JSE Journal of Systematics and Evolution

Journal of Systematics and Evolution 51 (1): 71–85 (2013) doi: 10.1111/j.1759-6831.2012.00220.x

Research Article

Phylogenetic beta diversity in tropical forests: Implications for the roles of geographical and environmental distance

[1,3]Jin-Long ZHANG [2]Nathan G. SWENSON [4]Sheng-Bin CHEN [1]Xiao-Juan LIU
[5]Zong-Shan LI [1]Ji-Hong HUANG [1]Xiang-Cheng MI [1]Ke-Ping MA*

[1](*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences,* Beijing 100093, China)
[2](*Department of Plant Biology, Michigan State University, East Lansing,* Michigan 48824, USA)
[3](*Graduate University of Chinese Academy of Sciences,* Beijing 100049, China)
[4](*Nanjing Institute of Environmental Sciences, Ministry of Environmental Protection,* Nanjing 210042, China)
[5](*State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Science, Chinese Academy of Sciences,* Beijing 100085, China)

Abstract Various mechanistic theories of community assembly have been proposed ranging from niche-based theory to neutral theory. Analyses of beta diversity in a phylogenetic context could provide an excellent opportunity for testing many of these hypotheses. We analyzed the patterns of phylogenetic beta diversity in tropical tree communities in Panama to test several community assembly hypotheses. In particular, the degree to which the phylogenetic dissimilarity between communities can be explained by geographical or environmental distance can yield support for stochastic or deterministic assembly processes, respectively. Therefore, we examined: (i) the existence of distance decay of phylogenetic similarity among communities and its degree of departure from that expected under a null model; and (ii) the relative importance of geographical versus environmental distance in predicting the phylogenetic dissimilarity of communities. We found evidence that the similarity in the phylogenetic composition of communities decayed with geographical distance and environmental gradients. Null model evidence showed that beta diversity in the study system was phylogenetically non-random. Our results highlighted not only the role of local ecological mechanisms, including environmental filtering and competitive exclusion, but also biogeographical processes such as speciation, dispersal limitation, and niche evolution in structuring phylogenetic turnover. These results also highlight the importance of niche conservatism in structuring species diversity patterns.
Key words community, distance decay, environmental filtering, neotropical forests, niche conservatism, null model.

Understanding the mechanisms determining species distribution patterns is a central issue in basic and applied ecology. A large number of studies have focused on the species richness within communities (i.e. alpha diversity) and the dissimilarity between communities (i.e. beta diversity) (Condit et al., 2002; Ruokolainen & Tuomisto, 2002; Webb et al., 2002; Tuomisto et al., 2003; Buckley & Jetz, 2008; La Sorte et al., 2008; Qian, 2009; Thrush et al., 2010; Anderson et al., 2011). The debate regarding whether beta diversity is structured relatively more by stochastic or deterministic processes has received a great deal of attention. The relative contribution of stochastic versus deterministic processes to patterns of beta diversity is often estimated by quantifying the amount of variation in community dissimilarity that is predicted by spatial distance, environmental distance, and their interaction. Variation explained by spatial distance is generally attributed to stochastic assembly and dispersal limitation, whereas variance explained by environmental distance is attributed to deterministic niche-based processes.

Despite the central role measures of species beta diversity have played in the debate regarding stochastic versus deterministic community assembly, the approach suffers from one critical problem: that the phylogenetic history and functional traits were not taken into account in many beta diversity studies. Species are, of course, not functionally identical or evolutionarily independent and this can lead to faulty ecological inferences from measures of species beta diversity (Swenson, 2011; Swenson et al., 2011). Thus, community ecologists are increasingly considering functional and phylogenetic measures of beta diversity in order to provide stronger inferences regarding community assembly (Bryant et al., 2008; Graham & Fine, 2008; Ricotta & Burrascano, 2008;

Received: 10 April 2012 Accepted: 22 June 2012
* Author for correspondence. E-mail: kpma@ibcas.ac.cn. Tel.: 86-10-62836223. Fax: 86-10-82599518.

Swenson, 2011; Swenson et al., 2011). The present paper focuses on patterns of phylogenetic beta diversity on a regional scale and the amount of variation in phylogenetic beta diversity explained by spatial and/or environmental distance. Previous phylogenetic beta diversity research has been carried out on regional scales. For example, Bryant et al. (2008) quantified the distance decay in phylogenetic similarity in microbial and plant assemblages along an altitudinal gradient, Swenson (2011) examined the phylogenetic dissimilarity among Indian tree assemblages, and Fine & Kembel (2011) examined the phylogenetic beta diversity in Amazonian tree assemblages. Although some of this research has examined the environmental correlates of phylogenetic beta diversity (Swenson, 2011), none has attempted to partition variance between spatial and environmental components to infer the relative influence of stochastic versus deterministic assembly processes.

Empirical patterns of phylogenetic beta diversity coupled with variance partitioning analyses can provide insights into community assembly beyond what can be gleaned from traditional analyses of species beta diversity. In particular, it is reasonable to expect that the amount of variance in community dissimilarity explained by the geographical distance will be greater in comparison with the cases of taking phylogenetic relationship into account. This could be explained as, a species may be dispersal limited, but a clade may be less dispersal limited. Inferences from phylogenetic beta diversity are further strengthened if the level of phylogenetic signal in traits or niches is quantified (Swenson et al., 2011).

Here, we aim to infer the relative degree to which stochastic or deterministic processes dictate the assembly of tropical tree communities in Panama. Specifically, we integrate two independent measures of phylogenetic beta diversity, null modeling analyses and variance partitioning, to ask the following questions: (i) is the nonrandom pattern of phylogenetic turnover between forest plots suggesting a role of deterministic processes in community assembly at regional scale? (ii) is geographical or environmental distance more strongly linked to the observed patterns of species and phylogenetic beta diversity? and (iii) are null models commonly used in community phylogenetic alpha diversity analysis suitable for phylogenetic beta diversity analysis and how similar are the results from different null models?

1 Material and methods

1.1 Plot descriptions

This study analyzed 100 plots located in central Panama, including the 50 1-ha quadrats from the Barro Colorado Island (BCI) forest dynamics plot (Hubbell et al., 1999) and 50 satellite forest plots (Condit et al., 2002) (Fig. 1). Plots with an area larger than 1 ha, which included BCI 50-ha forest dynamics plots, were divided into multiple 1-ha plots and treated separately. The forest plots are scattered in the Panama Canal Watershed with the lowest elevation 10 m and the highest elevation 830 m above sea level. The forests are in a fragmented landscape, divided by the canal, railways, and agricultural lands (Chust et al., 2006). Annual mean precipitation in the plots ranges from 1887 mm to 4002 mm with the mean of 2588.7 mm. All trees with a diameter above 10 cm at breast height were tagged and identified (Hubbell et al., 1999; Condit et al., 2002). Five species that were unidentified to family level were removed from the analysis. Species not identified to genus level were treated as a separate genus in its family. The community matrix included 792 taxa (species, subspecies and varieties), 318 genera in 68 families (APGIII, Chase et al., 2009). The Fabaceae, Sapotaceae, Moraceae, Rubiaceae, Lauraceae, Malvaceae, Myrtaceae, Annonaceae, Euphorbiaceae, and Melastomataceae are the 10 top families in species richness. The dominant genera

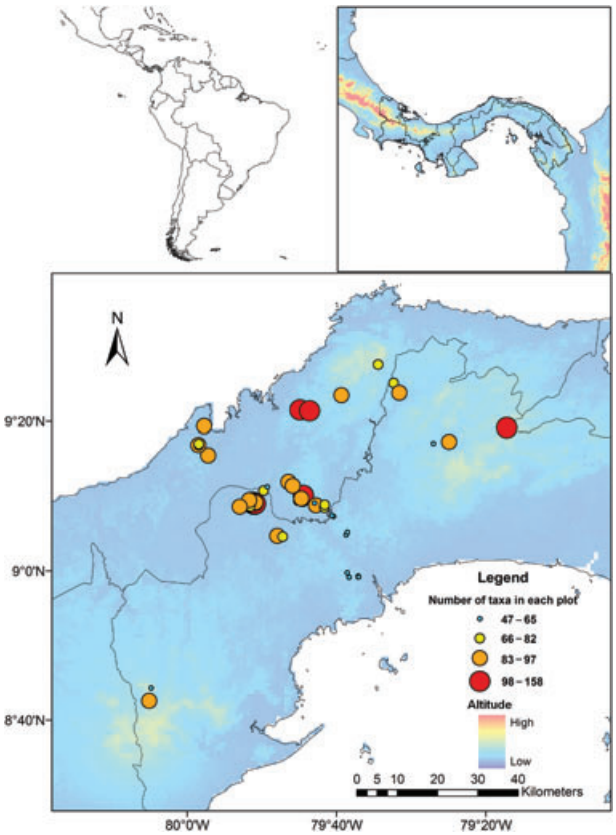

Fig. 1. Locations of the plots scattered in Panama, including 50 ha of Barro Colorado Island divided into 50 1-ha satellite plots.

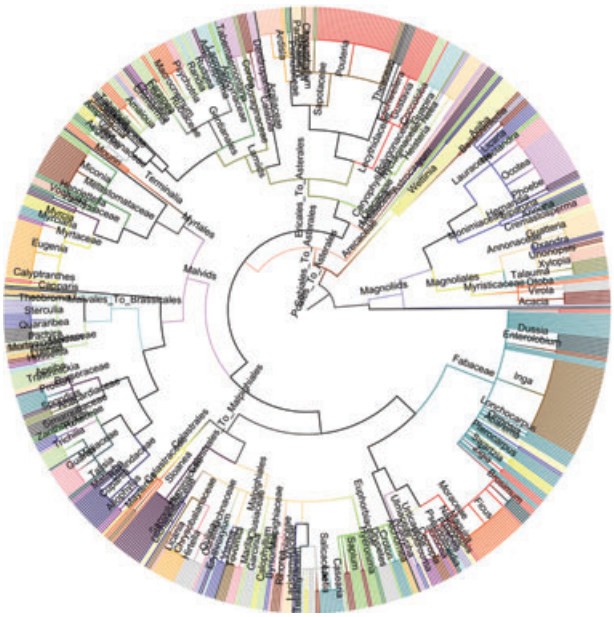

Fig. 2. Phylogenetic tree reconstructed using Phylomatic to APGIII, including 792 taxa, 319 genera, in 70 families.

include *Inga* Mill., *Pouteria* Aubl., *Eugenia* L., *Ficus* L., *Ocotea* Aubl., *Miconia* Ruiz & Pav., *Guarea* L., *Sloanea* L., *Ardisia* Sw., *Casearia* Jacq., *Licania* Aubl., *Eschweilera* Mart. ex DC., *Cupania* L., and *Dussia* Krug & Urb. ex Taub.

1.2 Phylogenetic tree reconstruction

A phylogenetic tree (Fig. 2) was reconstructed using the online eco-informatics software Phylomatic (Webb & Donoghue, 2005) that uses the APGIII (Chase et al., 2009) topology as the backbone tree onto which taxonomic relationships are grafted. Branch lengths were assigned to the tree using the BLADJ algorithm in Phylocom 4.1 (Webb et al., 2008) and estimates of angiosperm node ages taken from Wikström et al. (2001). This approach suffers from the generation of a phylogenetic tree containing multiple soft polytomies using crudely assigned branch lengths. This likely reduces the statistical power of the analyses (Kress et al., 2009; Swenson, 2009), but is the most suitable approach for the present study system where many trees species have no DNA sequence information available.

1.3 Statistical analysis

1.3.1 Measures of species and phylogenetic beta diversity The statistical analyses and data processing were mainly carried out in R statistical software 2.12.0 (R-Core-Team, 2010) (see Doc. S1 for R codes). Various measures of phylogenetic beta diversity have been proposed in recent years, including the mean phylogenetic dissimilarity (D_{pw}) between the individuals or species in two communities (Rao, 1982; Webb et al., 2008), the mean nearest taxon distance (D_{nn}) between the individuals or species in two communities (Ricotta & Burrascano, 2008; Webb et al., 2008), and the amount of phylogenetic branch length shared between species in two communities (PhyloSor, Bryant et al., 2008; Graham & Fine, 2008; UniFrac, Lozupone et al., 2006). Some of these metrics are mathematically identical to existing functional trait beta diversity metrics (e.g. Rao, 1982; Ricotta & Burrascano, 2008; Swenson, 2011).

We used the following phylogenetic beta diversity metrics, using both abundance weighted and presence–absence data: D_{pw}, D_{nn} and their standard effective size (Webb et al., 2008). Previous work has shown that the D_{pw} metric is largely identical to Rao's D, which is often used in published reports on functional diversity (Swenson, 2011), and that the D_{nn} metric is highly correlated with PhyloSor, UniFrac, and Phylogenetic Community Dissimilarity (Ives & Helmus, 2010). That said, D_{pw} and D_{nn} are generally uncorrelated. Therefore, using D_{pw} and D_{nn} allows for coverage of the two main classes of phylogenetic dissimilarity metrics while avoiding the redundancy of calculating other nearly identical metrics (Swenson, 2011).

1.3.2 Null model comparisons Null models have been used to evaluate the importance of certain species assembly mechanisms in community phylogenetics. These processes often include biotic interactions and abiotic filtering (Webb, 2000; Kembel & Hubbell, 2006; Swenson et al., 2006, 2007). For example, the net relatedness index (*NRI*) and the nearest taxon index (*NTI*), which are the standardized effect size quantified from null model output, tells us about whether co-occurring species are more or less phylogenetically related than random. This approach can be extended to analyses of phylogenetic beta diversity where one can ask whether the phylogenetic relatedness between species in two plots is any different from that randomly expected. Specifically, a standardized effect size (*S.E.S.*) of the phylogenetic beta diversity metrics, D_{pw} and D_{nn}, can be quantified as follows:

$$S.E.S.\ D_{pw} = -1 \times \frac{D_{pw_{observed}} - D_{pw_{random}}}{sd(D_{pw_{random}})} \quad (1)$$

$$S.E.S.\ D_{nn} = -1 \times \frac{D_{nn_{observed}} - D_{nn_{random}}}{sd(D_{nn_{random}})} \quad (2)$$

S.E.S. D_{pw} and *S.E.S.* D_{nn} are the standard effective size of D_{pw} and D_{nn}, respectively, where negative values indicate higher than expected phylogenetic dissimilarity, and positive values indicate lower than

expected dissimilarity. For each plot, the random distribution was generated by four algorithms of randomization with each run 999 times, as shown below.

Null model 0. This null model shuffles the names of species across the tips of the phylogenetic tree. This algorithm randomized the relatedness of species to one another, but it maintained the observed community data matrix. Therefore, species occupancy rates, abundances, and spatial distributions were fixed in each randomization. This null model also fixes the observed level of species beta diversity and has the advantage of fixing any observed levels of dispersal limitation in space while breaking up any signal in the phylogenetic distribution of dispersal limitation.

Null model 1. This null model randomly generates communities by sampling the observed number of species in a community from the species pool. This null model fixes the observed community alpha diversities and phylogenetic relatedness between species, but not the occupancy rates, spatial distributions of species, or the observed species beta diversity.

Null model 2. This null model is largely identical in concept to null model 1 except for the pool of species from which the random communities are assembled. In this null model, the random communities are drawn from the list of species in the phylogeny, whereas in null model 1 species are drawn from the list of species in the community data matrix. Thus, these nulls would generally be expected to produce similar results unless the number of species in the phylogeny was much larger than the number of species in the community data matrix. Note the reverse could not occur as all species in the community data matrix must be represented in the phylogeny for the analyses to be carried out.

Null model 3. This last null model is often referred to as an "independent swap", in which the observed species richness of communities and occupancy rates of species are fixed in the randomization (Gotelli, 2000). During the randomizations, species richness per sample and the frequency of each species across the samples were kept as constant, while the co-occurrences in samples were randomized. Only the co-occurrence for each species was randomized for 1000 times. This null model does not necessarily maintain the observed levels of dispersal limitation, spatial distributions, or species beta diversity.

We calculated the *NRI* and *NTI* for each plot (Fig. S1), based on the null models listed above. To test the effect of null models on the phylogenetic structure, the correlations between the *NRI* and *NTI* indices were also computed (Fig. S2).

In order to quantify the relationships between the output of different null models, we calculated Pearson's correlation of *NRI* and *NTI* for each plot and *S.E.S.* D_{pw} and *S.E.S.* D_{nn} between plots, generated by the four null models using the R package "hydroTSM" (Zambrano-Bigiarini, 2012). A pairwise *t*-test was used to test whether any differences could be found among the means of *S.E.S.* D_{pw} or *S.E.S.* D_{nn}, calculated using different null models.

1.3.3 Quantifying the relative importance of explanatory variables Geographical distance between each pair of plots was calculated using GPS coordinates taken from each plot and the R package "fossil" (Vavrek, 2011). Environmental distances were estimated by calculating the Euclidean distances between plots based on their precipitation and elevation. The relative importance of roles played by geographical distance and environmental distance was assessed using the statistical methods described below.

We used Mantel's tests to quantify the correlation between the matrix of the community phylogenetic dissimilarity, geographical distance, and environmental distance. Each Mantel's test generated an *r* value similar to Pearson's correlation index, which represents the correlation between the distance matrices. Permutation tests were applied to assess the significance of the correlation by randomizing the distance matrix 999 times.

In order to assess the performance of null models, we calculated a Mantel correlogram to examine the relationship between phylogenetic distance and geographical distances. A Mantel correlogram computes a Mantel's *r* for each geographic distance class between phylogenetic distance and geographical distance. This method allows for the examination of the correlation between two distance matrices in detail. Number of classes of geographical distance in Mantel correlograms was defined according to Sturges' rule. A Mantel's *r* was also calculated between phylogenetic distance generated by null models and the species dissimilarity. For abundance weighted metrics, we used Bray-Curtis dissimilarity, and Jaccard's dissimilarity for presence–absence weighted metrics.

The variances in D_{pw} and D_{nn} were partitioned using multiple regression on distance matrices (MRM) (Lichstein, 2007). Multiple regression on distance matrices is based on Mantel's test, and thus could be used to determine the explanatory power of independent distance matrices. The metrics were regressed on geographical distances and environmental distances (Ruokolainen & Tuomisto, 2002; Tuomisto et al., 2003). Variance partitioning allowed us to examine the contribution of independent effects and joint effects of the factors (Qian & Ricklefs, 2012). For D_{pw} and D_{nn}, we converted the community dissimilarity matrices into pairwise lists. We combined the distances of

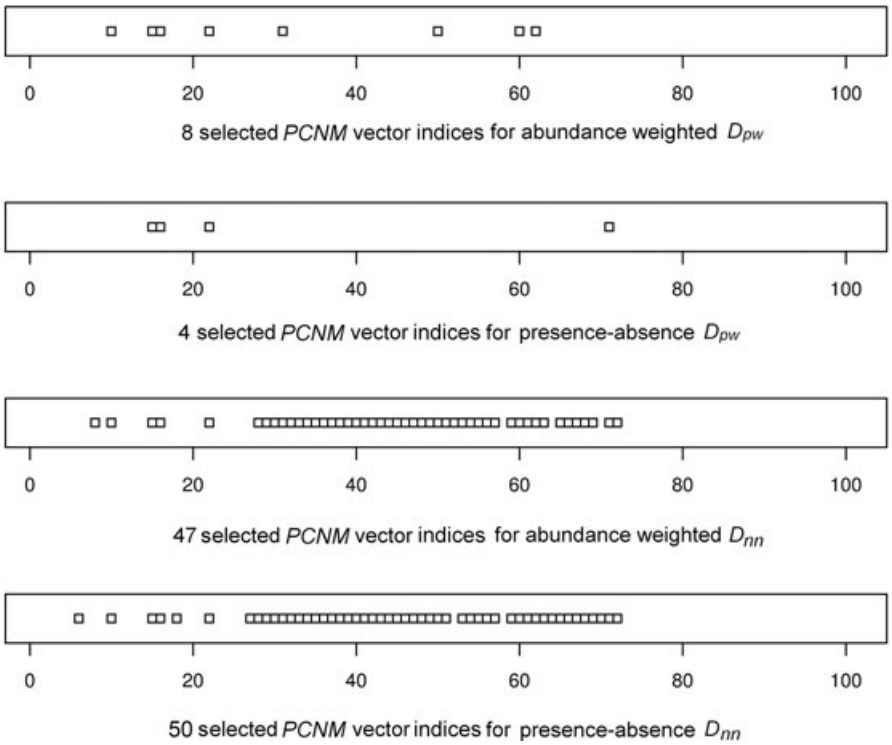

Fig. 3. Selected principal coordinates of neighbor matrices (*PCNM*) eigenvectors using forward selection.

precipitation and elevation as a representative matrix of environmental heterogeneity and subsequently partitioned the variance. Although some have suggested that MRM-like methods would greatly underestimate the variation explained by the variables (Legendre et al., 2008), this partitioning method has the benefit of being able to indicate the relative importance of the environmental and spatial factors. The MRM analyses were carried out using the R package "ecodist" (Goslee & Urban, 2007) and "vegan" (Oksanen et al., 2012.)

The function "adonis" in the R package "vegan" was also used to partition the sum of squares of the D_{pw} and D_{nn} distance matrices. This method is analogous to MANOVA (Anderson, 2001; McArdle & Anderson, 2001) and redundancy analysis (Legendre & Anderson, 1999). In order to understand the relative power of spatial structure in explaining the phylogenetic dissimilarity, principal coordinates of neighbor matrices (*PCNM*) was applied to simulate the spatial relationship between each pair of plots (Borcard & Legendre, 2002; Legendre, 2008; Legendre et al., 2009) using R package "vegan" (Oksanen et al., 2012). We obtained 99 eigenvectors representing the spatial relationship of the plots. Only the factors significantly correlated with D_{pw} and D_{nn} were selected (Fig. 3) using forward selection as implemented in R package "packfor" (Dray, 2011). Before forward selection, the phylogenetic distances matrices for D_{pw} and D_{nn} were transformed by principle coordinate analysis (pcoorda) in R package "ape" (Paradis et al., 2004). These factors with environmental factors (precipitation, elevation) were further used as explanatory factors.

2 Results

2.1 Phylogenetic signal, beta diversity, space, and environment

The inferences in this study stem from an assumption that species' niches have phylogenetic signal in our study system. This was tested using drought tolerance data previously published (Engelbrecht et al., 2007) (see Doc. S2). The results show that there is indeed phylogenetic signal (Blomberg's $K = 0.5659$, $P < 0.05$) (Blomberg & Garland, 2002; Blomberg et al., 2003) in this key trait, suggesting that inferences from phylogenetic distances are tractable.

The phylogenetic dissimilarity of the tree communities studied was significantly correlated with geographic and environmental distance using the D_{pw} and D_{nn} metrics weighted by abundance or presence–absence data (Table S1). For example, the abundance weighted D_{pw} values were strongly correlated with geographical distance (Mantel's $r = 0.291$, $P < 0.01$), the

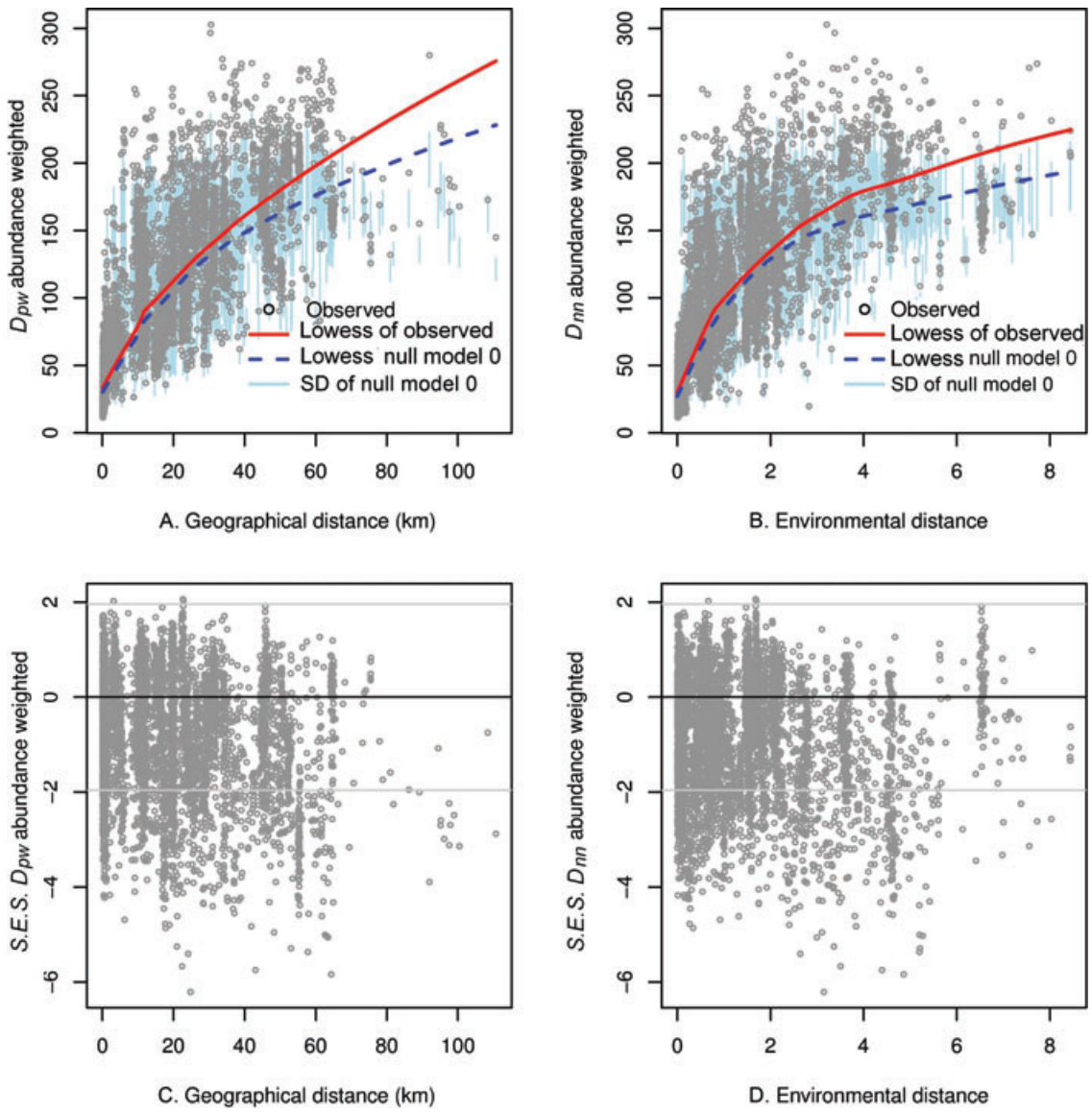

Fig. 4. The *S.E.S.* D_{pw} and *S.E.S.* D_{nn} (standard effective size for mean pairwise phylogenetic distance/mean nearest taxon distance between each pair of plots) generated using null model 0. Null model 0 shuffled the tips of a phylogeny and maintained species similarity across plots, thus producing a distance increasing pattern. Red lines are the lowess fitting for observed values; dotted blue lines are the lowess fitting for the randomized values, with light blue bars indicating the standard deviation of the null distribution.

change of elevation (Mantel's $r = 0.291$, $P < 0.01$), and change of precipitation (Mantel's $r = 0.182$, $P < 0.01$).

We carried out null model analyses to determine whether the observed patterns of phylogenetic dissimilarity were higher or lower than expected given the observed data and the species pool. A total of four different null models were used (Figs. S2, S3). The results of the null model analyses show that phylogenetic dissimilarity was largely non-random with respect to the underlying environmental gradient (Figs. 4, 5, S4–S17).

Geographical distance and environmental distance were both correlated with the observed patterns of phylogenetic dissimilarity, but we were primarily interested in the relative contribution of each to phylogenetic dissimilarity. Only a small proportion of the variance in abundance weighted D_{pw} and D_{nn} could be explained by geographical distance together with environmental distance ($R^2 = 0.148$, $P < 0.01$). The explanatory power of environmental distance is greater ($R^2 = 0.148$, $P < 0.01$) than that of geographical distance ($R^2 = 0.107$, $P < 0.01$) if we take

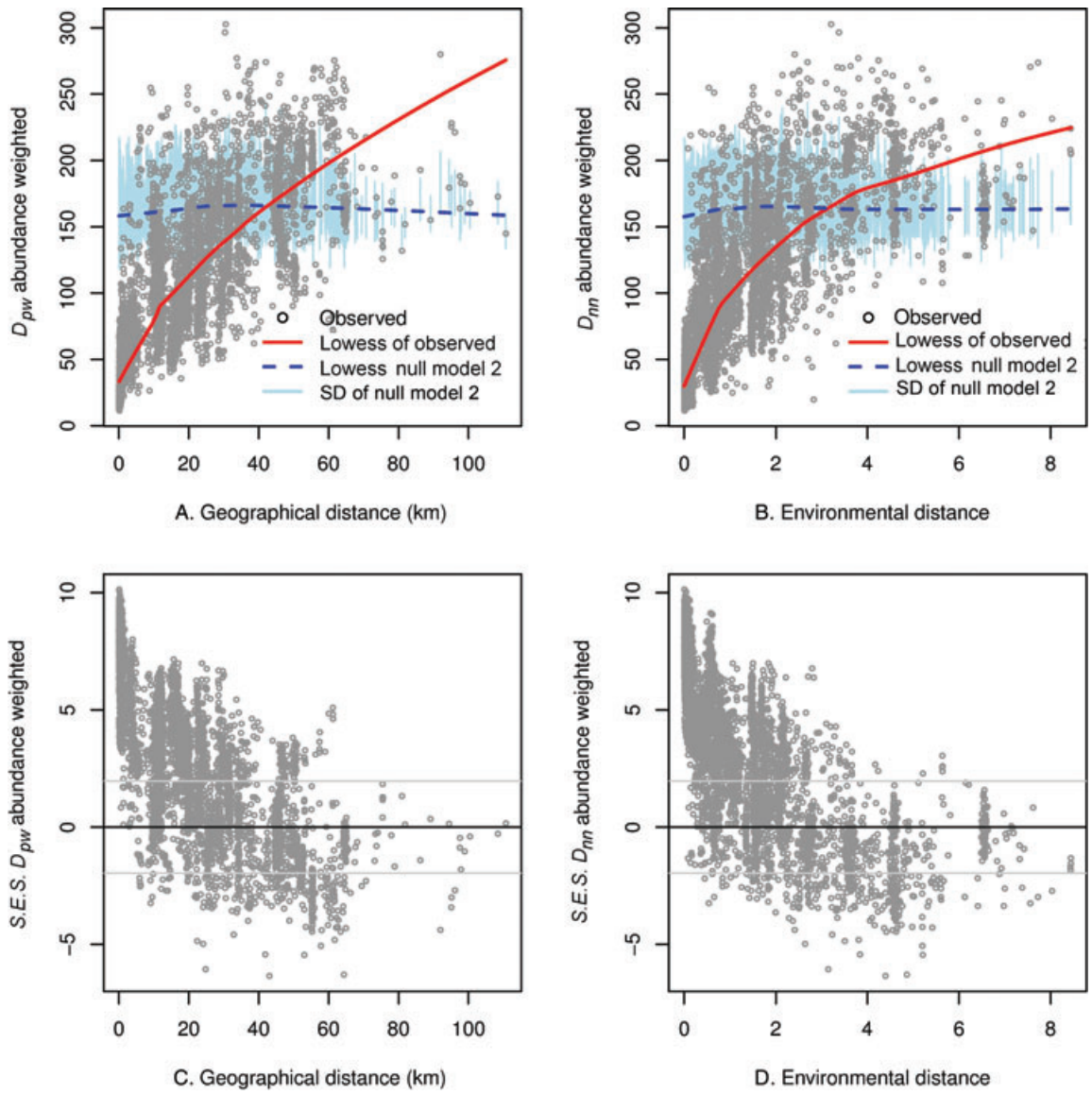

Fig. 5. The *S.E.S.* D_{pw} and *S.E.S.* D_{nn} (standard effective size for mean pairwise phylogenetic distance/mean nearest taxon distance between each pair of plots) results generated using null model 2. Null model 2 randomized the species list extracted from the community, thus a non-spatial pattern of phylogenetic decreasing could be observed from this null model. Red lines are the lowess fitting for observed values; dotted blue lines are the lowess fitting for the randomized values, with light blue bars indicating the standard deviation of the null distribution.

presence–absence D_{pw} as an example (Tables S2, S3). Variance partitioning highlighted the roles of environmental difference, if taking D_{pw} as an example (Table 1). In contrast, the dominating factor for D_{nn} is geographical distance (Table 1).

2.2 Null model comparisons

Both patterns of *NRI* and *NTI* were consistent across null models (Fig. S1), but with considerable differences in mean values (Table S4), and strongly correlated with each other (Fig. 6: A). Although *S.E.S.* D_{pw} and *S.E.S.* D_{nn} are strongly correlated between these models (Fig. 6: B), pairwise mean difference of *S.E.S.* D_{pw} and *S.E.S.* D_{nn} tend to be different under different null models (Table 2). For example, the pairwise *t*-tests reveal that the disparity between different null models for *S.E.S.* D_{pw} could be relatively larger than with *NRI* (Bartlett's K-squared $= 2.8561$, $d.f. = 1$, $P = 0.091$), as in the case of *S.E.S.* D_{nn} with *NTI* (Bartlett's K-squared $= 32.8594$, $d.f. = 1$, $P < 0.001$).

Table 1 Results from the permutational multivariate analysis of variance using phylogenetic beta diversity indices by "adonis"

Phylogenetic beta diversity index	Selected *PCNM*	Environmental distance matrix	Joined effects of selected *PCNM* and environmental distance matrix	Variation unexplained
S.E.S. D_{pw} abundance weighted	0.096^{***}	0.024^{***}	0.142^{*}	0.738
S.E.S. D_{pw} presence–absence	0.043^{***}	0.022^{***}	0.070^{**}	0.865
S.E.S. D_{nn} abundance weighted	0.952^{**}	0.006^{**}	0.018^{**}	0.025
S.E.S. D_{nn} presence–absence	0.883^{***}	0.008^{*}	0.032ns	0.078

ns, Not significant; *PCNM*, principal coordinates of neighbor matrices of geographical distance between each pair of plots, used to quantify the contribution of spatial distance; *S.E.S.* D_{nn}, standard effective size of mean nearest taxon distance between each pair of plots; *S.E.S.* D_{pw}, standard effective size of mean pairwise phylogenetic distance between each pair of plots. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

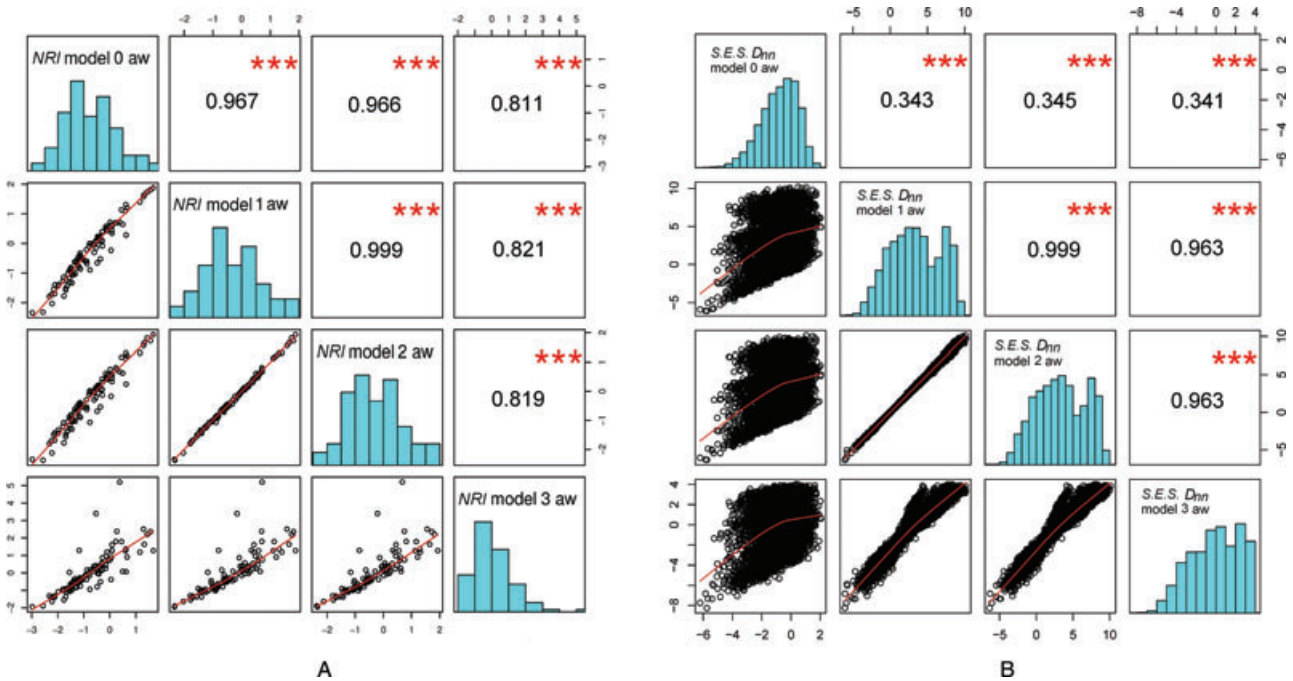

Fig. 6. Correlation between net relatedness index (*NRI*) (**A**) calculated using different null models and the correlation between *S.E.S.* D_{nn} (standard effective size for the mean nearest taxon distance between each pair of plots) (**B**), calculated using different null models. Note that the results from null model 0 tend to be distinct from the other null models. aw, abundance weighted.

2.3 Correlation between null model and geographical distance

Strong correlations between phylogenetic dissimilarity and geographical distance were observed for null model 0 using abundance weighted and presence–absence data (Tables S5, S6). Further it should be noted that the Mantel's *r*-values for null models 1, 2, and 3 were lower than that generated using null model 0. This indicates that the spatial relationships in the null phylogenetic pattern were lost in these three null models. The Mantel correlograms further show how the correlation changes with geographical distance (Figs. S18–S21). In the correlograms, significant correlations can be observed for null model 0, whereas few can be observed for other null models.

3 Discussion

Patterns of beta diversity have been some of the central pieces of empirical evidence in the study of the mechanisms underlying community structure and assembly (Condit et al., 2002; Cavender-Bares et al., 2004; Swenson et al., 2006, 2007; Kraft et al., 2008; Verleyen et al., 2009; Kraft & Ackerly, 2010; Soininen, 2010; Stokes & Archer, 2010; Anderson et al., 2011; Svenning et al., 2011). Here we argue that, although patterns of species beta diversity are interesting, additional insights into community assembly can be achieved through the measurement of phylogenetic beta diversity coupled with variance partitioning analyses. We carried out such analyses on a series of 100 forest plots located

Table 2 Pairwise *t*-tests for the standard effective size of mean pairwise phylogenetic distance (*S.E.S.* D_{pw}) and mean nearest taxon distance (*S.E.S.* D_{nn}) between each pair of plots generated by four null models (0–3)

		Null model I	Null model II	*t*	*d.f.*	*P*-value	Mean difference
S.E.S. D_{pw}	Abundance weighted	0	1	−128.52	4949	< 0.001	−0.846
		0	2	−126.54	4949	< 0.001	−0.843
		0	3	−68.75	4949	< 0.001	−0.440
		1	2	4.40	4949	< 0.001	0.003
		1	3	180.35	4949	< 0.001	0.406
		2	3	182.91	4949	< 0.001	0.403
	Presence– absence	0	1	−179.30	4949	< 0.001	−1.307
		0	2	−176.44	4949	< 0.001	−1.302
		0	3	−54.48	4949	< 0.001	−0.470
		1	2	6.12	4949	< 0.001	0.005
		1	3	279.98	4949	< 0.001	0.837
		2	3	276.74	4949	< 0.001	0.832
S.E.S. D_{nn}	Abundance weighted	0	1	−92.36	4949	< 0.001	−4.165
		0	2	−92.55	4949	< 0.001	−4.158
		0	3	−21.18	4949	< 0.001	−0.712
		1	2	3.26	4949	0.001124	0.007
		1	3	203.71	4949	< 0.001	3.453
		2	3	205.12	4949	< 0.001	3.446
	Presence– absence	0	1	−97.98	4949	< 0.001	−5.184
		0	2	−98.03	4949	< 0.001	−5.176
		0	3	−8.36	4949	< 0.001	−0.421
		1	2	2.82	4949	0.004896	0.008
		1	3	494.31	4949	< 0.001	4.763
		2	3	496.59	4949	< 0.001	4.755

S.E.S. D_{nn}, standard effective size of mean nearest taxon distance between each pair of plots; *S.E.S.* D_{pw}, standard effective size of mean pairwise phylogenetic distance between each pair of plots.

in Panama where all trees 10 cm in diameter or larger were inventoried.

3.1 Is species turnover phylogenetically non-random and why?

To answer our first question we implemented a series of null models. The results showed that species turnover between forest plots along both spatial and environmental gradients was non-random with respect to phylogeny (Figs. S4–S17). From this result we infer that non-random deterministic processes underlie the sorting and assembly of species into communities in our study system. The direction of the results shows that the phylogenetic turnover between tree plots was on average larger than that expected (Figs. 4, 5). From this we can infer that the turnover of species between plots is not simply a replacement of one congener with another from plot to plot along spatial and environmental gradients, but rather more phylogenetically "basal" turnover. This was particularly true for plots on opposing ends of the spatial and environmental gradients in our study system. The phylogenetic signal results from our study suggest closely related species typically share trait values that are more similar than that expected under a Brownian motion model of trait evolution (Blomberg & Garland, 2002; Blomberg et al., 2003). Thus, we can infer that the observed patterns of higher than expected phylogenetic turnover along spatial and environmental gradients indicate a higher than expected functional turnover along these same gradients, which further supports our inference of the importance of deterministic assembly.

3.2 Relative contribution of geographical and environmental distances to phylogenetic beta diversity

The second central question posed in this research was addressed by variation partitioning analyses that reported the amount of variance in phylogenetic beta diversity accounted for by spatial and/or environmental gradients. Correlative results show that phylogenetic beta diversity is correlated with the environmental gradients in our system (Table S1), but this result is impossible to disentangle from the influence of dispersal limitation without variance partitioning analyses. The results of the partitioning analyses showed that spatial and environmental distances both explained significant amounts of the variance in phylogenetic beta diversity with spatial distance typically accounting for slightly more of the variance (Tables S2, S3). Thus, while we can infer that phylogenetic turnover is typically non-random between tree plots, we cannot rule out the influence of dispersal limitation on the assembly of the tree communities in our study system. It is important to note that the 100 tree plots in our system are arrayed across the Panama Canal Zone. There is a significant rainfall gradient across the Canal Zone, which makes it difficult to separate environmental from spatial effects. Further, the size of the tree plots makes it more likely that dispersal limitation will be observed in the system.

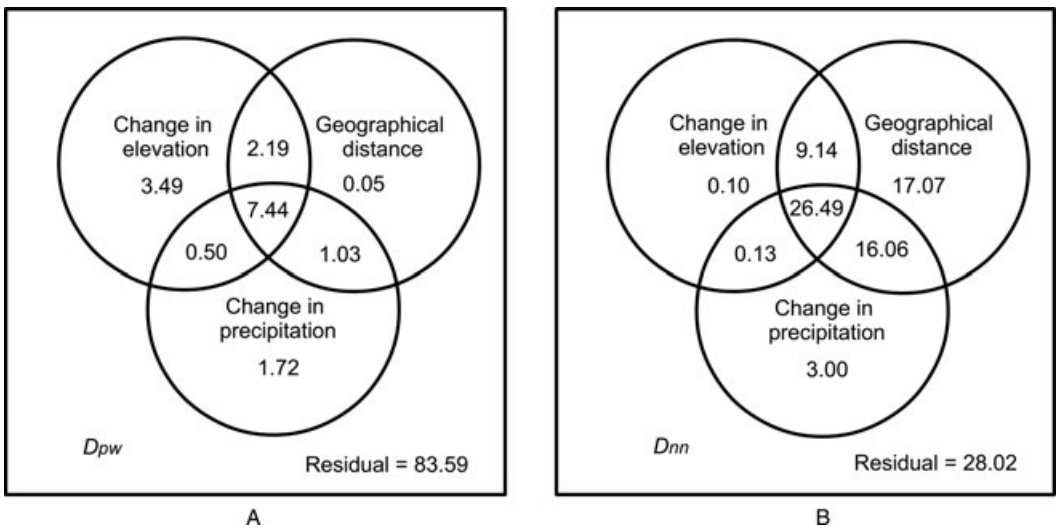

Fig. 7. Percentage of variance of phylogenetic beta diversity across 100 plots explained by change in elevation, geographical distance, and change in precipitation. **A,** Variation partitioning for presence–absence D_{pw} (mean pairwised phylogenetic distance). **B,** Variation partitioning for presence–absence D_{nn} (mean nearest taxon distance).

In particular, species turnover is likely to be inflated when the community sample is smaller in spatial scale. This would be particularly true in a diverse tropical system. Therefore, it may not be surprising that a significant amount of variance in phylogenetic beta diversity is explained by spatial distance. Our results showed that altitude and precipitation are more important in determining the mean pairwised phylogenetic distance (D_{pw}) (Fig. 7), whereas the geographical distance governs the mean nearest taxon distance (D_{nn}) between each pair of plots, indicating less power of D_{nn} in reflecting the phylogenetic diversity beta diversity patterns. The D_{nn} had been found to be closely related with PhyloSor and UniFrac (Feng et al., 2012). D_{nn} has also been reported to be able to reflect the species similarities in comparison with D_{pw} (Swenson, 2011). This indicates the D_{pw} (phylogenetic distance between each pair of species) could capture more information about the phylogenetic relationship than D_{nn} (only the most closely related taxon of one species over the phylogenetic tree in D_{nn}) (Table S1).

3.3 Null model comparison

The third goal of our study was to quantify the degree to which different null models produce similar results and therefore inferences. Our results show that different null models tend to yield different *S.E.S.* D_{pw} and *S.E.S.* D_{nn} results (Table S4, Fig. 8: A, B). This suggests that great care should be paid to the selection of null models. The results from null model 0 show higher than expected phylogenetic turnover between forest plots. This null model maintains the observed species beta diversity and patterns of dispersal limitation while only randomizing phylogenetic relationships.

These properties of null model 0 described in the preceding paragraph make this null model particularly powerful for analyses of phylogenetic beta diversity where one is typically interested in the influence of dispersal limitation and whether phylogenetic beta diversity is greater than that expected given the observed species beta diversity. Null models that do not constrain the randomization by the observed patterns of dispersal limitation and species beta diversity therefore make it difficult to address questions regarding dispersal limitation and non-random species turnover with respect to phylogeny. Contrary to null model 0, null models 1, 2, and 3 do not retain information for dispersal limitation or species beta diversity. This largely explains why the results from these null models are different from those obtained when using null model 0. Thus, although null models 1, 2, and 3 may be extremely useful in revealing community phylogenetic structure within communities (i.e. *NRI* or *NTI*), they may be less useful in phylogenetic beta diversity studies.

3.4 Limitations of the current study

The results of this study show that species turnover is non-random with respect to phylogeny in the study system and that patterns of phylogenetic turnover are often strongly correlated with regional scale spatial and environmental gradients. From this evidence we infer a large role for deterministic processes in the assembly of tree communities in this region. That said, we believe our study has three key limitations that should be discussed.

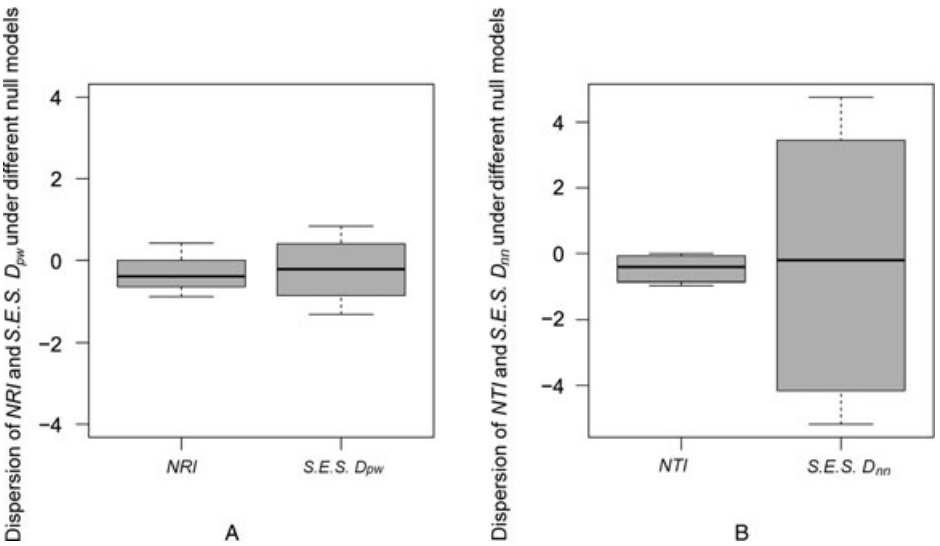

Fig. 8. Dispersion of net relatedness index/nearest taxon index (*NRI*/*NTI*) versus standard effective size of mean pairwise phylogenetic distance/mean nearest taxon distance between each pair of plots (*S.E.S.* D_{pw}/*S.E.S.* D_{nn}) under different null models. **A,** Dispersion of *NRI*/*S.E.S.* D_{pw} calculated under different null models. **B,** Dispersion of *NTI*/*S.E.S.* D_{nn} calculated under different null models. Note the dispersion of *S.E.S.* D_{pw} /*S.E.S.* D_{nn} is much larger than *NRI*/*NTI*. This is due to the poor performance of null models 1, 2, and 3 in randomizing species assembly among communities.

First, scale dependency is omnipresent in ecological studies and the strength of various processes is expected to vary with spatial scale (Cavender-Bares et al., 2006; Swenson et al., 2006; Lira-Noriega et al., 2007; Gardezi & Gonzalez, 2008; Qian & Kissling, 2010; Smith et al., 2011). In our study, we were limited to analyzing the phylogenetic beta diversity between all species or individuals in 1-ha forest plots in the Panama Canal Zone. We were unable to scale this research up to include additional regions or down to include fine scale spatial and environmental gradients. Thus, we are unable to determine how general the observed patterns may or may not be across several spatial scales. Future research that could achieve such multiscale analyses would be interesting and would be helpful to identify the degree to which our results can be generalized.

A second key limitation to our study is that we constructed and used a phylogenetic tree that was not fully resolved and that had crudely estimated branch lengths. The extent to which the polytomies and crude branch lengths may bias measures of phylogenetic alpha diversity have been previously explored (Kress et al., 2009; Swenson, 2009), but the bias introduced into studies of phylogenetic beta diversity are not known. It is reasonable to expect that the biases will be similar given the mathematical similarity of the phylogenetic alpha and beta diversity metrics used. Thus, we expect that our results are likely to have been biased by the phylogeny that we used and the non-random phylogenetic turnover would be less likely to be detected (Swenson, 2009).

The final key limitation of our study that we would like to highlight has to do with partitioning variance in beta diversity into spatial and environmental components. There has been a healthy debate regarding which statistical procedures should be preferred in partitioning studies of beta diversities. The Mantel test and MRM (Legendre et al., 1994; Goslee, 2010) have received a great deal of criticism in published works (see Legendre et al., 2008). The criticism leveled is that these methods often are incapable of explaining the actual amount of variance that should be explained by environmental distance. Further, the square of a Mantel's *r* does not reflect the variance of raw data, making inferences from this statistic less tractable (Tuomisto & Ruokolainen, 2008).

4 Conclusion

In conclusion, we have presented a study of the phylogenetic beta diversity in 100 tropical tree plots in Panama. We report that species turnover in this system is generally non-random with respect to phylogeny and that species traits in this system have phylogenetic signal indicating a non-random functional turnover. From this pattern, we infer the importance of deterministic processes in the assembly of our study communities. We have also shown that both spatial and environmental distances are significant correlates of phylogenetic beta diversity, suggesting that dispersal limitation, along with determinism, is important in our system. Lastly,

we compared and contrasted phylogenetic beta diversity results generated from four different null models. We found that phylogenetic beta diversity results can be very sensitive to null model choice and that three of the four null models implemented have undesirable qualities.

Acknowledgements We thank Dr. Richard CONDIT for permission to use the dataset, and for the people who collected the data for BCI and other plots. We are grateful to Dr. Campbell WEBB for helpful suggestions and Dr. Stéphane DRAY for statistical comments. We thank two anonymous reviewers for their valuable comments. Additionally, we thank Miss Wenjing YANG, Dr. Nancai PEI, Dr. Guoke CHEN, Dr. Lixin LÜ, and Dr. Yongbo LIU for helpful discussion and constructive suggestions. This work was financially supported by a key innovation project of the Chinese Academy of Sciences (Grant No. KZCX2-YW-430).

References

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46.

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF. 2011. Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. Ecology Letters 14: 19–28.

Blomberg SP, Garland Jr T. 2002. Tempo and mode in evolution: Phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology 15: 899–910.

Blomberg SP, Garland Jr T, Ives AR. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution 57: 717–745.

Borcard D, Legendre P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153: 51–68.

Bryant JA, Lamanna C, Morlon H, Kerkhoff AJ, Enquist BJ, Green JL. 2008. Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences USA 105: 11505–11511.

Buckley LB, Jetz W. 2008. Linking global turnover of species and environments. Proceedings of the National Academy of Sciences USA 105: 17836–17841.

Cavender-Bares J, Ackerly DD, Baum DA, Bazzaz FA. 2004. Phylogenetic overdispersion in Floridian oak communities. The American Naturalist 163: 823–843.

Cavender-Bares J, Keen A, Miles B. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87: 109–122.

Chase MW, Fay MF, Reveal JL, Soltis DE, Soltis PS, Anderberg AA, Moore MJ, Olmstead RG, Rudall PJ. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161: 105–121.

Chust G, Chave J, Condit R, Aguilar S, Lao S, Pérez R. 2006. Determinants and spatial modeling of tree β-diversity in a tropical forest landscape in Panama. Journal of Vegetation Science 17: 83–92.

Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Nunez P, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E, Hubbell SP. 2002. Beta-diversity in tropical forest trees. Science 295: 666–669.

Dray S. 2011. packfor: Forward selection with permutation. R package version 0.0–8/r100 [online]. Available from: http://r-forge.r-project.org/projects/sedar/ [accessed 5 July 2012].

Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80–82.

Feng G, Zhang JL, Pei NC, Rao MD, Mi XC, Ren HB, Ma KP. 2012. Comparison of phylobetadiversity indices based on community data from Gutianshan forest plot. Chinese Science Bulletin 57: 623–630.

Fine PVA, Kembel SW. 2011. Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. Ecography 34: 552–565.

Gardezi T, Gonzalez A. 2008. Scale dependence of species-energy relationships: Evidence from fishes in thousands of lakes. The American Naturalist 171: 800–815.

Goslee SC. 2010. Correlation analysis of dissimilarity matrices. Plant Ecology 206: 279–286.

Goslee SC, Urban DL. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22: 1–19.

Gotelli NJ. 2000. Null model analysis of species co-occurrence patterns. Ecology 81: 2606–2621.

Graham CH, Fine PVA. 2008. Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. Ecology Letters 11: 1265–1277.

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, de Lao SL. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283: 554–557.

Ives AR, Helmus MR. 2010. Phylogenetic metrics of community similarity. The American Naturalist 176: E128–E142.

Kembel SW, Hubbell SP. 2006. The phylogenetic structure of a neotropical forest tree community. Ecology 87: 86–99.

Kraft NJB, Ackerly DD. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs 80: 401–422.

Kraft NJB, Valencia R, Ackerly DD. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322: 580–582.

Kress WJ, Erickson DL, Jones FA, Swenson NG, Perez R, Sanjur O, Bermingham E. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. Proceedings of the National Academy of Sciences USA 106: 18621–18626.

La Sorte FA, McKinney ML, Pyšek P, Klotz S, Rapson GL, Celesti-Grapow L, Thompson K. 2008. Distance decay of similarity among European urban floras: The impact of

anthropogenic activities on β diversity. Global Ecology and Biogeography 17: 363–371.
Legendre P. 2008. Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. Journal of Plant Ecology 1: 3–8.
Legendre P, Anderson MJ. 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69: 1–24.
Legendre P, Borcard D, Peres-Neto PR. 2008. Analyzing or explaining beta diversity? Comment. Ecology 89: 3238–3244.
Legendre P, Lapointe FJ, Casgrain P. 1994. Modeling brain evolution from behavior: A permutational regression approach. Evolution 1487–1499.
Legendre P, Mi X, Ren H, Ma K, Yu M, Sun IF, He F. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90: 663–674.
Lichstein JW. 2007. Multiple regression on distance matrices: A multivariate spatial analysis tool. Plant Ecology 188: 117–131.
Lira-Noriega A, Soberón J, Navarro-Sigüenza AG, Nakazawa Y, Peterson AT. 2007. Scale dependency of diversity components estimated from primary biodiversity data and distribution maps. Diversity and Distributions 13: 185–195.
Lozupone C, Hamady M, Knight R. 2006. UniFrac—an online tool for comparing microbial community diversity in a phylogenetic context. BMC Bioinformatics 7: 371.
McArdle BH, Anderson MJ. 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82: 290–297.
Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2012. vegan: community ecology package. R package version 2.0–4 [online]. Available from http://CRAN.R-project.org/package=vegan [accessed 6 July 2012].
Paradis E, Claude J, Strimmer K. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289–290.
Qian H. 2009. Beta diversity in relation to dispersal ability for vascular plants in North America. Global Ecology and Biogeography 18: 327–332.
Qian H, Kissling WD. 2010. Spatial scale and cross-taxon congruence of terrestrial vertebrate and vascular plant species richness in China. Ecology 91: 1172–1183.
Qian H, Ricklefs RE. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. Global Ecology and Biogeography 21: 341–351.
R-Core-Team. 2010. R: A language and environment for statistical computing. ISBN 3-900051-07-0. Vienna: R Foundation for Statistical Computing [online]. Available from http://www.r-project.org/ [accessed 10 June 2012].
Rao CR. 1982. Diversity and dissimilarity coefficients: A unified approach. Theoretical Population Biology 21: 24–43.
Ricotta C, Burrascano S. 2008. Beta diversity for functional ecology. Preslia 80: 61–71.
Ruokolainen K, Tuomisto H. 2002. Beta-diversity in tropical forests. Science 297: 1439.
Smith AC, Fahrig L, Francis CM. 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34: 103–113.
Soininen J. 2010. Species turnover along abiotic and biotic gradients: Patterns in space equal patterns in time? BioScience 60: 433–439.
Stokes CJ, Archer SR. 2010. Niche differentiation and neutral theory: An integrated perspective on shrub assemblages in a parkland savanna. Ecology 91: 1152–1162.
Svenning JC, Fløjgaard C, Baselga A. 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction. Journal of Animal Ecology 80: 393–402.
Swenson NG. 2009. Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. PLoS One 4: e4390.
Swenson NG. 2011. Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. PLoS One 6: e21264.
Swenson NG, Anglada-Cordero P, Barone JA. 2011. Deterministic tropical tree community turnover: Evidence from patterns of functional beta diversity along an elevational gradient. Proceedings of the Royal Society B: Biological Sciences 278: 877–884.
Swenson NG, Enquist BJ, Pither J, Thompson J, Zimmerman JK. 2006. The problem and promise of scale dependency in community phylogenetics. Ecology 87: 2418–2424.
Swenson NG, Enquist BJ, Thompson J, Zimmerman JK. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. Ecology 88: 1770–1780.
Thrush SF, Hewitt JE, Cummings VJ, Norkko A, Chiantore M. 2010. β-diversity and species accumulation in Antarctic coastal benthos: Influence of habitat, distance and productivity on ecological connectivity. PLoS One 5: e11899.
Tuomisto H, Ruokolainen K. 2008. Analyzing or explaining beta diversity? Reply. Ecology 89: 3244–3256.
Tuomisto H, Ruokolainen K, Yli-Halla M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. Science 299: 241–244.
Vavrek MJ. 2011. fossil: Palaeoecological and palaeogeographical analysis tools. Palaeontologia Electronica 14(1): 16.
Verleyen E, Vyverman W, Sterken M, Hodgson DA, De Wever A, Juggins S, Van de Vijver B, Jones VJ, Vanormelingen P, Roberts D, Flower R, Kilroy C, Souffreau C, Sabbe K. 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. Oikos 118: 1239–1249.
Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. The American Naturalist 156: 145–155.
Webb CO, Donoghue MJ. 2005. Phylomatic: Tree assembly for applied phylogenetics. Molecular Ecology Notes 5: 181–183.
Webb CO, Ackerly DD, Kembel SW. 2008. Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24: 2098.
Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475–505.

Wikström N, Savolainen V, Chase MW. 2001. Evolution of the angiosperms: Calibrating the family tree. Proceedings of the Royal Society of London, Series B: Biological Sciences 268: 2211–2220.

Zambrano-Bigiarini M. 2012. hydroTSM: Time series management, analysis and interpolation for hydrological modelling. R package version 0.3–4 [online]. Available from http://CRAN.R-project.org/package=hydroTSM [accessed 10 February 2012].

Supporting Information

The following supplementary material is available for this article at http://onlinelibrary.wiley.com/doi/10.1111/j.1759-6831.2012.00220.x/suppinfo:

Doc. S1. R codes for analyzing phylogenetic beta diversity.

Doc. S2. Test of the phylogenetic signal.

Table S1. Results of the Mantel test correlating phylogenetic, geographic, environmental, and species dissimilarity

Table S2. Results of multiple regression where phylogenetic dissimilarity is being regressed onto geographic and environmental distance matrices based on multiple regression of distance matrices (MRM)

Table S3. Results of multiple regression where phylogenetic distance between two plots is being regressed onto geographic and environmental distance between two plots (i.e. a pairwise list analysis instead of a distance matrix analysis)

Table S4. Pairwise *t*-tests for net relatedness index (*NRI*) and the nearest taxon index (*NTI*) generated using four null models

Table S5. Mantel test results correlating phylogenetic D_{pw}/D_{nn} null models and geographical distance

Table S6. Mantel test results correlating null phylogenetic distance and species beta diversity

Fig. S1. Net relatedness index (*NRI*) and nearest taxon index (*NTI*) value of plots calculated using different null models. Note the similar patterns of *NRI* and *NTI* both for the abundance weighted data and presence–absence data.

Fig. S2. Correlation of net relatedness index (*NRI*) and nearest taxon index *(NTI*) using different null models. Null model 0 tends to behave more distinctively than other null models when analyzing abundance weighted data.

Fig. S3. Correlation between the standard effective size of mean nearest taxon distance between each pair of plots (*S.E.S* D_{pw}) and the standard effective size of mean pairwise phylogenetic distance between each pair of plots (*S.E.S.* D_{nn}) using different null models.

Fig. S4. Decay and standard effective size calculated using null model 1 of mean nearest taxon distance (D_{nn}) (abundance weighted) along geographical and environmental distances.

Fig. S5. Decay and standard effective size calculated using null model 3 of mean nearest taxon distance (D_{nn}) (abundance weighted) along geographical and environmental distances.

Fig. S6. Decay and standard effective size calculated using null model 0 of mean nearest taxon distance (D_{nn}) (presence−absence) along geographical and environmental distances.

Fig. S7. Decay and standard effective size calculated using null model 1 of mean nearest taxon distance (D_{nn}) (presence−absence) along geographical and environmental distances.

Fig. S8. Decay and standard effective size calculated using null model 2 of mean nearest taxon distance (D_{nn}) (presence–absence) along geographical and environmental distances.

Fig. S9. Decay and standard effective size calculated using null model 3 of mean nearest taxon distance (D_{nn}) (presence–absence) along geographical and environmental distances.

Fig. S10. Decay and standard effective size calculated using null model 0 of mean pairwised phylogenetic distance (D_{pw}) (abundance weighted) along geographical and environmental distances.

Fig. S11. Decay and standard effective size calculated using null model 1 of mean pairwised phylogenetic distance (D_{pw}) (abundance weighted) along geographical and environmental distances.

Fig. S12. Decay and standard effective size calculated using null model 2 of mean pairwised phylogenetic distance (D_{pw}) (abundance weighted) along geographical and environmental distances.

Fig. S13. Decay and standard effective size calculated using null model 3 of mean pairwised phylogenetic distance (D_{pw}) (abundance weighted) along geographical and environmental distances.

Fig. S14. Decay and standard effective size calculated using null model 0 of mean pairwised phylogenetic distance (D_{pw}) (presence–absence) along geographical and environmental distances.

Fig. S15. Decay and standard effective size calculated using null model 1 of mean pairwised phylogenetic distance (D_{pw}) (presence–absence) along geographical and environmental distances.

Fig. S16. Decay and standard effective size calculated using null model 2 of mean pairwised phylogenetic distance (D_{pw}) (presence–absence) along geographical and environmental distances.

Fig. S17. Decay and standard effective size calculated using null model 3 of mean pairwised phylogenetic distance (D_{pw}) (presence–absence) along geographical and environmental distances.
Fig. S18. Mean nearest taxon distance (D_{nn}) correlogram and distance decay (abundance weighted).
Fig. S19. Mean nearest taxon distance (D_{nn}) correlogram and distance decay (presence–absence).
Fig. S20. Mean pairwised phylogenetic distance (D_{pw}) correlogram and distance decay (abundance weighted).
Fig. S21. Mean pairwised phylogenetic distance (D_{pw}) correlogram and distance decay (presence–absence).