for this study. Thus, each FDP had a separate supertree representing the species pool for each size class analysis, which combined all species across all spatial scales and for each size class of canopy species at one spatial scale. This method avoids

the difficulty caused by small-stature trees not being present in the large size classes for reasons of their morphology rather than the result of competitive exclusion. More details concerning supertree construction are available in the Appendices. It should be emphasized that the supertrees generated in this study generally had polytomies (unknown topologies) within generic and family level clades due to current limitations of fully resolved published phylogenies. Therefore, while species are represented as the tips of the phylogenetic supertree, the absolute topology of relatedness between species within a genus could not be determined, and they were treated as equally related. This unavoidable consequence of analyzing hyper-diverse tropical forests with phylogenetic methods reduces the power of the study to detect nonrandom patterns, yet still allows for coarse preliminary insights into the influence of phylogenetic relatedness on tropical forest community structure.

Community phylogenetic analyses

Using the software Phylocom (Webb et al. 2004), the mean observed pairwise distance (MPD; in 1×10^6 years) and mean minimum phylogenetic distance (MMPD; in 1×10^6 years) between co-occurring taxa in each quadrat was calculated (Webb 2000). The MPD represents the mean of all the pairwise phylogenetic distances between all taxa within a local assemblage and is generally considered to be a tree-wide (i.e., basal) metric. The MMPD represents the mean of the phylogenetic distance for each taxa to its nearest relative within a local assemblage and is generally considered a more terminal metric. The MPD and MMPD for each stem diameter size class or quadrat dimension were compared to the same measure calculated from 1000 randomly generated local assemblages from the species pool supertree, rndMPD and rndMMPD respectively, for each individual quadrat. For each quadrat an independent swap algorithm randomization process was performed to generate the random assemblages (Gotelli and Entsminger 2001). The independent swap algorithm conserves both the observed row and column totals in the binary presence/absence matrix when generating null communities. The difference between rndMPD and MPD as well as the difference between rndMMPD and MMPD for all the quadrats within each FDP was analyzed using a Wilcoxon test. This difference was initially calculated without accounting for spatial autocorrelation by reducing the degrees of freedom. We then used the software SAM (Rangel et al. 2006; *available online*)⁴ to correct our degrees of freedom as outlined by Griffith (2003).

A net relatedness index (NRI) and nearest taxon index (NTI) sensu Webb et al. (2002, 2004) were also used to determine the proportion of individual quadrats within

⁴ (<http://www.ecoevol.ufg.br/sam/>)

TABLE 1. Results of a tree-wide phylogenetic conservatism analysis.

FDP	No. species	Wood density		Seed size		Specific leaf area		Leaf nitrogen (%)		Leaf phosphorus (%)		Reference†
		<i>n</i>	<i>Q</i>	<i>n</i>	<i>Q</i>	<i>n</i>	<i>Q</i>	<i>n</i>	<i>Q</i>	<i>n</i>	<i>Q</i>	
Luquillo	151	56	4	46	480	47	460	44	390	38	250	Ovington and Olson (1970); KEW Seed Size Database
BCI	301	124	8	124	9							Chave et al. (2003, 2004); KEW Seed Size Database
Cocoli	175	67	19	73	12							Chave et al. (2003, 2004); KEW Seed Size Database
Sherman	237	67	21	77	10							Chave et al. (2003, 2004); KEW Seed Size Database
San Emilio	173	134	5	49	375	127	237	155	10	155	33	Malavassi (1992); KEW Seed Size Database; N. G. Swenson, unpublished data

Notes: Quantile scores (*Q*) ≤ 500 signify traits that are significantly conserved on the phylogeny for the number of species (*n*) in each forest dynamics plot (FDP) for which trait values are available. Each analysis used 9999 randomizations of trait values across the tips of the phylogeny. Site abbreviations are: LFDP, Luquillo Forest Dynamics Plot, Puerto Rico; BCIFDP, Barro Colorado Island Forest Dynamics Plot, Panama; CFDP, Cocoli Forest Dynamics Plot, Panama; SF, Sherman Forest Dynamics Plot, Panama; SEFDP, San Emilio Forest Dynamics Plot, Costa Rica.

† KEW Seed Size Database: Kew Millennium Seed Bank Project (<http://www.rbgekew.org.uk/msbp/index.html>).

each FDP that was significantly overdispersed or clustered. These metrics were calculated as follows:

$$\text{NRI} = -1 \times (\text{MPD} - \text{rndMPD}) / \text{sdrndMPD}$$

$$\text{NTI} = -1 \times (\text{MMPD} - \text{rndMMPD}) / \text{sdrndMMPD}$$

where sdrndMPD represents the standard deviation of the 1000 rndMPD values and sdrndMMPD represents the standard deviation of the 1000 rndMMPD values. Stated another way the NRI metric is a standardized version of the MPD, and the NTI metric is a standardized version of the MMPD. These metrics can then also be used to assess phylogenetic overdispersion (negative values) or clustering (positive values). Note that the MPD and MMPD metrics can provide different results according to how they are calculated. For example it is possible for a community to be comprised of species from two clades distant to one another on the phylogenetic supertree. In this case the MPD (NRI) metric would detect phylogenetic overdispersion, yet the MMPD (NTI) would detect phylogenetic clustering.

RESULTS

Phylogenetic niche conservatism

All functional traits analyzed were ranked in low quantiles for all FDPs indicating significant tree-wide trait conservatism (see Table 1). Thus five traits in tropical trees generally considered to be important in determining tree life histories (Enquist et al. 1999, Westoby et al. 2002, Wright et al. 2004, Moles et al. 2005a, b) showed significant phylogenetic conservatism. Therefore, measures of phylogenetic dispersion of co-occurring species seem to provide reliable insights into whether biotic, abiotic, or stochastic processes are the most important in determining tropical-plant commu-

nity structure and diversity and at which scales these processes occur.

Spatial scaling

Restricting our analyses to changes in quadrat area reveals a suite of interesting results. Three of the five FDPs, the Luquillo, Sherman, and Cocoli, had significant phylogenetic overdispersion at the smallest quadrat sizes using the MPD and NRI metrics (Fig. 1), thereby providing some support for a competitive exclusion model. In contrast, at medium to larger spatial scales, >100 m², most of the FDPs were characterized by phylogenetic signals indistinguishable from the neutral or random expectation again using MPD and NRI. When the individual quadrats are analyzed a larger-than-expected proportion are nonrandom assemblages (i.e., clustered or overdispersed) with more quadrats being overdispersed than clustered at small scales in all FDPs (see Appendices).

When using the MMPD and NTI metrics the generality of the patterns of phylogenetic structure of communities across plots is less obvious on average in each FDP. Both of the dry forests, San Emilio and Cocoli, are significantly phylogenetically overdispersed at the smallest spatial scales whereas the three moist forests, BCI, Sherman, and Luquillo, are significantly phylogenetically clustered at the smallest scales on average (see Appendices). Yet, as with the MPD and NRI metrics, a larger number of overdispersed quadrats compared to clustered quadrats are evident at the smallest scales in each FDP. Further, a greater-than-expected proportion of nonrandomly assembled communities (i.e., clustered or overdispersed) were evident across spatial scales (see Appendices). After accounting for spatial autocorrelation in the above analyses the results did not change.

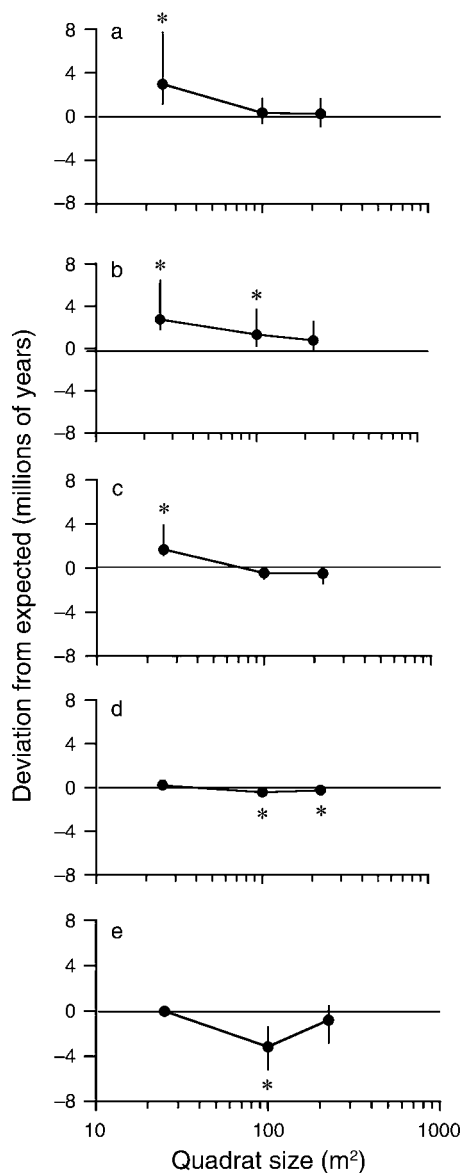


FIG. 1. The median deviation of mean observed pairwise distance (MPD) from expected randomly generated MPD (rndMPD) for (a) Cocoli, (b) Sherman, (c) Luquillo, (d) Barro Colorado Island, and (e) San Emilio at the three smallest quadrat sizes ($*P < 0.05$, Wilcoxon test). Positive values indicate phylogenetic overdispersion, and negative values indicate phylogenetic clustering. The error bars represent 95% confidence intervals. A test for concordance among forest dynamics plots gave a significant result (Kendall's $W = 0.91$, $P < 0.01$).

Plant size, age, and spatial scaling

The general pattern of phylogenetic structuring becomes clearer when the effects of spatial scale and plant size are incorporated into the analysis. At the smallest spatial scale almost all of the FDPs showed significant and increasing degrees of phylogenetic overdispersion with increasing tree size no matter which

community phylogenetic metric was utilized (Fig. 2, Appendices). At the 100-m² scale, the BCI FDP was significantly overdispersed at the two largest tree size classes and San Emilio was overdispersed at only the largest size class. At the 225-m² scale, only BCI was overdispersed at the largest size class (Fig. 2, Appendices). For larger quadrat sizes (>225 m²), no significant deviation from random was found. Furthermore, there was no significant deviation from random for the three smallest size classes for any FDP at the 100-m² scale or for the largest size class in BCI at the 225-m² scale when the degrees of freedom were reduced to account for spatial autocorrelation in the data. The general reduc-

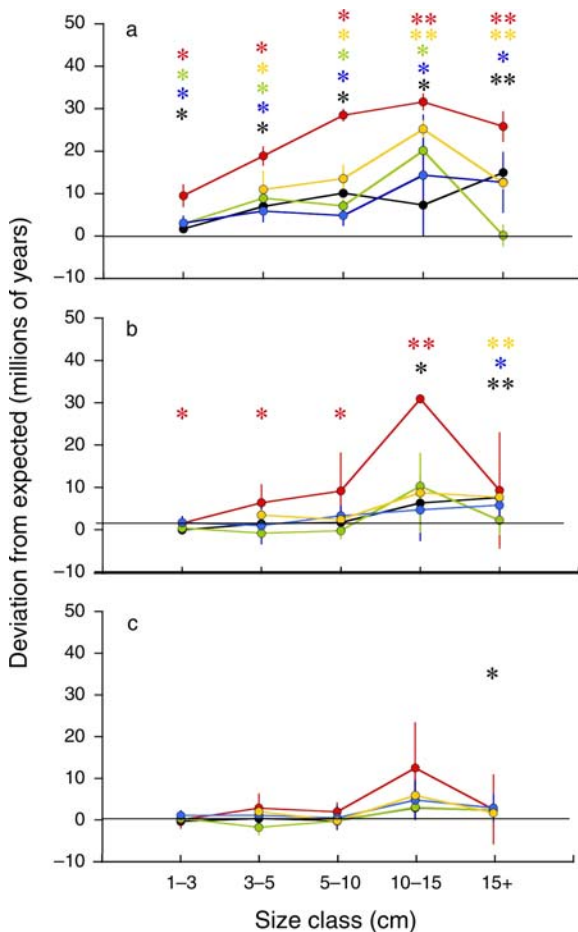


FIG. 2. The median deviation of mean observed pairwise distance (MPD) from expected randomly generated MPD (rndMPD) for all size classes for Barro Colorado Island (BCI; black), Sherman (blue), Luquillo (green), Cocoli (red), and San Emilio (yellow) at the three smallest quadrat sizes: (a) 25 m²; (b) 100 m²; (c) 225 m² (Wilcoxon test: $*P < 0.05$; $**P < 0.0001$). Positive values indicate phylogenetic overdispersion, and negative values indicate phylogenetic clustering. The error bars represent 95% confidence intervals. A test for concordance among forest dynamics plots for each quadrat size gave a significant result (25 m², Kendall's $W = 0.536$, $P < 0.05$; 100 m², Kendall's $W = 0.496$, $P < 0.05$; 225 m², Kendall's $W = 0.544$, $P < 0.05$).

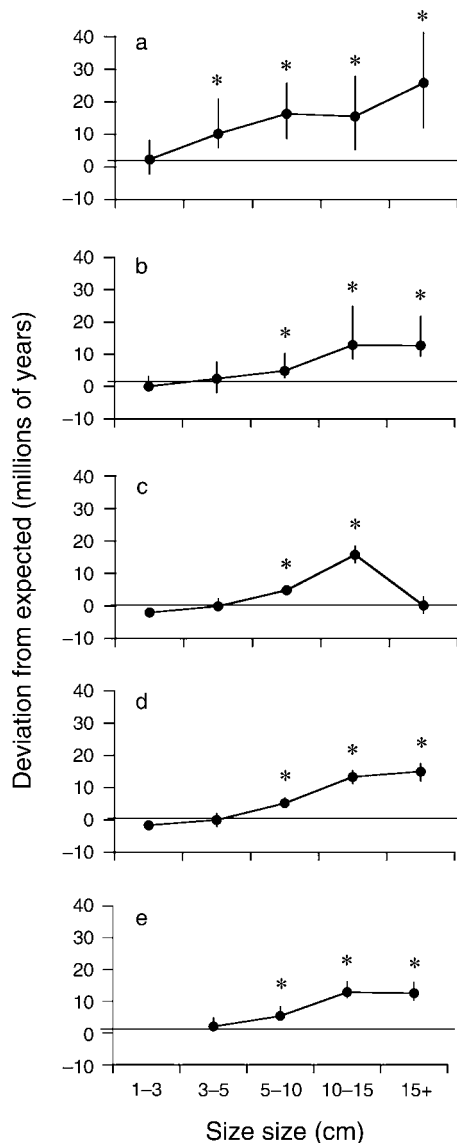


FIG. 3. The median deviation of mean observed pairwise distance (MPD) from expected randomly generated MPD (rndMPD) for canopy tree species in (a) Cocoli, (b) Sherman, (c) Luquillo, (d) Barro Colorado Island, and (e) San Emilio in 25-m² quadrats ($*P < 0.05$, Wilcoxon test). Positive values indicate phylogenetic overdispersion, and negative values indicate phylogenetic clustering. The error bars represent 95% confidence intervals.

tion of phylogenetic structuring at larger spatial scales could also be due to a decrease of statistical power because a smaller number of quadrats could be analyzed at this spatial scale.

The canopy species analyses, which were used to assess the effect of a temporal axis, showed that at the spatial scale of 25 m², across all FDPs, local assemblages of young cohorts (small size classes of canopy species) are generally random to phylogenetically clustered. In the older cohorts (larger size classes of canopy species)

all FDPs were phylogenetically overdispersed on average, and at the largest size class San Emilio, BCI, Cocoli, and Sherman were overdispersed on average (Fig. 3). These results were not influenced by spatial autocorrelation in the data.

DISCUSSION

In each of the forests studied, key functional traits that are indicative of tree life-history strategies were found to be phylogenetically conserved across the phylogeny. This suggests that the degree of phylogenetic relatedness between co-occurring species can be used to test the phylogenetic predictions made by the three models of community structuring (neutral, competitive exclusion, and abiotic filtering). The results from assessing pairwise community phylogenetic metrics, MPD and NRI, across spatial scales suggest that the degree of phylogenetic relatedness may be important in determining community structure of these FDPs but only at small spatial scales. However, the BCI and San Emilio FDPs did not differ from random at the smallest scale. Interestingly, in support of an abiotic filtering model, both BCI and San Emilio were characterized by significant phylogenetic clustering at medium spatial scales (Fig. 1).

The nearest neighbor phylogenetic metrics, MMPD and NTI, showed phylogenetic clustering to be more prominent in moist forests when they were analyzed as a whole, yet phylogenetic overdispersion was more prominent than phylogenetic clustering in individual quadrats in each FDP. Thus, no matter which metric was utilized, phylogenetic overdispersion was increasingly prevalent at the smallest scales for three of the FDPs, yet not for the remaining two.

The spatial scaling results for BCI in this study are similar to those of a recent study by Kembel and Hubbell (2006) that mapped phylogenetic composition across a smaller subset of spatial scales for BCI. Their study did not include the smallest spatial scale reported here and found a slightly clustered signal for BCI as a whole and greater-than-expected proportions of quadrats showing nonrandom phylogenetic associations (i.e., phylogenetically clustered or overdispersed). An interesting result from the present study, which uses the 1995 census data, is that we found slightly more phylogenetic clustering on average than the Kembel and Hubbell (2006) study, which used the 1982 census data. A large demographic shift inside the BCI FDP has been documented and attributed to the 1983 El Niño drought (Condit et al. 1996). If local mortality was nonrandom across species then the observed demographic shift could account for the slight increase in phylogenetic clustering observed in the present study (Weiher and Keddy 1995, 1999). Further community phylogenetic analyses of tropical FDPs, which have been censused multiple times, would likely prove instructive.

Scaling along a spatial axis provided some preliminary evidence in support of phylogenetic overdispersion

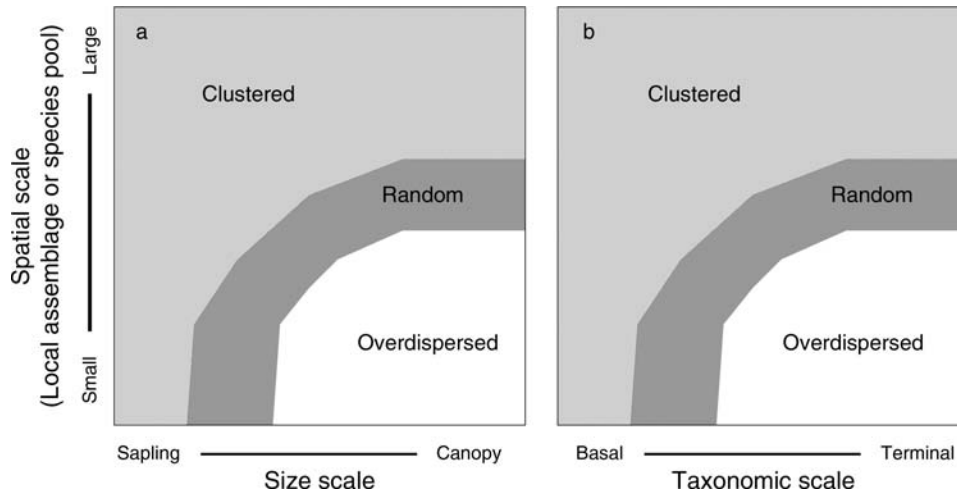


FIG. 4. (a) A figure adapted from Weiher and Keddy (1995), depicting a graphical model of the effect of spatial and body size scale on phylogenetic dispersion in ecological communities. (b) A graphical model of the spatial and taxonomic scale dependency of phylogenetic dispersion in ecological communities. The graphical predictions presented are based on and consistent with the findings of this study and Swenson et al. (2006).

on fine scales and is consistent with recent work by Cavender-Bares et al. (2006) that also found increased phylogenetic overdispersion at fine spatial scales, although it is important to note that we only found this result in three of the five FDPs. The evidence for phylogenetic overdispersion becomes more pronounced when both spatial and plant size (or age) scaling axes were incorporated. When the degree of phylogenetic relatedness is plotted as both a function of size and spatial scale (Fig. 2), the importance of spatial scale and plant size becomes clearer. We argue that because the three models of community structure presently discussed simultaneously make predictions concerning space and time, the incorporating of both of these axes in the same analysis provides a more powerful test.

These size results were also similar to the findings of Enquist et al. (2002) who found that within woody plant communities the taxonomic ratios (genus:species and family:genus) across several hundred 0.1-ha community plots declined with increases in plant size. Furthermore, the increase in overdispersion with age (stem size) in the canopy tree analyses is consistent with the expectation that as cohorts of trees grow, biotic interactions “play out” to influence community structure (Fig. 3).

Our analyses reveal preliminary evidence in support of general spatial and plant size scaling relationships that govern phylogenetic associations of species within hyper-diverse tropical forests. The similarity of pattern across FDPs suggests shared mechanisms. A phylogenetically overdispersed signal was observed only at the smallest spatial scales and become increasingly stronger in the largest size classes. However, when each FDP was analyzed at larger spatial scales and smaller size classes, the overdispersed signal progressively dissipates into a random to clustered signal. This suggests that the degree

of phylogenetic relatedness between co-occurring species is the most important at very small and large spatial scales and as cohorts age. At this point it is still unclear whether the random pattern detected at meso-scales in this study is due to the mixing of overdispersion and clustering or is actually indicative of neutral processes (Hubbell 2001, 2005).

The finding that local assemblages that are delineated on fine spatial scales are often phylogenetically overdispersed has now been found in three studies including the present (Cavender-Bares et al. 2006, Slingsby and Verboom 2006), yet the influence of other issues such as the taxonomic scale of the analysis and the spatial scale of the regional species pool have received less attention in community phylogenetics. Recent work by Swenson et al. (2006) has shown that as the spatial scale of the species pool is increased in relation to the local assemblage scale, phylogenetic clustering becomes more common. The taxonomic delineation of the communities also seems to be largely important in detecting nonrandom phylogenetic associations in communities. Cavender-Bares et al. (2006) and Swenson et al. (2006) have independently found that as communities are more finely defined taxonomically (i.e., a collection of species within a genera as compared to a collection of genera in a family), phylogenetic overdispersion is common. Thus the conceptual problem of melding all of this information regarding scale dependency in community phylogenetics is now confronting researchers as it did for researchers studying trait dispersion a decade ago (Weiher and Keddy 1995, 1999, Swenson et al. 2006). In Fig. 4 we present a graphical model adapted from the work of Weiher and Keddy (1995, 1999) that predicts generalities in phylogenetic dispersion simultaneously along two axes (space and taxonomy or size/age). As

more studies that incorporate scaling and phylogenetic analyses of communities begin to amass it will be possible to test the generality of this graphical model. If it is indeed found to be general it may provide a good starting point for trying to discern the scales at which competition and abiotic filtering and/or local and regional processes gain primacy in the assembly of plant communities.

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APPENDIX A

An explanation of species pool supertree construction (*Ecological Archives* E088-105-A1).

APPENDIX B

Analysis of the influence of number of taxa in a quadrat vs. significance (*Ecological Archives* E088-105-A2).

APPENDIX C

A table showing forest types analyzed and quadrat sample sizes (*Ecological Archives* E088-105-A3).

APPENDIX D

A figure showing the distribution of the net relatedness index and the nearest taxon index in 25-m² quadrats across organismal size scales in each forest dynamics plot (*Ecological Archives* E088-105-A4).

APPENDIX E

A figure showing the median deviation of mean minimum phylogenetic distance (MMPD) from expected randomly generated MMPD (rndMMPD) for Cocoli, Sherman, Luquillo, Barro Colorado Island (BCI), and San Emilio at the three smallest quadrat sizes (*Ecological Archives* E088-105-A5).

APPENDIX F

A figure showing the median deviation of MMPD from expected rndMMPD for all size classes for BCI, Sherman, Luquillo, Cocoli, and San Emilio at the three smallest quadrat sizes (*Ecological Archives* E088-105-A6).