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The role of functional traits and individual variation in the co-occurrence of *Ficus* species

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Abstract. The processes that structure assemblages of species in hyper-diverse genera, such as *Ficus* (Moraceae), are not well understood. Functional diversity of co-occurring species can reveal evidence for assembly processes; however, intraspecific variation may weaken species-level patterns. We studied whether functional and phylogenetic diversity of *Ficus* species indicated the effects of spatial variation in filters associated with topography or niche partitioning related to resource use and biotic interactions. We also asked whether individual trait patterns supported species-level patterns. We studied six traits (leaf area, succulence, specific leaf area [SLA], maximum diameter breast high [dbh], fruit size, and latex exudation) for 22 *Ficus* species and 335 individuals $\geq$10 cm dbh on a 20-ha forest plot in China. We found that higher elevation was correlated to changes in mean and reduced diversity of five traits, possibly due to frequent disturbances at higher elevations that favored fast-growing, poorly defended species with high SLA. Maximum dbh showed phylogenetic conservatism but high diversity among co-occurring species, suggesting adult stature is an important axis of within-quadrat niche partitioning. At the individual level, trait patterns were qualitatively consistent but were stronger than species-level patterns, especially for the leaf traits with the greatest intraspecific variation (SLA and succulence). Individual-level SLA exhibited the strongest evidence for both traits among and within-quadrat niche partitioning and indicated elevational filtering. Local niche partitioning and elevational filtering likely play an important role in maintaining species and functional diversity in the most speciose genus at our study site. Our results highlight the importance of individual variation, as it may reveal otherwise obscured niche effects.

Key words: community assembly; dipterocarp rain forest; habitat disturbance; herbivore defense; permutation test; spatial scale.

INTRODUCTION

Co-occurrence of closely related species, a hallmark of tropical forest diversity (Harrison 2005), presents a paradox because theory predicts that evolutionary niche conservatism and niche overlap prevent coexistence (Darwin 1859, MacArthur and Levins 1967). This has led some to propose neutral mechanisms of unstable coexistence for species assumed to be equivalent in fitness (Hubbell 2001), whereas others highlight the role of niche partitioning even among closely related congeners (Cavender-Bares et al. 2004, Ackerly et al. 2006, Sedio et al. 2012). However, approaches to elucidate the processes maintaining diversity may be hindered by a failure to consider functional variation at the individual level (Bolnick et al. 2011, Violle et al. 2012). Here we report a study of species and individual-level trait variation that asks whether several key processes maintain diversity of a set of closely related tropical tree species across a forest plot.

Spatial environmental gradients can drive variation in species relative performance, favoring different species at different sites (possibly mediated by competition [Lasky et al. 2013]). Filtering may be associated with spatial niche partitioning among species, which can maintain species diversity across regions with environmental heterogeneity (Pacala and Tilman 1994, Chesson 2000). Such filters are evidenced by high between-site but low within-site trait diversity (and by proxy phylogenetic diversity) of co-occurring species (Weiher and Keddy 1995, Webb et al. 2002). Shifts in trait mean and diversity along abiotic gradients are additional evidence for trait-mediated abiotic filters (Cornwell and Ackerly 2009, Schamp and Aarssen 2009), though patterns are often scale specific (Swenson and Enquist 2009, Kraft and Ackerly 2010). Environmental gradients associated with topography, such as soil moisture and disturbance, can have filtering effects on tropical tree survival and species distributions (Engelbrecht et al.

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2005, 2007, Lasky et al. 2013). Tropical seasonal rain forests experience a strong dry season (e.g., five months below 30 mm precipitation at our study site), when some species are partly deciduous (Zhang and Cao 1995). Seasonal drought stress may be highest at high elevations on convex ridges (Daws et al. 2002). Furthermore, dry sites may favor shifts in trait means and reduced trait diversity favoring species with conservative traits, such as low specific leaf area (SLA; Cornwell and Ackerly 2009, Sterck et al. 2011).

Species traits may also correlate to niche variation within sites, which can promote species and trait diversity (MacArthur and Levins 1967, Weiher et al. 1998). Niches may be partitioned within sites based on resource specialization, interactions with natural enemies, and within-site environmental heterogeneity (Kraft and Ackerly 2010). In tropical forests, traits associated with resource acquisition and leaf life span, such as SLA (Oren et al. 1986, Reich and Walters 1994, Westoby et al. 2002, Wright et al. 2004), may exhibit high local trait diversity indicative of within-site niche variation (Kraft et al. 2008, Swenson and Enquist 2009). However, an important gap in existing studies on tree functional diversity is that few have asked whether herbivore defense traits are related to niche partitioning associated with herbivory.

Herbivory can play a central role in plant community assembly, partly via negative density effects (Janzen 1970, Connell 1971, Carson and Root 2000, Ryerson and Parmenter 2001, Becerra 2007). *Ficus* (Moraceae) represents a useful model system for studying how herbivory affects plant diversity. Phytophage assemblages overlap among *Ficus* species (Basset and Novotny 1999); thus co-occurring *Ficus* may indirectly compete via shared enemies. Nearly all species of *Ficus* exude latex, which is rich in secondary defense compounds and impedes herbivores (Agrawal and Konno 2009). Thus the quantity of latex exudate may be a direct measure of defense strategy (Rasmann et al. 2009).

Latex variation may structure *Ficus* assemblages via two alternative mechanisms. First, if latex production trades off with other defenses, then latex variation represents diversity in defense strategies (Rudgers et al. 2004, Moles et al. 2013). Thus herbivore-mediated niche partitioning (Janzen 1970) is expected to increase the diversity of defense strategies and reduce herbivore overlap among species (Chaneton and Bonsall 2000, Kursar et al. 2009). Second, if latex defense trades off with growth rate, then latex levels represent strength of defenses (Fine et al. 2004). Thus marginal sites with low resource (e.g., light) availability should filter out fast-growing, poorly defended species, causing low latex diversity within sites but high diversity across sites (Janzen 1974, Fine et al. 2004, Agrawal 2007). At our study site, light availability may be greater at higher elevations on steep ridges where disturbance from tree fall and landslides is likely highest (Ohkubo et al. 2007), although soil nutrients are more abundant at lower elevations in valleys (Hu et al. 2012).

Intraspecific variation in functional traits

Trait-based community studies typically assume that all individuals of a species have traits equal to the species mean (e.g., Cavender-Bares et al. 2004, Swenson and Enquist 2009, Kraft and Ackerly 2010, Lasky et al. 2013). However, assembly processes are fundamentally driven by individual fitness; individual variation in traits, fitness, and niche can be extensive (reviewed by Bolnick et al. 2011, Violle et al. 2012). Ignoring intraspecific variation can result in inaccurate estimation of trait diversity (Jung et al. 2010), and thus obscure assembly mechanisms. Because individual-level patterns are closely linked with individual-level processes, individual trait diversity may provide stronger evidence and indicate distinct axes of niche partitioning compared to species-level patterns (Paine et al. 2011). Additionally, high intraspecific variation may reduce the strength of intraspecific competition and weaken the potential for species niche partitioning (Chesson 2000, Bolnick et al. 2011).

Ficus *as a model of tropical tree diversity*

Ficus assemblages are representative of the diversity of lowland tropical rain forests in that they are extremely diverse and often comprise many closely related and functionally similar species (Gentry 1982, Harrison 2005). *Ficus* is composed of ~800 species and is diverse at lowland tropical forest sites worldwide (Berg 1989, Harrison 2005). *Ficus* is the most diverse genus in nearly all completed florulas from Paleotropical lowland rain forests, being most speciose in Southeast Asia (Berg 1989, Harrison 2005). Additionally, *Ficus* is a keystone taxon for maintaining biodiversity because of its role in supporting frugivore communities (Terborgh 1986, Lambert and Marshall 1991, Shanahan et al. 2001, Kissling et al. 2007). Hypotheses for the diversity of *Ficus* have focused on reproductive isolation and rapid speciation (Janzen 1979, Herre et al. 2008), while few studies have investigated niche partitioning (see Harrison et al. 2003, Harrison and Shanahan 2005, Hao et al. 2011).

We studied functional and phylogenetic diversity of co-occurring *Ficus* species and individuals in a 20-ha forest plot in order to characterize mechanisms maintaining diversity across the plot. We asked whether filtering associated with topography drove spatial variation in *Ficus* assemblages, promoting diversity across topographic gradients. We asked whether traits associated with resource use and biotic interactions were associated with niche partitioning, promoting species and functional diversity among neighboring trees. We studied whether evolutionary relatedness was associated with trait similarity and whether co-occurring species were more or less related than expected. Finally, we asked whether individual-level trait patterns changed

TABLE 1. Nonparametric rank correlation among species mean values for functional traits used in analyses (Spearman's ρ, species is the unit of observation).

Correlation	Syconium diameter	Latex exudation	Leaf succulence	Specific leaf area	Leaf area
Maximum dbh	−0.24	0.37	0.46	−0.81	−0.09
Syconium diameter		0.53	0.03	0.21	0.52
Latex exudation			0.50	−0.47	0.35
Leaf succulence				−0.72	0.23
Specific leaf area					0.15

our interpretation of the mechanisms that promote *Ficus* species and functional diversity.

METHODS

Study site

Our study site was the 20-ha tropical seasonal rain forest dynamics plot in Xishuangbanna prefecture, Yunnan Province, China (21°36′50″ N, 101°34′36″ E) at 765 m above sea level (asl; range, 708–869 m; see Plate 1). Approximately 50 km from the plot at 560 m asl lies the Xishuangbanna Tropical Botanical Garden (XTBG), which receives 1493 mm/yr rainfall, ~85% of it arriving during a six-month rainy season (Cao et al. 2006). Mean annual temperature at XTBG is 21.8°C (Cao et al. 2006). Soils in the elevational band of the forest plot are laterite, derived from siliceous rocks, and have deep solum but thin humus (Cao et al. 2006). The plot is found near the northern limit of dipterocarp rain forests and is characterized by the emergent *Parashorea chinensis* (Dipterocarpaceae), which reaches 60 m tall (Zhang and Cao 1995).

We studied three topographical variables: elevation, convexity, and slope (Daws et al. 2002, Engelbrecht et al. 2007, Ohkubo et al. 2007, Lasky et al. 2013). Elevation was measured at the corners of 10-m quadrats. Convexity was calculated as the elevation of a quadrat minus the mean elevation of the eight neighboring quadrats. We calculated slope as the mean angular deviation from horizontal of each of the four triangular planes formed by three quadrat corners. We also calculated the average of each of these three variables for 20- and 50-m quadrats.

In 2007, all arborescent stems ≥ 1 cm diameter dbh (breast height; 1.3 m) were mapped, measured for dbh, and identified following established protocol (Condit 1998). The census recorded 111 177 stems belonging to 469 species and morphospecies. *Ficus* was the most speciose genus, with 19 identified species and 3 morphospecies. *Ficus* was represented by 3221 stems (2.9% of total), 4.6% of the total basal area in the plot (Appendix: Table A1), and a substantial portion of the seedbank (Tang et al. 2006). *Ficus* stems were most frequent along the steep slopes of the plot, and less frequent along ridges and at the bottom of ravines (Appendix: Fig. A1).

Trait sampling

Species trait values used in species analyses were taken as the mean of sampled individuals. We sampled four leaf traits and two additional traits that may correspond to niche variation: (1) leaf succulence [(fresh mass − dry mass)/area], (2) specific leaf area (SLA, leaf area/dry mass), (3) leaf area, (4) syconium (i.e., the pseudocarp containing multiple *Ficus* fruits) diameter, (5) maximum dbh, and (6) leaf latex exudation (fresh latex mass exuded/width of leaf cut [Table 1; Appendix: Table A2]). Three traits (leaf succulence, leaf area, and SLA) were sampled on >300 individuals and were also analyzed at the individual level.

The traits we selected correspond to a number of trade-offs identified in large-scale (e.g., global) data sets. Leaf succulence corresponds to a trade-off between leaf life span vs. productivity (Garnier and Laurent 1994). SLA variation corresponds to a trade-off between photosynthetic rate and cost of leaf growth (Wright et al. 2004). Leaf area trades off between increased light capture by large leaves and increased cooling in small leaves (Dolph and Dilcher 1980). Syconia size variation corresponds to variation in associated frugivore assemblages (Githiru et al. 2002, Lómascolo et al. 2010), and to an axis of reproductive investment and pollinator rewards (Herre 1989). Maximum dbh is a proxy for maximum height (Kraft and Ackerly 2010), which represents variation in the light niche of adults (King et al. 2006). Herbivory defense traits, such as latex exudation, may trade off with resource capture or other defenses (Fine et al. 2004).

For species-level analyses, leaf trait data were collected in 2010 from individuals in the 20-ha forest plot and in living collections at XTBG. We attempted to sample at least five individuals of each species. However, because some species were rare in the plot, too large to collect with pole shears, or absent from XTBG, we were unable to collect five for every species (Appendix: Table A1). For each individual, we collected three mature, sun-exposed leaves and processed leaves in the afternoon on the same day they were collected (Cornelissen et al. 2003). In addition to *Ficus* species, we sampled trait data of non-*Ficus* species using the same methods in order to account for interactions between *Ficus* and other species.

We sampled leaf size, leaf succulence, and SLA for 446 species, nearly all the non-*Ficus* species in the plot.

For individual-level analyses, we targeted *Ficus* individuals in the 20-ha plot with dbh $\geq$10 cm; however, we were limited to sampling 335 of 521 (64%) of those individuals because of the length of our telescoping shears. Only sampled individuals with dbh $\geq$10 cm were used in individual-level analyses. To compare individual-level variability among traits, we calculated the proportion of variance among individuals unexplained by species means as the residual $(1 - R^2)$ of an ANOVA for each trait.

Syconium diameter of species with known taxonomy was obtained from published species accounts (Wu et al. 2003). We followed previous approaches to reduce sampling bias in maximum dbh estimates (King et al. 2006, Kraft et al. 2008). Specifically, we took the average of the top three individual dbh's for species with $>$500 individuals, the average of the top two dbh's for species with 100–500 individuals, and the top dbh of species with $<$100 individuals. For analysis, we log-transformed traits that were highly right-skewed (all except SLA).

We adapted the assay of Rasmann et al. (2009) to measure interspecific variation in latex exudation using individuals at XTBG. For each individual, we collected latex from three mature, sun-exposed leaves that were the youngest mature leaf on their branch. While still attached to the tree, leaves were cut transversly 1 cm from the tip, perpendicular to the midrib. For leaves with narrow, elongate (e.g., acuminate) tips, we cut 1 cm from the base of the narrow tip toward the leaf petiole. Following Rasmann et al. (2009), latex that was exuded from the cut was collected onto preweighed strips of filter paper. Latex was collected until it stopped flowing, which usually occurred within 10 seconds. Paper strips with latex were placed into preweighed microcentrifuge tubes, which were then reweighed to obtain the fresh mass of latex exuded. We standardized latex exudation by the width of the transverse cut, because different leaf morphologies led to widely different widths of cuts. Thus our measure of latex exudation is in units of milligrams per millimeter, and is a metric of how much latex is exuded relative to leaf width. Latex exudation differed significantly among species (Kruskal-Wallis test, $\mathrm{df} = 17$, $P = 0.0251$), justifying its use in species-level analyses.

Phylogenetic data

We used a recently published molecular phylogeny of 208 *Ficus* species based on three nuclear rDNA genes (Xu et al. 2011), digitized using publicly available software (Laubach and von Haeseler 2007). Fifteen species, comprising 82% of *Ficus* stems and 64% of *Ficus* basal area on our 20-ha plot, were represented in the phylogeny. We pruned the remaining *Ficus* species not found in our plot and used the resulting tree in phylogenetic analyses (Appendix: Fig. A2).

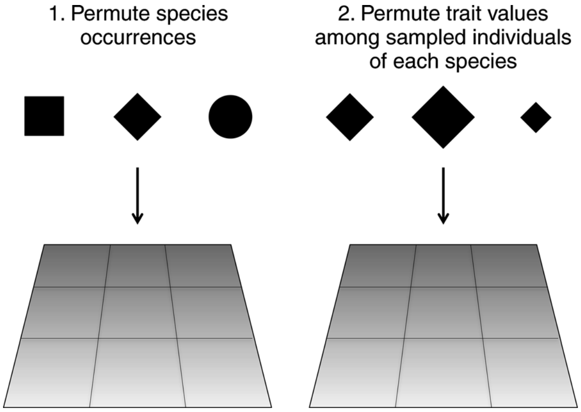

FIG. 1. Illustration of permutation strategy. Black shapes represent different species and their size represents different individual trait values, which were permuted across the plot grid of quadrats (in gray). (1) For species-level analyses, species occurrences in quadrats were permuted, while the number of quadrats occupied by each species and number of species in each quadrat was fixed. Quadrat trait metrics were calculated using species mean traits. (2) For individual-level analyses, we first performed step 1, permuting species. In step 2 we then permuted the trait values measured on *Ficus* stems $\geq$10 cm dbh among individuals within each species. Quadrat trait metrics were calculated using individual values.

Statistical analyses

Null Ficus *assemblages*.—Our strategy in testing for evidence of filtering and within-site niche partitioning was to compare observed trait and phylogenetic diversity in each quadrat to null assemblages and to quadrat topography (Fig. 1). Here, trait diversity and phylogenetic diversity simply refer to functional or evolutionary differences among species (or individuals in the case of traits), which are quantified using metrics presented in the following paragraphs. We permuted species occurrences in quadrats, while fixing the frequency of each species' occurrence across the plot (the number of quadrats where each species was present) and the local species richness of each assemblage (the number of species in each quadrat [Gotelli and Entsminger 2001, Kembel 2009]). Non-*Ficus* species were similarly permuted. We generated 1000 null assemblages in quadrats for species-level analyses using the "vegan" package in R (Oksanen et al. 2011).

We also permuted trait data at the individual level in order to test the null hypothesis that trait diversity of co-occurring individuals was random. Recent studies permuted trait data among all individuals in plots to generate a null model for co-occurring individuals, but did not fix the number of quadrats occupied by each species (i.e., species frequency [Paine et al. 2011, Siefert 2012]). However, it is important to fix species frequency in order to incorporate dispersal limitation patterns into the null model (Gotelli and Entsminger 2001, Kembel 2009). Null models that do not fix species frequency may create unrealistically species-rich null assemblages and increase Type I error in detecting filtering (Kembel 2009).

We developed a new, two-step permutation approach for individual trait analysis (Fig. 1). First, we permuted species occurrences while maintaining frequency of species occurrences and richness in quadrats (as in species-level analyses, previously described). Second, we permuted individual leaf trait values within species, restricted to the trait-sampled individuals $\geq$10 cm dbh (n = 335 individuals). We aimed to constrain permuted assemblages to have a number of individuals equal to the observed. However, we were unable to simultaneously constrain the number of species and individuals in all quadrats. Thus we allowed variation in the total number of individuals in a quadrat, limited to within two individuals of the observed. In order to avoid bias toward greater trait diversity in quadrats with more individuals, we used trait metrics that controlled for the number of individuals (see trait variance and CVNN metrics below [Paine et al. 2011, Siefert 2012]). We generated 1000 null assemblages of plot quadrats for individual-level analyses. In order to compare species and individual-level patterns, we reanalyzed species-level data using only the occurrences and species trait means calculated from the sampled 335 individuals $\geq$10 cm dbh.

Trait and phylogenetic diversity metrics.—We used four metrics to characterize trait diversity indicative of filtering and niche partitioning. First, Trait Diversity (TD, Petchey and Gaston 2002) was measured along a dendrogram of species trait values as the sum of branch lengths in the dendrogram shared by species in a quadrat divided by the sum of branch lengths across the entire dendrogram (Petchey and Gaston 2002, Swenson and Enquist 2009). The second metric was variance in traits among species or individuals. High TD and trait variance are considered evidence for within-site niche partitioning, while low TD and trait variance suggest among-site partitioning. The third metric, standard deviation of nearest neighbor (SDNN), is defined as the standard deviation of the trait distance between each species or individual and its nearest neighbor in trait space. Low SDNN signifies that co-occurring trees are evenly distributed in trait space, suggesting within-site niche partitioning (Kraft and Ackerly 2010). We calculated nearest neighbors in trait space of each *Ficus* stem, where all species with trait data (including non-*Ficus*) were potential nearest neighbors of *Ficus* stems. We used a fourth metric that standardizes SDNN by quadrat trait range (SDNNr, range calculated using only *Ficus* stems) in order to avoid bias in SDNN due to trait range variation (Kraft and Ackerly 2010). However, in individual-level analyses we were unable to constrain the number of individuals in null quadrats, and more individuals cause downward bias in SDNN. Thus for individual-level analyses we standardized SDNN by dividing by the mean nearest neighbor distance, giving the coefficient of variation of nearest neighbor distance (CVNN), a metric unbiased by the number of individuals in a quadrat. We standardized the observed metric in each quadrat to a z score by subtracting the mean and dividing by the standard deviation of metrics for the 1000 null assemblages in each quadrat (Webb et al. 2002, Kraft et al. 2008, Swenson and Enquist 2009).

We used two measures of phylogenetic diversity of co-occurring species. The net relatedness index (NRI) quantifies phylogenetic clustering across depths of the phylogeny (Webb et al. 2002). NRI is defined as $-1 \times$ mean phylogenetic distance (branch length) separating all pairs of co-occurring species. Second, the nearest taxon index (NTI) measures diversity toward the tips of the phylogeny (Webb et al. 2002). NTI is calculated as $-1 \times$ mean phylogenetic distance (branch length) separating each species and the co-occurring species most closely related to it. Both NRI and NTI were standardized to the metrics from 1000 null assemblages. Positive NRI and NTI indicate that co-occurring species are more closely related than the null expectation.

We calculated trait diversity metrics in 100-, 400-, and 2500-m^2 quadrat scales (10-, 20-, and 50-m edges). However, we were unable to test phylogenetic diversity in 100-m^2 quadrats because there were too few quadrats with sufficient occurrences. We excluded trees in young successional stands of broadleaf forest that are recovering from agricultural use (defined as quadrats with indicator species *Castanopsis echinocarpa*, Fagaceae), because those stands may exhibit differences in community assembly compared to old-growth stands that comprise the majority of the 20-ha plot.

Testing trait, phylogenetic, and environmental patterns.—Standardized metrics among co-occurring species or individuals were tested using sign tests. The null hypothesis for the sign test was that diversity metrics are distributed evenly about zero, where zero was the expectation from null assembly permutations.

In order to test for topographic filtering, we tested whether standardized trait means, TD, and trait variance were related to topographic variables, using nonparametric Spearman's rank correlations. For each trait combination we report the environmental variable with the strongest correlation to trait mean and diversity across spatial scales in order to focus on the strongest pattern for each trait.

We tested for trait conservatism across the phylogeny using Blomberg's K and a permutation test (Blomberg et al. 2003). Values of K greater than one indicate greater conservatism than under trait evolution by Brownian motion. We used the "picante" package in R to test observed K for each trait against 1000 permutations of trait values across the tips of the phylogeny (Kembel et al. 2010).

RESULTS

Species-level trait diversity

The number of *Ficus* species in quadrats with at least one *Ficus* species had a mean of 1.8 species (range = 1,

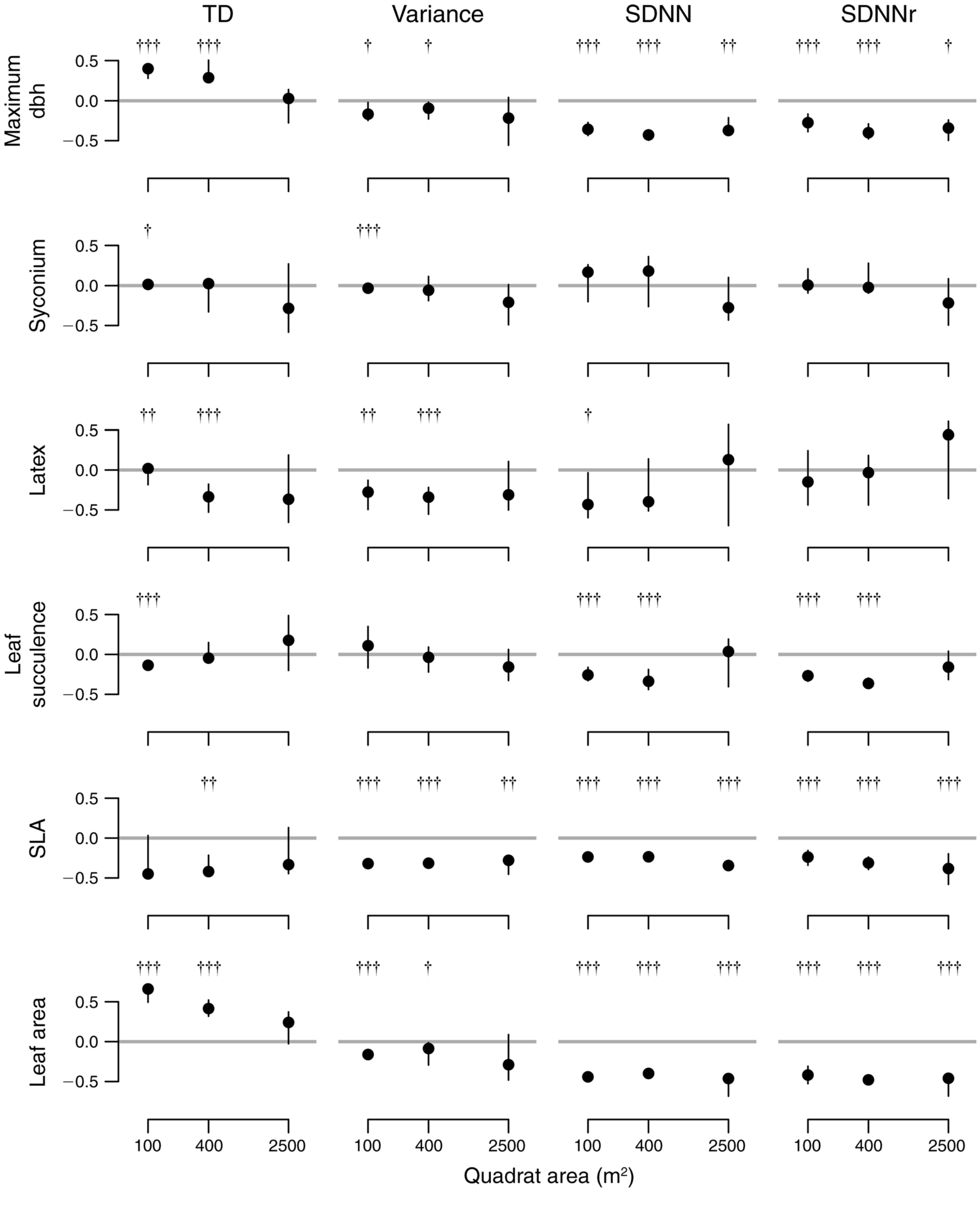

FIG. 2. Trait distributions of co-occurring species relative to null assemblages (permutations). The median and 95% CI of the median quadrat *z* score are shown for each trait–metric scale combination. The significance of sign tests on *z* score distributions are indicated as: † $0.05 > P > 0.005$; †† $0.005 > P > 0.0005$; ††† $0.0005 > P$. A conservative Bonferroni α for the species-level tests shown below would be $0.05/72 = 0.0007$. (Tests with the ††† significance level are significant under this criterion.) SLA is specific leaf area; TD is trait diversity; SDNN is standard deviation of the nearest neighbor; SDNNr is SDNN standardized by quadrat trait range.

6), 2.9 (range = 1, 9) and 6.1 (range = 2, 13) for 100-, 400- and 2500-m^2 quadrats, respectively. In species-level analyses on all stems, trait metrics exhibited stronger patterns in 100- and 400-m^2 quadrats compared to 2500-m^2 quadrats. Most traits showed significant deviations from null expectations, although the direction of patterns differed among metrics and even among the most strongly correlated traits (e.g., between SLA and maximum dbh; rank correlation $\rho = -0.81$; Table 1, Fig. 2). SLA among co-occurring species had significantly

TABLE 2. Topographic variables most strongly related to mean and either trait diversity (TD) or variance for each trait, which provide evidence for environmental filtering and among-quadrat niche partitioning.

Group and trait	Trait metric	Strongest topographical correlate	Quadrat size (m^2)	Spearman's ρ	*P*
All species					
Maximum dbh	mean	elevation	100	0.06	0.0612
	TD	concavity	400	−0.16	0.0102
Syconium diameter	mean	elevation	100	−0.27	<0.0001
	TD	elevation	100	−0.15	0.0054
Latex exudation	mean	elevation	100	−0.22	<0.0001
	variance	elevation	100	−0.20	0.0002
Leaf succulence	mean	elevation	100	−0.31	<0.0001
	TD	elevation	100	−0.21	<0.0001
SLA	mean	elevation	100	0.28	<0.0001
	TD	elevation	100	−0.14	0.0043
Leaf area	mean	elevation	100	−0.27	<0.0001
	TD	elevation	100	0.18	0.0002
Sampled individuals ≥10 cm dbh					
Leaf succulence	mean	elevation	100	−0.54	<0.0001
	variance	slope	100	0.26	0.0355
SLA	mean	elevation	100	0.50	<0.0001
	variance	concavity	2500	−0.17	0.2606
Leaf area	mean	concavity	400	−0.48	<0.0001
	variance	slope	100	0.30	0.0148

Notes: A negative correlation (ρ) for TD or variance suggests that as the topographical variable increased, trait diversity decreased, suggesting stronger filtering. Both species-level and individual-level results are shown. Note that TD and variance were tested for species-level analyses, while only variance was tested for individual-level analyses to control for differences in the number of stems in quadrats.

lower variance than expected, but also had significantly lower SDNN and SDNNr than expected (significant for all scales, sign test, $\alpha = 0.05$ throughout). Among traits, SLA and leaf area exhibited the most significant evidence for both filtering and niche variation across scales and metrics. Latex exudation and leaf succulence showed a similar pattern to SLA, whereby TD and variance indicated low trait diversity, while SDNN indicated even spacing of trait values.

Topography.—Across traits, the strongest topographical correlates of TD and variance were almost always elevation. Mean syconium diameter, latex exudation, leaf succulence, and leaf area decreased significantly with elevation, while SLA increased (Table 2; Spearman's rank correlation). Four traits showed significantly lower TD or variance at higher elevations, while one trait (leaf area) had significantly greater diversity at higher elevations.

Individual-level trait diversity

Intraspecific variation in leaf traits among the 335 sampled individuals ≥10 cm dbh in the 20-ha plot represented a substantial portion of total variation (residual portion of individual variation in ANOVA using species identities: leaf area 10%, SLA 73%, succulence 58%; Appendix: Fig. A3). However, interspecific variation among these individuals was significant for all three traits (Kruskal-Wallis test, $P < 10^{-16}$ for all). In general we observed stronger evidence for filtering and niche partitioning in individual-level trait metrics compared to species mean analyses of the same trees ≥10 cm dbh (Fig. 3). All three leaf traits exhibited significantly less variance among co-occurring individuals than expected at all scales. SLA showed the strongest evidence for even trait spacing, having significantly lower CVNN than expected at all scales. The significance of trait metrics decreased at larger spatial scales in species-level analysis, although this trend was less evident at the individual level (e.g., leaf succulence, Fig. 3).

Topography.—As quadrat concavity increased, individual leaf area significantly decreased (Table 2; Appendix: Fig. A3). As elevation increased, leaf succulence decreased and SLA significantly increased. Variance in leaf succulence and leaf area significantly increased as slope increased, while SLA variance decreased nonsignificantly with concavity.

Phylogenetic analyses

Maximum dbh ($K = 1.20$, $P = 0.005$) and SLA ($K = 1.08$, $P = 0.005$) showed significant phylogenetic conservatism; all other traits were nonsignificantly conserved (permutation *z* scores < 0, Table 3; Appendix: Fig. A2). Both measures of relatedness among co-occurring species indicated that *Ficus* assemblages in quadrats were significantly phylogenetically over-dispersed (i.e., negative NRI and NTI; Fig. 4). In 400-m^2 quadrats, NRI (sign test, $P = 0.0165$) and NTI were significantly negative ($P = 0.0002$), although patterns in

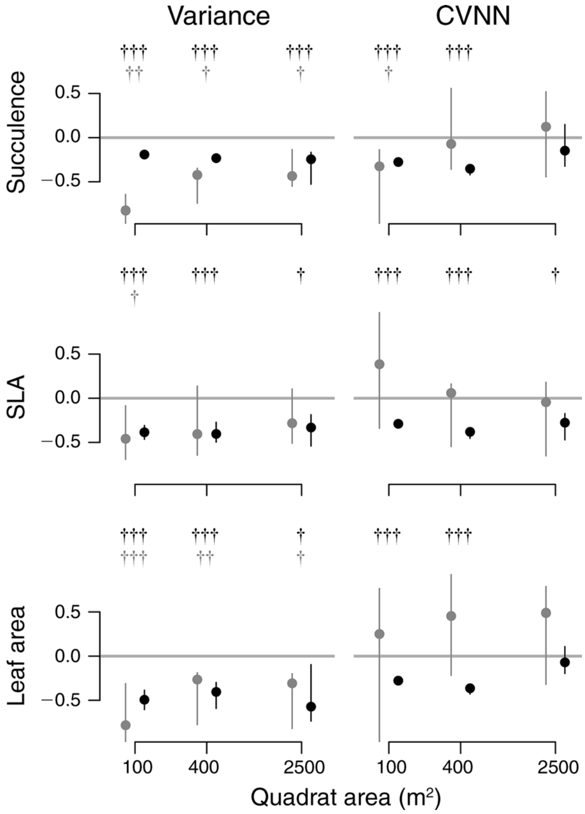

FIG. 3. Trait distributions of co-occurring individuals (shown with black symbols) and species (shown with gray symbols) relative to null assemblages (permutations). Species-level analyses were done on the trees with dbh ≥10 cm used in individual-level analysis in order to compare results. The median and 95% CI of the median quadrat *z* score are shown for each trait–metric scale combination. The significance of sign tests on *z* score distributions are indicated as: † $0.05 > P > 0.005$; †† $0.005 > P > 0.0005$; ††† $0.0005 > P$. A conservative Bonferroni α for the species-level or individual-level tests shown below would be $0.05/18 = 0.003$ (†† tests are significant under this criterion). CVNN is coefficient of variation of nearest neighbor distance; SLA is specific leaf area.

2500-m^2 quadrats were not significant (NRI ($P = 1$), NTI ($P = 0.3123$).

TABLE 3. Permutation tests of phylogenetic signal (Blomberg's *K*) in interspecific trait variation.

Trait	*K*	*z* score	*P*
Maximum dbh	1.20	−1.59	0.005
Syconium diameter	0.71	−0.77	0.159
Latex exudation	0.49	−0.20	0.552
Leaf succulence	0.54	−0.42	0.414
Specific leaf area	1.08	−1.26	0.005
Leaf area	0.68	−0.73	0.214

Note: Negative *z* scores indicate greater phylogenetic conservatism than the null expectation from permutations.

DISCUSSION

Our analysis reveals three key properties of mechanisms that likely maintain diversity among closely related *Ficus* species in Xishuangbanna. First, filters associated with elevation appear to promote *Ficus* functional diversity across our study plot, potentially caused by defense–growth trade-offs across habitats. Second, within-site niche variation associated with leaf traits may promote diversity of co-occurring *Ficus* and neighboring species. Third, evidence for trait-based topographic filtering and within-site niche variation was strongest when considering individual-level variation, suggesting intraspecific variation in response to environment that may weaken the role of species-level niche partitioning in promoting species diversity.

Trait diversity metrics suggested that niche partitioning within sites by *Ficus* and co-occurring non-*Ficus* species promotes local species co-occurrence, while topographic filters cause turnover in assemblages. Given that the traits we study are associated with broad differences in ecological strategies, it is unsurprising that they may be related simultaneously to niche partitioning among sites and within sites (Adler et al. 2013). A previous study on the 20-ha Xishuangbanna plot found that tree species distributions were spatially random for larger size classes, potentially indicating a limited role for species turnover driven by environmental filtering (Lan et al. 2009). However, another study at the plot identified many species distributions, including at large size classes, which were better predicted by environmental variables than putative dispersal patterns (Hu et al. 2012).

In general, the strongest topographic correlate of trait mean, TD, and variance was elevation at the scale of 100-m^2 quadrats. Although low trait diversity can result when certain trait values confer the greatest fitness (Mayfield and Levine 2010), we observed shifts in multiple trait means and reduced diversity at higher elevations, suggesting an important role for trait-mediated filtering, albeit potentially mediated by com-

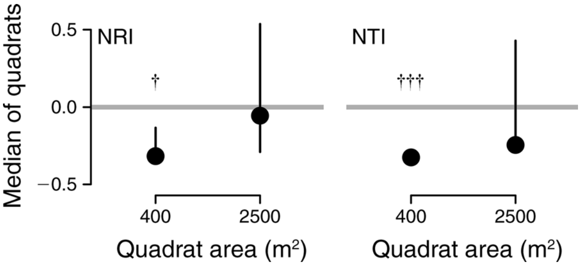

FIG. 4. Phylogenetic relatedness of co-occurring species relative to null assemblages (permutations). NRI is net relatedness index; NTI is nearest taxon index. The median and 95% CI of the median quadrat *z* score are shown for each metric-scale combination. The significance of sign tests on *z* score distributions are indicated as: † $0.05 > P > 0.005$; ††† $0.0005 > P$. A conservative Bonferroni α for the species-level or individual-level tests shown below would be $0.05/4 = 0.01$ (††† tests are significant under this criterion).

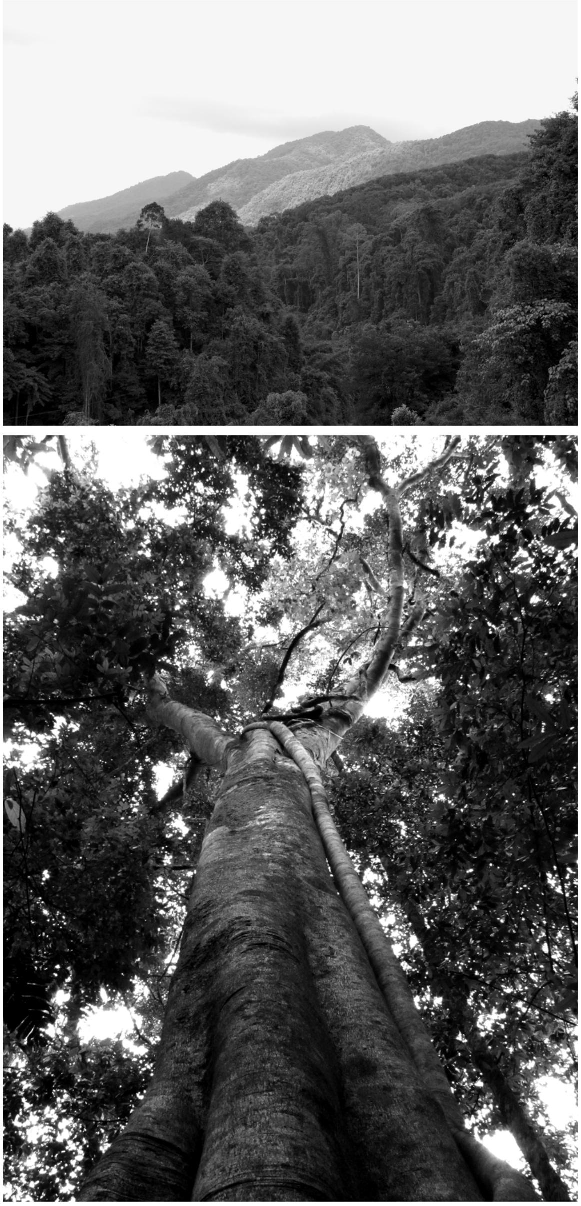

PLATE 1. (Top) Forests surrounding the 20-ha plot in Xishuangbanna, China, and (bottom) an adult *Ficus benjamina* on the plot, one of 22 study species. Photo credits: J. R. Lasky.

petition (Cornwell and Ackerly 2009, Schamp and Aarssen 2009, Adler et al. 2013). We expected filtering due to moisture limitation at higher elevations; however, trait means shifted toward species and individuals with higher SLA, contrary to expectations that dry conditions favor low SLA (Wright et al. 2004, Lasky et al. 2013). Instead, the increase in SLA may be related to greater disturbance from tree fall and landslides at higher elevations that create light gaps and favor younger successional strategies (Ohkubo et al. 2007).

Among co-occurring species, we expected high latex diversity would indicate latex trade-offs with other defense traits resulting in herbivory-mediated niche partitioning, i.e., low herbivore overlap among species (Janzen 1970, Rudgers et al. 2004, Moles et al. 2013), while we expected low latex diversity would indicate defense–growth trade-offs and filtering (Janzen 1974, Fine et al. 2004, Agrawal 2007, Zhao and Chen 2012). We found evidence that both processes might be occurring at our study site. SDNN indicated significant even spacing of latex production in 100-m^2 quadrats, supporting a role for within-site niche variation associated with latex and reduced herbivore overlap. However, we simultaneously observed significantly low TD and variance in 400-m^2 quadrats, suggestive of filtering, with decreasing mean and variance of latex at higher elevations. Latex exudation was negatively correlated with SLA (Spearman's $\rho = -0.47$, $P = 0.05$), which can be positively associated with fast growth (Shipley 2006), consistent with the hypothesis of a latex defense–growth trade-off. The decrease in latex at higher elevations may be due to increased disturbance at higher elevations (Ohkubo et al. 2007) that increases light availability and allows communities to be dominated by poorly defended fast-growing early-successional species (Coley et al.1985, Fine et al. 2004). We found latex production was evolutionarily convergent (though not significantly); one explanation is that adaptation to habitats with distinct resource availability drives evolution of latex production (Fine et al. 2006). Our study is one of the few in vegetation plots that addresses how a trait directly involved in herbivore defense mediates species co-occurrence. In a study of *Inga* (Fabaceae) on two tropical forest plots, Kursar et al. (2009) found that co-occurring species showed significant dispersion in multivariate defenses. Additionally, Becerra (2007) found that the diversity of defense compounds in *Bursera* (Burseraceae) was greater in locations where phytophages were more specialized, suggesting herbivory-mediated niche differentiation.

Individual-level trait patterns

We found that trait patterns revealed stronger evidence for niche partitioning at the individual-level compared to species-level analyses, consistent with our expectation and recent studies (Paine et al. 2011, Siefert 2012). For example, many of the significant trait patterns among co-occurring individuals were also significant at the species level, but weakly so. Trait-associated ecophysiological processes that affect species patterns also likely affect individual patterns, where functional variation is more directly related to performance. However, functionally diverse individuals of two species could exhibit local niche partitioning even if the two species occupy identical niches averaged across individuals. The extensive intraspecific variation we observed in SLA and leaf succulence may reduce the strength of intraspecific competition, weakening the role of species-level niche partitioning associated with these traits (Chesson 2000, Bolnick et al. 2011). When species niche differences are small, greater similarity in fitness is required for species coexistence (Chesson 2000). Thus the reduced signal of niche partitioning that we observed among species could indicate that *Ficus* coexist through neutral, unstable fitness-equalizing mechanisms (Hubbell 2001, Vellend 2006, Adler et al. 2007, Lichstein et al. 2007). However, additional, unobserved axes of niche partitioning may also promote species diversity.

The greatest increase in significant tests between individual and species-level analyses was for SLA, the leaf trait with the highest intraspecific variation. Additionally, SLA and leaf succulence were more strongly correlated to elevation at the individual level compared to the species level. SLA is often highly variable among individuals in plant communities (Wilson et al. 1999, Garnier et al. 2001). In a temperate grassland, SLA showed the greatest intraspecific variation and also the greatest differences between community-wide species patterns and individual level patterns (Jung et al. 2010). The fact that SLA is strongly related to photosynthetic rate (Oren et al. 1986, Reich and Walters 1994) supports the hypothesis that intraspecific SLA variation has fitness consequences or is associated with niche partitioning among individuals.

Among significant relationships, there were no sign differences in species vs. individual-level analyses, indicating that species-level analyses would not suggest opposite conclusions to individual-level analyses (Paine et al. 2011). We believe that our null model of individual-level assembly, which maintained the number of quadrats in which a species occurred, was appropriately more conservative than those used previously (Paine et al. 2011, Siefert 2012). However, the construction of appropriate null permutation models in spatial ecology is challenging because of the difficulty of representing spatially autocorrelated processes, such as dispersal, in permutations (Kembel 2009, Guillot and Rousset 2013).

Trait diversity at the individual level may have been partly affected by co-occurring individuals plastically matching their phenotype to the environment in a correlated or repelling manner (Rausher 1992). Although individual-level patterns may partly result from plasticity, the evolutionary origin of plasticity may also involve environmental filtering or selection. Understanding the role of community-wide plasticity will require determining the heritability of functional traits in co-occurring species (Cornwell and Ackerly 2009, Jung et al. 2010, Paine et al. 2011).

Our results affirm that species mean patterns should be interpreted with caution, especially for traits with high intraspecific variability, and that negative results may be due to the ignorance of intraspecific variation (Messier et al. 2010, Bolnick et al. 2011, Violle et al. 2012). Individual-level measurement of the most intraspecifically variable but ecologically important traits can be critical to detecting trait-associated niche variation (Albert et al. 2010, 2011, Paine et al. 2011, Siefert 2012). Highly variable traits, such as SLA in *Ficus*, could be identified through pilot sampling followed by extensive individual sampling. In our study, the relative strength of individual-level compared to species-level patterns was greatest in the largest quadrats (2500 m^2). The largest quadrats were necessarily the fewest in number, and have also showed weak species-level trait patterns in a previous study (Swenson and Enquist 2009). The change in power across scales is determined by both the resulting sample size (number of quadrats) and the scale of sampling relative to the scale at which niche processes occur (Kraft and Ackerly 2010).

Phylogenetic diversity

Co-occurring *Ficus* species showed higher phylogenetic diversity than expected, possibly due to filtering of traits that evolved convergently, or due to within-site niche partitioning for phylogenetically conserved traits. At one extreme, local niche partitioning of highly conserved SLA could explain the low relatedness of co-occurring species. At the other extreme, more convergent latex production associated with herbivore-mediated filtering could explain the low relatedness of co-occurring species. Our results are consistent with previous findings that co-occurring plant species of a single lineage exhibit low relatedness (Cavender-Bares et al. 2006), though others have found high relatedness or site-dependent patterns (Kursar et al. 2009, Sedio et al. 2012). Our use of highly resolved phylogenies (e.g., the *Ficus* phylogeny employed here [Xu et al. 2011]) may increase the accuracy of community analyses beyond approaches that use (phylogenetic) super-trees with poorly resolved tips (Webb 2000, Kress et al. 2009, Swenson 2009, Davies et al. 2012, Srivastava et al. 2012). However, note that competitive exclusion at the plot level among closely related species may reduce power to observe phylogenetic trait conservatism (Srivastava et al. 2012); thus a larger, regional sample of *Ficus* species might reveal even stronger conservatism than we detected.

Large-scale environmental, evolutionary, and dispersal processes have likely influenced the patterns we observed in this study. Xishuangbanna occurs near the northern range limit of dipterocarp rain forests, and nearly all of the study species are near their northern range limit in the prefecture, although they are found across larger areas to the south (e.g., Sundaland [Wu et al. 2003]). Abiotic limitations may be more important to limiting species distributions near their north or south temperate range boundaries as opposed to at tropical boundaries (Wiens 2011). Whether abiotic limitations near poleward range boundaries also are more important drivers of local distributions (e.g., across a forest plot) merits further exploration. Additionally, the distribution of environmental conditions across Southeast Asia and the evolutionary history of *Ficus* can affect whether species evolve specialization along environmental gradients (Brown and Pavlovic 1992). These large-scale forces might limit the number of species sensitive to quadrat-level environmental filtering, thus limiting our ability to observe spatial niche partitioning (Ricklefs 1987, Hugueny et al. 1997).

Conclusions

Ficus is an example of the speciose genera that underlie a large portion of tropical plant diversity (Harrison 2005). Recent studies of woody species in three diverse neotropical genera have found evidence for niche partitioning along spatial environmental gradients (Sedio et al. 2012) and within local sites (Becerra 2007, Kursar et al. 2009), suggesting that partitioning is prevalent even among closely related species. Our findings suggest that niche partitioning along abiotic gradients and within sites promotes functional diversity of *Ficus* species, although high intraspecific variation may reduce the role of niche partitioning in species coexistence. As efforts expand to sample intraspecific trait variation, we expect researchers to further illuminate mechanisms that maintain diversity that may be obscured by species-mean approaches.

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SUPPLEMENTAL MATERIAL

Appendix

Additional information on functional traits, distribution, sampling, and phylogeny of *Ficus* species on our study plot (*Ecological Archives* E095-082-A1).