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Drought tolerance as a driver of tropical forest assembly: resolving spatial signatures for multiple processes

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Abstract. Spatial patterns in trait variation reflect underlying community assembly processes, allowing us to test hypotheses about their trait and environmental drivers by identifying the strongest correlates of characteristic spatial patterns. For 43 evergreen tree species (>1 cm dbh) in a 20-ha seasonal tropical rainforest plot in Xishuangbanna, China, we compared the ability of drought-tolerance traits, other physiological traits, and commonly measured functional traits to predict the spatial patterns expected from the assembly processes of habitat associations, niche-overlap-based competition, and hierarchical competition. We distinguished the neighborhood-scale (0–20 m) patterns expected from competition from larger-scale habitat associations with a wavelet method. Species' drought tolerance and habitat variables related to soil water supply were strong drivers of habitat associations, and drought tolerance showed a significant spatial signal for influencing competition. Overall, the traits most strongly associated with habitat, as quantified using multivariate models, were leaf density, leaf turgor loss point (π_{tlp}; also known as the leaf wilting point), and stem hydraulic conductivity (r^2 range for the best fit models = 0.27–0.36). At neighborhood scales, species spatial associations were positively correlated with similarity in π_{tlp}, consistent with predictions for hierarchical competition. Although the correlation between π_{tlp} and interspecific spatial associations was weak ($r^2 < 0.01$), this showed a persistent influence of drought tolerance on neighborhood interactions and community assembly. Quantifying the full impact of traits on competitive interactions in forests may require incorporating plasticity among individuals within species, especially among specific life stages, and moving beyond individual traits to integrate the impact of multiple traits on whole-plant performance and resource demand.

Key words: community assembly; competition; drought tolerance; environmental filtering; functional traits; habitat associations; spatial associations; tropical forest; turgor loss point.

Introduction

Species spatial distribution patterns are shaped by underlying community assembly processes (McIntire and Fajardo 2009). Non-neutral processes influence plant species distributions through their interactions with species traits (Adler et al. 2013), enabling spatial patterns in trait variation to provide powerful evidence of the drivers of community assembly. Tropical forests exhibit spatial signatures of multiple processes, including trait associations with microhabitats, and, at the neighborhood scale (<20 m), trait patterns that are consistent with the effects of competitive interactions (Kraft et al. 2008, Paine 2012). However, inferring processes from patterns has been hampered by the inability of earlier statistical methods to disentangle multiple patterns, and, hence, the underlying processes, occurring at overlapping spatial scales (Wiegand et al. 2009, Detto and Muller-Landau 2013). Identifying the traits and environmental characteristics that most strongly impact assembly has also been limited by the use of traits that capture an important but narrow range of plant function (Wright 2004, Kraft et al. 2008, Bartlett et al. 2012).

Plant vegetative traits impact several ecological processes simultaneously: (1) habitat association, wherein species with similar traits co-occur in microhabitats due to similar resource requirements; (2) niche-based competition, wherein species trait differences enhance coexistence by reducing niche overlap, so competitive exclusion is strongest among similar species; and (3) hierarchical competition, wherein species trait differences reduce coexistence by increasing fitness differences, so the strongest competitors have similar trait values and exclude species with different, less competitive, trait values (Chesson 2000, Kraft et al. 2008, Mayfield and Levine 2010, Kunstler 2012). These processes can be identified by spatial signatures in trait variation

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(Fig. 1A–C). Habitat association is predicted to result in the aggregation of functionally similar species in similar environments, at the scale of edaphic and topographic environmental variation. Competition, which is expected to act at the scale of neighborhood interactions (<20 m), is predicted to cause neighboring species to differ in traits that influence niche differences (sensu Chesson 2000). Alternatively, for traits that influence fitness in general, hierarchical competition may result in the aggregation of similar species at the neighborhood scale, excluding species that differ strongly from the competitively superior. These patterns will also emerge for closely related species if traits are phylogenetically conserved (Mayfield and Levine 2010).

Evidence for traits influencing community structure through habitat association is strong, but still coarse. Previous studies have found a spatial signature for habitat associations through strong relationships between traits and habitat categories within communities (i.e., ridges and valleys or soil types [Becker et al. 1988, Comita and Engelbrecht 2009, Katabuchi et al. 2012]), and smaller ranges in trait variation within subsamples of a community than would be expected if trait values were distributed randomly throughout (Kraft et al. 2008, Swenson and Enquist 2009). These studies laid the groundwork for a higher resolution of the drivers of habitat associations. One important advance is the use of quantitative rather than categorical habitat variables, an approach that identified a significant relationship between topography and functional traits at the Xishuangbanna long-term forest dynamics plot (XSBN), a seasonal tropical rainforest in Yunnan, China (Liu et al. 2014). Species with trait values often associated with fast growth,

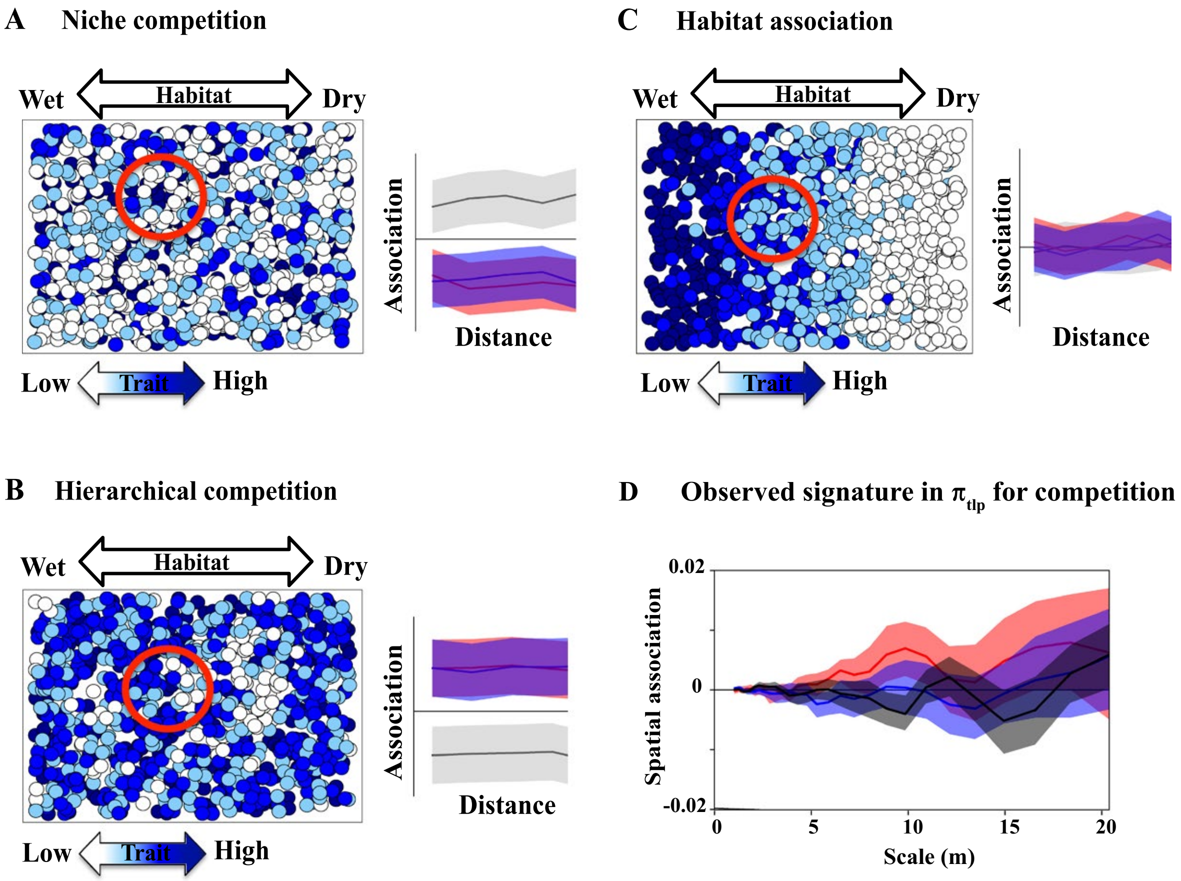

FIG. 1. Simulations showing characteristic spatial patterns in trait variation and results of the wavelet analysis for each assembly process (A–C), and the observed signature of hierarchical competition for the drought tolerance trait turgor loss point (π_{tlp}) (D). Niche competition spatially clusters neighbors with different trait values (A, indicated by the colors in the neighborhood in the red circle), while hierarchical competition and habitat association aggregate similar trees (B, C). Habitat association also correlates trait values with habitat (C). Wavelet analyses separate neighborhood patterns from larger-scale habitat associations and show that species with similar trait values (red, high; blue, low) are more clustered than species with contrasting trait values (gray) for hierarchical competition (B), with no differences under habitat association (C). The trait π_{tlp} was the only trait with a signal for competition (D) (Appendix S5: Fig. S1). The larger trees of drought-tolerant species pairs (red; n = 190 pairs) were more aggregated than those with contrasting π_{tlp} values (gray, n = 420) at scales from 8 to 11 m, consistent with hierarchical competition. Bands show 95% confidence intervals. There were no differences for analyses unweighted by tree size (Appendix S5: Fig. S2).

including lower seed mass and wood density, occurred in valleys rather than on ridges (Liu et al. 2014). Further, while previous studies have often focused on leaf and stem economic spectrum traits, such as leaf mass per area and wood density (Kraft et al. 2008, Liu et al. 2014), which capture important trade-offs between rapid growth and the mechanical strength and longevity of leaf and wood tissue (Wright 2004), species differences in water use or drought tolerance are increasingly recognized as important drivers of species distributions within and across communities (Baltzer et al. 2008, Comita and Engelbrecht 2009, Bartlett et al. 2012). Species that experience hydraulic dysfunction, wilting and leaf death at greater leaf water deficits occur in drier ecosystems and drier habitat categories within ecosystems (Becker et al. 1988, Choat et al. 2007, Baltzer et al. 2008, Comita and Engelbrecht 2009, Bartlett et al. 2012). Thus, we sampled traits that characterize drought tolerance and water use as well as quantitative environmental variation to test hypotheses about the trait and environmental drivers of habitat associations in a tropical community (detailed in Tables 1 and 2). We sampled the turgor loss point (π_{tlp}), a key drought tolerance trait that represents leaf vulnerability to wilting, and sapwood area- and leaf-area-specific stem conductivity (K_S and K_L), physiological traits contributing to the capacity to transport water to sustain transpiration and photosynthetic carbon gain (Choat et al. 2007, Bartlett et al. 2012). Species with more negative π_{tlp} values typically maintain photosynthesis under drier conditions, while higher conductivity is often associated with lower drought tolerance due to anatomical trade-offs (Brodribb et al. 2003, Choat et al. 2007). To broadly characterize plant function, we also sampled the commonly-measured leaf structural and economic spectrum traits leaf dry mass per area (LMA), leaf density (ρ), leaf dry matter content (LDMC), and nitrogen concentration per unit mass (N_{mass}) (Wright 2004). To quantify habitat, we not only used topographic variables, but also variables that characterize solar radiation and vegetation structure, which can drive landscape variation in water supply more strongly than topography under dry conditions (Grayson et al. 1997).

Previous studies have also found spatial signatures for competition. For example, studies have reported lower trait similarity among co-occurring species than expected from dispersal, consistent with trait differences reducing niche overlap between species (Kraft et al. 2008, Swenson and Enquist 2009). However, these studies did not test for a spatial signature for hierarchical competition, which may be even more important as a process influencing assembly if traits contribute to fitness differences across species (Chesson

Table 1. Hypothesized relationships between key ecological processes and spatial patterns in trait variation

Process	Pattern	Hypotheses
Habitat association	Functionally similar species will co-occur at the spatial scale of environmental variation.	(1) Trait values will correlate with habitat variables across species. (2) Drought tolerance and physiology traits will be strong drivers of habitat association and strong correlates with habitat, as established for economic spectrum traits. More drought-tolerant species will occur in drier habitats, while species with greater conductivities will occur in wetter sites. Species with higher nutrient and lower structural investment will occur in less shaded habitats, and these traits will relate weakly to water supply. (Habitat and trait variables are described in Table 2 and Fig. 2). (3) Traits will strongly correlate with habitat variables that determine water supply in dry conditions, including neighborhood crowding, solar radiation, and topographic aspect and convexity (Table 2).
Competition	Species will show significant spatial associations at the neighborhood scale when accounting for larger-scale habitat patterns.	(4) Spatial associations weighted by tree size will show a stronger spatial signal for competition, as larger trees are typically stronger competitors. (5) Drought tolerance and physiology traits will show strong spatial patterns, as they directly impact ability to deprive neighbors of resources. (6) Pairwise differences in phylogenetic relatedness will show the same correlations with spatial associations as phylogenetically conserved traits.
Niche overlap based competition	Functionally distinct species will be more clustered at the neighborhood scale.	(7) Species pairs with distinct trait values will be more clustered than pairs where both species have high or low trait values. (8) The absolute value of pairwise trait differences will significantly correlate with pairwise spatial associations.
Hierarchical competition	Functionally similar species will be more clustered at the neighborhood scale.	(9) Species pairs where both members have high or low mean trait values will be significantly more aggregated than pairs with contrasting means. (10) The absolute value of pairwise trait differences will not correlate with pairwise spatial associations.

TABLE 2. Habitat variables' relationships to light and water supply and predicted correlations with traits.

Habitat variable	π_{tlp}	C	LI	Values	Functional significance
Elevation (m)	−	−	+	731, 760, 805	Higher elevation sites receive less water drainage and shading from upslope areas (Becker et al. 1988).
Convexity (m/m)	−	−	+	−3.4, −0.08, 1.5	Elevation relative to surroundings. Convex, drier sites receive more light and less drainage (Daws et al. 2002).
Slope (°)	−	−	0	18.4, 25.3, 29.8	More sloping sites may receive less drainage (making them drier) or less light (wetter) (Galicia et al. 1999).
Topographic wetness index (TWI)	+	+	0	4.4, 5.5, 7.7	Ratio of upslope area to local slope. Wetter sites, with a higher TWI, receive more drainage from upslope areas than they lose due to local slope (Sorensen et al. 2006).
East/west aspect	+	+	−	−0.55, −0.21, 0.70	Western, drier sites (−) have more light at the hottest time of day, increasing evaporation (Bennie et al. 2008).
North/south aspect	+	+	−	−0.63, −0.21, 0.28	Southern, drier sites (−) have more light, and thus evaporation, in the northern hemisphere (Leij et al. 2004).
Solar radiation (W/m^2)	−	−	+	3778, 3955, 4091 1077, 1122, 1186 2291, 2739, 3145 853, 888, 939	Values are for mean direct light during the wet season, diffuse light during the wet season, direct light during the dry season, and diffuse light during the dry season, respectively. Sites with greater light exposure have more evaporation (Galicia et al. 1999). Direct light should induce more evaporation than diffuse, and dry season radiation should influence water supply more than the wet season (Grayson et al. 1997).
Crowding	−	−	0	4.16, 5.48, 6.58 7838, 20249, 47712 507, 610, 725 22.9, 25.5, 28.3	Values are for crowding measured as the mean total neighborhood basal area (BA; m^2), mean neighborhood basal area normalized by focal tree area (Neighborhood-scaled BA), mean total neighborhood tree density (Density), and mean neighbor size (cm^2), respectively. Drought-tolerant species should occur in crowded neighborhoods, which will deplete water faster; however, greater density could also increase shading (Canham et al. 2004).

Notes: A + predicts that higher values are associated with greater leaf structural investment (LI; higher leaf dry mass per area [LMA], leaf dry matter content [LDMC], and leaf density [ρ]; lower nitrogen concentration per unit mass [N_{mass}]), higher conductivity (C; higher sapwood-area- and leaf-area-specific stem conductivity [K_S and K_L]), or lower drought tolerance (π_{tlp}), as $\pi_{tlp} < 0$. A - predicts a correlation in the opposite direction, and a 0 predicts no correlation. Values are the minimum, mean, and maximum.

2000, Mayfield and Levine 2010). Indeed, previous studies of neighborhood interactions have found increased growth and survival in trees with functionally similar interspecific neighbors, consistent with both habitat association (Uriarte 2010, Paine 2012) and hierarchical competition (Kunstler 2012), but a previous study at the XSBN plot found that trait similarity was lower in valley than ridge habitats, suggesting stronger competition among fast-growing species (Liu et al. 2014). We distinguished for the first time between a signature of trait influence on habitat associations and competition (niche-based and hierarchical) using statistical methods that separate neighborhood from larger-scale spatial patterns (Fig. 1A–C), by implementing a wavelet transform of tree coordinates to produce analytically tractable functions for the correlation between two species' points at given distances (e.g., 2 and 5 m from focal trees), that are independent of correlations at other distances (Detto and Muller-Landau 2013). Further, competition can be strongly influenced by size (Canham et al. 2004, Uriarte 2010), and we developed a novel analysis to account for tree size in determining species associations across spatial scales. These approaches allowed us to rigorously test hypotheses about the impact of drought tolerance, physiology and functional traits on community assembly in a diverse tropical system (Table 1).

METHODS

Trait measurements

Physiological and functional traits were measured for three to six saplings (dbh ranged from 1 to 10 cm) of 43 evergreen species (see Appendix S1 for methods). We focused on saplings to minimize variation due to life stage and canopy position. The study species account for 71% of the total stem density at the 20-ha (400 × 500 m) Xishuangbanna (XSBN) forest-dynamics plot in Yunnan, China (101°34′26″–47″E and 21°36′42″–58″N; Lan et al. 2011*b*). All trees ≥1 cm in diameter have been censused and the topography mapped at 10-m intervals according to standard Center for Tropical Forest Science protocols (Condit 1998). The plot is a seasonal tropical rain forest with a mean annual temperature of 21.0°C and precipitation of 1532 mm, with 80% of rainfall occurring during the May–October wet season (Lan et al. 2011*b*). For the traits that are expected to exhibit seasonal plasticity, we measured

π_{tlp}, LMA, LDMC, and ρ during the dry season and N_{mass} during the wet season (Appendix S1). We assessed K_{S} and K_{L} in both seasons.

Testing for habitat associations

Species' habitats were characterized with variables previously shown to be associated with landscape variation in water and energy fluxes in other forests: (1) elevation; (2) slope; (3) the ratio of the upslope area to the local slope, or topographic wetness index *(TWI)*; (4) convexity; the linearly transformed aspect variables (5) eastness and (6) northness; and average daily (7) direct and (8) diffuse light in the wet season and (9 and 10) dry season (Appendix S2: Tables S1–S3, Figs. S1–S3). Previous studies have established that sites with higher daily light exposure or a more southern or western aspect are drier due to greater evaporation (Grayson et al. 1997, Bennie et al. 2008), sites with a lower topographic wetness index (TWI) are drier due to greater water drainage away from the area (Sorensen et al. 2006), and sites with higher elevation (Becker et al. 1988) or convexity (more ridge than valley shaped) are drier due to both greater evaporation and greater water drainage away (Daws et al. 2002, Leij et al. 2004) (Table 2). Sites with a higher slope may be drier due to greater drainage (Leij et al. 2004) or wetter due to lower light interception (Galicia et al. 1999). Diffuse and direct light were considered separately because long-term carbon balance is more strongly associated with diffuse light, but direct light may induce greater evaporation and soil dryness (Mercado 2009). These variables were calculated from the plot elevation map for each 10 × 10 m quadrat with ArcGIS 9.3 (ESRI, Redlands, California, USA), and species means for each variable were calculated from the number of individuals in each quadrat. We compared the predictive ability of species means for environmental variables (e.g., Elevation) and of species means weighted by species abundance relative to the total density in each quadrat, to quantify the habitats where a species is over-represented in the community (e.g., $\mathrm{Elevation}_{\mathrm{WA}}$, see Appendix S1). We also characterized habitat with vegetation structure variables for "neighborhood crowding" in 20 m radius circular neighborhoods. We determined (1) average neighbor basal area, (2) overall neighborhood basal area, (3) tree density (i.e., number of stems per ground area), and (4) neighborhood basal area scaled by focal tree size, or the ratio of total neighborhood basal area to focal tree area (Appendix S2: Table S2, Fig. S4), using all trees in the neighborhood. We expected crowding to increase competition for water, although crowding can also reduce evaporation through greater shading (Coomes and Grubb 2000, Canham et al. 2004).

We first tested univariate correlations between species trait means and habitat variables (Appendix S3: Table S1, S2), and then multivariate correlations, since many of the habitat variables were significantly correlated. We predicted trait means from multivariate habitat models (Appendix S3: Table S3) and determined the best-fit models using the Akaike information criterion corrected for small sample sizes (AIC_c), then assessed which best-fit models were robust to spatial autocorrelation using torus translation tests (Harms et al. 2001). Best-fit models were defined as those with an $\mathrm{AIC}_c \leq$ 2 units from the minimum AIC_c identified for each trait variable and for which a more parsimonious model with a subset of the same predictor variables was not also identified as a best-fit model (Burnham and Anderson 2010). If the model with the minimum AIC_c value was rejected for a more parsimonious model, it was used to define the threshold AIC_c value for the best-fit models, but it was not considered to be supported enough to be discussed further.

Testing for spatial signals of interspecific competition using wavelet analyses

To identify spatial patterns for competition, we used a wavelet method to calculate the pairwise interspecific spatial association for each combination of species pairs at 32 scales between 0 and 20 m (Detto and Muller-Landau 2013; n = 820 pairs). The wavelet method separates the correlation between two spatial processes into independent values at each scale, so the correlations at local scales are independent from larger-scale patterns. Values are >0 for clustered species, 0 for randomly associated species, and <0 for segregated species. We used 20 m as the largest scale because neighborhood effects on performance dissipate beyond that distance in tropical forests (Hubbell et al. 2001, Uriarte et al. 2004). Previous spatial analyses at XSBN, which did not distinguish between processes with wavelet decomposition, found largely random associations beyond that distance (Lan 2012). We excluded the gap-distributed species *Mallotus garrettii* and *Microcos chungii* from these analyses, as we expected associations between gap and understory species to reflect gap locations more strongly than competitive outcomes.

Because larger trees exhibit greater resource uptake, and, thus, a stronger exclusionary influence on neighbors than smaller trees (Canham et al. 2004), we tested the hypothesis that large trees would show the strongest characteristic spatial patterns for competition (Table 1). Spatial analyses that do not account for tree size weight co-occurrence with small and large trees equally, despite the greater exclusionary pressure of the large trees. We implemented a novel analysis that weighted each tree according to its basal area, so that the spatial patterns of large trees were more influential to the overall spatial association (see Appendix S4 for detailed methods). This weighting makes species pairs with clustered large trees positively associated and pairs with segregated large trees negatively associated.

Testing for hierarchical competition

To test for a signature of hierarchical competition, we classified species means for each trait as high (species mean > 50th percentile of species means) or low (species mean ≤ 50th percentile of species means) and categorized each species pair as "both high," "both low," or "contrasting" for each trait. We then calculated the mean spatial association and 95% confidence intervals from 1000 bootstraps for each category. We considered the trait categories to exhibit significantly different spatial associations at scales for which their 95% confidence intervals did not overlap.

Testing for niche-overlap-based competition

To test for niche-overlap-based competition, we tested the Pearson and rank correlations of the absolute values of differences in species means for each trait with the spatial association between each species pair at each of the 32 scales. Correlations were considered significant if the P value for both the rank and Pearson correlations was $P \leq 0.0083$, which is a significance level of 0.05 corrected for 224 multiple tests (32 scales for 7 traits; Benjamini and Yekutieli 2001).

Testing for an influence of phylogeny on habitat association and competition

We generated a phylogeny for the 42 species with available sequence data (Yang 2014*a*), excluding *Walsura robusta*. We calculated Pagel's λ statistic for each trait and habitat variable, applied phylogenetic least-squared regression to the univariate and best-fit multivariate models relating traits to habitat, and tested for an effect of relatedness on competition by correlating spatial associations with the branch lengths separating the species in each pair.

RESULTS

Tests of habitat association: leaf drought tolerance is a strong trait driver of habitat preference

Five of the six measured traits were significantly correlated with habitat, as expected from hypothesis 1, with r^2 for the best-fit models ranging from 0.04 to 0.36 (Table 3, Fig. 2). We report only the best-fit models that were more predictive than spatial autocorrelation (Appendix S3: Table S4).

Supporting hypothesis 2, which predicted the drought tolerance and physiology traits would correlate with habitat (Tables 1 and 3), leaf density (ρ) was strongly correlated with habitat (r^2 for best-fit models = 0.34–0.36), as was the drought tolerance trait π_{tlp} (r^2 for best-fit models = 0.18–0.32) and the physiology traits K_{L} and K_{S} (r^2 for best-fit models = 0.24–0.27 and 0.22, respectively). These traits were more strongly correlated with habitat than the economics spectrum traits LDMC and N_{mass} (r^2 for best-fit models = 0.10–0.11 and 0.04, respectively), and LMA was the only trait for which none of the best-fit models were significant (Appendix S3: Table S4).

In the best-fit models for ρ, species with denser leaves were associated with more crowded neighborhoods and sites with a greater topographic wetness index (TWI; Table 3; Fig. 2). The correlation between ρ and neighborhood density supports hypothesis 2, which predicts that species with lower leaf investment will occur in less shaded habitats. Four of the five best-fit models for π_{tlp} supported hypothesis 2, with drought-tolerant species associated with drier values for four of the five habitat variables identified as predictors. In those four models, more drought-tolerant species were associated with sites with a higher convexity, more western aspect, greater scaled neighborhood basal area, and larger neighboring trees. In the remaining model, drought tolerance was associated with a more western aspect, as predicted, but with less dense neighborhoods, contrary to expectation (Table 2). By contrast, none of the best-fit models for K_{L} and K_{S} fully supported hypothesis 2. Species with a greater K_{L} occurred in sites with a higher elevation, slope, and neighborhood basal area, contrary to prediction (Tables 2 and 3), although a greater K_{L} was also associated with lower light exposure, as expected if shaded sites are wetter. Species with a higher K_{S} were associated with higher convexity and neighborhood basal area, contrary to hypothesis 3.

The functional traits LDMC and N_{mass} were weakly correlated with habitat (r^2 range = 0.04–0.11) (Table 3). Species with a greater LDMC were found in more western sites and those with higher N_{mass} were found in more crowded neighborhoods, contrary to our prediction that species with greater leaf nutrient investment and lower structural investment would be associated with greater light exposure and not with indicators of habitat water supply (Tables 1 and 2). However, the low r^2 values indicate that these traits are not strongly linked with habitat.

Tests of hierarchical competition: large trees of drought-tolerant species are spatially clustered

Large trees were significantly more clustered for species pairs with more negative mean π_{tlp} values, or greater drought tolerance, than species pairs with contrasting π_{tlp} values at scales from 8 to 11 m, supporting hypotheses 5, 6, and 10 (Fig. 1D). The mean spatial association (i.e., the correlation between the spatial patterns of the species in each pair) for each of these two categories and the difference in mean spatial association between them were small in magnitude; the mean spatial association at 8–11 m was 0.006 to 0.007 for the "high drought tolerance" category, where both species have a more negative π_{tlp} than the 50th

TABLE 3. The best-fit models predicting traits from habitat that were more predictive than autocorrelation (Appendix S3: Table S4), their r^2 values, number of parameters fit (K), and difference in AIC_c from the model with the lowest AIC_c (ΔAIC_c) Habitat variables defined in Table 2.

Predictors	R^2	K	ΔAIC_c
Predicted variable: ρ			
+Neighborhood density, $+\text{TWI}_{\text{WA}}$	0.36	4	0
+Neighborhood density, +TWI	0.34	4	1.1
Predicted variable: π_{tlp}			
−Average neighbor BA, +Eastness	0.24	4	$0.9^{\dagger}$
−Neighborhood-scaled BA, −Convexity, +Eastness, +Neighborhood-scaled BA × Convexity	0.32	6	1.2
$+\text{Eastness}_{\text{WA}}$	0.18	3	1.5
+Neighborhood density, +Eastness	0.22	4	1.8
−Average neighbor BA, −Convexity, +Eastness, +Average neighbor BA × Convexity	0.31	6	1.8
Predicted variable: K_L			
$+\text{Elevation}_{\text{WA}}$, +Neighborhood BA, $+\text{Slope}_{\text{WA}}$, $-\text{Elevation}_{\text{WA}}$ × Neighborhood BA	0.27	6	0
$+\text{Elevation}_{\text{WA}}$, +Neighborhood BA, −Direct light wet $\text{season}_{\text{WA}}$, $+\text{Elevation}_{\text{WA}}$ × Neighborhood BA	0.25	6	1.8
+Elevation, +Neighborhood BA, +Slope, −Elevation × Neighborhood BA	0.24	6	1.8
Predicted variable: K_S			
$+\text{Convexity}_{\text{WA}}$, +Neighborhood BA, $-\text{Convexity}_{\text{WA}}$ × Neighborhood BA	0.22	5	0
Predicted variable: LDMC			
$-\text{Eastness}_{\text{WA}}$	0.11	3	0
−Eastness	0.10	3	0.1
Predicted variable: N_{mass}			
+Average neighbor BA	0.04	3	0

[†] The model with the lowest AIC_c was rejected for a more parsimonious model. Leaf density (ρ) was the strongest correlate with habitat, followed by π_{tlp}, and these correlations largely matched our hypotheses (Table 2).

percentile of species means, and −0.004 to −0.003 for the category of contrasting species pairs. The large trees of more drought-tolerant species were thus more significantly clustered than random, while those of species with contrasting drought tolerances were significantly segregated. The less drought-tolerant species did not exhibit significantly different associations from the other categories. No other traits showed significant differences in spatial association among categories (Appendix S5: Fig. S1, S2).

Tests of niche-overlap-based competition: spatial associations were unrelated to trait differences

Pairwise spatial associations were not significantly correlated with species differences in any trait, either for associations unweighted (maximum r^2 for each trait = 0.004–0.008, minimum P = 0.02–0.07, p_{rank} = 0.03–0.07, n = 820 pairs) or weighted by tree size (maximum r^2 for each trait = 0.004–0.008, min. P = 0.02–0.07, p_{rank} = 0.03–0.07), contrary to hypotheses 5 and 8 (Appendix S5: Fig. S3). (The P value threshold for significance is 0.0083; i.e., 0.05 corrected for multiple correlations).

Tests of phylogenetic effects: relatedness does not influence spatial patterning for these species

None of the trait or habitat variables exhibited Pagel's λ values significantly greater than 0 (Appendix S6: Table S1, Fig. S1, S2). A significant phylogenetic signal was found for univariate correlations between ρ and LMA, and ρ, LDMC, and habitat (Appendix S6: Table S2, S3), but not the best-fit habitat models for any trait (Appendix S6: Table S4). Relatedness was not correlated with pairwise spatial associations, either unweighted (maximum r^2 across scales = 0.006; minimum P = 0.03; p_{rank} = 0.006) or weighted by size (maximum r^2 across scales = 0.004; minimum P = 0.05; p_{rank} = 0.02; Appendix S5: Fig. S3H).

DISCUSSION

Trait variation at the Xishuangbanna plot exhibited spatial signatures for habitat associations and competition. The drought tolerance trait π_{tlp} produced the only signal for both competition and habitat association, providing the first demonstration that leaf drought tolerance plays a critical role in multiple assembly processes in tropical communities.

We expected trait and habitat correlations to be strong, since many species here show significant associations with topography and soil type (Lan et al. 2011*a*, Hu 2012), and these species' functional traits have been found to correlate with topography (Liu et al. 2014). Indeed, five of the six traits, with the exception of LMA, were more strongly correlated with habitat than expected from spatial autocorrelation (Table 3, Appendix S3: Table S4,; hypothesis 1 in Table 1). While LMA is known to vary across

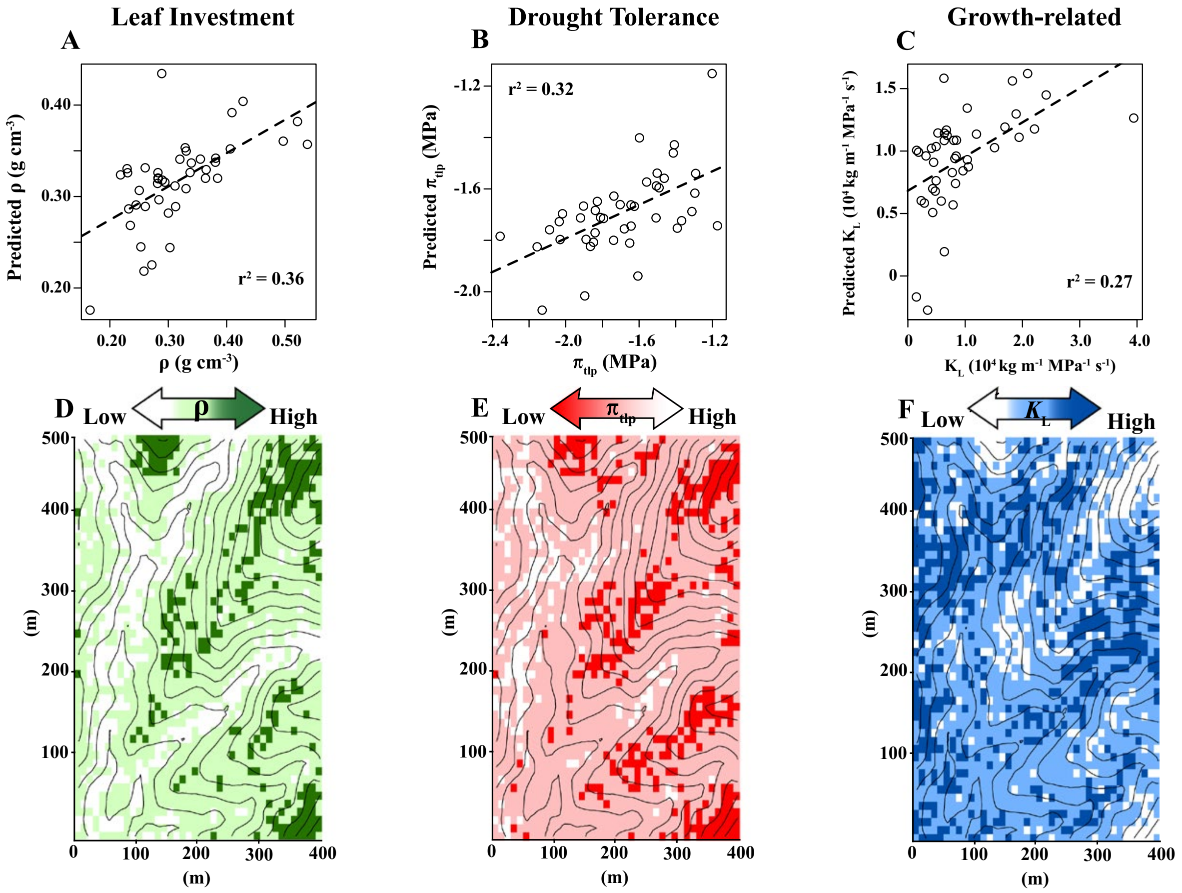

FIG. 2. The predictive power of habitat variables for the traits characterizing leaf structural investment, drought tolerance, and plant growth rate. The strongest correlates in each category are leaf density (ρ, $r^2 = 0.36$; A), turgor loss point (π_{tlp}, $r^2 = 0.32$; B), and leaf-area-specific stem conductivity (K_L, $r^2 = 0.27$; C). Greater leaf structural investment is also quantified by higher leaf dry mass per area (LMA; range = 36–134, mean = 62 g/m^2) and leaf dry matter content (LDMC; 0.22–0.62, 0.35 g/g), and faster growth is also associated with higher sapwood-area-specific conductivity (K_S; 0.14–2.19, 0.91 kg·m^{-1}·MPa^{-1}·s^{-1}) and nitrogen concentration per unit mass (N_{mass}; 1.2–3.1, 2.1%; Wright 2004, Fan et al. 2012; see Appendix S2: Fig. S1 for trait variation across species). Mean ρ (D), π_{tlp} (E), and K_L (F) in each 10 × 10 m quadrat vary strongly across the landscape in accordance with habitat heterogeneity (see Appendix S3: Figs. S1 and S2 for maps of variation in the habitat predictors).

habitats in tropical forests (Kraft et al. 2008), this pattern may reflect a correlation between LMA and traits that more directly drive habitat associations, as supported by the significant correlation and co-evolution between LMA and leaf density ($r^2 = 0.09$, $P = 0.04$, $\lambda = 1$; Appendix S3: Tables S1 and S2, Appendix S6: Tables S2 and S3). Leaf density (ρ) was the strongest trait correlate with habitat (maximum r^2 for best-fit models = 0.36). Species with higher ρ occurred in sites with denser neighborhoods and a higher topographic wetness index (TWI; Table 3, Fig. 2). These results are consistent with predictions from the leaf economics spectrum that species with greater structural investment will occur in more shaded, and hence more crowded neighborhoods (Wright 2004); indeed, increased crowding during succession in a tropical forest favors species with greater leaf structural investment, with a stronger trend found for ρ than LMA or LDMC (Lohbeck 2013). These results are also consistent with the correlation between topography and leaf area index (LAI) found in other tropical forests, suggesting that sites with a higher TWI exhibit a higher LAI and thus more shade from neighboring trees (Moser et al. 2007).

This is the first study to quantify an impact of variation in drought tolerance on species differences in habitat preference within a forest (Fig. 2). Our findings importantly extend previous studies that contrasted π_{tlp} between one species each from different habitat categories within a forest, which found that the more drought-tolerant species occurred in the drier ridge habitats, thus suggesting an important role for π_{tlp} in driving habitat preferences within forests (Becker et al. 1988, Gibbons and Newberry 2002). The π_{tlp} was the trait with the second strongest correlation with environment (maximum $r^2 = 0.32$), demonstrating for the first time across habitats within a forest the stronger alignment of species distributions with π_{tlp} than with K_S, K_L, and LMA, as has been observed across forests and biomes globally (Choat et al. 2007, Bartlett et al. 2012). Species with a more negative π_{tlp} were generally found in drier sites, showing expected correlations (Tables 2 and 3) for four of the five best-fit habitat predictors, including a more western aspect and a higher scaled basal area, average neighbor size, and convexity. A western aspect was especially important, present in every best-fit model for π_{tlp}, and consistent with strong effects of aspect on performance in tropical seedlings (Inman-Narahari et al. 2014). Contrary to prediction, more drought-tolerant species also occurred in less dense neighborhoods, suggesting that decreased shading impacted water supply more than reduced competition, as observed in some other tropical forests (Lebrija-Trejos et al. 2010). The stem conductivity traits K_L and K_S were more weakly correlated with habitat (maximum $r^2 = 0.27$ and 0.22, respectively), and more conductive species did not occur in wetter sites, contrary to expectation from the trade-offs between conductivity and drought tolerance (Choat et al. 2007). Thus, while K_S and K_L are important drivers of growth rate (Fan et al. 2012), these traits weakly impact distributions within the forest. A more negative π_{tlp} was also associated with denser leaves ($r^2 = 0.19$, $P = 0.003$; Tables C1, C2); however, these traits were most strongly related to different habitat variables (Table 3). Thus, the correlation of π_{tlp} with habitat was not driven by ρ; rather, habitat associations reflect the impact of environmental variation on integrated plant function, such as this coordinated investment in leaf structure and drought tolerance (Fig. 2).

Vegetation structure was an especially important environmental driver, with crowding variables identified as predictors in 11 of the 14 best-fit models (Table 3). The predictors for the strongest best-fit models ($r^2 > 0.3$) included convexity, aspect, and crowding, as expected, since these variables drive landscape-level patterns in water supply during drought (hypothesis 3) (Grayson et al. 1997), but not canopy-level solar radiation, suggesting vegetation structure has a stronger impact on light availability. Further, only six of the best-fit models included predictors corrected for quadrat density, suggesting that mean variable values are representative of habitat.

We found novel evidence for a significant impact of leaf drought tolerance on neighborhood interactions, although the spatial signature for competition was weak. As hypothesized for hierarchical competition, species pairs where both species have more negative π_{tlp} values had significantly more aggregated large trees than pairs with contrasting π_{tlp} values at scales from 8 to 11 m (hypothesis 9; Fig. 1D), while pairwise differences were not correlated with interspecific clustering for any trait (hypothesis 10; Appendix S5: Fig. S3). This pattern is consistent with species that have greater drought tolerance being superior competitors. Indeed, ecohydrology models show that species with more negative π_{tlp} values exhibit greater transpiration and depletion of soil water (Laio et al. 2001). We found no significant signal for niche-overlap-based competition (hypotheses 7, 8). These results concur with previous studies showing that position in a trait hierarchy predicts competitive impacts on growth and survival more strongly than trait differences (Kunstler 2012, Kraft et al. 2014), while demonstrating a novel role for leaf drought tolerance in determining species fitness differences. A previous study found greater trait differences among valley-associated species at the XSBN plot and interpreted this result as evidence for stronger competition among species with traits that produce rapid growth and mortality (i.e., lower wood density; Liu et al. 2014). However, our results did not support such a relationship, which would have reduced clustering among drought sensitive species and among species with low K_S, as those trait values are associated with valley sites (Table 3). The signal in π_{tlp} alone suggests drought tolerance more directly impacts resource depletion than leaf economics traits (hypothesis 5; Laio et al. 2001). The presence of a signal for competition in associations weighted by tree size and not unweighted associations is consistent with large trees more strongly impacting competitive interactions (hypothesis 4). This analysis does not identify which life stage drives exclusion; this pattern is consistent with drought-tolerant species excluding drought sensitive trees slowly over time, as the trees become larger, or with drought-tolerant adults preventing less tolerant juveniles from establishing. Overall, these results provide novel support for the further development of size-weighting methods for spatial point patterns.

The spatial signature for competition was statistically significant but extremely weak ($r^2 < 0.01$), which is expected for several reasons. First, we quantified traits for saplings to represent differences among all trees larger than 1 cm in diameter. This is a common study design (e.g., Kraft et al. 2008, Katabuchi et al. 2012), as traits are generally correlated across life stages, and variation within species is typically smaller within than across species (Thomas and Winner 2002, Markesteijn et al. 2007). However, shifts in traits across life stages and plasticity among individuals may widen the range of tolerable habitats or alter competitive outcomes, weakening the spatial signatures of trait means measured for saplings. Second, this weak relationship is also consistent with the difficulty of scaling up individual traits to the whole-plant performance and resource demand that determine competitive impacts (Hérault 2011). Strongly predicting the effect of traits on competition is likely to require a mechanistic approach for predicting whole-plant performance and resource use from many traits. These results may also be consistent with interspecific competition having a relatively small impact on assembly compared to pest/pathogen interactions or conspecific competition. Indeed, conspecific neighbors impact growth and survival more strongly than heterospecifics (Uriarte 2010, Terborgh 2012).

We did not find a phylogenetic pattern in any trait, an impact of phylogeny on the best-fit habitat models, or a correlation between relatedness and spatial association (Appendix S6: Tables S1-S4, Fig. S2). Previous studies in this plot found significant lability in LDMC and SLA and coevolution between SLA and topography (Yang 2014*a*,*b*), suggesting that sampling such a large number of species (>200) enabled the resolution of these phylogenetic patterns. Greater sampling within clades may be especially important, as long branch lengths can obscure phylogenetic signal (Townsend et al. 2010), and our species span 38 genera and 25 families.

Spatial patterns in trait variation can provide powerful insights into the drivers of community assembly, as well as an analytical framework that can be applied to other forests to identify global patterns in the impact of different traits and habitat variables on assembly. Applying these analyses to other forests will raise several important considerations. Here we assessed evergreen species, which potentially exhibit greater resource demand and, thus, competition than deciduous species during the dry season so that analyzing both functional types could obscure the effects of trait differences on competitive interactions. Deciduous species account for 2% of stem density at XSBN, allowing patterns in evergreens to capture important processes at this site, but accounting for differences in competitive interactions between functional types will be crucial in forests with more deciduous trees. Disturbance history can also strongly impact spatial patterns in trait variation. Over 80% of the XSBN forest has been unlogged for at least 200 years, while part of the ridge was logged 40 years ago (Lan et al. 2011*a*). This management history is consistent with the association between drought-tolerant species and ridge sites, as disturbed sites favor drought-tolerant species (Lebrija-Trejos et al. 2010), and with the greater spatial aggregation found among drought-tolerant adults than adults with contrasting trait values, if drought-tolerant species colonized logged areas and excluded sensitive species. While the continuous variation in drought tolerance observed across this landscape (Fig. 2E) suggests that localized disturbance is not sufficient to explain these patterns, future studies should consider these effects in more disturbed forests. Overall, these findings suggest that leaf drought tolerance and structural investment are promising avenues for further research. In addition, the low predictive power for interspecific associations indicates the need to progress from correlative trait signatures to a mechanistic framework to quantitatively infer ecological processes from traits to further resolve the drivers of assembly across communities.

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