Functional traits of tree species with phylogenetic signal co-vary with environmental niches in two large forest dynamics plots

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Abstract

Aims

While using phylogenetic and functional approaches to test the mechanisms of community assembly, functional traits often act as the proxy of niches. However, there is little detailed knowledge regarding the correlation between functional traits of tree species and their niches in local communities. We suggest that the co-varying correlation between functional traits and niches should be the premise for using phylogenetic and functional approaches to test mechanisms of community assembly. Using functional traits, phylogenetic and environmental data, this study aims to answer the questions: (i) within local communities, do functional traits of co-occurring species co-vary with their environmental niches at the species level? and (ii) what is the key ecological process underlying community assembly in Xishuangbanna and Ailaoshan forest dynamic plots (FDPs)?

Methods

We measured seven functional traits of 229 and 36 common species in Xishuangbanna and Ailaoshan FDPs in tropical and subtropical China, respectively. We also quantified the environmental niches for these species based on conditional probability. We then analyzed the correlations between functional traits and environmental niches using phylogenetic independent contrasts. After examining phylogenetic signals of functional traits using Pagel's λ, we quantified the phylogenetic and functional dispersion along environmental gradients within local tree communities.

Important Findings

For target species, functional traits do co-vary with environmental niches at the species level in both of the FDPs, supporting that functional traits can be used as a proxy for local-scale environmental niches. Functional traits show significant phylogenetic signals in both of the FDPs. We found that the phylogenetic and functional dispersion were significantly clustered along topographical gradients in the Ailaoshan FDP but overdispersion in the Xishuangbanna FDP. These patterns of phylogenetic and functional dispersion suggest that environmental filtering plays a key role in structuring local tree assemblages in Ailaoshan FDP, while competition exclusion plays a key role in Xishuangbanna FDP.

Keywords: forest dynamics plot, local scale, phylogenetic independent contrast, phylogenetic signal, phylogenetic dispersion, functional dispersion

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INTRODUCTION

Plant functional traits are the traits that are linked to organismal performance in a given environment and therefore are expected to provide critical information regarding how organismal form and function relate to resource acquisition and ecological strategies (Díaz and Cabido 2001; McGill *et al.* 2006; Lavorel *et al.* 1997; Westoby *et al.* 2002). A large body of the literature on functional traits has developed over the past two decades. The expected trait-performance linkage in these studies has resulted in implicit use of traits as surrogates for local-scale niches by many researchers (e.g. Ackerly *et al.*

2006; Böhning-Gaese *et al.* 2003; Slingsby and Verboom 2006; Swenson *et al.* 2007; Violle and Jiang 2009). Thus it is critical for all downstream analyses and inferences that the traits measured in these studies and others are linked to environmental niches at the species level.

Linking traits to niches is important not only for functional trait-based ecology but also for community phylogenetics. In recent years there has been a tremendous interest in using phylogenetic and functional approaches in unison to infer the ecological processes underlying species coexistence and community assembly (Swenson 2013; Webb *et al.* 2002; Vamosi *et al.* 2009). Many of previous studies in this field simply assumed phylogenetic relatedness was a solid proxy of niche similarity, but this assumption is now generally greatly debated (Swenson 2013). Rather, researchers now often quantify phylogenetic signal in functional trait data to determine if phylogenetic relatedness actually does serve as a proxy for niche similarity. In these studies, if phylogenetic signal in functional traits is detected, then phylogenetic dispersion (clustering or overdispersion) is often used to infer an ecological process (environmental filtering or biotic interactions) that plays a dominant role in structuring community composition. For example, if functional traits have phylogenetic signal, phylogenetic clustering can indicate that environmental filtering is important (e.g. Kraft *et al.* 2010; Swenson *et al.* 2006; but see Mayfield and Levine 2010). Thus, the phylogenetic approach, when there is phylogenetic signal in traits, effectively uses the same inference pathway as that used by ecologists directly using functional trait dispersion patterns (e.g. Ackerly and Cornwell 2007; Garnier and Navas 2012; Kraft *et al.* 2008; Siefert *et al.* 2013). Importantly, both approaches make the implicit assumption that functional traits are actually indicative of species niches.

Given the heavy reliance of phylogenetically and functional trait-based community ecology on trait-niche relationships, investigations that explicitly link traits to the environment a species occupies are critical for a mechanistic understanding of community structure. Such investigations could then lead to the linkage of niches to traits to phylogenies and ultimately towards understanding what patterns of trait and phylogenetic dispersion in communities do or do not tell us regarding the mechanisms underlying community structure. Without forging such explicit linkages it is possible that we may be wrongly using functional trait data as a proxy of niche differentiation on local scales when investigating community patterns.

Here, we integrate functional trait data, well-resolved molecular phylogenies and topographical data from two large forest dynamics plots in Chinese tropical and subtropical forests to test whether there are explicit linkages between traits, niches, phylogenetic relatedness and community phylogenetic and functional trait dispersion patterns. Specifically, we first ask: is there a significant relationship between traits and environmental niches? We address this question by quantifying the correlation between functional traits and topographical niches using phylogenetic independent contrasts where

topographical niches are based upon four attributes (aspect, convexity, elevation and slope). We then ask whether the traits linked to topographical niches have phylogenetic signal. Lastly, we ask whether we can formulate an explicit linkage between traits and niches, the evolutionary history of traits and the phylogenetic and functional dispersion of tree communities in the two forest dynamics plots along local-scale topological gradients. We utilize two forest dynamics plots in highly dissimilar environments to determine whether there are any consistencies between different types of forests.

MATERIALS AND METHODS

Study sites and target species

This study was conducted in the 20-ha Xishuangbanna Forest Dynamics Plot (FDP) (21°36′N, 101°34′E) and the 6-ha Ailaoshan FDP (24°32′N, 102°01′E) located in the Yunnan Province, southwest China (Fig. 1). The Xishuangbanna FDP is characterized as a seasonal tropical rainforest and is dominated by large individuals of *Parashorea chinensis* (Dipterocarpaceae). The climate is strongly seasonal with distinct alterations between the wet season (from May to October) and the dry season (from November to April). The annual mean precipitation is 1493 mm, of which 1256 mm (84%) occurs in the wet season (Cao *et al.* 2006). Elevation within this FDP ranges from 708.2 to 869.1 m. The Ailaoshan FDP is characterized as an evergreen broadleaved forest and it is dominated by *Castanopsis wattii* (Fagaceae) and *Lithocarpus xylocarpus* (Fagaceae). The annual mean precipitation is 1931 mm with 85% of the annual precipitation falling between May and October (Gong *et al.* 2011). Elevation within this FDP ranges from 2490 to 2530 m. The Xishuangbanna and Ailaoshan FDPs were established in 2007 and 2008, respectively, where all freestanding woody stems ≥1 cm diameter at 130 cm from the ground (DBH, diameter at breast height) were measured, mapped, tagged and identified to species (Gong *et al.* 2011; Lan *et al.* 2009). There are 468 and 76 tree and shrub taxa in the Xishuangbanna and Ailaoshan FDPs, respectively. In this study, we selected 229 and 36 common tree species with more than 20 individuals (Xishuangbanna plot) and 6 individuals (Ailaoshan plot) ≥1 cm in diameter as the target species for investigation, in order to assure robust estimations of environmental niches.

Phylogenetic tree reconstruction

We generated two molecular phylogenetic trees using 229 and 36 target species for Xishuangbanna FDP and Ailaoshan FDP, respectively. The molecular phylogenies were generated from four sequence regions—*rbcL*, *matK*, *trnH-psbA* and ITS (Kress *et al.* 2009). The *rbcL* and *matK* DNA region alignment follows the methods described in Kress *et al.* (2009, 2010). The *trnH-psbA* and ITS DNA regions were aligned with in families using software package SATé (Liu *et al.* 2012). The DNA supermatrix was then analyzed using RAxML (Stamatakis 2006) via the CIPRES supercomputer cluster (Miller *et al.* 2009) to infer a maximum likelihood phylogeny using the APG III
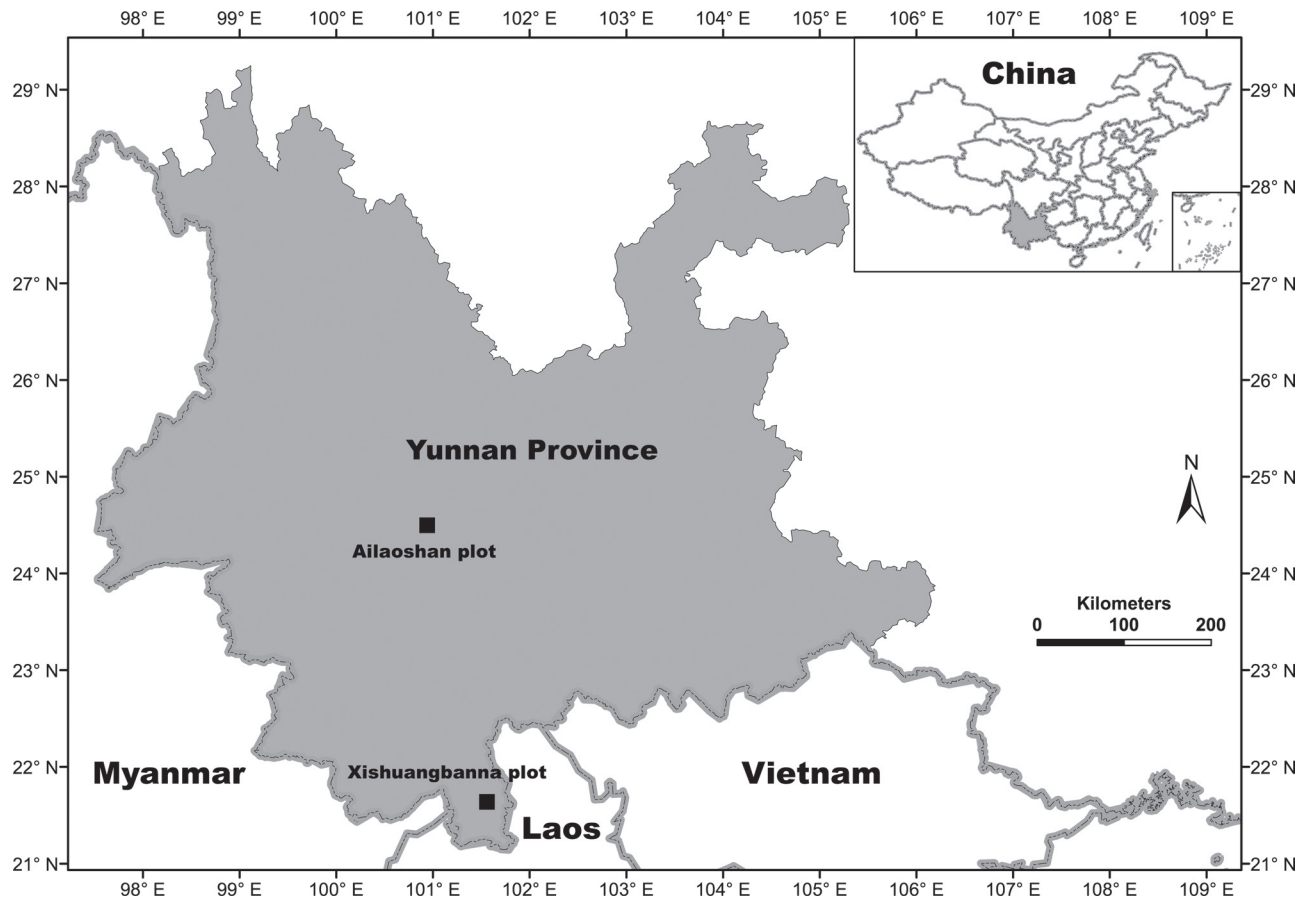
Figure 1: geographic location of the Ailaoshan and Xishuangbanna forest dynamics plots in Yunnan Province, China.

phylogenetic tree as a constraint or guide tree as described in Kress *et al.* (2010). A constraint tree approach helps assure the basal topology of a molecular community phylogeny is consistent with the global working hypothesis for the angiosperm basal topology. Node support was estimated using bootstrap values with nodes with <50% support being collapsed into soft polytomies. Finally, an ultrametric tree was obtained using the non-parametric rate smoothing approach in the r8s software package (Sanderson 2003).

Trait selection and measurement

Seven functional traits for the target species in the Xishuangbanna and Ailaoshan FDPs were selected and measured following globally standardized protocols (Cornelissen *et al.* 2003) with the exception of leaf chlorophyll content and stem specific resistance. These functional traits (Table 1) are believed to represent fundamental functional trade-offs in leaves, wood and seeds among tree species (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013; Westoby 1998; Westoby *et al.* 2002). Leaf area has important consequences for the leaf energy and water balance (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013); specific leaf area (SLA) represents a trade-off between construction costs photosynthetic capacity and leaf life spans (Cornelissen *et al.* 2003; Wright

et al. 2004); leaf chlorophyll content is directly involved in the photosynthesis calculation of plants (Coste *et al.* 2010; Gitelson *et al.* 2003); leaf thickness is related to leaf life span, litter decomposition and nutrient cycling (Onoda *et al.* 2011; Pérez-Harguindeguy *et al.* 2013). Maximum tree DBH represents adult size and adult light niche (Cornelissen *et al.* 2003). Wood density, as a trade-off between volumetric growth rates and mechanical strength, is traditionally determined by calculating the volume and mass of wood cores. While this method is accurate it can be a very destructive measurement that could alter the growth of individuals being permanently monitored in the FDP (Isik and Li 2003). Isik and Li (2003) have used a new device termed a Resistograph (Rinntech Co., Germany) for rapid assessment of stem specific resistance. It has been shown that stem specific resistance is strongly correlated with wood density (Isik and Li 2003) and it is frequently used by horticulturalists for non-destructive analyses of stem health and density. Therefore, we used the stem specific resistance to represent the similar trade-off as wood density in this study. Seed mass is important traits related to the dispersal of species and their regeneration niche (Cornelissen *et al.* 2003).

Leaf traits were quantified from randomly collected mature leaf samples (relatively young but fully expanded and hardened) from the outer canopy of adult trees without obvious

Table 1: correlation coefficients of phylogenetically independent contrasts between functional traits and topographical niches for 36 and 229 tree species in the Ailaoshan and Xishuangbanna forest dynamics plots, respectively

	SM	DBH$_{max}$	WR	LT	LA	SLA	LC
Ailaoshan plot							
Aspect niche	0.164*	0.128*	−0.281**	−0.410***	0.375***	0.284**	−0.407*
Convexity niche	−0.050*	−0.104	−0.077	0.078	−0.399**	0.070	0.144*
Elevation niche	0.229**	0.145	−0.403**	−0.233*	−0.184*	0.010	−0.218
Slope niche	0.195**	−0.001	−0.226**	0.036	−0.308*	−0.170*	0.046
Xishuangbanna plot							
Aspect niche	−0.014*	−0.064*	0.087*	−0.069*	−0.025*	−0.120*	−0.042
Convexity niche	−0.074*	−0.040*	0.104*	−0.110*	−0.108*	0.018*	−0.025
Elevation niche	−0.019*	0.009	0.122*	−0.049	−0.088*	−0.098	0.128*
Slope niche	0.045*	−0.137	−0.119	−0.182	−0.093	−0.022	0.156*

SM = seed mass (milligram); DBH$_{max}$ = maximum DBH (millimeter); WR = wood resistance (N); LT = leaf thickness (millimeter); LA = leaf area (square centimeter); SLA = specific leaf area (square centimeter per gram); LC = leaf chlorophyll content (SPDA). ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

symptoms of pathogen or herbivore attack and without substantial cover of epiphylls (Cornelissen *et al.* 2003). More than 25 leaves were sampled from five individuals of each taxon. Each leaf was scanned as a computer image and leaf area (square centimeter) was measured by using ImageJ software (Abramoff *et al.* 2004) then dried to a constant weight at 60°C. SLA (square centimeter per gram) was the ratio of one-sided area of a fresh leaf to oven-dry mass. Leaf thickness (millimeter) was measured by electronic digital micrometer (CANY Co., Shanghai, China) on fresh leaves (Seelig *et al.* 2012). Relative leaf chlorophyll content was measured by using a hand-held 'SPAD-502 Chl meter' (Minolta Camera Co., Osaka, Japan). Three readings were taken from the widest portion of the leaf blade to the narrow portion at ~15 mm from the leaf margin (Marenco *et al.* 2009; Uddling *et al.* 2007). Stem specific resistance (N) was measured on the five largest individuals for each taxon by using Resistograph (Rinntech Co., Germany). Maximum tree DBH (centimeter) was from the largest individuals in the 2007 census. Each seed mass was an average value of oven-dry mass (<80°C for 48 h) from 30 to 200 collected mature seeds for each species without any appendages.

Environmental variables and environmental niches measurement

Four continuous topographical variables (aspect, convexity, elevation and slope) were used to quantify environmental niches. For each 20 m × 20 m quadrat, elevation was calculated as the mean of values at its four corners. Slope was calculated as the mean angular deviation from horizontal of each of the four triangular planes formed by connecting three of its corners (Harms *et al.* 2001). Convexity was calculated as the elevation of a focal quadrat minus the mean elevation of the eight surrounding quadrats. For edge quadrats, convexity was calculated as the elevation of the center point minus the mean of the four corners (Valencia *et al.* 2004). Aspect was calculated as the following formula:

$$Aspect = 180 - \arctan(fy / fx) \cdot (180 / 3.141592) + 90 \cdot (fx / |fx|)$$

fx was the elevation difference from east to west in the quadrat and *fy* was the elevation difference from north to south in the quadrat. Finally, the value of aspect represents the direction (the degree from north to south, regardless of west and east) to which the slope of a quadrat faces.

The conditional probability of tree occurrence (E) for a given habitat variable x: p(E|x) represents the probability that a focal species exists at the selected point when the environmental variable of the point is x. Values of p(E|x) are not affected by the frequency distribution of x within a study plot. We therefore calculated the environmental niche as the x when p(E|x) achieves its maximum. For each species we can therefore find the environmental variable value on which species occurs with maximum probability (hereafter this value was referred to as environmental niche). We calculated the environmental niche for each topographical variable for each target species. The details to estimate p(x|E), p(x) and p(E|x) can be found in Itoh *et al.* (2010).

To test whether the average phylogenetic and functional dispersion in 20 m × 20 m quadrats changes along topographical gradients, we divided all quadrats into different orders for each topographical variable. Because the topography is relatively homogeneous in Ailaoshan plot (Fig. S1a, see online supplementary material), we divided each topographical variable equally into two orders, low and high. Considering the relatively heterogeneous topography in Xishuangbanna plot (Fig. S1b, see online supplementary material), we divided the each topographical variable equally into four orders, with the sequence from order one to order four representing the sequence from low to high level.

Phylogenetic comparative methods

Phylogenetic independent contrasts (PICs) were calculated to correlate all functional traits with environmental niches

(Felsenstein 1985; Garland *et al.* 1992). For N species, N-1 contrasts were computed for each variable. All traits and niches data were log10 transformed prior to approximate a normal distribution. To examine the correlation between functional traits and niches throughout the phylogeny, a Pearson's correlation through the origin was calculated for all pairwise contrasts. A significant correlation between PICs for traits and niches indicates that the traits and niches have undergone changes in similar direction and magnitude across the phylogeny and supports a possible evolutionary link between the traits and niches (Jacobsen *et al.* 2007).

Phylogenetic signals of functional traits

The degree of phylogenetic signal in the seven functional traits for the target species was tested using Pagel's lambda estimator (λ) (Pagel 1999). A value of $\lambda = 0$ indicates no phylogenetic signal in the trait data, while a value of $\lambda = 1$ indicates that traits evolve according to Brownian motion on the given phylogeny. The λ value normally varies between 0 and 1 but it can exceed 1 depending on the shape of the phylogeny (Freckleton *et al.* 2002). We used a log-likelihood ratio test to examine the significance of phylogenetic dependence for the seven traits (Freckleton *et al.* 2002). Pagel's λ estimation and significance tests were conducted in the R (R Development Core Team, 2012) package 'Geiger' (Harmon *et al.* 2008).

Testing community-wide phylogenetic dispersion

The net relatedness index (NRI) and the nearest taxon index (NTI) were used to quantify the phylogenetic dispersion of co-occurring species in 20 m × 20 m quadrats. The NRI is the standardized effect size (S.E.S.) for the mean pairwise phylogenetic distance (MPD) for all individuals in each quadrat. The NTI is the standardized effect size for the mean nearest taxon index (MNTD) for all individuals in each quadrat. NRI and NTI metrics were abundance-weighted calculation, which used the following equations.

$$NRI = -(MPD_{obs} - mean(MPD_{null}))/sd(MPD_{null})$$

$$NTI = -(MNTD_{obs} - mean(MNTD_{null}))/sd(MNTD_{null})$$

MPD is the mean pairwise phylogenetic distance between all taxa within a local sample and MNTD the mean phylogenetic distance to the closest relative of each species in the sample. The MPD_{obs} and $MNTD_{obs}$ are the observed value of mean pairwise phylogenetic distances and mean nearest taxon phylogenetic distances for each quadrat. The mean(MPD_{null}) and mean($MNTD_{null}$) are the mean values from a null distribution where species names were randomly shuffled on the tips of the community phylogeny 999 times and the MPD and MNTD values were calculated each time for each quadrat. The sd(MPD_{null}) and sd($MNTD_{null}$) are the standard deviations of the null distribution. A negative NRI or NTI indicates that a community is phylogenetically overdispersed, whereas a positive NRI or NTI indicates that a community is phylogenetically clustered.

Because the NRI and NTI values in the quadrats were spatially auto-correlated, we estimated spatially independent NRI and NTI values within each quadrat using simultaneous spatial auto-regression (SAR). Following Kembel and Hubbell (2006), a generalized least-squares model with a first order spatial neighbor SAR in 'spdep' package (Bivand 2010) of R was used. A Wilcoxon's test was used to test for significant deviations of NRI or NTI from the expectation of zero.

Testing community-wide functional dispersion

We measure functional dispersion by first generating trait dendrograms from trait distance matrices allowing for direct comparisons between trait and phylogenetic results (Swenson *et al.* 2012). Trait dispersion within quadrats was quantified by calculating the mean pairwise trait distance (PW) and mean nearest neighbor trait distance (NN) between all individuals in a quadrat. The distances between taxa were calculated from a trait dendrogram that was generated from the Euclidean distance matrix for each of the log10 transformed trait variables. Hierarchical clustering was then applied to this matrix to generate the dendrogram and used as analogous to a phylogenetic tree. To determine whether the trait dispersion observed in a quadrat differed significantly from a randomly assembled community, we compared observed values with a distribution of 999 communities generated from a null model. As with phylogenetic analyses, the null model shuffles the names of species across the dendrogram 999 times. This randomization procedure retains observed trait combinations and correlations and only changes the identity of the species with a particular trait combination. S.E.S. PW and S.E.S. NN metrics were abundance-weighted calculation, which used the following equations.

$$S.E.S \ PW = -(PW_{obs} - mean(PW_{null}))/sd(PW_{null})$$

$$S.E.S \ NN = -(NN_{obs} - mean(NN_{null}))/sd(NN_{null})$$

A positive S.E.S. PW or S.E.S. NN indicates that traits are clustered in a quadrat, whereas a negative S.E.S. PW or S.E.S. NN indicates that traits are overdispersed in a quadrat. Because S.E.S. PW and S.E.S. NN values in the quadrats were spatially auto-correlated, we estimated spatially independent S.E.S. PW and S.E.S. NN values within each quadrat using simultaneous SAR analyses. Following Kembel and Hubbell (2006), a generalized least-squares model with a first order spatial neighbor SAR in 'spdep' package (Bivand 2010) of R was used. A Student's t test was used to test for significant deviations of S.E.S. PW or S.E.S. NN from the expectation of zero.

RESULTS

Correlations between functional traits and environmental niches

In both the Ailaoshan FDP and the Xishuangbanna FDP, each of the seven functional traits was significantly correlated with one or more of the four topographical niches (Table 1).

Correlation coefficients between functional traits and topographical niches are generally greater in the Ailaoshan plot than in the Xishuangbanna plot (Table 1). In the Ailaoshan plot, all functional traits were significantly correlated with the aspect niche. In the Xishuangbanna plot, all functional traits except leaf chlorophyll content were significantly correlated with the aspect and convexity niches. In both of the plots, seed mass was significantly correlated with all the four topographical niches.

Phylogenetic signal in functional traits

In both of the plots, the Pagel's λ values for all seven functional traits were significantly greater than 0, ranging from 0.272 to 0.811 in the Ailaoshan plot and from 0.060 to 0.831 in the Xishuangbanna plot (Table 2). All seven functional traits showed significant phylogenetic signal as quantified using the log-likelihood ratio test (Table 2).

Phylogenetic dispersion along topographical gradients

The means of both NRI and NTI metrics were significantly different from zero along all topographical gradients in both the Ailaoshan and Xishuangbanna plots (Wilcoxon test, $P < 0.05$), indicating that there were generally non-random phylogenetic structure in both of the plots. In the Ailaoshan plot, phylogenetic clustering was consistent along all topographical gradients (Figs 2a and b). In contrast, in the Xishuangbanna plot, phylogenetic overdispersion was consistent along all topographical gradients (Figs 3a and b).

Functional dispersion along topographical gradients

The means of both S.E.S PW and S.E.S NN metrics were significantly different from zero, both in Ailaoshan and Xishuangbanna plots (Wilcoxon test, $P < 0.05$), indicating that there was generally non-random functional structure in both of the plots. In the Ailaoshan plot, functional clustering was

consistent along all topographical gradients (Figs 2c and d). In contrast, in the Xishuangbanna plot, functional overdispersion was consistent along all topographical gradients (Figs 3c and 2d). In the Ailaoshan plot, functional clustering increased along low to high convexity, elevation and slope gradients, and decreased along north to south aspect gradients (Figs 2c and d). In the Xishuangbanna plot, functional overdispersion decreased along low to high convexity gradient. For the other three topographical gradients, there were no clear trends in the change of functional overdispersion.

DISCUSSION

In the present study, we argue that the correlation between traits and niches should be the premise for the use of phylogenetic and functional approaches to infer the role of deterministic or stochastic processes underlying community assembly. We found that the seven functional traits examined were significantly correlated with local-scale topographical niches in both of the Ailaoshan and Xishuangbanna plots, indicating that the difference of functional traits can be used as the proxy for local-scale environmental niche differentiation in these two local tree assemblages. We also found that these functional traits had significant phylogenetic signal in both of the plots. We further found that phylogenetic and functional clustering dominated in the Ailaoshan plot and overdispersion in the Xishuangbanna plot. Combined with these findings, we confirmed that environmental filtering played a key role in structuring tree communities in Ailaoshan plot and biotic interactions in Xishuangbanna plot.

Correlation between functional traits and environmental niches

Community ecologists have emphasized a central role of niche differentiation to explain patterns of community composition

Table 2: phylogenetic signal of seven functional traits examined using Pagel's λ for the target species in the Ailaoshan and Xishuangbanna forest dynamics plots

Functional traits	Ailaoshan plot					Xishuangbanna plot				
	n	λ	ln lik	ln lik (λ = 0)	ln lik (λ = 1)	n	λ	ln lik	ln lik (λ = 0)	ln lik (λ = 1)
SM	36	0.41	−84.64	**−86.79***	**−86.79*****	229	0.83	−497.31	**−568.70*****	**−568.70*****
DBH$_{max}$	36	0.81	−48.61	**−49.09***	**−49.09*****	229	0.44	−278.12	**−287.29*****	**−287.29*****
WR	36	0.70	−3.85	**−5.58***	**−5.58*****	229	0.54	−54.52	**−72.78*****	**−72.78*****
LT	36	0.76	−25.53	**−27.14***	**−27.14*****	229	0.25	29.44	**25.58***	**25.58*****
LA	36	0.27	−14.67	**−15.80***	**−15.80*****	229	0.16	−258.76	**−259.71***	**−259.71*****
SLA	36	0.33	−6.45	**−7.01***	**−7.01*****	229	0.22	−91.43	**−96.41*****	**−96.41*****
LC	36	0.78	14.73	**13.54***	**13.54*****	229	0.06	159.46	**159.16*****	**159.16*****

n = the number of target species; ln lik = the maximum likelihood estimate of λ is given together with its associated log likelihood; ln lik (λ = 0) = the log-likelihood values for the model with λ set to 0; ln lik (λ = 1) = the log-likelihood values for the model with λ set to 1; SM = seed mass (milligram); DBH$_{max}$ = maximum DBH (millimeter); WR = wood resistance (N); LT = leaf thickness (millimeter); LA = leaf area (square centimeter); SLA = specific leaf area (square centimeter per gram); LC = leaf chlorophyll content (SPDA). Values significantly different from the test value (determined from a log-likelihood ratio test) are indicated in bold. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.
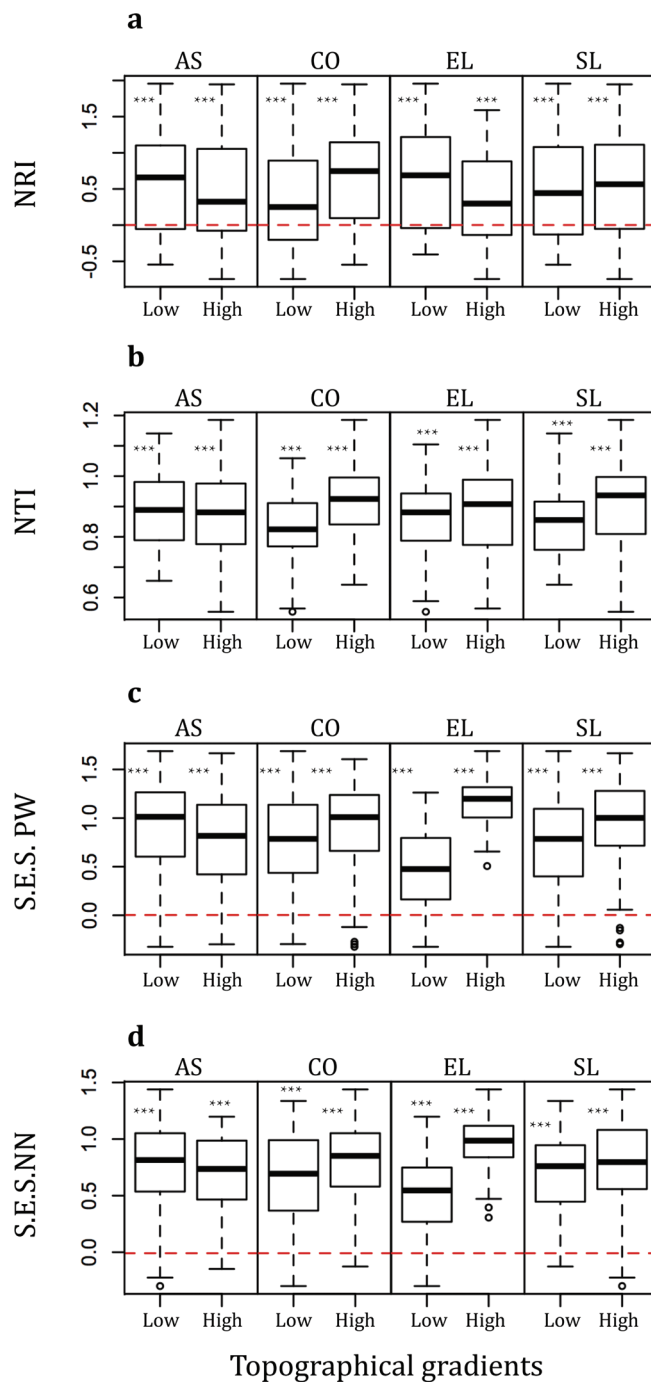
Figure 2: phylogenetic and functional dispersion in relation to topographical gradients in the 6-ha Ailaoshan forest dynamics plot. Positive values indicate phylogenetic or functional clustering, negative values indicate phylogenetic or functional overdispersion. AS: aspect; CO: convexity; EL: elevation; SL: slope; (**a**) phylogenetic pattern (NRI); (**b**) phylogenetic pattern (NTI); (**c**) functional pattern (S.E.S. PW); (**d**) functional pattern (S.E.S. NN). Wilcoxon tests were used to examine whether the means of NRIs, NTIs, S.E.S PWs and S.E.S NNs along topographical gradients are significantly different from zero. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, $P > 0.05$.

and species coexistence on local scales (e.g. Chesson 1991, 2000; Silvertown 2004). It is widely recognized that fine-scale environmental heterogeneity may promote species coexistence by the differentiation of environmental niches among coexisting species within local communities (e.g. Harms *et al.* 2001; Plotkin *et al.* 2000). However, there have been few reports using environmental data directly to measure local-scale environmental niches and extending those analyses to the analysis of niche differentiation (but see John *et al.* 2007; Schreeg *et al.* 2010). Some studies have used functional traits as surrogates of local-scale environmental niches (e.g. Ackerly *et al.* 2006; Böhning-Gaese *et al.* 2003; Kerkhoff *et al.* 2006; Slingsby and Verboom 2006; Violle and Jiang, 2009); however, there is still little knowledge regarding the correlation between functional traits and environmental niches in tree assemblages. Our results show that functional traits universally correlate with topographical niches in both of the plots examined (Table1), indicating the difference of functional traits could serve as a reasonable proxy for the topographical niche differentiation. Species distributions are often found to correlate with different topographical features (Legendre *et al.* 2009). Some recent studies have shown that there were significant contributions of topographical niches to species distribution in local tree communities (e.g. Gunatilleke *et al.* 2006; Hu *et al.* 2012; Legendre *et al.* 2009; Queenborough *et al.* 2007; Valencia *et al.* 2004). All the seven functional traits examined have a strong correlation with aspect niches in the Ailaoshan plot. Aspect is correlated with solar radiation, soil temperatures and moisture indicating why there is an expected general biological importance of this topographic variable (Ackerly 2004; Ackerly *et al.* 2002; Whitney 1991). Solar radiation, temperature and moisture differences may alter nutrient mineralization and availability along aspect and slope gradients (Miller 1983) and may also influence the trade-off between strategic allocations to construction costs, seedling establishment and subsequent species regeneration patterns (Kutiel 1997).

Seed mass was found to have a significant correlation with all the four topographical niches in both the Ailaoshan and Xishuangbanna plots (Table 1). Previously, Peco *et al.* (2009) have found that seed mass was significantly correlated with topography, especially seed mass of most annual species preferentially distributed on shallower slope zones. Topography-related spatial heterogeneity may be expected to produce a differential distribution of diaspore size so that small-seeded species will establish towards the drier and less productive upper slope and elevation zones (Azcárate *et al.* 2002).

Key ecological processes underlying species coexistence in the two FDPs

The tight correlation between functional traits and environmental niches (Table 1) supports the premise for using phylogenetic and functional approaches in order to infer the importance of deterministic and stochastic assembly
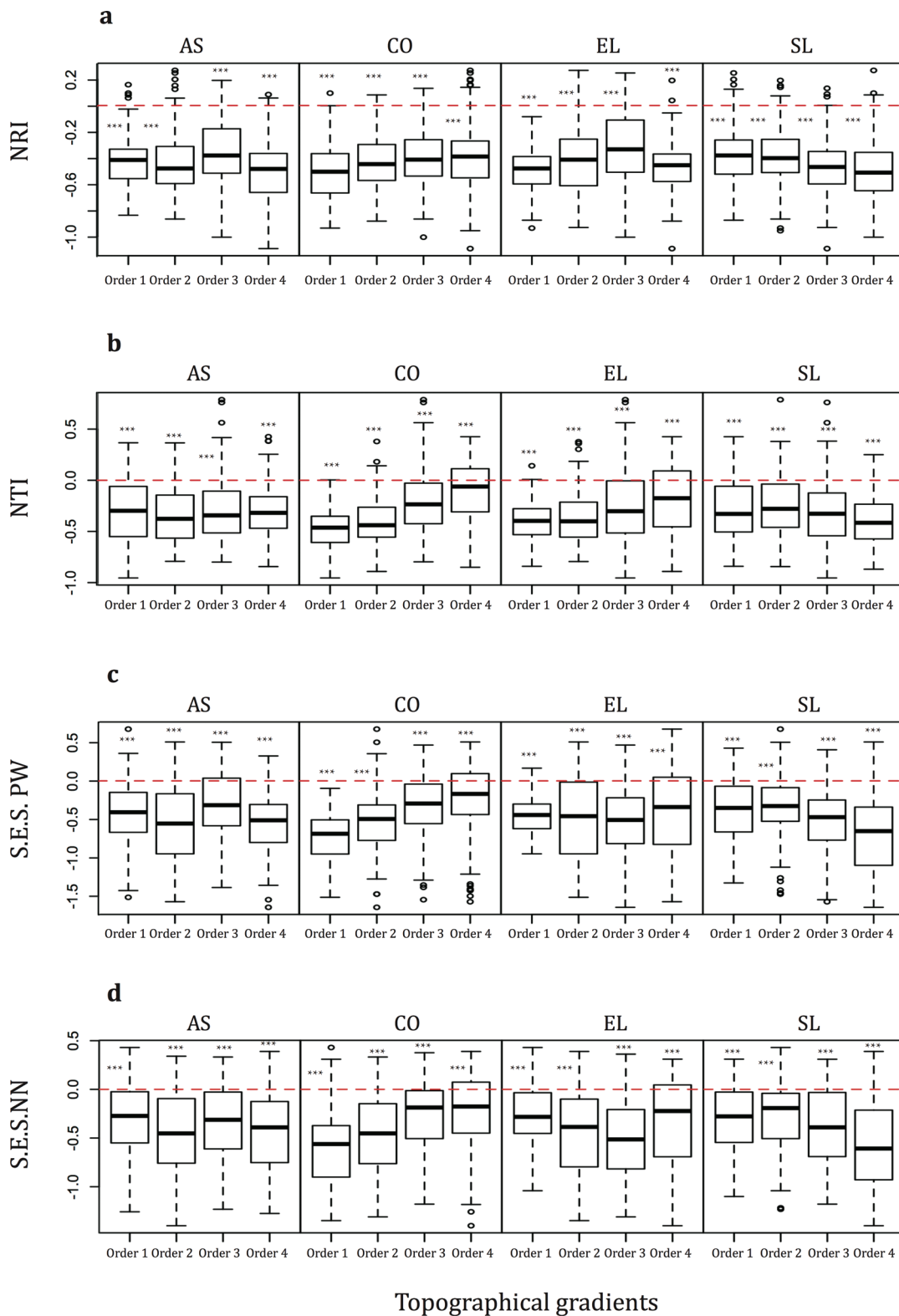
Figure 3: phylogenetic and functional dispersion in relation to topographical gradients in the 20-ha Xishuangbanna forest dynamics plot. Positive values indicate phylogenetic or functional clustering, negative values indicate phylogenetic or functional overdispersion. AS: aspect; CO: convexity; EL: elevation; SL: slope; (**a**) phylogenetic pattern (NRI); (**b**) phylogenetic pattern (NTI); (**c**) functional pattern (S.E.S. PW); (**d**) functional pattern (S.E.S. NN). Wilcoxon tests were used to examine whether the means of NRIs, NTIs, S.E.S PWs and S.E.S NNs along topographical gradients are significantly different from zero. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, $P > 0.05$.

processes. In this study, the phylogenetic and functional dispersion were significantly clustered along topographical gradients in the Ailaoshan plot, while overdispersion in the Xishuangbanna plot (Figs 2 and 3). The consistent results between phylogenetic and functional approaches may be due to the significant phylogenetic signal in functional traits (Table 2). Thus, we inferred that environmental filtering played a key role in structuring tree assemblages in the Ailaoshan plot and biotic interactions in the Xishuangbanna plot. The topography in the Xishuangbanna plot is very rugged with elevation ranging from 869.1 to 708.2 m, but the topography in Ailaoshan plot is relatively flat with elevation ranging from 2530 to 2490 m. Why does the relatively homogeneous topographical environment in the Ailaoshan plot consistently produce phylogenetic and functional clustering, while relatively heterogeneous topographical environment in the Xishuangbanna plot consistently produce phylogenetic and functional overdispersion? We postulate that the extent of topographical heterogeneity might be an important factor that caused the contrasting patterns of phylogenetic and functional structures between these two plots (Fig. S1, see online supplementary material).

Lastly, we would like to discuss some potential limitations of this study. Whether the functional traits and environmental niches examined are those that are the most reliable indicators of assembly processes is a critical question. For example, if the functional traits examined do not represent a full representation of the main aspects of plant function, or the environmental niches measured do not represent important niches axis along which co-occurring tree species differentiate, a significant correlation between functional traits and environmental niches can not guarantee the reliability of phylogenetic and functional approaches for inferring the importance of different ecological processes. Nevertheless, it is unrealistic to measure all functional traits and niches in communities. The seven functional traits examined in this study have been widely considered as important indicators of plant functional strategies (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013).

SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Plant Ecology online.

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