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Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities

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Abstract. The study of biodiversity has tended to focus primarily on relatively information-poor measures of species diversity. Recently, many studies of local diversity (alpha diversity) have begun to use measures of functional and phylogenetic alpha diversity. Investigations into the phylogenetic and functional dissimilarity (beta diversity) of communities have been far less numerous, but these dissimilarity measures have the potential to infer the mechanisms underlying community assembly and dynamics. Here, we relate levels of phylogenetic and functional alpha diversity to levels of phylogenetic and functional beta diversity to infer the mechanism or mechanisms responsible for the assembly of tree communities in six forests located in tropical and temperate latitudes. The results show that abiotic filtering plays a role in structuring local assemblages and governing spatial turnover in community composition and that phylogenetic measures of alpha and beta diversity are not strong predictors of functional alpha and beta diversity in the forests studied.

INTRODUCTION

The quantification of biodiversity has tended to focus primarily on species alpha and beta diversity. This research program has been successful in providing initial insights into the distribution of biodiversity and the potential mechanisms governing those patterns (e.g., Gentry 1982, Condit et al. 2002, Legendre et al. 2005). A species diversity-centric approach to the study of biodiversity is a logical starting point, but measures of species diversity alone are relatively information poor (Webb et al. 2002, McGill et al. 2006, Cavender-Bares et al. 2009, Swenson 2011*b*, Swenson et al. 2011). That is, they convey little to no information regarding the evolutionary history or functional diversity of the system under study. In other words, metrics of species

diversity treat all species as evolutionarily independent and ecologically equivalent. Alternative axes of biodiversity such as phylogenetic and functional diversity have the ability to convey this nonindependence and substantially improve our understanding of the mechanisms underlying biodiversity patterns (e.g., Faith 1992, Webb et al. 2002, Petchey and Gaston 2006, Swenson 2011*b*).

The widespread implementation of a phylogenetically and functionally centric approach to studying biodiversity has been hindered by the difficulty of estimating the phylogenetic relatedness and functional similarity of hundreds to thousands of species across broad gradients. That said, these traditional obstacles are quickly being removed. Informatics tools (e.g., Webb and Donoghue 2005) that rely on advances in our knowledge of major groups (e.g., Soltis et al. 2011) and large-scale community DNA sequencing efforts (e.g., Kress et al. 2009, 2010, Pei et al. 2011) are now enabling ecologists to quickly estimate the phylogenetic diversity of assemblages around the world. Coincidental with the

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phylogenetic diversity revolution has been a movement in plant functional ecology toward identifying key plant traits that are robust indicators of ecological strategies (e.g., Westoby et al. 2002) and, importantly, that can be measured relatively quickly on hundreds of co-occurring species allowing for estimates of the functional diversity within assemblages. While the quantification of phylogenetic and functional diversity will continue to be refined with more sophisticated tools and metrics, the fundamental building blocks are now in place to explore the distribution of phylogenetic and functional diversity in plant assemblages along broad gradients (Swenson and Weiser 2010, Swenson 2011*b*).

Perhaps one of the most conspicuous biodiversity patterns on Earth is the increase in species diversity from the poles toward the equator (e.g., Gentry 1982, Weiser et al. 2007). Indeed, the spectacular degree of biodiversity in the tropical environments has fascinated biologists for well over a century. When compared to the relatively depauperate temperate latitudes, the tropics are remarkable in their levels of biodiversity in two ways. First, there is a tremendous diversity within sites (i.e., alpha diversity), and second, there is a high diversity between sites (i.e., beta diversity) (Koleff et al. 2003, Kraft et al. 2011). Investigations into alpha diversity have often sought to identify the mechanisms underlying local-scale co-occurrence. Importantly, the vast majority of these mechanisms predict the degree to which the similarity of species should or should not influence their local co-occurrence. For example, negative biotic interactions should result in co-occurring species that are dissimilar in traits relating to competition or predation. For example, negative biotic interactions should result in co-occurring species that are dissimilar in traits relating to competition or predation; for example, environmental filtering should result in species co-occurring that are similar in trait values that relate to abiotic gradients. Conversely, purely stochastic processes should leave no consistent pattern of ecological similarity between co-occurring species. Thus, strong tests of these hypotheses require the quantification of the similarity of co-occurring species (Webb et al. 2002). For nearly a century, beginning with genus-to-species ratios, ecologists have tested these hypotheses by quantifying the evolutionary relatedness of co-occurring species as a proxy for their similarity (see Jarvinen 1982, Webb 2000), but the strength of this assumption is often rightly questioned (see Cavender-Bares et al. 2009). An alternative approach has been to directly quantify the functional similarity of species. These functionally based investigations of alpha diversity have now been implemented in temperate (e.g., Weiher et al. 1998, Cavender-Bares et al. 2004) and tropical (e.g., Kraft et al. 2008, Swenson and Enquist 2009) plant assemblages, with the results often rejecting a purely stochastic model of community assembly.

The study of beta diversity has generally lagged behind the study of alpha diversity, but interest in the

topic has begun to explode over the last decade (Anderson et al. 2011). Beta diversity serves as the scalar between local biodiversity and regional biodiversity (i.e., gamma diversity; Whittaker 1960) and can provide substantial insights into the mechanisms underlying community structure and assembly. The development of beta diversity research programs is therefore critical for a comprehensive understanding of biodiversity. To date, beta diversity research has primarily focused on two major themes. First, researchers have focused on the partitioning of gamma diversity into its alpha and beta components (e.g., Whittaker 1960). Second, community ecologists have attempted to quantify the degree to which the environment, space, or their interaction is the best predictor of community dissimilarity in the search for the dominant mechanisms underlying community structure and assembly (e.g., Condit et al. 2002, Legendre et al. 2005). This second theme has proved to be a difficult one due to the heavy correlation between space and the environment with the potential consequence of the overestimation of the influence of purely spatial processes (Legendre et al. 2005, Peres-Neto et al. 2012). An additional, less well recognized issue with the second theme is that species vary in their degree of similarity. Indeed, it is possible to have a complete turnover of the species composition between two communities, but have little to no turnover in the functional composition (Fig. 1). Traditional species-centric analyses may attribute such turnover to dispersal limitation and stochasticity, while functionally informed analyses would recognize dispersal limitation and ecological determinism governing community structure. Thus, it is conceivable that species beta diversity analyses that do not consider the similarity of species could lead to seriously misleading inferences (Fig. 1; Swenson 2011*a, b*).

In recognition of the potential limitations of focusing solely on species beta diversity, ecologists are increasingly attempting to quantify the evolutionary and functional dissimilarity between communities. The evolutionary dissimilarity of communities has been accomplished utilizing traditional measures of beta diversity on lists of genera and families in communities rather than lists of species (e.g., Terlizzi et al. 2009). This approach was refined using phylogenetic trees by microbial ecologists that have necessarily been at the leading edge of phylogenetically based analyses of communities (Martin 2002, Lozupone and Knight 2005, Lozupone et al. 2007). Relatively recently nonmicrobial ecologists have also embraced phylogenetic analyses of beta diversity (e.g., Hardy and Senterre 2007, Bryant et al. 2008, Graham and Fine 2008, Swenson 2011*a*). Analyses of functional beta diversity have also become more common with a large sum of work focusing on the development of functional beta diversity metrics that are often implemented in relatively species-poor temperate systems (e.g., Ricotta and

Burrascano 2009), with only one study, to our knowledge, being conducted in a highly diverse tropical system (Swenson et al. 2011).

Ultimately, the number of phylogenetically and functionally informed analyses of community structure and assembly has rapidly increased, with increasingly sophisticated tools and analyses being implemented. Recent reviews that have sought to synthesize this increase in the literature have focused on phylogenetic and functional alpha diversity, spatial scale, and the relative influence of biotic and abiotic filters governing community assembly as a guiding framework (Weiher and Keddy 1995, Cavender-Bares et al. 2009). This work has highlighted a general finding that abiotic and biotic filters often operate at different spatial scales, and that this can be detected by varying the spatial scale of the analysis. In particular, phylogenetic and functional analyses of community structure often find closely related or functionally similar species co-occurring on larger spatial scales, and distantly related or functionally dissimilar species co-occurring on finer spatial scales (Weiher and Keddy 1995, Cavender-Bares et al. 2006, Swenson et al. 2006).

This interesting cumulative result suggests that the observed scaling transitions or changes in scaling domains (sensu Wiens 1989) support a hierarchical model of community assembly where species sequentially pass through historical, abiotic, and biotic filters to result in the local assemblage observed on the ground (Webb et al. 2002, 2008b, Algar et al. 2011). This hierarchical filtering model of community assembly can be further tested by considering the predictions it makes regarding phylogenetic and functional beta diversity and spatial scale (Fig. 1). For example, an initial step in the assembly process would be the abiotic filtering of species into large homogeneous patches of environment (i.e., dry forest or rain forest), which should result in similar species co-occurring at this spatial scale, but it should also result in little to no phylogenetic or functional compositional turnover between large neighboring assemblages within the large swath of homogeneous habitat (Fig. 1c). At the next level of the hierarchy, species are proposed to abiotically filter into homogeneous habitats partitioned at a finer scale (i.e., soil types) where similar species are still expected to co-occur, but there is substantial phylogenetic and functional compositional turnover between assemblages due to turnover in habitat types (Fig. 1a; see Fine and Kembel 2011). At the next finest level in the hierarchy, biotic interactions within a largely homogeneous abiotic habitat are expected to play a dominant role, resulting in dissimilar species co-occurring and far less turnover in the phylogenetic and functional composition between assemblages within an abiotically homogeneous habitat type (Fig. 1d). It is also possible to observe high dissimilarity within and across assemblages presumably due to strong sorting of lineages or traits along a habitat

gradient and negative biotic interactions between species at individual sites on the gradient (Fig. 1b).

As noted in the previous paragraph, previous phylogenetic and functional analyses of assemblages have generally considered alpha diversity and spatial scale to test the hierarchical community assembly model. The present work seeks to inject analyses of beta diversity into this framework to provide a more refined exploration of the hierarchical assembly hypothesis by testing these predictions regarding the relationship between alpha and beta diversity (Fig. 1). The analyses were conducted in six large-scale forest inventory plots arrayed across latitude, allowing for initial insights into whether the inferred assembly mechanisms changes among plots with vastly different numbers of co-occurring species.

MATERIALS AND METHODS

Forest dynamics plots

The present study utilized a series of six large forest dynamics plots located in Asia and the Americas. The forest plots range in latitude from 45.55° N to 9.15° N, and the species diversity ranges from 36 to 299 (Table 1). In each forest dynamics plot, each free-standing woody stem ≥ 1 cm diameter at breast height was identified, mapped, and measured (Condit 1998). This mapping of stems allows for spatial analyses of tree community composition including the quantification of species, and phylogenetic and functional beta diversity.

Community phylogenies

A molecular phylogeny was generated for each forest dynamics plot. The phylogenies were generated using three sequence regions: *rbcL*, *matK*, and *trnH-psbA*. In all plots except Wabikon Lake in Wisconsin, USA, the sequences were generated from vouchered material collected from tagged individuals within the forest dynamics plots. The sequence data for the Wabikon Lake forest plot came from previously deposited sequences in National Center for Biotechnology Information (NCBI; Bethesda, Maryland, USA). The sequence alignment for all six plots followed the methods described in Kress et al. (2009, 2010). Specifically, the *rbcL* and *matK* regions were globally aligned, and the *trnH-psbA* sequences were aligned only within families and concatenated onto the *rbcL* and *matK* alignments to constitute a supermatrix. The supermatrix and maximum likelihood were used to infer the community phylogeny representing species pool for each forest dynamics plot.

Functional traits and phylogenetic signal

Five functional traits were quantified for all species in four of the six forest dynamics plots. Specifically, specific leaf area, leaf area, seed mass, wood density, and maximum height were determined for the tree species in the Barro Colorado Island, Panama (BCI; Wright et al. 2010), Luquillo, Puerto Rico (LUQ; Swenson et al.

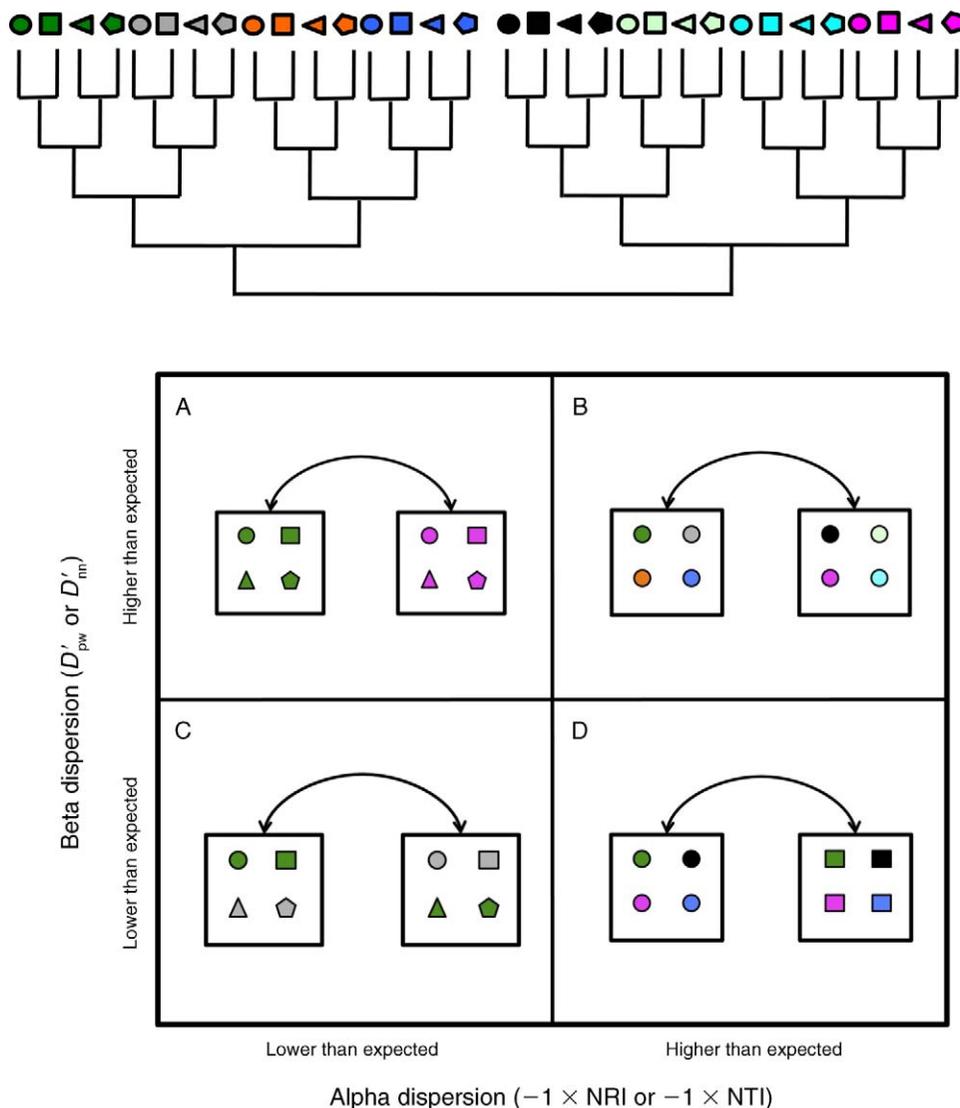


FIG. 1. A schematic relating levels of phylogenetic (or functional) alpha dispersion to levels of phylogenetic (or functional) beta dispersion. The tree at the top of the figure might refer to phylogenetic or to functional similarity. The color of the shapes indicates the ecological strategy or niche of each species. The unique combination of shape and color indicates a unique species. The small black squares represent local assemblages of species. Species or alpha diversity is equal within each assemblage. Species turnover or beta diversity is also equal (100%) between assemblages within each example. But, the level of phylogenetic (or functional) alpha and beta diversity varies among the four examples. In example (A), species abiotically filter into homogeneous habitats where similar species are expected to co-occur, but there is substantial phylogenetic (or functional) turnover between assemblages due to turnover in habitat types. In example (B), a strong sorting of lineages (or traits) along a habitat gradient and local negative biotic interactions between species at individual sites on the gradient governs assembly. In example (C), abiotic filtering of species into large homogeneous patches of environment results in similar species co-occurring locally and little-to-no phylogenetic (or functional) turnover between neighboring assemblages within the large swath of homogeneous habitat. In example (D), negative biotic interactions in a large swath of homogeneous habitat are expected to produce local dispersion but little turnover in phylogenetic (or functional) composition. In example (D), species turnover results from chance draws from a large species pool and subsequent interactions among co-occurring species. Abbreviations are: NRI, net relatedness index; NTI, nearest taxon index; D'_{min} , nearest neighbor dissimilarity; and D'_{pw} , pairwise dissimilarity.

2011), Wabikon Lake (WAB; data collected by N. G. Swenson), and Gutianshan, China (GTS; data collected by X. Liu) forest dynamics plots. Maximum height, seed mass, and wood density for the Smithsonian Conservation Biology Institute, Virginia, USA (SCBI) plot were gathered from the literature. These traits clearly do not

represent a full representation of all aspects of plant function. For example, root and defense traits and physiological rates would ideally also be quantified. That said, the traits presently utilized do provide robust indicators of where species fall along several major axes of plant functional strategy. Maximum height was used

TABLE 1. Characteristics of the forest dynamics plots (with abbreviations) used in this study.

Forest dynamics plot	Latitude (°N)	Elevation (m)	Total species richness	Plot area (ha)
Wabikon Lake, Wisconsin, USA (WAB)	45.55	501	36	25
Smithsonian Conservation Biology Institute, Virginia, USA (SCBI)	38.89	330	62	25.6
Gutianshan, China (GTS)	29.25	715	159	24
Dinghushan, China (DHS)	23.16	470	210	20
Luquillo, Puerto Rico (LUQ)	18.33	428	138	16
Barro Colorado Island, Panama (BCI)	9.15	160	299	50

to indicate the adult light niche of species (Moles et al. 2009). Leaf area was used to represent the leaf area deployed for light capture. Seed mass was used to represent the trade-off between the number and size of seeds produced (Moles and Westoby 2006) and the regeneration niche (Grubb 1977). Specific leaf area (SLA) was used to represent the leaf economics spectrum where high structural investment, long leaf life spans, and low photosynthetic rates are contrasted with low structural investment, short leaf life spans, and high photosynthetic rates (Wright et al. 2004). Wood density was used to represent a trade-off between high structural investment and low growth and mortality rates vs. low structural investment and high growth and mortality rates (Chave et al. 2009). Trait values were quantified using globally standardized protocols (Cornelissen et al. 2003) with few exceptions (see Wright et al. 2010). In particular, wood density in the Luquillo and Wabikon plots was estimated from branch wood (Swenson and Enquist 2008), and seed mass in the forest plots was calculated using entire diaspore weights. Finally, leaf traits were quantified from leaves collected from the crowns of individuals, but these were not necessarily “sun-exposed” leaves, as many species attain their maximum size in the understory and never experience full sun exposure. In all plots, except BCI, sample sizes typically exceeded 10 individuals. At BCI, sample sizes were typically around five or six individuals (Wright et al. 2010). A recent power analysis of functional traits in tropical trees (Hulshof and Swenson 2010) has suggested that this sample size can allow for robust estimates of species mean values. The present work does not explicitly incorporate within-species or within-individual trait variation into the statistical analyses. Our analyses therefore underestimate trait beta diversity where traits vary within a species from subplot to subplot within the forests studied (Swenson et al. 2011).

The analyses in this work compare and contrast measurements of phylogenetic and functional beta diversity. It is expected that patterns of functional beta diversity should mirror the patterns of phylogenetic beta diversity if significant phylogenetic signal is present in the functional trait data. To test whether or not phylogenetic signal was present in the trait data, we calculated the *K* statistic of Blomberg et al. (2003) for each trait.

Phylogenetic and functional alpha dispersion

The phylogenetic alpha dispersion of each assemblage was calculated using two widely implemented metrics: the net relatedness index (NRI) and the nearest taxon index (NTI) (Webb 2000). The NRI is a standardized effect size (SES) of the observed mean pairwise phylogenetic distance (MPD) of all individuals or species in an assemblage. The pairwise nature of this metric makes it an indicator of the “basal” dispersion of the assemblage. Specifically, the NRI is often calculated as the observed MPD minus the mean MPD of many random assemblages divided by the standard deviation of the random MPD values. This value is then generally multiplied by -1 , such that higher than expected observed MPD values (i.e., phylogenetic overdispersion) provides a negative NRI value and lower than expected observed MPD values (i.e., phylogenetic clustering) provides a positive NRI value. Therefore, negative values represent clustering, and positive values represent overdispersion in all results shown. This tends to create confusion as higher than expected MPD values give lower NRI values. The NTI is also a SES measure, except that the observed value being calculated is the mean nearest phylogenetic neighbor distance (MNND) between individuals or species in a community. The NTI therefore only considers nearest neighbors and indicates the “terminal” phylogenetic structure of the assemblage complementing the basal NRI metric. Both NRI and NTI can be calculated using species presence-absence data, but in this study, all measures were abundance weighted. In the present study, we transformed all NRI and NTI values by multiplying it again by -1 . As such, in all figures we present $-1 \times \text{NRI}$ and $-1 \times \text{NTI}$ so that the positive values on the axes represent overdispersion and negative values represent clustering.

The NRI and NTI are measures of phylogenetic alpha dispersion, but identical measures of functional alpha dispersion can be calculated using trait dendrograms or trait distance matrices allowing for direct comparisons between trait and phylogenetic results. The present work generated trait dendrograms from Euclidean trait distances and quantifying analogous SES measures of functional alpha dispersion, which we term SES PW for pairwise trait dispersion and SES NN for nearest neighbor trait dispersion. The phylogenetic and functional alpha dispersion values were calculated in each forest plot with the analyses being repeated at multiple

spatial scales: 20 × 20 m, 40 × 40 m, and 100 × 100 m. Previous work has demonstrated clear relationships between trait and phylogenetic dispersion and spatial and size scales utilized in the study (e.g., Swenson et al. 2007, Swenson and Enquist 2009), but finer spatial scales and size-scaling analyses could not be implemented presently due to computational limitations. Future work that examines these scaling dimensions further, particularly with respect to beta diversity would likely prove interesting.

Phylogenetic and functional beta dispersion

The present study also measured the phylogenetic and functional beta diversity in the forest plots. Two phylogenetic and functional beta diversity metrics were utilized. The first metric used is abundance weighted and calculates the mean nearest phylogenetic or functional neighbor between two communities (Ricotta and Burrascano 2009)

$$D'_{\text{nn}} = \frac{\sum_{i=1}^{nk_1} f_i \min \delta_{ik_2} + \sum_{j=1}^{nk_2} f_j \min \delta_{jk_1}}{2} - 1$$

where $\min \delta_{ik_2}$ is the nearest phylogenetic neighbor to species i in community k_1 in community k_2 , and $\min \delta_{jk_1}$ is the nearest phylogenetic neighbor to species j in community k_2 in community k_1 , and f_i and f_j are the relative abundance of species i and species j . The resulting values of this metric, when presence-absence data are used, are strongly correlated with two other presence-absence phylogenetic beta diversity metrics, UniFrac (Lozupone and Knight 2005) and PhyloSor (Bryant et al. 2008), which are themselves nearly identical (Swenson 2011a). The benefit of the D'_{nn} metric is that it can incorporate abundance information if desired. The nearest neighbor metric is ideal for detecting subtle turnover in composition from subplot-to-subplot that may not be detected with pairwise metrics.

The second metric is an abundance weighted, pairwise phylogenetic or functional dissimilarity measure

$$D'_{\text{pw}} = \frac{\sum_{i=1}^{nk_1} f_i \overline{\delta_{ik_2}} + \sum_{j=1}^{nk_2} f_j \overline{\delta_{jk_1}}}{2} - 2$$

where $\overline{\delta_{ik_2}}$ is the mean pairwise phylogenetic distance between species i in community k_1 to all species in community k_2 , and $\overline{\delta_{jk_1}}$ is the mean pairwise phylogenetic distance between species j in community k_2 to all species in community k_1 , and f_i and f_j are the relative abundances of species i and species j . This metric is highly correlated with the more broadly known metric Rao's D (Rao 1982), but weakly correlated with the nearest neighbor metric (Swenson 2011a). This pairwise metric is likely better at detecting major compositional turnover from community to community.

The phylogenetic and functional beta diversity values were calculated between all pairwise combinations of subplots in each forest plot at the scale of 20 × 20 m, with the analyses being repeated at the 40 × 40 m and 100 × 100 m scale. As the forest plots vary in their size and overall heterogeneity, comparing the overall beta diversity found in forest plots is uninformative. We took an alternative and more tractable approach by quantifying the mean dissimilarity of a focal subplot and its surrounding eight subplots. This allowed for the quantification of neighborhood plot dissimilarity and reduces analytical biases due to differences in plot size and heterogeneity. It is also important to note that all analyses were contained within a plot such that all observed statistics and randomizations were constrained to a particular forest plot such that plot-to-plot differences in species diversity, functional diversity, phylogenetic diversity, plot size, and plot heterogeneity had less influence on the statistical output.

Null model

A central goal of the present work was to determine when and whether the observed level of phylogenetic and functional alpha and beta diversity differs from that randomly expected, given the species alpha and beta diversity, and to calculate alpha and beta dispersion such as NRI, NTI, SES PW, SES NN, SES D'_{nn} , and SES D'_{pw} . In order to achieve this goal, we implemented a null model. The null model shuffled the names of taxa across the tips of the phylogeny 999 times. During each iteration, the phylogenetic and functional beta diversity was quantified to provide one null measurement. The 999 null measurements constituted a null distribution from which standardized effect sizes and probabilities could be calculated. This null model fixes the observed levels of species alpha diversity, species beta diversity, species occupancy rates, community abundance distributions, species abundance, and observed levels of individual spatial contagion within species (i.e., potential dispersal limitation). This null model has been frequently used in studies of alpha dispersion, but it is particularly powerful for studies of beta diversity since it fixes all observed spatial patterns, therefore making inferences more tractable. In other words, this null model fixes, in each randomization, all observed levels of dispersal limitation. Thus, the null model can “factor out” this observed pattern and investigate other processes, but it cannot explicitly address hypotheses regarding dispersal limitation itself. Given the goal of the present work was not to study dispersal limitation, per se, but to detect the potential influence of abiotic or biotic filtering, this null model was chosen. Standardized effect sizes are represented as the observed value minus the mean value of the 999 randomizations divided by the standard deviation of the 999 null values. Thus, high values indicate higher than expected alpha or beta diversity, and low values indicate lower than expected

TABLE 2. Phylogenetic signal in functional traits in five forest plots.

Trait	BCI	LUQ	GTS	SCBI	WAB
Maximum height	0.03	0.06	0.31	0.04	0.07
Leaf area	0.05	0.10	0.43	...	0.13
Seed mass	0.07	0.13	0.52	0.06	0.06
Specific leaf area (SLA)	0.02	0.06	0.12	...	0.17
Wood density	0.07	0.10	0.22	0.03	0.05

Notes: Phylogenetic signal was quantified using the K statistic of Blomberg et al. (2003). Values of one indicate phylogenetic signal similar to that expected from a Brownian motion model of trait evolution. Values greater than one indicate more than expected phylogenetic signal, and values less than one indicate less than expected phylogenetic signal. See Table 1 for site abbreviations. Ellipses indicate missing trait data for the SCBI plot.

alpha or beta diversity. All phylogenetic and trait dispersion and analyses can be conducted in the free software Phylocom (Webb et al. 2008a).

RESULTS

Phylogenetic signal

We measured phylogenetic signal in the functional trait data for the five plots where this data was available. The K statistic of Blomberg et al. (2003) was used to quantify phylogenetic signal. Values of $K < 1$ indicate less phylogenetic signal in the trait data than expected from a Brownian motion model of trait evolution. Values of $K > 1$ indicate more than expected phylogenetic signal. The results of the analyses are presented in Table 2. In sum, all trait data in all forest plots had less phylogenetic signal than expected, given a Brownian motion model of trait evolution.

Phylogenetic alpha and beta dispersion

Phylogenetic and functional alpha and beta dispersion was quantified using pairwise and nearest neighbor metrics. The pairwise alpha (NRI) and beta (SES D'_{pw}) dispersion of each subplot was plotted against one another (Fig. 2) and the nearest neighbor alpha (NTI) and beta (SES D'_{nn}) dispersion of each subplot was plotted against one another (Fig. 3). All NRI and NTI values were multiplied by -1 such that positive values on the x -axis indicated phylogenetic overdispersion within an assemblage and negative values indicated clustering. Positive values on the y -axis indicate higher than expected phylogenetic turnover between subplots, and negative values indicated lower than expected phylogenetic turnover.

The results of the pairwise metrics showed that NRI and SES D'_{pw} are highly correlated indices with the majority of the subplots falling in the upper right and lower left quadrants of the bivariate space (Fig. 2). In other words, subplots were generally phylogenetically overdispersed and phylogenetically dissimilar from their neighboring subplots or phylogenetically underdispersed and phylogenetically similar to their neighboring subplots. The BCI tropical forest was exceptional in that the vast majority of subplots were phylogenetically overdispersed, but were more phylogenetically dissimilar

than expected from their neighboring subplots. The remaining five forests did not have such a signature.

The results of the nearest neighbor alpha and beta metrics were largely uncorrelated (Fig. 3). Similar to the pairwise results, the dispersion was rather consistent across the spatial scales investigated. There were no consistent patterns of alpha dispersion across the forest plots or across spatial scales. The BCI forest plot had higher than expected phylogenetic turnover in the vast majority of the subplots using this metric, whereas the remaining forests had a relatively equal mix of higher and lower than expected phylogenetic turnover.

Functional alpha and beta dispersion

As with the phylogenetic results, the functional alpha and beta dispersion values for focal subplots were plotted against one another. For brevity, we only display the results from the 20×20 m scale, as the results at the large spatial scales were largely consistent with those found at this scale. The pairwise metrics were again correlated with the majority of points falling in the upper right and lower left quadrants (Fig. 4). The results were not consistent across plots or traits, so we highlight some generalities, while referring the reader to the figures for exceptions. Maximum height values tended to be clustered within subplots with little turnover between subplots. Leaf area was also clustered in the BCI, GTS, and Wabikon Lake (WAB) plots, but overdispersed in the Luquillo (LUQ) forest. Seed mass was less consistent across plots with underdispersion in LUQ, WAB, and SCBI, but overdispersed in BCI and GTS. Specific leaf area was clustered locally in BCI, GTS, and WAB, but not in LUQ. Finally, wood density was clustered in BCI and WAB, and overdispersed in SCBI, GTS, and LUQ.

Similar to the nearest neighbor phylogenetic results, the nearest neighbor functional alpha and beta dispersion values were largely uncorrelated (Fig. 5). Again, the results were not consistent across plots or traits, but here we highlight some of the more interesting findings per trait. Maximum height was often overdispersed within forest plots, which is the opposite of the pairwise result. Leaf area, specific leaf area, and wood density were also generally clustered within subplots. Seed mass was overdispersed at BCI, but generally clustered in the other forests. In most cases, the trait turnover was, on

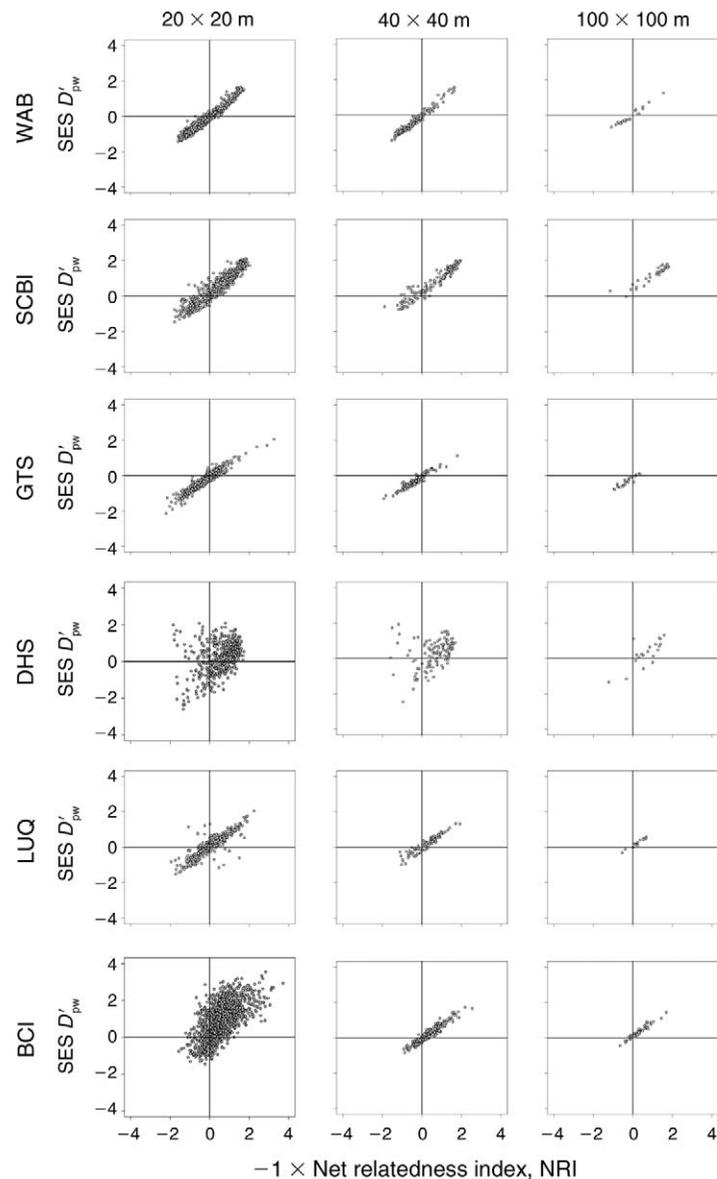


FIG. 2. Following the schematic presented in Fig. 1, here we plot the pairwise phylogenetic dispersion of the focal subplot on the x -axis vs. the pairwise phylogenetic dissimilarity between a focal subplot and its eight neighboring subplots on the y -axis (standardized effect size of pairwise dissimilarity, $SES D'_{pw}$). Higher values on the x -axis and y -axis indicate higher than expected alpha dispersion and beta dispersion, respectively. Lower values on the x -axis and y -axis indicate lower than expected alpha dispersion and beta dispersion, respectively. Results from all three spatial scales are shown. Site abbreviations are: BCI, Barro Colorado Island, Panama; LUQ, Luquillo, Puerto Rico; DHS, Dinghushan, China; GTS, Gutianshan, China; SCBI, Smithsonian Conservation Biology Institute, Virginia, USA; and WAB, Wabikon Lake, Wisconsin, USA.

average, higher than expected between neighboring subplots.

DISCUSSION

The present study aimed to relate phylogenetic alpha and beta dispersion, and functional alpha and beta dispersion across a series of forest plots in order to infer mechanisms of community assembly in six forest dynamics plots. Specifically, we quantified the phylogenetic and trait dissimilarity of individuals within forest subplots and compared that value to the phylogenetic and trait dissimilarity of all individuals between subplots using the framework presented in Fig. 1. This was done using pairwise metrics of alpha and beta dispersion, as well as nearest neighbor metrics of alpha and beta dispersion.

Phylogenetic and functional alpha and beta dispersion: pairwise metrics

The pairwise values were highly correlated with high phylogenetic turnover between subplots being related to high dispersion within subplots and low phylogenetic turnover and low within plot dispersion being related. This axis could be envisioned in terms of a stress gradient assembly mechanism where low local dispersion and low turnover occurs in relatively harsh and spatially contiguous habitats, and high dispersion and high turnover occurs in more benign and potentially patchy habitats (Helmus and Ives 2012). The relative proportion of subplots falling on either end of this spectrum was generally equivalent. The exception to this was the BCI forest plot, where more subplots were phylogenetically overdispersed with high phylogenetic

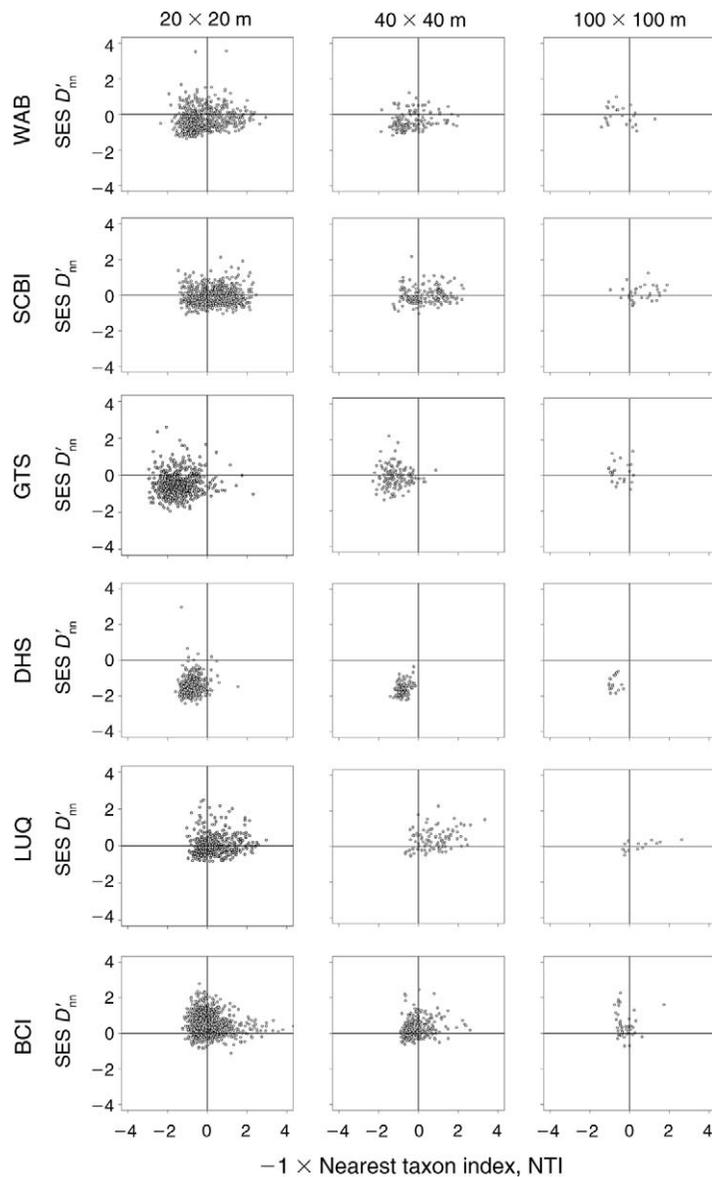


FIG. 3. Following the schematic presented in Fig. 1, here we plot the nearest neighbor phylogenetic dispersion of the focal subplot on the x -axis vs. the nearest neighbor phylogenetic dissimilarity between a focal subplot and its eight neighboring subplots on the y -axis (standardized effect size of the nearest neighbor dissimilarity, $SES D'_{nn}$). Higher values on the x -axis and y -axis indicate higher than expected alpha dispersion and beta dispersion, respectively. Lower values on the x -axis and y -axis indicate lower than expected alpha dispersion and beta dispersion, respectively. Results from all three spatial scales are shown. See Fig. 2 for site abbreviations.

dissimilarity between a subplot and its neighboring subplots. We should note that the BCI results may, in some cases, seem divergent from those previously reported from this forest (e.g., Kress et al. 2009), but we remind the reader that the present manuscript weighted all analyses by abundance, whereas previous work used presence-absence weighting. This could be taken as evidence that negative biotic interactions and among-subplot habitat heterogeneity are important for understanding the phylogenetic diversity at the scales studied in the BCI forest plot. We do caution that the present work did not directly measure abiotic filtering using environmental data. This is a weakness of the approach and could not be strengthened due to a lack of consistent and meaningful environmental data sets from all plots studied. Ideally, the inferences made here and in

the rest of the discussion will be more strongly substantiated in the future when consistent and informative environmental data are available for these forests and others.

The pairwise trait metrics were similarly correlated with many traits being underdispersed locally in most plots indicating nonrandom processes structuring local communities in these forests. This result is similar to previous work in tropical forests that found strongly deterministic trait dispersion (Swenson and Enquist 2007, Kraft et al. 2008, Swenson and Enquist 2009). For example, maximum height, specific leaf area, and wood density were often clustered in local communities suggesting that abiotic filtering may increase the similarity of traits in these communities. The beta dispersion results showed a large number of subplots

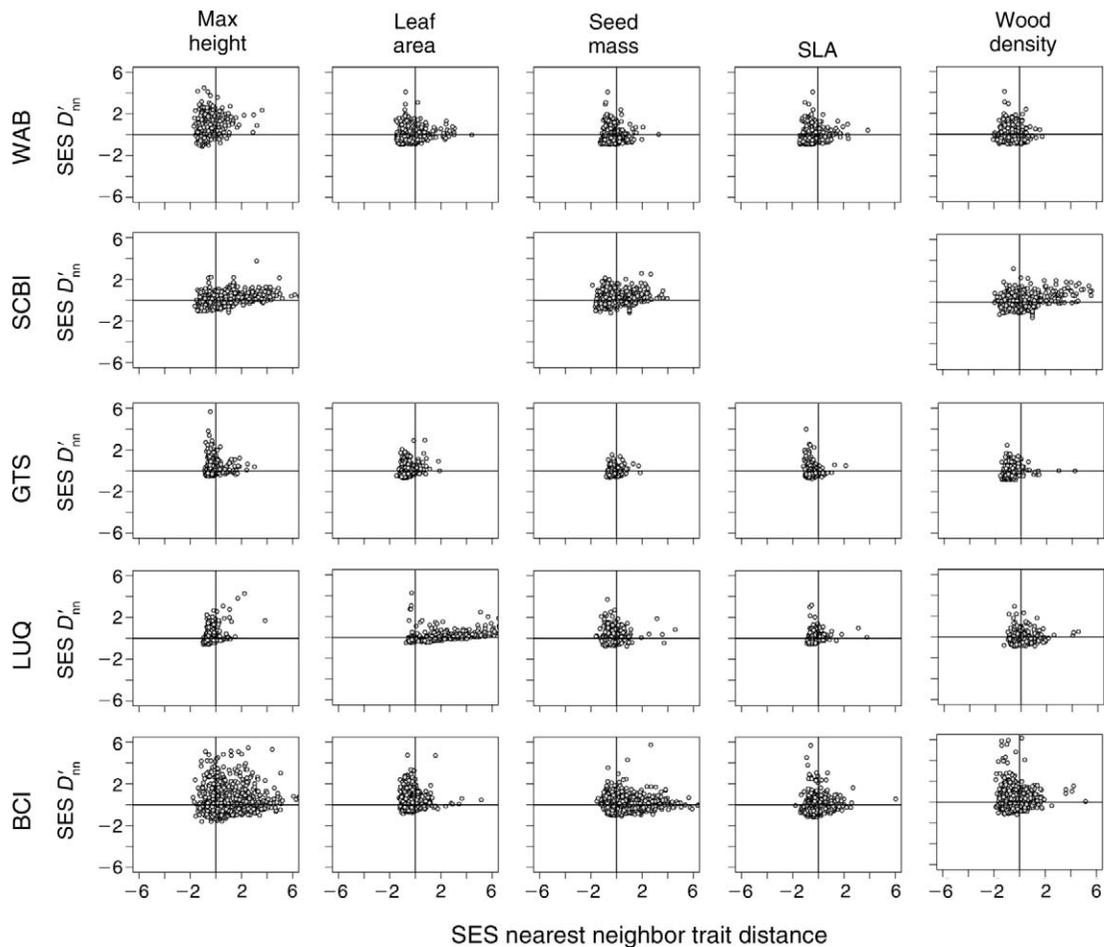


FIG. 4. Following the schematic presented in Fig. 1, here we plot the pairwise functional dispersion of the focal subplot on the x -axis vs. the pairwise functional dissimilarity between a focal subplot and its eight neighboring subplots on the y -axis. Higher values on the x -axis and y -axis indicate higher than expected alpha dispersion and beta dispersion, respectively. Lower values on the x -axis and y -axis indicate lower than expected alpha dispersion and beta dispersion, respectively. Only results from 20×20 m are shown. See Fig. 2 for site abbreviations; SLA, specific leaf area. The two missing panels indicate missing trait data for the SCBI plot.

having little functional differentiation from one subplot to the next. For example, for the majority of traits, except seed mass, the BCI forest subplots had lower than expected trait turnover between subplots, suggesting that, although species turnover from subplot to subplot occurs, there is relatively little functional turnover. Such a pattern could result from functionally deterministic community assembly with dispersal limitation. This would be particularly expected given the relatively homogeneous topography in the BCI forest plot. A similar pattern was also uncovered in the Wabikon Lake forest plot in Wisconsin, USA, where most traits, except leaf area, had lower than expected trait turnover among subplots. Thus, the BCI result cannot be explained as a tropical phenomenon. That said, it is important to recognize that these are null modeling results and that the raw turnover may be quite high in the tropics, but not higher than that expected given the observed

elevated patterns of species beta diversity and the trait pool (see Kraft et al. 2011).

It is important to note that the phylogenetic results showed local overdispersion and higher than expected phylogenetic turnover, while the majority of the trait results were the opposite. This was particularly true for the BCI forest plot and to a lesser extent the temperate plots. This suggests that there is likely substantial trait convergence between the species in the BCI forest plot community in particular, which is substantiated by the phylogenetic signal analyses we performed (Table 2). Biologically, this suggests that there is strong abiotic filtering of traits within and across subplots of this spatial scale in the BCI forest, but there is a substantial turnover of lineages from subplot to subplot that generally are functional replacements of one another. Thus, for the BCI forest, there is trait convergence, dispersal limitation of lineages, and deterministic abiotic filtering of most traits. In the other plots, there also

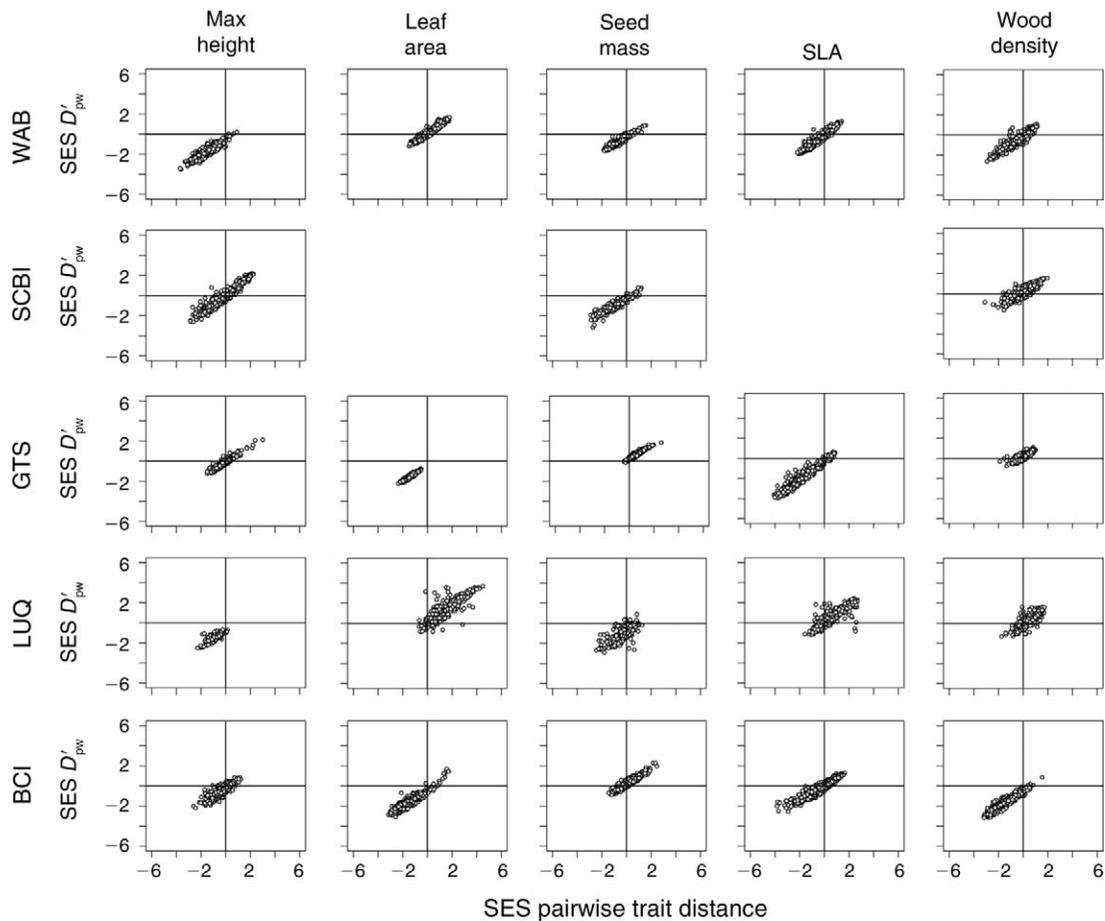


FIG. 5. Following the schematic presented in Fig. 1, here we plot the nearest neighbor functional dispersion of the focal subplot on the x -axis vs. the nearest neighbor functional dissimilarity between a focal subplot and its eight neighboring subplots on the y -axis. Higher values on the x -axis and y -axis indicate higher than expected alpha dispersion and beta dispersion, respectively. Lower values on the x -axis and y -axis indicate lower than expected alpha dispersion and beta dispersion, respectively. Only results from 20×20 m are shown. The two missing panels indicate missing trait data for the SCBI plot.

appears to be similar trait convergence, some dispersal limitation of lineages and again a deterministic abiotic filtering of most traits. As previously noted, this study did not analyze any defense traits of the species in these plots. Previous work has shown there to be varying degrees of phylogenetic signal in plant defense (e.g., Becerra 1997, 2007, Gilbert and Webb 2007, Kursar et al. 2009, Lamarre et al. 2012), and the strength of the signal may depend on the phylogenetic breadth of the taxa being studied; thus, it is not entirely clear whether results from defense trait analyses would mirror our phylogenetic results.

Aside from the biological implications of the mismatch between phylogenetic and trait results is the practical implication that measures of phylogenetic alpha and beta diversity or dispersion are not always strong predictors of functional patterns. In other words, studies of phylogenetic alpha and beta diversity alone may be poor predictors of the actual functional alpha and beta diversity (Swenson 2011a, Swenson et al. 2012).

Thus, as many others have stressed, phylogenetic relatedness is not always a good predictor of species similarity, and assembly studies that only use phylogenetic information may be misleading.

Phylogenetic and functional alpha and beta dispersion: nearest neighbor metrics

The nearest neighbor alpha and beta dispersion metrics were generally uncorrelated with one another using both phylogenetic and trait information. In all forest plots except BCI, the phylogenetic nearest neighbor turnover was lower than that expected given the null model. This result largely contrasts with the results of the pairwise metric. This is due to large shifts in the abundance distribution from subplot to subplot, driving a large pairwise dissimilarity between subplots, but not a large nearest neighbor turnover. In other words, species A could have 50 individuals and species B could have 4 individuals in subplot 1, while in subplot 2, the each have 2 and 75 individuals, respectively. Such a

pattern would result in large pairwise dissimilarity, but no nearest neighbor dissimilarity. The phylogenetic nearest neighbor alpha dispersion results ranged from strongly overdispersed to strongly clustered depending on the forest plot, and there was no relationship with latitude. Thus, the one general finding was that nearest neighbor turnover was typically lower than expected from subplot to subplot in all forests except BCI.

The nearest neighbor alpha dispersion for most traits was lower than expected for many traits, while maximum height, leaf area, seed mass, and wood density were occasionally more diverse than expected in many of the plots (Fig. 5). This indicates abiotic filtering of some traits in some forests, and a role for biotic interactions with respect to other traits. In other words, there were no clearly defined patterns that emerged from the nearest neighbor analyses of trait alpha dispersion. The beta trait dispersion was also inconsistent across traits and plots, making general inferences difficult. It appears that most nearest neighbor trait dispersion results largely hovered around zero, or randomness. Thus, while local trait dispersion was constrained within a subplot, patterns of nearest neighbor similarity between subplots cannot be easily explained and random turnover cannot be rejected.

CONCLUSIONS

The present study analyzed the relationship between phylogenetic and functional alpha and beta dispersion in a series of six forest plots located in the tropics and the temperate zone. Three main conclusions may be drawn from this study. First, the alpha and beta pairwise trait dispersion in most forests was clustered. This pattern is expected from strong abiotic filtering within and between subplots, highlighting a dominant role for this process at the scale of this study. A second conclusion is that the nearest neighbor alpha and beta dispersion of traits and phylogeny showed very little relationship with one another and was inconsistent across plots and traits. Thus, no strong inferences supporting the importance of limiting similarity and negative biotic interactions can be made from the present results. Instead, abiotic filtering appears to be the dominant mechanism operating in these forests, but again we stress that this inference remains to be substantiated with environmental data from the plots. Third, the phylogenetic results often were not indicators of the trait results. In particular, while the pairwise turnover of traits between subplots was often lower than expected, the phylogenetic turnover was often higher than expected. Taken together, this suggests that traits are filtered into subplots (alpha clustering) that occur within large homogeneous habitats, generating little functional turnover (beta clustering) and a lack of phylogenetic signal in trait data (Table 2). The question now becomes whether patterns of phylogenetic beta diversity are useful to the ecologist. Indeed, the lack of phylogenetic signal (*sensu* Blomberg et al. 2003) is concerning for those interested in making inferences

from a phylogenetic measure alone. That said, measures of phylogenetic beta diversity are likely still to be useful, particularly at larger spatial scales or in clade-specific investigations. The increase in spatial scale will likely increase the taxonomic scale of the analysis, and therefore, likely increase the degree of phylogenetic signal allowing for perhaps stronger inferences (Fine and Kembel 2011). Investigations into specific clades could potentially compare patterns of phylogenetic and functional beta diversity. For example, the convergent evolution of communities should lead to low functional beta diversity and high phylogenetic beta diversity, whereas dispersal-based assembly of phylogenetically conserved niches into communities should lead to a pattern of low phylogenetic and functional beta diversity. Thus, future analyses of phylogenetic beta diversity would benefit from a clade-centric approach and/or expanding the spatial scale of the study, while substantial caution should be taken particularly when making inferences regarding local-scale assemblages.

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