

Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology

NATHAN G. SWENSON¹ AND BRIAN J. ENQUIST

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA

Abstract. Species diversity is promoted and maintained by ecological and evolutionary processes operating on species attributes through space and time. The degree to which variability in species function regulates distribution and promotes coexistence of species has been debated. Previous work has attempted to quantify the relative importance of species function by using phylogenetic relatedness as a proxy for functional similarity. The key assumption of this approach is that function is phylogenetically conserved. If this assumption is supported, then the phylogenetic dispersion in a community should mirror the functional dispersion. Here we quantify functional trait dispersion along several key axes of tree life-history variation and on multiple spatial scales in a Neotropical dry-forest community. We next compare these results to previously reported patterns of phylogenetic dispersion in this same forest. We find that, at small spatial scales, coexisting species are typically more functionally clustered than expected, but traits related to adult and regeneration niches are overdispersed. This outcome was repeated when the analyses were stratified by size class. Some of the trait dispersion results stand in contrast to the previously reported phylogenetic dispersion results. In order to address this inconsistency we examined the strength of phylogenetic signal in traits at different depths in the phylogeny. We argue that: (1) while phylogenetic relatedness may be a good general multivariate proxy for ecological similarity, it may have a reduced capacity to depict the functional mechanisms behind species coexistence when coexisting species simultaneously converge and diverge in function; and (2) the previously used metric of phylogenetic signal provided erroneous inferences about trait dispersion when married with patterns of phylogenetic dispersion.

Key words: *community ecology; Costa Rica; forest ecology; functional diversity; functional ecology; Neotropical dry forest; spatial scale; tropical forest dynamics plot.*

INTRODUCTION

The problem of how and why so many species coexist continues to be an important focus in ecology and evolution (Chesson 2000). Proposed mechanisms range from niche-based assembly rules (e.g., MacArthur and Levins 1967, Diamond 1975) to neutral assembly with dispersal limitation (e.g., Hubbell 1979, Bell 2001, Hubbell 2001). Given the breadth of empirical results and the possibility that the centerpiece of most species coexistence theory, the niche, may be less important than previously thought, ecologists are now tasked with reexamining species coexistence using alternative approaches. For example, phylogenetic community ecology (e.g., Losos 1996, Webb et al. 2002), functional community ecology (McGill et al. 2006), and scaling (Wiens 1989, Levin 1992, Weiher and Keddy 1995, Swenson et al. 2006, 2007) are three potentially

complementary alternative lines of inquiry into the problem of coexistence.

Phylogenetic community ecology builds upon a long history of using taxonomic similarity to address hypotheses regarding community assembly. For example, genus-to-species ratios have been used to determine whether or not closely related species are more likely to co-occur (e.g., Elton 1946, Simberloff 1970, Jarvinen 1982). When compared to a null model, a higher than expected genus-to-species ratio is considered to be evidence of limiting similarity structuring the community (Grant and Abbott 1980). The central assumption underlying this method is that closely related species are likely to be more ecologically and functionally similar than distantly related species, allowing inferences regarding the relative influence of abiotic and biotic interactions in structuring communities.

The rapidly accumulating literature regarding the phylogenetic structure of communities is largely dominated by analyses of coexisting plants. To date the reported results range from nonrandom patterns of phylogenetic dispersion to phylogenetic dispersion being no different from a random expectation (Webb 2000, Cavender-Bares et al. 2006, Kembel and Hubbell 2006, Swenson et al. 2006, Chave et al. 2008). The inferences

Manuscript received 31 May 2008; revised 21 November 2008; accepted 8 December 2008. Corresponding Editor: K. D. Woods.

¹ Present address: Center for Tropical Forest Science–Asia Program, Arnold Arboretum, Harvard University, Cambridge, Massachusetts 02138 USA.

E-mail: nswenson@oeb.harvard.edu

made in many studies rest upon the same central assumption, often termed phylogenetic conservatism, that closely related species are more ecologically and functionally similar. Other work tests the assumption of phylogenetic conservatism and marries the results of these tests with observed patterns of phylogenetic dispersion to allow for stronger inferences regarding the ecological and functional similarity of coexisting species (Webb et al. 2002, Cavender-Bares et al. 2004). Cavender-Bares et al. (2004) have shown that some ecological traits are phylogenetically conserved while others are not. Thus, their work clearly shows the importance of testing the assumption of phylogenetic conservatism and suggests that such tests should become requisite (Losos 2008).

The expanded framework originally proposed by Webb et al. (2002) and later implemented by Cavender-Bares et al. (2004) requires the collection of ecological trait data from the species in the communities of interest in order to gain deeper insights into mechanisms that promote species coexistence. In other words, analyses of the phylogenetic dispersion in a community alone will not necessarily provide the mechanistic detail needed to infer which traits or interactions are influencing the composition of an assemblage at a given spatial and temporal scale (Brooks and McLennan 2002, Cavender-Bares et al. 2004, McGill et al. 2006, Losos 2008).

Here we build upon a previous investigation of the phylogenetic dispersion and trait conservatism in a Neotropical dry-forest community (Swenson et al. 2007) to assess whether the functional trait dispersion in this forest mirrors the phylogenetic dispersion results. We use functional traits, individually and in combination, representing fundamental trade-offs shared by all land plants (Westoby 1998, Westoby et al. 2002, Westoby and Wright 2006) to quantify: (1) relationships between trait diversity and species richness at various spatial scales; and (2) trait dispersion along spatial and size scaling axes. Our analyses use the same methodology as the previous phylogenetic analysis (Swenson et al. 2007), substituting functional trait dendrograms in place of the phylogenetic tree. We show that patterns of trait dispersion in this forest do not match patterns of phylogenetic dispersion. The previous phylogenetic study quantified the phylogenetic signal (sensu Blomberg et al. 2003) in trait data to infer the degree of phylogenetic conservatism in these traits. Thus, the present results were unexpected. We test the hypothesis that this unexpected result was due to a lack of phylogenetic signal in trait data basally and terminally on the phylogeny, a possibility that was unexamined in the previous study. We argue on the basis of our results that two fundamental mechanisms of community assembly, abiotic filtering and biotic interactions, can be simultaneously and equally important at a given spatial scale, a result that could not be detected by phylogenetic analyses alone. Further we argue that measuring the degree of phylogenetic signal in trait data at different

depths in the phylogenetic tree can yield insights into when and why marrying metrics of phylogenetic dispersion and phylogenetic signal may lead to misleading inferences.

METHODS

Study location

The study was conducted in the ~16-ha San Emilio Forest Dynamics Plot (SEFDP) in Santa Rosa National Park, Area de Conservación Guanacaste, Guanacaste Province, Costa Rica. This forest is characterized as seasonally dry with the majority of the annual rainfall (~1500 mm) occurring between the months of June and December. The SEFDP has been censused in 1976, 1996, and 2006 (Hubbell 1979, Enquist et al. 1999; N. G. Swenson, *unpublished data*). Each census recorded the diameter and spatial position of every woody stem 3 cm or greater in diameter 1.3 m from the ground. For the purposes of this study, which is only concerned with the tree community, all lianas were excluded from the analyses. All of the analyses and results presented were generated from the 1996 census data.

Functional traits that characterize central life-history axes

We selected six plant functional traits that are often cited as representing fundamental functional trade-offs defining how species differentiate from each other. Specifically, we quantified leaf area, specific leaf area (SLA), leaf succulence, wood specific gravity, maximum height, and seed mass. Variation in leaf area is thought to reflect a trade-off between the laminar area deployed for light capture and increased leaf temperatures due to an increased boundary layer (Dolph and Dilcher 1980). Specific leaf area (SLA: ratio of leaf area to dry leaf mass) is often cited as representing a trade-off between low construction costs, high photosynthetic rates, and short leaf life spans vs. high construction costs, low photosynthetic rates, and long leaf life spans (Reich et al. 1997, Wright et al. 2004). Leaf succulence (i.e., leaf water content per unit area) represents a trade-off between long persistence and low productivity vs. short persistence and high productivity (Garnier and Laurent 1994). Wood specific gravity represents a trade-off between high volumetric growth rates, low construction costs, and high mortality rates vs. low volumetric growth rates, high construction costs, and low mortality rates (Enquist et al. 1999, Swenson and Enquist 2007). Maximum height is indicative of adult light niche (Kohyama 1993, Aiba and Kohyama 1997, Kohyama et al. 2003). Finally, seed mass represents a trade-off between producing many small seeds per unit energy vs. producing a few large seeds per unit energy (Venable 1996, Moles and Westoby 2006).

Functional trait measurement

Sun-exposed leaves were collected from at least 3–5 individuals of each species within the SEFDP. Leaves were collected from the outer canopy as leaves deeper in

TABLE 1. All pairwise Pearson's product-moment correlations (r) between the six functional traits used in this study of the San Emilio Forest Dynamics Plot, Santa Rosa National Park, Costa Rica.

| Trait | LA | SLA | LS | Maximum height | Seed mass | WSG |
|----------------|------|------|-------|----------------|-----------|-------|
| LA | 1.00 | 0.17 | 0.02 | 0.38 | 0.13 | -0.26 |
| SLA | | 1.00 | -0.22 | -0.01 | -0.34 | -0.25 |
| LS | | | 1.00 | -0.01 | 0.01 | -0.31 |
| Maximum height | | | | 1.00 | 0.33 | -0.11 |
| Seed mass | | | | | 1.00 | 0.11 |
| WSG | | | | | | 1.00 |

Note: Key to abbreviations: LA, leaf area; SLA, specific leaf area; LS, leaf succulence; WSG, wood specific gravity.

the canopy are likely more variable in their trait values and may not provide a good estimate of whole plant function. Care was also taken not to sample senescing or heavily damaged leaves. All leaf areas were measured using a handheld leaf area meter, and leaf masses were recorded before and after being dried for two days at 60°C or until their mass stabilized. These measurements were used to calculate average leaf area, specific leaf area (SLA; ratio of area to dry mass), and leaf succulence [(wet mass – dry mass)/leaf area].

Wood cores were collected using an increment borer at 100 cm from the ground for 2–3 individuals of each tree species recorded in the SEFDP during the 1996 census. For shrub species we took a basal stem section from 2–3 individuals near the SEFDP; when this was not possible we estimated the stem wood density from a branch section using the methods and conversion equations from Swenson and Enquist (2008). For all cores and sections, length and diameter were measured immediately in the field after removal of cortex, and green volume was calculated from these measurements (sample sections of wood were selected for minimal tapering or bending). Water displacement measurement of wood specific gravity value was not possible at the field location, so wood samples were then dried in a drying oven at 60°C for two days or until their mass stabilized and wood specific gravity was calculated as the ratio of dry mass to green volume.

The maximum height of each species was recorded using literature sources (Appendix A). If reported maximum heights varied substantially, we utilized the value from the region most climatically similar to the SEFDP (i.e., tropical dry forest). For 33 species without literature values for maximum height in the literature we used field measurements by range finder of the largest known individual in Santa Rosa National Park.

Seed mass was obtained for 54 of the 139 species in the SEFDP from the Kew Millennium Seed Database (*available online*),² and 43 of the 139 species were obtained from personal field collections by N. G. Swenson. For the 42 species lacking a species-specific value, we used the mean of the congeneric values. Although this is not a preferred method, most of the

global variation in seed mass is contained in taxonomic levels higher than genera (Moles et al. 2005), and the results of this study were not differentially affected by the use of seed mass.

Last, because some of the six functional traits measured were highly correlated (Table 1), we conducted a principal components analysis (PCA) of measured traits for the 139 species in the 1996 census. The first axis of the PCA space explained 65.9% of the variance and the second axis explained an additional 24.0% of the variance (Appendix B). Therefore we used the PCA1 and PCA2 scores as composite measurements of functional similarity for the spatial scaling analyses. For the analyses that included maximum height quartiles we excluded maximum height and recalculated the PCA1 and PCA2 scores. In both cases, the first PCA axis was representative of leaf area and seed mass (68.9% of variance) and the second axis of leaf area, seed mass, and SLA (24.5% of variance). The trait values and PCA scores were then used to generate trait and PCA score dendrograms using hierarchical clustering using R statistical software (R Development Core Team 2007) so that the distance between two taxa on the dendrogram represented functional similarity in the same way that the distance between two taxa on a phylogenetic tree represents their degree of relatedness.

Spatial scaling analyses

In order to account for the influence of spatial scale we examined trait diversity at six different scales in this study. For each spatial scale we divided up the SEFDP into quadrats and recorded the presence of all species in each quadrat. The spatial scales used were 25, 100, 400, 2500, and 10 000 m². Inside each quadrat we quantified the trait diversity using the functional trait dendrograms and the functional diversity metric of Petchey and Gaston (2002) where the trait diversity is the sum of the length of the branches on the dendrogram shared by taxa in the community divided by the sum of all branch lengths in the dendrogram.

In order to determine whether increased trait diversity within quadrats was different than what is expected given their species richness, we generated 1000 random assemblages for each quadrat at each spatial scale within the SEFDP using an Independent Swap null model

² (<http://ftp.rbgekew.org.uk/msbp/index.htm>)

(Gotelli and Entsminger 2001). The Independent Swap algorithm fixes the observed species richness and species occupancy rates. The species pool for the null model, as in our previous study (Swenson et al. 2007), was the 1996 census species list. We chose this null model because of its low error rates (Gotelli and Entsminger 2001) and because it was used in the previous phylogenetic study (Swenson et al. 2007), and the comparative nature of this study required consistency in our methodological approach. For each of these random assemblages we calculated the trait diversity to generate a null distribution. This null distribution was used to calculate a standardized effect size as follows:

$$Z_{td} = (TD_{obs} - TD_{null}) / TD_{sdnull}$$

where TD_{null} is the mean value of the null distribution of random assemblage trait diversities and TD_{sdnull} is the standard deviation of the null distribution (Gotelli and Graves 1996). We then tested whether the median Z_{td} for all of the SEFDP quadrats was different from a null expectation of zero using a Wilcoxon test. We quantified the spatial autocorrelation in Z_{td} values using the software SAM (*available online*),³ and reduced the degrees of freedom in all of our statistical tests.

Size class analyses

A previous phylogenetic study of this forest has shown that for trees that will eventually reach the canopy, the degree of phylogenetic relatedness increases when only small individuals are examined and that the relatedness decreases when only larger individuals are examined (Swenson et al. 2007). This was taken as evidence that as cohorts age, closely related individuals tend to be competitively excluded because closely related species are likely functionally similar (Swenson et al. 2007). Here we directly test whether coexisting species really are more functionally overdispersed in larger individuals. This was done first by splitting the species into maximum height quartiles. Within each quartile we separated the species into size bins based upon their diameters at breast height (3–4.9, 5–9.9, 10–14.9, and 15+ cm). Next, we divided the SEFDP into 400-m² quadrats and examined the degree of trait dispersion in each size bin for each quartile in each quadrat using the Independent Swap null model. The deviation from expected was again quantified by using a Wilcoxon test.

Relative timing of functional trait divergences

In previous work in this forest we have shown that some of the traits in this study have significant phylogenetic signal (*sensu* Blomberg et al. 2003, Swenson et al. 2007). Phylogenetic signal quantifies the statistical relationship between the entire phylogenetic tree and trait data, and it is often used to infer the degree of phylogenetic conservatism (the degree to which related species have

similar traits) in phylogenetic investigations of communities (e.g., Ackerly 2004, Cavender-Bares et al. 2004, Swenson and Enquist 2007). Here we refine this approach by examining the degree of phylogenetic signal at different depths in the phylogeny in order to gain deeper insights into how differential phylogenetic patterns of functional trait evolution produced similarities and dissimilarities between the present trait dispersion results and the prior phylogenetic dispersion results. To accomplish this we first generated a phylogenetic supertree using the software Phylomatic (Webb and Donoghue 2005). We next resolved some of the larger polytomies using recently published phylogenies (i.e., Malpighiales; Davis et al. 2005) as described in Swenson et al. (2006, 2007). Species-specific trait values were arrayed across the tips of the phylogeny. At each internal node of the phylogeny the root mean square deviation of descendent trait values was calculated (Moles et al. 2005, Swenson and Enquist 2007). In the following we refer to this value as the divergence size. Next, all trait values were permuted across the tips of the phylogeny 1000 times. For each iteration, a divergence size was calculated for each internal node. This produced a null distribution for each node that could be compared to the observed value. This was repeated for all traits and both PCA scores using the software Phylocom (Webb et al. 2004). The observed rank of the observed divergence size in the null distribution was recorded and plotted against the age of the node. Last, a locally weighted regression was calculated for each trait to qualitatively examine whether each trait tended to have lower or higher than expected phylogenetic signal at different depths in the phylogeny.

RESULTS

Spatial scaling results

We initially quantified the relationship between species richness and trait diversity in each quadrat. We found that species richness and trait diversity values were generally positively correlated with the strength of the relationship increasing as the spatial scale of the analysis decreased (Fig. 1). The significance of the relationship disappeared for some traits as the spatial scale increased, while for others the relationship remained strong (Fig. 1). In some cases the breakdown in the relationship was likely due to a reduction in statistical power.

As it is difficult to discern whether the observed trait diversity within a quadrat is simply due to variation in species richness, abiotic interactions, or biotic interactions, we conducted a null model analysis that controlled for species richness within quadrats and quadrat occupancy rates across the SEFDP. At larger spatial scales the trait dispersion in a quadrat was generally no different from the random expectation (Fig. 2). At mesoscales the trait dispersions were also generally no different from the random expectation with a few showing trait clustering (Fig. 2). At the smallest spatial scales (i.e., 25 m²) the dispersion for every trait and PCA

³ (www.ecoevol.ufg.br/sam/)

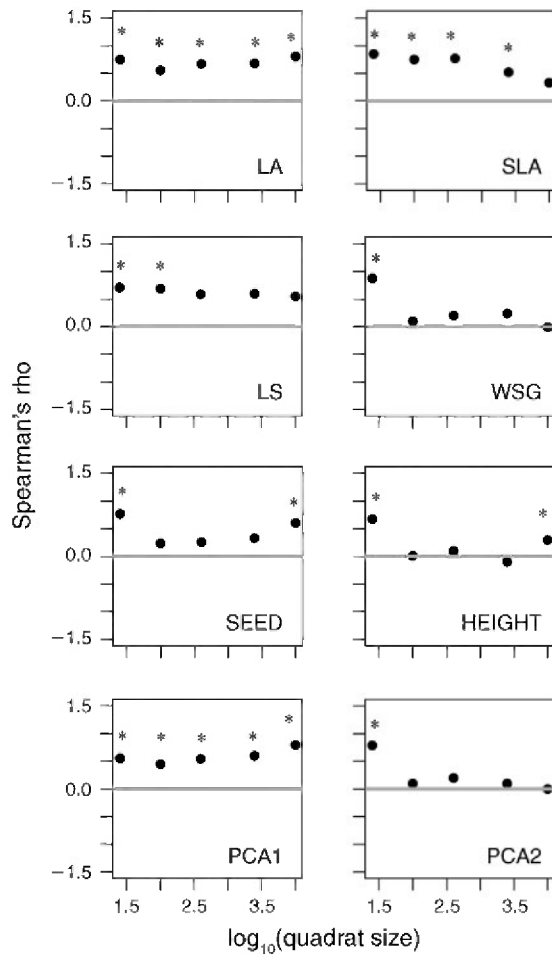


FIG. 1. The results of Spearman's rho correlational analyses between quadrat species richness and trait diversity for all quadrats plotted against spatial scale in the San Emilio Forest Dynamics Plot, Santa Rosa National Park, Costa Rica. Positive values indicate that trait diversity increases with increasing species diversity, or vice versa, at that spatial scale. Negative values indicate that trait diversity decreases with increasing species diversity or vice versa, at that spatial scale. Quadrat size was originally measured in m². Key to abbreviations: LA, leaf area; SLA, specific leaf area; LS, leaf succulence; WSG, wood specific gravity; HEIGHT, maximum height; SEED, seed mass; PCA1, PCA1 score; PCA2, PCA2 score. Asterisks indicate significant ($P \leq 0.05$) deviations from a null expectation using a Wilcoxon test.

score was nonrandom. We found that the majority of traits and both PCA scores showed high values of clustering (Fig. 2). Thus, coexisting species were more functionally similar than expected. However, there were two trait axes that violated this general pattern. Seed mass and maximum heights were found to be overdispersed at the smallest scales (Fig. 2).

Size class results

Maximum height was found to be overdispersed among coexisting species in this study (Fig. 2). However, a central question is, within groups of species sharing a

similar maximum height, does trait dispersion change directionally as cohorts age? Across all four maximum height quartiles, generally all traits were more clustered between coexisting species than expected (Fig. 3). As the diameter size class within a height quartile increased there was generally no change in the degree of clustering or only a slight increase. The lack of signal in larger diameter size classes in the first and second maximum height quartiles was likely due to a lack of statistical power. The increase in clustering would suggest a nonrandom increase in the mortality rates of functionally dissimilar species within cohorts. This is opposite to the patterns reported for phylogenetically based tests in this forest that showed an increase in phylogenetic

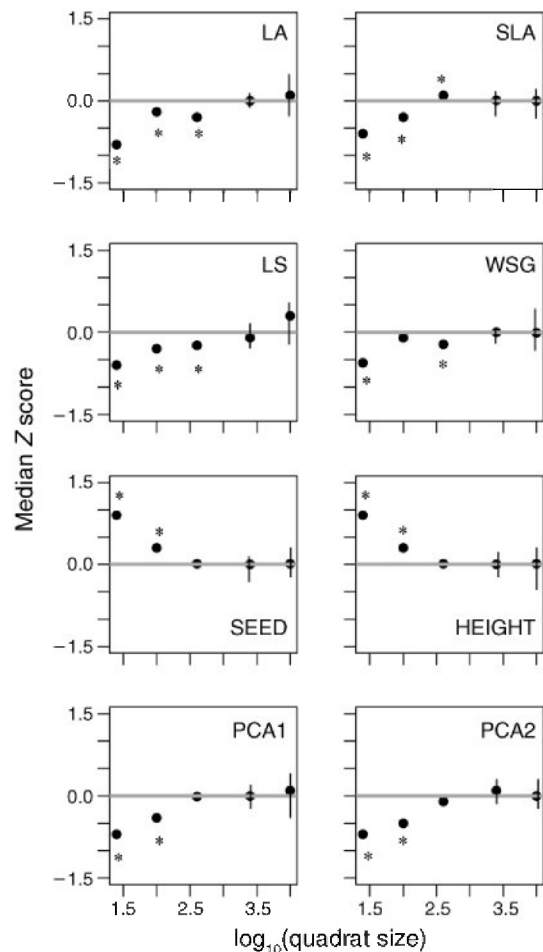


FIG. 2. The relationship between spatial scale and functional trait dispersion in the San Emilio FDP. Key to abbreviations: LA, leaf area; SLA, specific leaf area; LS, leaf succulence; WSG, wood specific gravity; HEIGHT, maximum height; SEED, seed mass; PCA1, PCA1 score; PCA2, PCA2 score. Positive Z scores indicate trait values in an assemblage are more dissimilar than expected by chance. Negative Z scores indicate trait values in an assemblage are less dissimilar than expected by chance. Error bars are 95% confidence intervals. Asterisks indicate significant ($P \leq 0.05$) deviations from a null expectation using a Wilcoxon test.

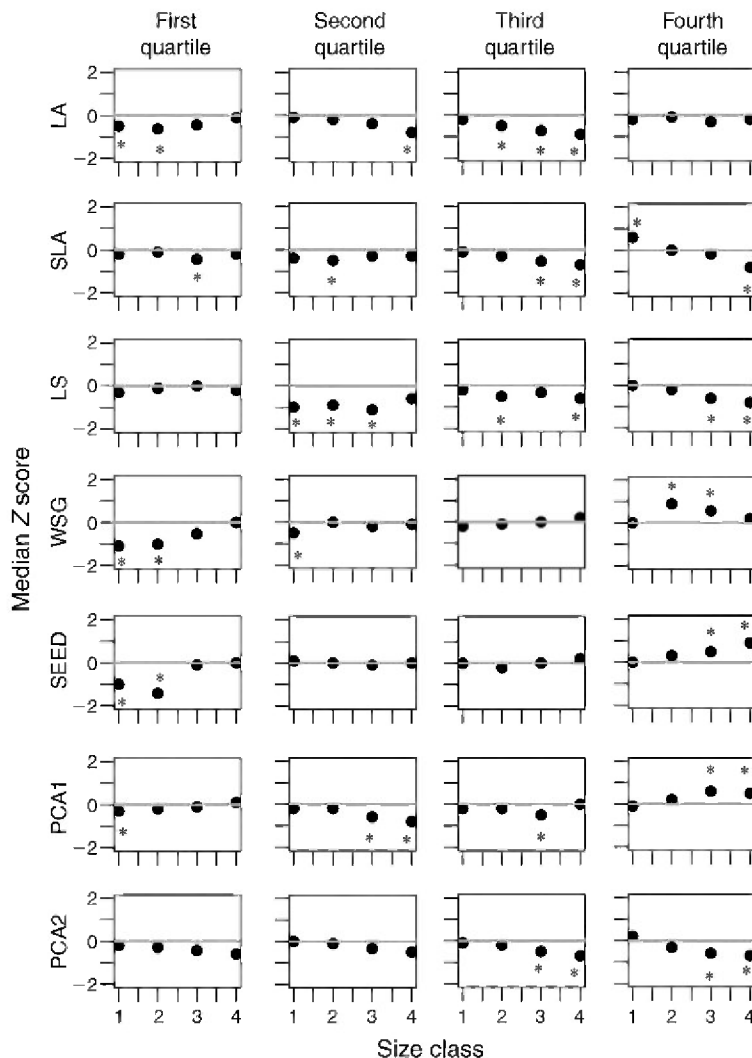


FIG. 3. The relationship between functional trait dispersion in different-sized individuals in the four height quartiles in the San Emilio FDP. Definitions of size classes: 1, 3–4.9 cm stem diameter; 2, 5–9.9 cm stem diameter; 3, 10–14.9 cm stem diameter; 4, 15+ cm stem diameter. Key to abbreviations: LA, leaf area; SLA, specific leaf area; LS, leaf succulence; WSG, wood specific gravity; HEIGHT, maximum height; SEED, seed mass; PCA1, PCA1 score; PCA2, PCA2 score. Positive Z scores indicate that trait values in an assemblage are more dissimilar than expected by chance. Negative Z scores indicate that trait values in an assemblage are less dissimilar than expected by chance. Error bars are omitted for clarity. Asterisks indicate significant ($P \leq 0.05$) deviations from a null expectation using a Wilcoxon test.

overdispersion with increasing size bins of canopy tree species (Swenson et al. 2007).

Timing of trait evolution results

In an effort to uncover what may cause inconsistencies between trait dispersion and phylogenetic dispersion such as those found presently, we examined the phylogenetic signal in trait data at different depths in the phylogeny. The test examined the continuous distribution of divergence sizes along the entire phylogenetic super tree. Basally and terminally, seed mass and maximum height generally had a stronger phylogenetic signal than the remaining traits (Fig. 4). It should be reiterated that genus means were used for

many of the seed masses in this study. This clearly biases the tests toward a high degree of phylogenetic signal terminally for seed mass, and therefore we only show this data for reference and will not discuss it any further.

DISCUSSION

Spatial scaling

The present study was designed to ask if, in the same forest, does the dispersion of several key traits match patterns of phylogenetic dispersion (Swenson et al. 2007)? The answer appears to be both “yes” and “no.” Specifically, on small spatial scales the functional trait dispersion, unlike the previous phylogenetic dispersion

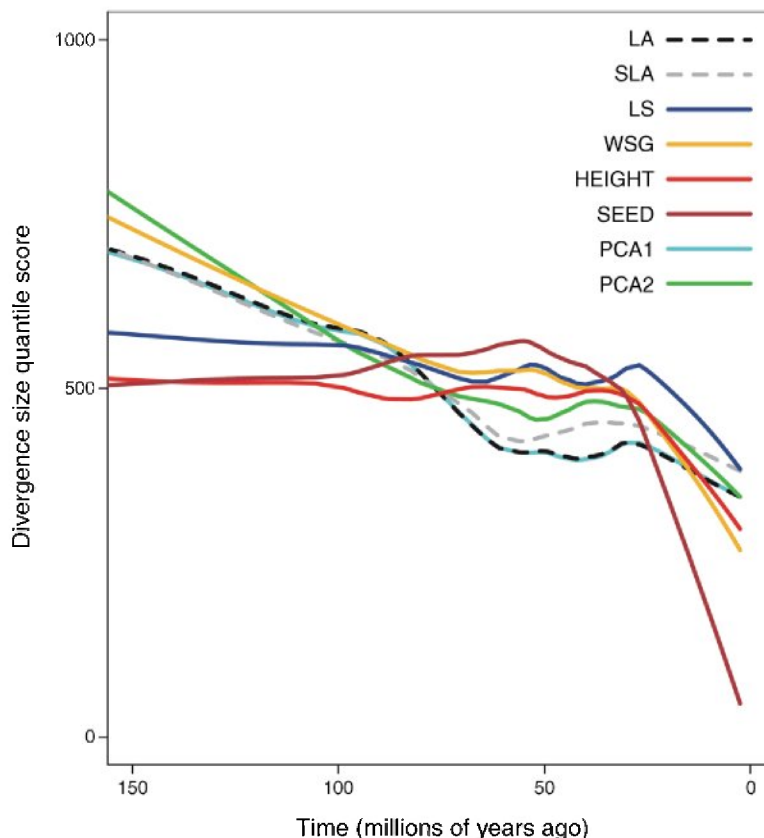


FIG. 4. Locally weighted regressions (66% weighting window) of divergence size quantile scores of internal nodes of the super tree on the *y*-axis vs. the node age on the *x*-axis. The node ages were estimated on the phylogenetic super tree using the software Phylomatic. Key to abbreviations: LA, leaf area; SLA, specific leaf area; LS, leaf succulence; WSG, wood specific gravity; HEIGHT, maximum height; SEED, seed mass; PCA1, PCA1 score; PCA2, PCA2 score. Higher quantile scores indicate a higher than expected observed divergence size. Lower quantile scores indicate a lower than expected observed divergence size.

results, of coexisting species tended to be a nonrandom subset of the species pool (Fig. 2). The present analyses of trait dispersion show that, on small spatial scales four of the six functional traits and both PCA scores were more clustered, but that within assemblages on small scales the remaining two traits (seed size and maximum height) were overdispersed.

We suggest that the simultaneous functional clustering and overdispersion found in the present study may largely explain why we found random phylogenetic dispersion in our original work. Thus, analyses of phylogenetic dispersion that produce a random result do not necessarily imply that there is no functional mechanism of coexistence in the community analyzed. In fact, it could be the exact opposite where orthogonal trait axes are simultaneously being influenced by abiotic filters and limits to similarity. Previous analyses have shown simultaneous clustering and overdispersion in functional traits in tree communities (Cavender-Bares et al. 2004). Our work builds upon the work by Cavender-Bares et al. (2004) and highlights how opposing assembly mechanisms may provide a random phylogenetic dispersion in communities.

The majority of the traits examined in this study show a high degree of clustering in small-scale assemblages. This suggests that the local abiotic template allows for the coexistence of only a winnowed functional subset of the species pool. Grime (2006) recently proposed that local scale functional clustering in plant communities should be found in trait axes related to productivity. In particular, traits such as relative growth rate, leaf life span, and leaf nutrients should be locally clustered. The present study does not directly measure any of these traits, but it does analyze correlates of each such as SLA and WSG (wood specific gravity) that are important indicators of plant resource acquisition and growth strategies (Reich et al. 1991, 1997, Enquist et al. 1999, Westoby et al. 2002, Wright et al. 2004, Enquist et al. 2007). For the traits that are linked to plant productivity, we find a high degree of local functional clustering (Fig. 2). Thus the hypothesized general clustering of productivity related traits in temperate herbaceous communities proposed by Grime and colleagues (Thompson et al. 1996, Grime 2006), appears to be supported by our analyses of this tropical tree community.

There were two trait axes in the present study, maximum height and seed mass, that disobeyed the general finding of functional clustering on small scales. Both of these traits were found to be locally overdispersed. Previous empirical and theoretical evidence has suggested that maximum height may be important in promoting species diversity and coexistence in light limited forested ecosystems (e.g., Thomas and Weiner 1989, Kohyama et al. 2003, King et al. 2006). Our present results lend further support to the importance of this trait in promoting species diversity and coexistence in tropical forests.

Seed mass represents a fundamental trade-off between producing many small seeds vs. producing few large seeds per unit energy (Venable 1996, Moles and Westoby 2006). Seed mass has also been suggested to be a good indicator of the regeneration niche of a species (Grubb 1977). The seed mass results presented suggest that species may differ in their regeneration niche thereby allowing for local coexistence. Thus, the overdispersion of seed mass also supports the prediction of Grime and colleagues (Thompson et al. 1996, Grime 2006) that the traits that should be overdispersed locally should be related to disturbance and regeneration. Last, we note that seed mass and maximum height are correlated. Thus, it is difficult to infer whether one of these traits plays a predominant role in promoting coexistence in this forest or whether both traits play a role. It may be that both traits play an important role at different times during the life cycle of the tree, but because they are correlated they may appear to be important at stages in the life cycle when they may not be. For example, the maximum possible height of a tree likely plays little role in determining the distribution and coexistence of species early during the life cycle, but it likely is very important during the adult stage. The seed mass of a tree likely plays a large role in determining the distribution and coexistence of species early during the life cycle, but it likely has less importance in the adult stage.

Along with spatial scale, communities may be differentially clustered or overdispersed functionally as cohorts age. Previous phylogenetic analyses in this forest have shown that as one examines larger diameter individuals within a maximum height size class, the degree of phylogenetic overdispersion increases suggesting that as cohorts age they represent a more dissimilar phylogenetic subset of the species pool (Swenson et al. 2007). We tested this possibility by examining the trait dispersion in diameter size classes of coexisting species that will attain similar maximum heights. In general, coexisting species tended to be functionally clustered no matter the diameter size class or maximum height quartile examined (Fig. 3).

Phylogenetic–functional mismatch

The present functional trait dispersion results are inconsistent with previous phylogenetic dispersion results from this forest. It was not surprising that the

spatial scaling results differed because simultaneous clustering and overdispersion in function could produce a random phylogenetic dispersion in the forest. The size-scaling mismatch was more surprising. This is because, it has been suggested that measuring the phylogenetic conservatism in trait data and the phylogenetic dispersion of species in a community in unison, one can infer the dispersion of that trait in the community (e.g., Webb et al. 2002, Cavender-Bares et al. 2004, Swenson et al. 2007). The present results show that this may not be the case when one uses the metric of phylogenetic signal (sensu Blomberg et al. 2003) that was used in the previous study (Swenson et al. 2007) as a method for inferring the phylogenetic conservatism in trait data.

In an effort to uncover how and why the observed disparity between phylogenetic and functional dispersion exists in this forest, we performed a phylogenetic analysis that quantified the phylogenetic signal in trait data at different depths in the phylogenetic tree. The expectation was that a lack of phylogenetic signal in trait data basally and terminally in the phylogeny would weaken the ability to accurately infer the degree of phylogenetic conservatism in that trait and thereby weaken inferences of trait dispersion using metrics phylogenetic dispersion. We found that maximum height had a high degree phylogenetic signal basally and terminally on the phylogeny while the other traits generally had little signal throughout the phylogeny (Fig. 4). This result was consistent with our expectation. Specifically, the trait dispersion result that was consistent with the phylogenetic dispersion result was for a trait that had a high degree of phylogenetic signal terminally and basally in the phylogenetic tree, maximum height. The remaining four traits had little phylogenetic signal terminally and basally in the phylogeny, and we suggest that this may have led to the observed inconsistencies in the phylogenetic and trait dispersion results. Thus, we suggest that analyses based only on measuring phylogenetic dispersion and the metric of phylogenetic signal sensu Blomberg et al. (2003) that do not examine the degree of phylogenetic signal at different depths in the phylogeny may be prone to erroneous inferences of trait dispersion. We do not find this to be a fatal flaw for the framework proposed by Webb et al. (2002) that describes how measuring phylogenetic dispersion and phylogenetic conservatism in trait data in unison could be used to infer trait dispersion, but we do suggest that perhaps the metric of phylogenetic signal is not a good tool for inferring the degree of ecological similarity between closely related taxa (i.e., phylogenetic conservatism). We note that recent simulation analyses (Revell et al. 2008) have come to similar conclusions and our empirical results yield further support to their findings.

Conclusions

The present study was designed to examine the role of functional similarity in promoting species diversity and

coexistence in a diverse tropical forest and whether previous phylogenetic dispersion results in this forest accurately predicted the degree of functional dispersion. We have found that phylogenetic dispersion does not accurately predict the dispersion of all functional traits in this forest. We argue that this is due to the simultaneous clustering and overdispersion in functional traits, the distribution of large trait divergences along the phylogenetic tree, and that the phylogenetic signal metric used in the original study (Swenson et al. 2007) may be a poor indicator of phylogenetic conservatism (Revell et al. 2008). Last, we point out that similar patterns of trait dispersion have recently been uncovered in an Ecuadorian rain forest dynamics plot (Kraft et al. 2008) suggesting that our results are not peculiar to our system. Despite this continuity, future work will need to be conducted in other systems to address the generality of our findings, and the role of other traits will need to be examined.

ACKNOWLEDGMENTS

We thank Nathan Kraft and David Ackerly for providing us with preliminary results from their work in Ecuador and for comments. We also thank Cathy Hulshof for assisting in the field collection of functional trait values. Conservation International and a NSF CAREER award to B. J. Enquist supported N. G. Swenson and B. J. Enquist.

LITERATURE CITED

- Ackerly, D. D. 2004. Evolution of leaf form in the California chaparral: adaptation and community assembly. *American Naturalist* 163:654–671.
- Aiba, S. I., and T. Kohyama. 1997. Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. *Journal of Ecology* 85:611–624.
- Bell, G. 2001. Neutral macroecology. *Science* 293:2413–2418.
- Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.
- Brooks, D. R., and D. A. McLennan. 2002. *The nature of diversity*. University of Chicago Press, Chicago, Illinois, USA.
- Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163:823–843.
- Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87(Supplement):S109–S122.
- Chave, J., G. Chust, and C. Thebaud. 2008. The importance of phylogenetic structure in biodiversity studies. Pages 151–167 *in* D. Storch, P. L. Marquet, and J. H. Brown, editors. *Scaling biodiversity*. Cambridge University Press, Cambridge, UK.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review in Ecology and Systematics* 31:343–366.
- Davis, C. C., C. O. Webb, K. J. Wurdack, C. A. Jaramillo, and M. J. Donoghue. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *American Naturalist* 165:E36–E65.
- Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 *in* M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Dolph, G. E., and D. L. Dilcher. 1980. Variation in leaf size with respect to climate in Costa Rica. *Biotropica* 12:91–99.
- Elton, J. 1946. Competition and the structure of ecological communities. *Animal Ecology* 15:54–68.
- Enquist, B. J., A. J. Kerkhoff, S. C. Stark, N. G. Swenson, M. C. McCarthy, and C. A. Price. 2007. A general integrative model for scaling plant growth, carbon flux and functional trait spectra. *Nature* 449:218–222.
- Enquist, B. J., G. B. West, E. L. Charnov, and J. H. Brown. 1999. Allometric scaling of production and life history variation in vascular plants. *Nature* 401:907–911.
- Garnier, E., and G. Laurent. 1994. Leaf anatomy, specific mass and water content in congeneric and perennial grass species. *New Phytologist* 128:725–736.
- Gotelli, N. J., and G. L. Entsminger. 2001. Swap and fill algorithms in null model analysis: rethinking the knight's tour. *Oecologia* 129:281–291.
- Gotelli, N. J., and G. R. Graves. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, D.C., USA.
- Grant, P. R., and I. Abbott. 1980. Interspecific competition, island biogeography and null hypotheses. *Evolution* 34:332–341.
- Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17:255–260.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the regeneration niche. *Biological Reviews* 52: 107–145.
- Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203:1299–1309.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Jarvinen, O. 1982. Species-to-genus ratios in biogeography: a historical note. *Journal of Biogeography* 9:363–370.
- Kemml, S. W., and S. P. Hubbell. 2006. The phylogenetic structure of a Neotropical forest tree community. *Ecology* 87(Supplement):S86–S99.
- King, D. A., S. J. Wright, and J. H. Connell. 2006. The contribution of interspecific variation in maximum tree height to tropical and temperate diversity. *Journal of Tropical Ecology* 22:11–24.
- Kohyama, T. 1993. Size-structured tree populations in gap-dynamic forest: the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology* 81:131–143.
- Kohyama, T., E. Suzuki, T. Partomihardjo, T. Yamada, and T. Kubo. 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *Journal of Ecology* 91: 797–806.
- Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580–582.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Losos, J. 1996. Phylogenetic perspectives on community ecology. *Ecology* 77:1344–1354.
- Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* 11:995–1007.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- McGill, B., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005. A brief history of seed size. *Science* 307:576–580.

- Moles, A. T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113:91–105.
- Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness, and community composition. *Ecology Letters* 5:402–411.
- R Development Core Team. 2007. R: a language and environment for statistical computing. (<http://www.R-project.org>)
- Reich, P. B., C. Uhl, M. B. Walters, and D. S. Ellsworth. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* 86:16–24.
- Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences (USA)* 94:13730–13734.
- Revell, L. J., L. J. Harmon, and D. C. Collar. 2008. Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* 57:591–601.
- Simberloff, D. 1970. Taxonomic diversity of island biotas. *Evolution* 24:23–47.
- Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94:451–459.
- Swenson, N. G., and B. J. Enquist. 2008. The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. *American Journal of Botany* 95:516–519.
- Swenson, N. G., B. J. Enquist, J. Pither, J. Thompson, and J. K. Zimmerman. 2006. The problem and promise of scale dependency in community phylogenetics. *Ecology* 87:2418–2424.
- Swenson, N. G., B. J. Enquist, J. Thompson, and J. K. Zimmerman. 2007. The influence of spatial and size scales on phylogenetic relatedness in tropical forest communities. *Ecology* 88:1770–1780.
- Thomas, S. C., and J. Weiner. 1989. Including competitive asymmetry in measures of local interference in plant populations. *Oecologia* 80:349–355.
- Thompson, K., S. H. Hillier, J. P. Grime, C. C. Bossard, and S. R. Band. 1996. A functional analysis of a limestone grassland community. *Journal of Vegetation Science* 7:371–380.
- Venable, D. L. 1996. Packaging and provisioning in plant reproduction. *Philosophical Transactions of the Royal Society Series B* 351:1319–1329.
- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* 156:145–155.
- Webb, C. O., D. D. Ackerly, and S. Kembel. 2004. Phylocom version 3.21: software for the analysis of community phylogenetic structure and character evolution. (<http://www.phylodiversity.net/phylocom>)
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475–505.
- Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5:181–183.
- Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74:159–164.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33:125–159.
- Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21:261–268.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Wright, I. J., et al. 2004. The world-wide leaf economics spectrum. *Nature* 428:821–827.

APPENDIX A

Literature sources for height data (*Ecological Archives* E090-151-A1).

APPENDIX B

The results of the principal components analysis of the six functional traits quantified for all of the species in the LFDP (*Ecological Archives* E090-151-A2).