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E-Article

The Contribution of Rare Species to Community Phylogenetic Diversity across a Global Network of Forest Plots

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abstract: Niche differentiation has been proposed as an explanation for rarity in species assemblages. To test this hypothesis requires quantifying the ecological similarity of species. This similarity can potentially be estimated by using phylogenetic relatedness. In this study, we predicted that if niche differentiation does explain the co-occurrence of rare and common species, then rare species should contribute greatly to the overall community phylogenetic diversity (PD), abundance will have phylogenetic signal, and common and rare species will be phylogenetically dissimilar. We tested these predictions by developing a novel method that integrates species rank abundance distributions with phylogenetic trees and trend analyses, to examine the relative contribution of individual species to the overall community PD. We then supplement this approach with analyses of phylogenetic signal in abundances and measures of phylogenetic similarity within and between rare and common species groups. We applied this analytical approach to 15 long-term temperate and tropical forest dynamics plots from around the world. We show that the niche differentiation hypothesis is supported in six of the nine gap-dominated forests but is rejected in the six disturbance-dominated and three gap-dominated forests. We also show that the three metrics utilized in this study each provide unique but corroborating information regarding the phylogenetic distribution of rarity in communities.

Keywords: rare species, community phylogenetic diversity, species abundance distribution, phylogenetic relatedness, niche differentiation, community assembly.

Introduction

A central goal in community ecology is to determine the mechanisms underlying the relative abundances of species. Addressing this question is particularly challenging and interesting in diverse communities where a large proportion of the species are relatively rare. Thus, basic research into species abundances, particularly in diverse communities, requires a consideration of the forces underlying species rarity. Two opposing families of hypotheses have been proposed to explain rarity in species assemblages. One family, which focuses on niche differentiation, stresses the importance of specialization and spatiotemporal resource partitioning. For example, the niche position hypothesis (Gaston 1994; Kunin 1997) and similar hypotheses, such as Hanski's (1982) core-satellite species hypothesis and Grime's (1998) classification of dominant, subordinate, and transient species, postulate that rare species utilize spatially scarce resources that are underutilized by common species. Similar hypotheses that focus on temporal partitioning of the environment, such as the storage effect, have also been proposed to explain the recruitment of rare species (Chesson 2000; Kelly and Bowler 2002). Contrary to this family of niche differentiation hypotheses are neutral models (e.g., Hubbell 2001). Neutral models assume that species are interchangeable and species abundances are not best explained by niche differences but rather may be better explained by dispersal limitation, the

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structure of the metacommunity, and demographic stochasticity. A niche differentiation hypothesis and a neutral model make opposing predictions regarding the similarity of rare and common species. In particular, a niche differentiation hypothesis predicts that rare species will be dissimilar from common species and other rare species, whereas a neutral model predicts no significant dissimilarity between rare and common species or between rare species.

The main challenge in testing the validity of the above hypotheses lies in quantifying the ecological similarity between rare and common species (Keddy 1989; Clark et al. 2007). For years ecologists have utilized evolutionary relatedness as a proxy for ecological similarity (Jarvinen 1982; Webb et al. 2002; Cadotte et al. 2008; Wiens et al. 2010). The rationale for this approach has been that common descent from a recent ancestor should result in closely related species being, on average, more similar to one another than they are to a distantly related species. Of course, divergent evolution between closely related species is often demonstrated, for example, during an adaptive radiation, and in these cases the assumption that closely related species are similar will inevitably break down (Losos 2008). That said, in instances where the analyses incorporate taxa from a broad sampling of the tree of life, the assumption may be more reasonable (Wiens et al. 2010). For example, two palm species in a rain forest tree community are likely to be much more ecologically similar to one another than to a species in the common shrub genus *Piper* (Piperaceae). Aside from the potential utility of the assumption that closely related species are likely to be ecologically similar, is the reality that quantifying the multidimensional ecological similarity of hundreds or thousands of species in diverse assemblages is often unreasonable. A further rationale for using phylogenetic relatedness in ecological studies comes from recent research that has compared and contrasted results from trait and phylogenetic analyses. This work has reported that phylogenetic measures can capture additional information not contained in the small set of traits that ecologists often measure (Cadotte et al. 2008, 2009; Burns and Strauss 2011). In other words, the phylogeny may contain information pertaining to important and unmeasured traits that have phylogenetic signals (Cadotte et al. 2009).

Phylogenetic analyses of rarity in communities can be utilized to address several key questions. Perhaps the most fundamental question involves determining the degree to which rare species are closely or distantly related to common species. Phylogenetic assessments of a niche differentiation hypothesis would therefore test the degree of phylogenetic relatedness between common and rare species. Indeed, recent phylogenetically based work has aimed to test this expectation. For example, studies from a diverse Mexican tree community and a cactus yeast community have found that common species are distantly related to rare species (Anderson et al. 2004; Kelly et al. 2008). However, these results are not totally consistent with the predictions of a niche differentiation hypothesis. Specifically, rare species are expected to utilize locally or temporally scarce resources, and thus rare species are expected to be not only dissimilar to common species but also dissimilar to one another. This dissimilarity of rare species to common species and to one another is therefore expected to result in rare species disproportionately contributing to the overall phylogenetic diversity (PD) in a community. Thus, the question becomes, do rare species disproportionately contribute to the community PD as expected by a niche differentiation hypothesis, or is their contribution random as expected by a neutral model?

A second important question regarding the relationship between relatedness and rarity is simply to determine whether there is phylogenetic signal (Blomberg et al. 2003; Swenson and Enquist 2009) in the relative abundances of species in communities. A niche differentiation hypothesis would predict that there is phylogenetic signal in abundances in communities because of the expected distinctiveness between common and rare species.

A third important question regarding phylogeny and rarity is what is the degree of phylogenetic dissimilarity within and between groups of common and rare species? A niche differentiation hypothesis predicts that rare species would be dissimilar to common species. Further common species should also be closely related to one another, but rare species should be distantly related to one another.

In this study, our central objective is to test the niche differentiation hypothesis by addressing these three central questions: (1) what is the contribution of rare species to the community PD? (2) Is there phylogenetic signal in rank abundance across forest plots? (3) What is the level of phylogenetic similarity within and between common and rare species in forest plots? We utilize 15 forest dynamics plots (FDPs; 16–52 ha in size) located across temperate, subtropical, and tropical forests of Asia and America (fig. A1; tables A1, A2, available online) as our study systems. The results of these tests will be used to indentify the degree to which a niche differentiation hypothesis can be invoked to explain the distribution of rarity across varied tree communities.

Material and Methods

Study Sites and Data

We analyzed 15 FDPs from around the world (fig. A1). The majority of these FDPs exist within extensive primary forests either without anthropogenic disturbance or with only slight anthropogenic disturbance (tables A1, A2). The Fushan, Luquillo, Palanan, and Dinghushan FDPs suffer from hurricane damage to varying degrees, and the Luquillo plot also has a history of anthropogenic disturbance (Losos and Leigh 2004). The Mudumalai plot in India has been influenced by logging operations since the early twentieth century, and it experiences frequent and widespread ground fires. The La Planada FDP was logged lightly decades ago, and the Lambir FDP is frequently affected by landslides generated by continuous heavy rain. Although most of the Barro Colorado Island (BCI) plot is primary forest, about 2 ha of the plot is secondary forest. The FDPs cover 16–52 ha within which the locations of all trees with diameters ≥1 cm at 1.3 m above the ground are mapped, measured, and identified to the species level when possible.

In this study we define rare species within the FDPs following Hubbell and Foster (1986), who state that rare species have an average density of fewer than one individual per hectare. The abundance data for the plots were available from either the published standard books of the plots (table A2) or from the website of the Smithsonian Institution Global Earth Observatories (http://www.sigeo.si.edu/). The 15 FDPs vary widely with respect to both species richness and their proportion of rare species (table A2). In total, the data set we utilized represents 5,637 species and 2,167 rare species in a wide variety of forests.

Community Phylogenetic Analyses

For the community phylogenetic analyses a phylogenetic tree was constructed for each plot, using the plant phylogeny database Phylomatic (Webb and Donoghue 2005). In the Yasuní plot, 26 species (14 of which are rare species according to the criteria of Hubbell and Foster [1986]) were identified only to the family level and were excluded from the analysis. Phylomatic used the latest Angiosperm Phylogeny Group classification (Angiosperm Phylogeny Group III 2009) as the phylogenetic tree backbone. The phylogenetic branch lengths were calibrated by implementing the BLADJ algorithm in Phylocom 4.1 (Webb et al. 2008) with estimated molecular and known fossil dates (Wikstrom et al. 2001). These branch lengths are taken as rough estimates, but they provide a substantial advantage over using nodal distances where all branch lengths are treated as equivalent (Webb 2000). To explore the potential impact of using a Phylomatic-generated phylogeny instead of a molecular phylogeny, we performed an additional set of analyses, using highly resolved community phylogenies for the BCI and Luquillo plots (Kress et al. 2009, 2010). While there were a few differences in the results, our results are generally robust to differences in the phylogeny estimates (data not shown).

A Framework for Quantifying the Contribution of Rare Species to Community PD

The first goal of this study is to quantify the contribution of rare species to the overall community PD. We start by defining community PD and standardized community PD (stdPD). Community PD is defined as the sum of the branch lengths throughout a phylogenetic tree connecting all taxa in a community or sample (Faith 1992). We define stdPD as the difference between the observed PD of subsets of a community or sample and the mean PD value of 999 null communities or samples generated by shuffling the names of species across the tips of the phylogeny.

We now integrate the stdPD metric with species rank abundance to quantify the contribution of rare species to overall community PD. Specifically, we first quantify the cumulative PD by adding increasingly rare species to the sample starting with the second-most abundant species, then the third-most abundant species, and so on. Next we standardize the cumulative PD values by quantifying stdPD. The stdPD value of the most abundant species will always be undefined, because PD cannot be calculated from a sample of one species, and the cumulative stdPD value upon adding the rarest species is 0, because all species are included in the PD calculation, assuring that the mean null value equals the observed value.

Trends in the species rank abundance–stdPD (SAPD) curve can now be used to reveal the contribution of an individual species to the overall community PD while weighing that observation by that randomly expected. Specifically, a decrease in the stdPD from one species to the next in the rank abundance distribution shows that the added species was more closely related than expected by chance to the species that are more abundant in the community (i.e., it adds little to the community PD). Thus, if rare species contribute little to the overall community PD, we would expect a decreasing trend toward the right end of the SAPD. For example, in the hypothetical community represented in figure 1*b*, adding the rare species E and C to a community containing the common species B and D results in a decreasing trend of stdPD in species rank 4 and 5 (fig. 1*b*). Conversely, an increase in the stdPD from one species to the next in the rank abundance distribution shows that the added species was more distantly related than expected by chance (i.e., it adds greatly to the community PD). Thus, if rare species contribute greatly to the overall community PD, we would expect an increasing trend toward the right end of the SAPD. For example, in the hypothetical community in figure 1*c*, the addition of the rare species D and G to a community containing the distantly related common species A and B leads to an increasing trend of stdPD from species rank 3 to 4 (fig. 1*c*). Finally, if rare species contribute a random amount

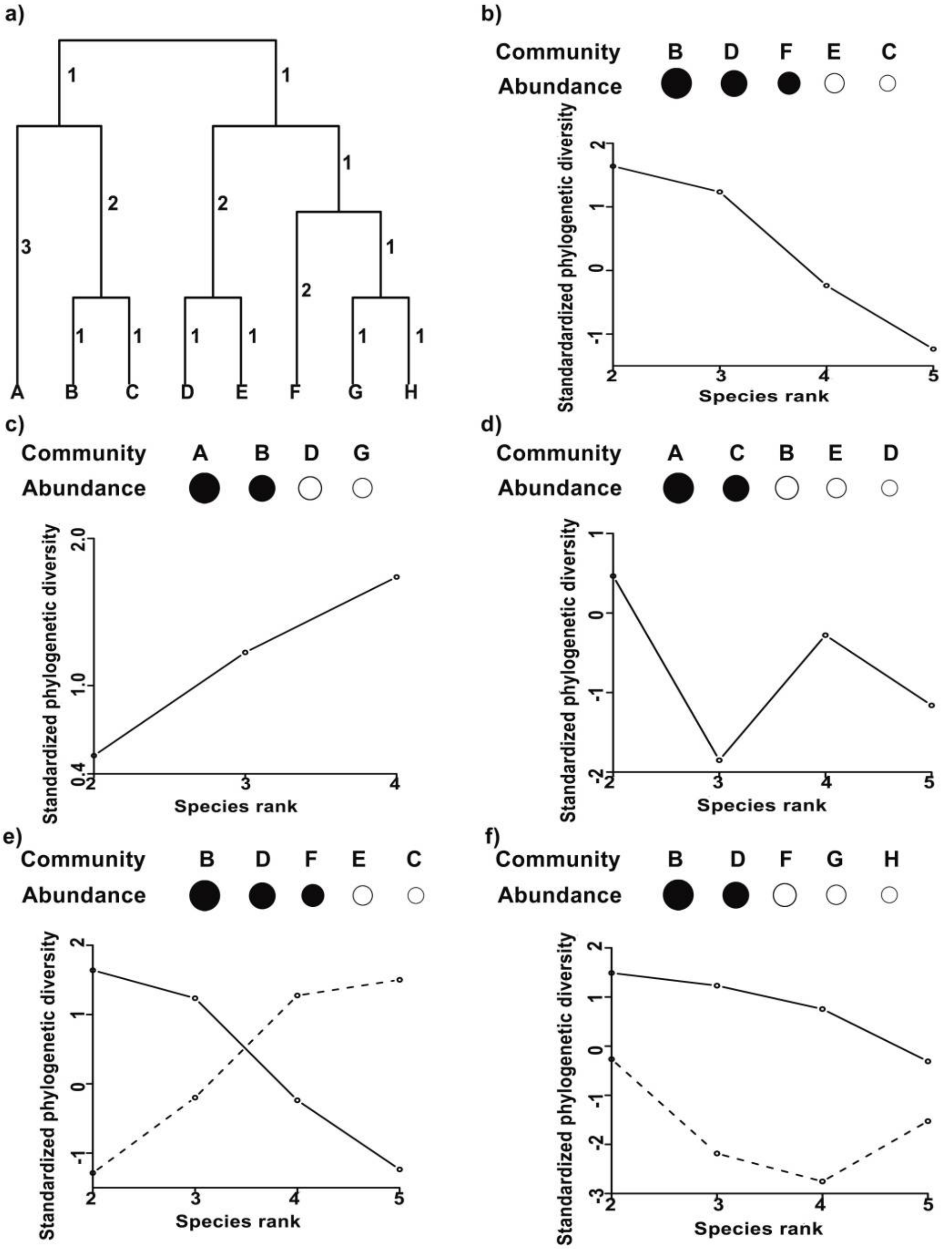

Figure 1: Highly simplified illustration of how the species abundance rank–standardized phylogenetic diversity (SAPD) curves are generated and interpreted. *a*, Hypothetical phylogenetic tree of the species pool; *b*, standardized community PD (stdPD) increases along species rank when rare species are distantly related to common species; *c*, stdPD decreases along species rank when rare species are closely related to common species; *d*, stdPD randomly fluctuates along species rank when rare species are randomly distributed in the phylogenetic tree; *e*, reverse stdPD decreases along species rank from a peak value when rare species are distantly related to common species; and *f*, reverse SAPD curves are concave because of closely related rare species. Note that the species numbers in the hypothetical communities of this figure are lower than the species numbers in the species pool. The stdPD values for the SAPD curves of the rarest species in this figure are not 0, and so the SAPD curves in this figure are slightly different from those generated when all species are included in the analysis, such as in figure 2 and figure C1, available in a zip file. The filled circles represent common species and the open circles represent rare species. The size of the circle indicates species abundance. The solid lines are SAPD curves and the dashed lines are reverse SAPD curves.

to the overall community PD, then the SAPD would fluctuate randomly. For example, in the hypothetical community in figure 1*d*, the rare species B and D were closely related to the more abundant species A and E, whereas E was distantly related to the common species. This causes a fluctuation of stdPD values in the SAPD curve.

Note that the scenario of decreasing stdPD against species rank from common species to rare species shown in figure 1*c* may not only be explained by the high relatedness between rare and common species, but also be interpreted as the high relatedness between rare species (fig. 1*e*, 1*f*). Fortunately, these two situations of decreasing stdPD against species rank can be distinguished by reversing the SAPD curves where the curve is quantified beginning with the second-rarest species. The reverse SAPD along reverse abundance rank (i.e., starting from the second-rarest species) will decrease from a peak value if rare species are more closely related to common species than chance would predict (fig. 1*e*). For example, stdPD decreases along reverse species rank because of high relatedness between rare species E and C and common species B, D, and F (fig. 1*e*). A second scenario is that the reverse SAPD would first exhibit a downward trend and then display an increasing trend along reverse species rank if the rare species are more closely related (fig. 1*f*). For example, in the highly simplified hypothetical community in figure 1*f*, the reverse SAPD curve first decreases from species rank 5 to 4 because of close relatedness between rare species G and H. Then the reverse SAPD curve increases from species rank 4 to 2 because of distant relatedness between common species B and D and rare species F, G, and H. Therefore, the reverse SAPD curve is not simply the complement of the SAPD curve, it also contains useful information of its own.

Statistical analyses of the SAPD curves require the quantification of trends in stdPD values along the rank abundance axis and a single SAPD curve may present multiple trends in different subseries. Thus, it is necessary to identify significant trends across all subseries. In other words, it is necessary to identify regions of the SAPD curve that are significantly increasing or decreasing. The potential breakpoints between subseries were analyzed using piecewise regression (Muggeo 2003, 2011; Toms and Lesperance 2003; Betts et al. 2007):

$$\text{stdPD}_i = \beta_0 + \beta_1 i + \sum_{j \geq 2} \beta_j (i - \alpha_j) I(i > \alpha_j), \tag{1}$$

where stdPD_i is the value of stdPD for *i*th species rank; i is the corresponding species abundance rank from 2 to $n - 1$; n is the species richness in a community; α_j is the *j*th breakpoint (i.e., the breakpoint between subseries); the slopes of the lines are β_1, $\beta_1 + \beta_2$, and so on; β_j is the difference in slope values; and I is an indicator variable. We built piecewise linear regression models with one or more breakpoints in a SAPD curve by using Muggeo's (2003) method. The significance of the breakpoints in the piecewise regressions was evaluated by using Zeileis et al.'s (2003) method. We also determined the weight of evidence for breakpoints in relation to linear models with j breakpoints in relation to model with $j - 1$ breakpoints by using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). The relative likelihood of each model in relation to the best model was determined based on evidence ratios (ERs) derived from AIC values (Burnham and Anderson 2002).

To quantify the trend of an identified subseries in the SAPD curve, we used a Mann-Kendall trend test to calculate the significance of the decreasing or increasing trends of stdPD values along species abundance rank. A Mann-Kendall test, commonly known as the Kendall's tau statistic, has been applied widely to test for randomness against trends in climatological and hydrological time series (Hirsch and Slack 1984; Yu et al. 1993; Douglas et al. 2000). In this test, the null hypothesis H_0 states that stdPD_1, stdPD_2, ..., stdPD_n are a sample of n independent and identically distributed random variables (Yu et al. 1993). The alternative hypothesis H_1 of a two-sided test is that the distributions of stdPD_k and stdPD_j are not identical for all k, where $j \leq n$ and $k \neq j$. The test statistic S is calculated using equations (2) and (3):

$$S = \sum_{k=1}^{n-1} \sum_{j=k+1}^{n} \operatorname{sgn}(\text{stdPD}_j - \text{stdPD}_k), \tag{2}$$

$$\operatorname{sgn}(\text{stdPD}_j - \text{stdPD}_k) = \begin{cases} +1 & \text{if } (\text{stdPD}_j - \text{stdPD}_k) > 0 \\ 0 & \text{if } (\text{stdPD}_j - \text{stdPD}_k) = 0, \\ -1 & \text{if } (\text{stdPD}_j - \text{stdPD}_k) < 0 \end{cases} \tag{3}$$

where S has a mean of 0 and variance of S is computed by $\operatorname{Var}(S) = [n(n-1)(2n+5) - \sum_t t(t-1)(2t+5)]/18$ and is asymptotically normal (Hirsch and Slack 1984), where t is the extent of any given tie and $\sum_t$ denotes the summation over all ties. The standard normal variable z is computed by using the following equation (Douglas et al. 2000):

$$z = \begin{cases} \dfrac{S - 1}{(\operatorname{Var}(S))^{1/2}} & \text{if } S > 0 \\ 0 & \text{if } S = 0\,. \\ \dfrac{S + 1}{(\operatorname{Var}(S))^{1/2}} & \text{if } S < 0 \end{cases} \tag{4}$$

A positive value of z indicates an increasing trend in the SAPD curve meaning that rare species in the community are more distantly related to common species than expected by chance, while a negative value of z indicates a decreasing trend in SAPD curve, meaning rare species in a community are more closely related to common species than expected by chance.

The SAPD curve is autocorrelated because of its cumulative nature, which may inflate type I error rates and result in the overestimation of significant increasing or decreasing trends. In order to account for the autocorrelation of stdPD values between neighboring species ranks, we randomly shuffled species abundance across the tips of the phylogeny 999 times and constructed 999 null SAPD curves. Then we calculated the probability that the observed z value of a subseries in the observed SAPD curve was greater or lower than z value of the subseries in null SAPD curves.

In this study we have proposed a new approach, the SAPD curve, to assess the contribution of rare species to community PD. Several other indices frequently used in phylogenetic community ecology, such as the mean pairwise phylogenetic distance (MPD), the net relatedness index (NRI; Webb 2000; Webb et al. 2002), phylogenetic species variability (PSV), phylogenetic species richness (PSR; Helmus et al. 2007), and evolutionary distinctiveness (ED; Redding and Mooers 2006; Isaac et al. 2007; Cadotte et al. 2010), may also have the potential to assess the contribution of rare species. That said, our choice of metrics, PD, stdPD, and SAPD, was conditional on the biological question being tested. For example, frequently used indices such as MPD, NRI, and PSV have their merit in measuring average relatedness of community across the entire phylogenetic tree, but the central focus in this study was on the relative contribution of an individual species or a range of species on the rank abundance distribution (app. B, available online), which is less interpretable when using MPD, PSV, PSR, or NRI. We did find that the integration of the evolutionary distinctiveness (ED) metric with the species rank abundance distribution—that is, species abundance rank–standardized ED—had a similar ability to assess relative contribution of individual species to community PD when compared with the SAPD; these results are presented in appendix B.

Phylogenetic Signal Analysis of Species Abundance

The SAPD curve analyses above consider the contribution of rare species to the overall community PD. Quantifying the phylogenetic signal in species rank abundance provides a complementary analysis that addresses the degree to which closely related species have similar rank abundances. We quantified the phylogenetic signal in rank abundance data of all species and of only rare species in each plot, using the K statistic proposed by Blomberg et al. (2003). The abundance data were $\log_{10}$ transformed before analysis to homogenize variances. The K statistic provides a comparison of the observed and expected level of phylogenetic signal under the assumption of Brownian motion trait evolution given a phylogenetic tree (Blomberg et al. 2003). If $K > 1$, then the abundance data have more phylogenetic signal than expected from Brownian motion, whereas if $K < 1$, then the abundance data have less phylogenetic signal than expected. We assessed the significance of the phylogenetic signal by randomly shuffling species abundance among species 999 times and calculating 95% confidence intervals.

Phylogenetic Similarity within and between Common and Rare Species

The last aim of this study was to calculate the phylogenetic similarity within and between groups of common and rare species in each forest plot. To accomplish this, we first calculated the phylogenetic dispersion within the group of common species and within the group of rare species, using the nearest taxon index (NTI). The NTI is a standardized effect size (SES) of the mean nearest phylogenetic neighbor distance (MNND) between species in a community (Webb et al. 2002; Swenson et al. 2007) or, in this case, the mean nearest neighbor distance between common species or between rare species. We calculated the phylogenetic similarity between the groups of common and rare species using a phylogenetic beta diversity metric based on nearest neighbor distances (D_{nn}; Swenson 2011; Swenson et al. 2011):

$$\mathrm{D}_{\mathrm{nn}} = \frac{\sum_{i=1}^{n} \min \delta_{i\mathrm{r}} + \sum_{j=1}^{m} \min \delta_{j\mathrm{c}}}{2}, \qquad (5)$$

where $\min \delta_{i\mathrm{r}}$ is the nearest phylogenetic neighbor from common species i to rare species, $\min \delta_{j\mathrm{c}}$ is the nearest phylogenetic neighbor from rare species j in common species, and m and n are the number of common and rare species, respectively. The SES of D_{nn} and MNND, SES (D_{nn}), and NTI, respectively, were calculated by implementing a null model analysis. The null model shuffled the names of taxa across the tips of the phylogeny 999 times. The SES (D_{nn}) and NTI were calculated as the observed D_{nn} or MNND minus the mean value of the 999 randomizations divided by the standard deviation of the 999 null values. The NTI and SES (D_{nn}) consider only the nearest phylogenetic neighbors and indicate the "terminal" phylogenetic structure. The NTI and SES (D_{nn}) therefore complement the SAPD curve and the standardized ED metrics in this study, which are more heavily influenced by the "basal" phylogenetic structure.

Most statistical analyses were performed in the free software R, version 2.9.0 (R Development Core Team 2009), Blomberg's K was computed using the R package "picante" (Kembel et al. 2010), Mann-Kendall tests were performed

Table 1: Estimates of the breakpoints in the species abundance rank–standardized phylogenetic diversity (SAPD) curves for the 15 plots in this study

Forest dynamics plot, breakpoints	95% CI	supF	*P*	$\mathrm{AIC_L}$ (× 10^3)	AIC_ψ (× 10^3)	ER (ψ)
Changbaishan:						
45.5	43.6, 47.4	16.3	<.001	.630	.608	>80,000
Gutianshan:						
91.7	85.9, 97.5	95.9	<.001	1.947	1.824	>80,000
141.4	134.6, 148.2	10.6	<.001		1.814	115.6
Dinghushan:						
40.9	39.3, 42.5	99.3	<.001	2.706	2.621	>80,000
57.0	54.8, 59.2	74.1	<.001		2.426	>80,000
Xishuangbanna:						
259	252.7, 265.3	862.2	<.001	6.740	6.020	>80,000
Sinharaja:						
185.4	181.4, 189.4	49.9	<.001	2.715	2.636	>80,000
Lambir:						
950.4	943.2, 957.5	268.4	<.001	15.637	15.184	>80,000
984.4	977.9, 990.9	230.9	<.001			
1,075.0	1,067.0, 1,082.0	243.1	<.001		14.965	>80,000
Pasoh:						
546	530.6, 561.4	348.8	<.001	10.680	10.178	>80,000
Yasuní:						
499.7	492, 507.4	3,143.3	<.001	16.417	14.332	>80,000
BCI:						
138.9	135.2, 142.6	88.2	<.001	3.820	3.747	>80,000
208.6	205.1, 212.1	51.7	<.001		3.329	>80,000
Huai Kha Khaeng:						
59.5	57.3, 61.72	75.1	<.001	3.689	3.577	>80,000
149.3	146.3, 152.3	.6	.527		3.547	>80,000
223.2	220.7, 225.6	33.5	<.001		3.090	>80,000
La Planada:						
81.1	77.7, 84.6	71.5	<.001	3.003		
150.1	146.1, 154.1	23.0	<.001		2.673	>80,000
Fushan:						
8.0	3.9, 12.1	5.3	.006	1.352	1.337	1,900.7
Palanan:						
122.2	115.7, 128.7	50.1	<.001	3.893	3.842	>80,000
198.0	191.1, 204.9	38.4	<.001		3.631	>80,000
Mudumalai:						
50.1	43.5, 56.7	9.9	<.001	.761	.746	1,299.9
Luquillo:						
124.9	122, 127.8	30.3	<.001	1.763	1.716	>80,000

Note: supF is a statistic used to test the significance of every potential breakpoint (Andrews 2003); $\mathrm{AIC_L}$ is the Akaike Information Criterion value of the linear model; AIC_ψ is the AIC value of the piecewise regression model with one, two, or three breakpoints; and ER (ψ) is the evidence ratio, to be interpreted as the evidence against the linear model or the j-breakpoints piecewise regression model against the $j-1$ breakpoint piecewise regression model. Blank cells indicate no converged j-breakpoints piecewise regression model. BCI, Barro Colorado Island.

using the R package "Kendall" (McLeod 2011), piecewise regressions were implemented using the R package "segmented" (Muggeo 2011), and the significance of breakpoints were evaluated using the R package "strucchange" (Zeileis et al. 2011). Finally, the NTI and SES of D_{nn} were calculated using the software "phylocom" (Webb et al. 2008).

Results

We first partitioned the SAPD curve for each forest plot into several subseries using piecewise regressions to dissect the presence of multiple trends (table 1). For example, rare species (with fewer than one individual per hectare; species rank, 188–305) in BCI were decomposed into two sub-

Table 2: Mann-Kendall trend test of common species and rare species in the forest dynamics plot communities

Forest dynamics plot	Common species	Rare species
Changbaishan	−.308 (.285) (2–34)[a]	.118 (.703) (35–51)[a]
	−.848 (.057) (2–45)[b]	.733 (.985)* (46–51)[b]
	−.226 (.378) (2–102)[a]	.629 (.968) (103–158)[a]
Gutianshan	−.369 (.347) (2–92)[b]	.765 (.994)** (93–141)[b]
		−.456 (.346) (142–158)[b]
Xishuangbanna	−.746 (.020)* (2–238)[a]	.542 (.927) (239–467)[a]
	−.786 (.010)* (2–259)[b]	.494 (.900) (260–467)[b]
Sinharaja	−.267 (.282) (2–161)[a]	.418 (.880) (162–205)[a]
	−.340 (.202) (2–185)[b]	.544 (.960) (186–205)[b]
	−.455 (.152) (2–781)[a]	.408 (.823) (782–1,191)[a]
	−.575 (.053) (2–950)[b]	.482 (.904) (950–984)[b]
Lambir		−.940 (.002)** (985–1,075)[b]
		.735 (.985)* (1,075–1,191)[b]
Pasoh	−.352 (.261) (2–533)[a]	.747 (.988)* (534–812)[a]
	−.332 (.249) (2–546)[b]	.744 (.990)* (547–812)[b]
Yasuní	−.738 (.021) (2–678)[a]	.634 (.940) (679–1,092)[a]
	−.907 (.001)*** (2–500)	.649 (.976)* (501–1,092)[b]
	−.402 (.392) (2–187)[a]	−.712 (.127) (187–304)[a]
BCI	−.679 (.083) (1–139)[b]	−.827 (.023)* (210–304)[b]
	.747 (.995)** (140–209)[b]	
	−.695 (.066) (2–96)[a]	−.056 (.518) (97–276)[a]
	−.878 (.005)** (2–60)[b]	.661 (.978)* (61–149)[b]
Huai Kha Khaeng		−.902 (.012)* (150–223)[b]
		.774 (.996)** (224–276)[b]
	.091 (.626) (2–155)[a]	−.667 (.122) (156–219)[a]
La Planada	−.614 (.090) (2–81)[b]	−.708 (.097) (151–219)[b]
	.767 (.992)* (82–150)[b]	
	.067 (.541) (2–102)[a]	−.087 (.536) (103–209)[a]
Dinghushan	−.822 (.015)* (2–41)[b]	.213 (.699) (58–209)[b]
	.294 (.762) (42–57)[b]	
Fushan	−.526 (.095) (2–77)[a]	.182 (.738) (78–109)[a]
	.500 (.781) (2–8)[b]	−.619 (.037) (9–109)[b]
	.334 (.861) (2–235)[a]	−.040 (.568) (236–321)[a]
Palanan	−.346 (.265) (2–122)[b]	−.404 (.313) (199–321)[b]
	.584 (.939) (123–198)[b]	
Mudumalai	.281 (.761) (2–22)[a]	.165 (.675) (23–66)[a]
	.381 (.992)* (2–50)[b]	−.662 (.162) (51–66)[b]
Luquillo	−.285 (.358) (2–82)[a]	−.011 (.601) (83–136)[a]
	−.493 (.087) (2–125)[b]	.600 (.932) (126–136)[b]

Note: The first number in each cell is the z value from the Mann-Kendall trend test, the number in the first set of parentheses indicates the probability that an observed z value in a subseries is greater than that in null species rank abundance–standardized phylogenetic diversity (SAPD) curves, and the range in the second set of parentheses indicates the species rank range. BCI, Barro Colorado Island.

[a] Species rank of common species and rare species, according to Hubbell and Foster (1986), who defined rare species as having fewer than one individual per hectare.

[b] Partitioning of the SAPD curve into several subseries by piecewise regression in order to identify multiple trends in a single SAPD curve.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

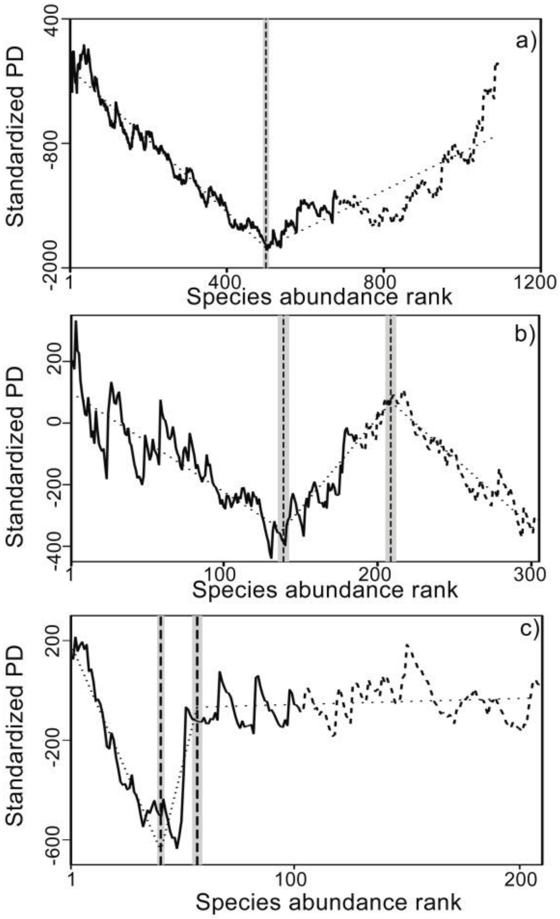

Figure 2: Three typical species abundance rank–standardized phylogenetic diversity (SAPD) curves for three forest dynamics plots. SAPD curves here describe the following: *a*, Yasuní, with a significant upward trend for rare species, indicating little relatedness between common and rare species; *b*, Barro Colorado Island (BCI), with a significant downward trend of rare species, indicating close relatedness between common and rare species; and *c*, Dinghushan, with random fluctuation of rare species along species abundance rank, indicating random relatedness between common and rare species. The solid line represents common species in the curves, while the dashed line stands for rare species (<1 individual/ha). Dashed vertical lines and shared zones indicate breakpoints and associated 95% CIs, respectively. The dotted lines are the segmented linear regression curves.

series by piecewise regression: the first part of the rare species region of the rank abundance distribution (species rank, 188–209) exhibited a significant increasing trend, whereas the second part of rare species region of the rank abundance distribution (species rank, 210–305) showed a significant decreasing trend (tables 1, 2). The significance of all breakpoints between neighboring subseries was assessed using piecewise regression, the supF statistic, and the evidence ratio (table 1). All 15 SAPD curves were partitioned into two to four subseries by piecewise regression (fig. 2; fig. C1, available in a zip file).

Next we quantified the significance of the trends for the groups of common and rare species in the forest plots, following the description of rarity used by Hubbell and Foster (1986), using a Mann-Kendall trend test to account for the autocorrelated nature of stdPD (table 2). Ultimately, we found no general result regarding the contribution of rare species to community PD in the 15 forest dynamic plots (FDPs; table 2). In particular, our observed SAPD curves for the 15 FDPs revealed that the contribution of rare species to community PD can range from significantly less than expected to significantly greater than expected (fig. 2; table 2; app. C, available in a zip file): the contribution of rare species to community PD in six FDPs (Changbaishan, Gutianshan, Xishuangbanna, Pasoah, Lambir, and Yasuní) was significantly greater than expected, whereas the contribution of rare species to community PD in BCI was significantly less than expected, the contribution of rare species in seven FDPs (Palanan, Dinghushan, Luquillo, Mudumalai, La Planada, Sinharaja, and Fushan) was not significantly different from expected, and rare species of Huai Kha Khaeng (HKK) showed multiple trends. We assigned rare species from the Xishuangbanna plot to the group supporting niche differentiation because most of the rare species (ranging from 259 to 290 and from 353 to 468) showed an increasing trend and there was a decreasing trend for rare species (species rank, 291–352) that was caused by close relatedness among rare species (see the reverse stdPD between species rank 291–352 in fig. E1*d*, available in a zip file).

Our second central question in this study was whether there is phylogenetic signal in abundance in the 15 FDPs. Species abundance in 11 FDPs (all except Luquillo, La Planada, Dinghushan, and Mudumalai) exhibited significant phylogenetic signals, indicating that closely related species tended to have similar abundances (table 4). In the Luquillo, La Planada, Dinghushan, and Mudumalai FDPs, abundance was randomly distributed with respect to phylogeny (table 4).

Our third and final question concerned the phylogenetic similarity within and between common and rare species in each of the 15 FDPs. To answer this question, we quantified the phylgenetic dispersion within and between common species and rare species groups in each FDP, using the nearest neighbor metrics NTI and D_{nn}. We found that common species were phylogenetically clustered in nine FDPs (Changbaishan, Xishuangbanna, Sinharaja, Pasoh, Yasuní, BCI, Huai Kha Khaeng, Luquillo, and Lambir; tables 3, 5) and were phylogenetically overdispersed in six FDPs (Gutianshan, Dinghushan, La Planada, Fushan, Palanan, and Mudumalai; tables 3, 5). Similarly, we also found that rare species were phylogenetically overdispersed

Table 3: Standardized phylogenetic diversity (stdPD) for common species and rare species

Forest dynamics plot	stdPD of common species	stdPD of rare species
Changbaishan	−151 (.225) (1–34)[a]	222 (.816) (35–52)[a]
	−436 (.003)** (1–45)[b]	329 (.957) (46–51)[b]
Gutianshan	−187 (.224) (1–102)[a]	291 (.834) (103–159)[a]
	−264 (.163) (1–92)[b]	238 (.795) (93–141)[b]
		−25 (.477) (142–159)[b]
Dinghushan	−89 (.040) (1–102)[a]	189 (.708) (103–210)[a]
	−517 (.042) (1–41)[b]	51 (.542) (58–210)[b]
	306 (.913) (42–57)[b]	
Xishuangbanna	−722 (.026) (1–238)[a]	630 (.958) (239–468)[a]
	−921 (.002)** (1–259)[b]	724 (.988)* (260–468)[b]
Sinharaja	−528 (.031) (1–161)[a]	607 (.976)* (162–205)[a]
	−409 (.017)* (1–185)[b]	61 (.557) (186–205)[b]
Lambir	−377 (.111) (1–781)[a]	131 (.629) (782–1,192)[a]
	−457 (.067) (1–950)[b]	731 (.984)* (951–984 and 1,076–1,192)[b]
		−698 (.004)** (985–1,075)[b]
Pasoh	−600 (.027) (1–533)[a]	665 (.968) (534–813)[a]
	−528 (.033) (1–546)[b]	706 (.979)* (547–813)[b]
Yasuní	−1,337 (.002)** (1–678)[a]	948 (.987)* (679–1,093)[a]
	−1,768 (.002)** (1–500)[b]	1,280 (.998)** (501–1,093)[b]
BCI	−59 (.590) (1–187)[a]	−434 (.092) (188–305)[a]
	−373 (.119) (1–139)[b]	−605 (.024)* (210–305)[b]
	811 (.992)** (140–209)[b]	
Huai Kha Khaeng	−470 (.047) (1–96)[a]	216 (.773) (97–278)[a]
	−553 (.013)* (1–60)[b]	750 (.999)*** (61–149 and 224–278)[b]
		−343 (.112) (150–223)[b]
La Planada	240 (.780) (1–155)[a]	−509 (.099) (156–220)[a]
	−605 (.070) (1–81)[b]	−543 (.064) (151–219)[b]
	1,055 (.997)** (82–150)[b]	
Fushan	−80 (.359) (1–77)[a]	−110 (.361) (78–110)[a]
	374 (.951) (1–8)[b]	−296 (.034) (8–110)[b]
Palanan	132 (.715) (1–235)[a]	−152 (.284) (236–323)[a]
	−213 (.194) (1–122)[b]	−293 (.146) (199–323)[b]
	159 (.727) (123–198)[b]	
Mudumalai	21 (.528) (1–22)[a]	−165 (.101) (23–67)[a]
	152 (.953) (1–50)[b]	−28 (.415) (51–67)[b]
Luquillo	−128 (.348) (1–82)[a]	162 (.701) (83–137)[a]
	−356 (.050) (2–125)[b]	347 (.935) (126–137)[b]

Note: The first number in each cell is the stdPD value, the number in the first set of parentheses indicates the probability of the observed PD being greater than that of the null communities, and the range in the second set of parentheses indicates the species rank. BCI, Barro Colorado Island.

[a] Species rank of common species and rare species, according to Hubbell and Foster (1986), who define rare species as having fewer than one individual per hectare.

[b] Partitioning of the species abundance rank–stdPD curve into several subseries by piecewise regression in order to identify multiple trends in a single species abundance rank–stdPD curve.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

in 11 FDPs (Changbaishan, Gutianshan, Dinghushan, Pasoh, HKK, Xishuangbanna, Fushan, Yasuní, Palanan, Sinharaja, and Lambir; tables 3, 5) and phylogenetically clustered in three FDPs (BCI, La Planada, and Mudumalai). The SES of D_{nn} of all plots except Luquillo was lower than expected (table 5), indicating that rare and common species are phylogenetically dissimilar.

Discussion

Despite the range of hypotheses that have been proposed to explain the assembly of common and rare species into communities, the question of whether spatial or temporal niche differentiation of species promotes their co-occurrence remains an open one (Keddy 1989; Clark et al. 2007).

Taking a phylogenetic approach, we asked three central questions. First, we asked what is the contribution of rare species to the overall PD of a community. It is predicted that if niche differentiation facilitates the co-occurrence of rare species with common species, then rare species are expected to contribute more to the community PD than would be expected by chance. Second, we asked whether there is phylogenetic signal in the abundance of species in communities. If there is phylogenetic signal, then rare species tend to be on average distantly related to common species. Finally, we asked about the phylogenetic similarity within and between the common and rare species in a community. A niche differentiation hypothesis predicts that rare species should be phylogenetically distinct from common species, thereby permitting their co-occurrence. Thus, we predicted that if niche differentiation is occurring, there should be phylogenetic signal in species abundance and rare species should be distantly related to common species and to each other.

The degree to which rare species contribute to the overall PD of a community was expected to reflect phylogenetic dissimilarity between common and rare species and also between rare species themselves. The contribution of rare species to the overall community PD was quantified using a SAPD curve. In six of the forest plots (Changbaishan, Gutianshan, Xishuangbanna, Pasoh, Lambir, and Yasuní), we found a significant increasing trend at the end of the SAPD curve, indicating that rare species contribute more than expected to overall community PD. This suggests that rare species are generally phylogenetically distinct from common species and from each other, providing partial support for the niche differentiation hypothesis. In the BCI forest plot we found the opposite result, with rare species contributing significantly less than expected to overall community PD, as indicated by a decreasing trend in the SAPD curve. This result shows that rare species in BCI forest areas typically come from clades that also contain common species and therefore are likely to be less differentiated in their niches. Finally, in the Dinghushan, Palanan, Luquillo, Fushan, Sinharaja, La Planada, and Mudumalai forests, the contribution of rare species to overall community PD was not different from random, while in the Huai Kha Khaeng (HKK) forest plot there was a mixture of significantly increasing and decreasing trends in the SAPD. Thus, in nine of the 15 forest plots, we failed to support the prediction of the niche differentiation hypothesis.

We found that among gap-dominated FDPs, six (Changbaishan, Gutianshan, Xishuangbanna, Pasoh, Lambir, and Yasuní) of nine FDPs showed evidence supporting the niche differentiation hypothesis. Conversely, all FDPs with dominant disturbance (Dinghushan, Palanan, Luquillo, Fushan, HKK, and Mudumalai) rejected the niche differentiation hypothesis. That the niche differentiation hypothesis was not supported for nine of the forests may be explained by different types of disturbance in these plots, such as frequent typhoons in Fushan and Palanan and widespread fires and browsing of elephants in Mudumalai. It is likely that disturbance selects for more closely related species with similar resistances to disturbances (Warwick and Clarke 1998; Abellán et al. 2006; Helmus et al. 2010), which supports an environmental filtering hypothesis (Webb 2000; Vamosi et al. 2009).

Our second main question was whether there is phylogenetic signal in the relative abundances of species in the 15 forest plots studied. The results of the phylogenetic signal analyses generally corroborated the results of the SAPD analyses. In particular, we expected that phylogenetic signal in abundance would cause an increasing trend in the SAPD curve. In each of the forest plots with a significant increasing trend in the SAPD curve, we detected phyogenetic signal in abundance (table 4; figs. 2, C1, available in a zip file). Thus, phylogenetic signal in relative abundance does influence the shapes of the SAPD curves.

Our last set of analyses quantified the phylogenetic similarity within and between groups of common and rare species in each of the 15 forest plots. The SES values in the between-group similarity analyses (SES (D_{nn})) were

Table 4: Phylogenetic signals in species abundance data

Forest dynamics plot	Value
Changbaishan	.295 (.01)
Gutianshan	.185 (.001)
Xishuangbanna	.227 (.032)
Sinharaja	.176 (.001)
Lambir	.104 (.001)
Pasoh	.103 (.001)
Yasuní	.074 (.001)
BCI	.099 (.001)
Huai Kha Khaeng	.199 (.001)
La Planada	.116 (.051)
Dinghushan	.136 (.059)
Fushan	.217 (.001)
Palanan	.128 (.021)
Mudumalai	.150 (.375)
Luquillo	.144 (.132)

Note: The data are K values, which indicate the comparison between the observed and the expected phylogenetic signal under the assumption of Brownian motion, followed by the numbers in parentheses, which indicate the probability that the observed phylogenetic signal is greater than the null expectation generated by randomly shuffling the species abundances across the tips of the phylogeny. BCI, Barro Colorado Island.

almost always negative, indicating that common and rare species tended to be phylogenetically dissimilar (table 5), but many of these results were not statistically significant. These results therefore only weakly corroborate the results of the above analyses, showing that on average, rare species are phylogenetically distinct from common species in the forests studied. This further supports the prediction of niche differentiation hypotheses, where common and rare species are expected to be dissimilar. It is also interesting to note that the results from the within-common-group analyses generally had positive NTI values and rare species had negative values (table 5). Thus, common species are typically phylogenetically clustered and rare species are phylogenetically overdispersed in the forests studied. This supports the prediction of niche differentiation hypotheses, where rare species are not only distinct from common species but also distinct from one another. Further, this demonstrates why measuring phylogenetic signal in relative abundances alone does not provide a complete picture of how commonness and rarity relate to phylogeny.

When the three lines of evidence—the SAPD curve, the phylogenetic signal analyses, and the phylogenetic similarity analyses—are considered together, we believe that the SAPD curve analyses provide the best window into the contribution of rare species to community PD and their phylogenetic similarity with respect to common species. This is because the SAPD curve can be used to detect fine-scale shifts in how abundance relates to phylogeny. This level of resolution is difficult to achieve by using measures of phylogenetic signal or phylogenetic similarity that effectively average over the entire phylogeny. For example, the less than expected contribution of rare species to community PD in the BCI plot according to the SAPD curves seems to contradict the evidence from the phylogenetic signal results for the plots. Upon closer examination, we see that rare species in the BCI plot had less PD than expected by chance (table 3) and rare species were phylogenetically clustered (table 5). Thus, by combining the similarity and signal analyses, we can link these results back to those from the SAPD curve. In other words, phylogenetic signal is likely detected in this plot because of species ranking from 1 to 131 and species ranking from 132 to 210 being distantly related to one another (fig. 2*b*) and rare species being phylogenetically clustered (table 5) such that they cumulatively contribute little to the community PD.

Conclusions

In summary, rare species were found to be distantly related to common species and to have significantly higher cumulative PD than expected by chance in six of the nine gap-dominated forests, supporting the predictions made by niche differentiation hypotheses. We therefore inferred

Table 5: Phylogenetic similarity within and between common and rare species for 15 forest dynamics plots

		NTI	
Forest dynamics plot	SES of D_{nn}	Common species	Rare species
Changbaishan	−1.620	.082	−.948
Gutianshan	−1.052	−.016	−1.083
Dinghushan	−.217	−.509	−.373
Xishuangbanna	−.169	1.009	−1.102
Sinharaja	−.624	1.514	−1.199
Lambir	−2.872**	.645	−.579
Pasoh	−.182	1.903*	−1.749*
Yasuní	−3.304***	2.358***	−1.096***
BCI	−.659	.453	.226
Huai Kha Khaeng	−3.323***	.941	−.059
La Planada	−1.174	−.971	1.092
Fushan	−.367	−.284	−.215
Palanan	−.534	−.976	−.051
Mudumalai	−1.633	−.749	1.293
Luquillo	.325	1.018	−.354

Note: Nearest taxon index (NTI) of common and rare species and standardized effect size of mean nearest neighbor distance (SES of D_{nn}) between common species and rare species. BCI, Barro Colorado Island.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

that in these six forests, rare species may have spatially or temporally divergent niches that permit their co-occurrence with common species in these forests. In contrast, rare species in six disturbance-dominated forests and three gap-dominated forests were found to be closely or randomly related to common species and have less cumulative PD or ED, meaning that niche differentiation hypotheses are rejected and the environmental filtering hypothesis is supported. Along with these biological inferences, we have presented a novel methodology for examining the contribution of increasingly rare or increasingly common species to community PD that provides finer-scale insights that cannot be achieved by using metrics that average over all species in a community.

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