

How does habitat filtering affect the detection of conspecific and phylogenetic density dependence?

JUNJIE WU,^{1,2} NATHAN G. SWENSON,^{1,3} CALUM BROWN,⁴ CAICAI ZHANG,^{1,2} JIE YANG,¹ XIUQIN CI,^{1,2}
JIE LI,¹ LIQING SHA,¹ MIN CAO,¹ AND LUXIANG LIN^{1,5}

¹Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China

²University of Chinese Academy of Sciences, Beijing 100049, China

³Department of Biology, University of Maryland, College Park, Maryland 20742, USA

⁴School of Geosciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom

Abstract. Conspecific negative density dependence (CNDD) has been recognized as a key mechanism underlying species coexistence, especially in tropical forests. Recently, some studies have reported that seedling survival is also negatively correlated with the phylogenetic relatedness between neighbors and focal individuals, termed phylogenetic negative density dependence (PNDD). In contrast to CNDD or PNDD, shared habitat requirements between closely related individuals are thought to be a cause of observed positive effects of closely related neighbors, which may affect the strength and detectability of CNDD or PNDD. In order to investigate the relative importance of these mechanisms for tropical tree seedling survival, we used generalized linear mixed models to analyze how the survival of more than 10 000 seedlings of woody plant species related to neighborhood and habitat variables in a tropical rainforest in southwest China. By comparing models with and without habitat variables, we tested how habitat filtering affected the detection of CNDD and PNDD. The best-fitting model suggested that CNDD and habitat filtering played key roles in seedling survival, but that, contrary to our expectations, phylogenetic positive density dependence (PPDD) had a distinct and important effect. While habitat filtering affected the detection of CNDD by decreasing its apparent strength, it did not explain the positive effects of closely related neighbors. Our results demonstrate that a failure to control for habitat variables and phylogenetic relationships may obscure the importance of conspecific and heterospecific neighbor densities for seedling survival.

Key words: competition; habitat association; Janzen-Connell hypothesis; mixed models; phylogenetic relatedness; tropical forest.

INTRODUCTION

Tree populations are often thought to be regulated by negative density dependence (NDD), thereby making NDD an important mechanism underlying the maintenance of species diversity across multiple life stages (e.g., Wills et al. 1997, Harms et al. 2000, Peters 2003, Volkov et al. 2005, Comita et al. 2010, 2014, Swamy et al. 2011, Johnson et al. 2012). Intraspecific competition and Janzen-Connell effects (Janzen 1970, Connell 1971) via species-specific natural enemies (seed predators, pathogens, and herbivores) are two main drivers of NDD (Wright 2002). Many studies have tried to demonstrate NDD by examining the relationship between plant survival, recruitment, or growth and the densities of conspecific neighbors. Such studies, typically conducted using seedlings, have frequently found conspecific negative density dependence (CNDD) in the species studied (e.g., Webb and Peart 1999, Chen et al. 2010, Comita et al. 2010, Johnson et al. 2012, Lin et al. 2012).

The effects of intra- and interspecific density on seedlings may be interchangeable if pathogens have wide host ranges where neighborhood density per se drives NDD and it is not necessary to invoke CNDD (Freckleton and Lewis 2006). However, tropical forest investigations that have partitioned their analyses into conspecific and heterospecific effects have often found significant differences in intra- and interspecific effects (e.g., Peters 2003, Comita and Hubbell 2009, Johnson et al. 2012, Lin et al. 2012). This has supported the widespread view that seedling performance is limited more by interactions with conspecific individuals than with heterospecific individuals. If generally valid, the greater strength of negative intraspecific effects relative to negative interspecific effects promotes stable species coexistence (Chesson 2000).

Interestingly, conspecific adult neighbor densities have been found to have a particularly strong negative influence on seedling survival (e.g., Comita and Hubbell 2009, Chen et al. 2010, Johnson et al. 2014). Seedling–seedling interactions, in contrast, are often relatively weak, presumably because the sizes and densities of seedlings in the understory of tropical forests are not

Manuscript received 5 January 2015; revised 8 September 2015; accepted 1 December 2015. Corresponding Editor: N. J. B. Kraft.

⁵E-mail: linluxa@xtbg.ac.cn

typically great enough to generate such large impacts (Paine et al. 2008, Svenning et al. 2008). Further, positive correlations between the probability of seedling survival and heterospecific neighbor densities have been found (Comita and Hubbell 2009), supporting the so-called “species herd protection hypothesis” (Peters 2003). Thus, seedling survival is likely to be lower in an area of high conspecific adult neighbor density and higher in an area with many heterospecific adult neighbors.

Due to the enormous diversity in the tropics, heterospecific neighbors are more common than conspecific neighbors. A simple division of neighbors into conspecifics and heterospecifics may therefore hide the potentially large variation in the degree to which heterospecific species are similar to the focal species. Such thinking led Webb et al. (2006) to characterize heterospecific species in terms of their phylogenetic distance from the focal individual, thereby moving neighborhood analyses beyond a potentially overly simplistic conspecific/heterospecific dichotomy.

The rationale for considering phylogenetic relatedness in studies of NDD rests on empirical evidence suggesting that there is often a phylogenetic signal in morphological and biochemical traits that dictate host–pest interactions (Mitter et al. 1991). In the most extensive syntheses to date, the probability of sharing a pest or pathogen between two host plants decays strongly with phylogenetic distance (Parker and Gilbert 2004, Novotny et al. 2006, Gilbert and Webb 2007, Gilbert et al. 2012). This pattern is expected to be more pronounced under broader taxonomic samples, and less pronounced under smaller taxonomic samples (e.g., a single genus). Phylogenetic negative density dependence, due to shared natural enemies between closely related species, may therefore be expected to emerge in a tropical forest containing many plant lineages (i.e., a broad taxonomic sample). In such cases, CNDD can be extended across evolutionary distance between two neighboring species (e.g., Webb et al. 2006, Metz et al. 2010, Liu et al. 2012, Paine et al. 2012, Lebrija-Trejos et al. 2014) therefore generating phylogenetic negative density dependence (PNDD).

Beyond biotic interactions, an important driver of local community composition is the abiotic environment (Metz et al. 2010). For example, variation in light availability (Comita et al. 2009, Queenborough et al. 2009, Rüger et al. 2009), soil water availability (Comita and Engelbrecht 2009, Lin et al. 2012), and soil nutrients (Bai et al. 2012) are all well-known drivers of species survival, coexistence, and diversity.

Findings that survival probability is positively correlated with conspecific density are often interpreted as being due to species’ habitat preferences (e.g., Comita and Hubbell 2009, Comita et al. 2009, Lin et al. 2012). Indeed, many studies examine species’ habitat preferences by analyzing the association between species occurrence and habitat variables (e.g., topography, light, soil nutrients, water availability, etc.) at the seedling stage (e.g., Webb and Peart 2000, Comita et al. 2007,

John et al. 2007, Comita and Engelbrecht 2009, Metz 2012). However, we argue that such results do not necessarily indicate a lack of biotic interactions in general or NDD in particular. Specifically, biotic interactions are dictated by the abiotic context, and a shared habitat preference does not negate the possibility of NDD. Rather, it is likely that habitat preferences and NDD operate simultaneously to produce observed species composition and population dynamics (e.g., Comita et al. 2009, Chen et al. 2010, Bai et al. 2012, Piao et al. 2013). In order to elucidate such a scenario, nested models that consider density effects without and with the abiotic context are needed.

In this study, we used a population dynamics data set of 10 316 seedlings for 269 woody plant species for four contiguous one-year census intervals in the 20-ha Xishuangbanna tropical seasonal rainforest dynamics plot in southwest China. Using generalized linear mixed models, we explored the relative importance of CNDD, PNDD, and habitat filtering for seedling survival. Specifically, we built models of seedling survival dependent on the densities of conspecific and heterospecific neighbors and on the phylogenetic dissimilarities between heterospecific neighbors and focal seedlings. Each of these models was built without and with habitat variables to determine the degree to which habitat filtering affected the apparent prevalence of NDD. We specifically ask (1) Does scaling the effects of neighbors by their phylogenetic distances improve model fit? (2) What is the relative importance of CNDD, PNDD, and habitat filtering in our study system? (3) How does habitat filtering affect the detectability of CNDD and PNDD?

METHODS

Study site

The study was conducted within the 20-ha Xishuangbanna Forest Dynamics Plot (XSBN), located in Mengla, Yunnan Province, Southwestern China (101°34' E, 21°36' N). The elevational range of the plot is from 709 m above sea level (asl) to 869 m asl (Lan et al. 2012; Appendix S1: Fig. S1). There is a rainy season from May to October and a dry season from November to April in the following year. Mean annual precipitation is approximately 1500 mm, of which 80% occurs from May to October (Cao et al. 2006).

The XSBN plot (400 × 500 m) was established in 2007 and censuses are carried out every five years. All woody stems with a diameter at breast height (DBH) ≥ 1 cm are tagged, identified, measured, and mapped (see detailed methods in Condit 1998). A detailed description of the climate, geology, and flora of XSBN can be found in Cao et al. (2008).

Seedling quadrats

During March 2010, a total of 500 seedling quadrats (2 × 2 m) were established in a regular pattern in the

center of each 20 × 20 m subplot in the 20-ha XSBN plot. Where obstacles such as streams, large trees, rocks or fallen woods prevented the establishment of seedling quadrats in these locations, they were placed instead in nearby 5 × 5 m subplots. In each of the 500 seedling quadrats, all woody (tree, shrub, and liana) seedlings with DBH < 1 cm and height ≥ 20 cm were tagged, identified to species, and measured for height. In this study, we used seedlings with height ≥ 20 cm as focal seedlings because seedlings with this height can be assumed to be established in our study system, and therefore more likely to be dependent upon relevant biotic and abiotic interactions rather than effects of chance events that drive mortality in younger seedlings. Seedling quadrats were subsequently censused in the late dry season (April and May) 2010, 2011, 2012, 2013, and 2014. In each census, the states (alive or dead) of all the woody seedlings alive at the previous census were recorded and all new recruits to the 20-cm height threshold were identified and tagged.

Neighborhood variables

At the first (2010) census, we defined total seedling neighbor density of each seedling quadrat as the number of seedlings within the quadrat. Conspecific and heterospecific seedling neighbor densities were defined in the same way. At subsequent censuses, we recalculated seedling neighbor densities by excluding dead seedlings and adding newly recruited seedlings. Tree, shrub, and liana seedlings were monitored at the censuses, and all were included in the calculation of heterospecific seedling neighbor densities, although lianas were not included as focal seedlings in our models. Seedlings that were impossible to classify by species (121 in the 2010 census) were included in heterospecific neighbor counts, but not as focal seedlings.

We calculated the total adult neighbor density (TA) as the summed basal area (BA) of nearby adults weighted by their distances to the focal seedling (Canham et al. 2004)

$$TA = \sum_i^N \frac{BA_i}{\text{Distance}_i}$$

where N is the number of adult neighbors. Conspecific and heterospecific adult neighbor densities were calculated in the same way. Models with densities calculated over a distance of 20 m had stronger support than those with densities calculated over distances of 10 m or 30 m (Appendix S1: Table S1). In the following analyses, we therefore used total, conspecific and heterospecific adult neighbor densities calculated over 20 m. As a result, data from 86 of the 500 seedling quadrats were excluded from the following analyses because these quadrats were within 20 m of the edge of the XSBN plot, and therefore had incomplete adult neighbor density values.

Construction of phylogenetic tree and indices of phylogenetic dissimilarity

We have previously produced a molecular phylogeny for 428 species in the 20-ha XSBN plot (Yang et al. 2014). A total of 121 species identified in the 20-ha plot and/or the seedling quadrats were added to this phylogeny using the APE package (Paradis 2006) in R software (v. 3.0.2; R Development Core Team 2014). These species were added at the crown node of the most closely related taxonomic level (genus, family, or order) in the original molecular phylogeny. For example, any species missing from the original phylogeny that had a congener in the original phylogeny was manually added to the phylogeny at the node for that genus. If there was no congener in the original phylogeny, then the species was added to the node for its family in the original phylogeny. A total of 18 species could not be added to the phylogeny because they were from orders not in the original phylogeny. These species only constituted < 1% of all individuals in the seedling quadrats and therefore had little influence on our results.

Four phylogenetic diversity indices quantifying phylogenetic dissimilarity between focal seedlings and their heterospecific neighbors were used in our analyses: total phylogenetic diversity (TOTPd), average phylogenetic diversity (AVEPd), relative average phylogenetic diversity (APd'), and relative nearest taxon phylogenetic diversity (NTPd'). The TOTPd and AVEPd are, respectively, the sum and average of the phylogenetic distances between a focal seedling and its heterospecific neighbors. The APd' and NTPd' (proposed by Webb et al. 2006) quantify the deviation of observed average phylogenetic distance between a focal seedling and its heterospecific neighbors from that expected under a null model and the equivalent deviation of observed phylogenetic distance between a focal seedling and its most closely related heterospecific neighbor, respectively. The null model used in this study shuffled the names of species on the phylogeny 999 times to produce a null distribution of neighborhood phylogenetic diversities. Positive APd' and NTPd' indicate that neighbors are less related to the focal seedling than expected under the null model and negative APd' and NTPd' indicate that the neighbors are more related than expected. We recalculated the four phylogenetic diversity indices at each census after 2010 to exclude dead seedlings and add newly recruited seedlings. The indices were calculated separately for heterospecific seedling neighbors and heterospecific adult neighbors (with the adult neighborhood again defined as having a radius of 20 m).

Habitat variables

Habitat variables for each of the 414 target seedling quadrats were characterized using measurements of canopy openness, soil properties, and topography.

Canopy openness.—For each seedling quadrat, hemispherical photographs were used to obtain a measure of canopy openness (Comita et al. 2009, Queenborough et al. 2009), which indicated the light condition in the understory. Hemispherical photographs were taken 1.3 m aboveground at the center of each quadrat, using a Nikon Coolpix 4500 camera equipped with a Nikon FC-E8 Fisheye Converter lens (Tokyo, Japan) in January 2014. The camera was arranged horizontally with the aid of a spirit level and pointed to the geographic south. Black and white .jpg images of 2272×1704 pixels were produced in accordance with the methods of Queenborough et al. (2009). The high contrast setting increased distinction between sky and foliage. Three to five replicate photos were taken using a fixed aperture of f/7.5 and shutter speeds between 1/1000 and 1/30 s. Photographs were taken in uniformly overcast weather, during either early dawn or late dusk. The photograph showing the highest contrast between sky and foliage for each quadrat was selected. Gap Light Analyser software (GLA, version 2.0) (Frazer et al. 1999) was used to convert photographs to a single canopy openness measure following the protocol of Beaudet and Messier (2002).

Soil properties.—Soils were sampled following the protocol of John et al. (2007). The 20-ha plot was divided into regular grid squares of 30×30 m, and two soil samples were taken at depths of 10 cm (without litter and humus) and random distance combinations of 2 and 5 m, 2 and 15 m, or 5 and 15 m in a random direction from the grid point. A total of 765 soil samples were obtained. Soil pH, organic matter content (C), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), available potassium (AK) and soil bulk density within each sample were measured (for details see Hu et al. 2012). We used the residuals from polynomial trend-surface regressions for these soil variables to compute empirical variograms, to which we fitted variogram models and used ordinary kriging to obtain spatial predictions of soil variables for each seedling quadrat. This kriging interpolation was implemented using the gstat package (Pebesma 2004) in R software (v. 3.0.2; R Development Core Team 2014). The volumetric soil water content (%) was measured in the late dry season of 2013, using the mean values of three replicates taken randomly around the center of each seedling quadrat using a TDR probe (MPM-160B, ICT International Pty Ltd., Armidale, New South Wales, Australia) at a depth of 5 cm (Song et al. 2013).

Topography.—The topographic variables used were elevation, convexity, slope, and aspect for each seedling quadrat. As above, the full plot was divided into 500 20×20 m subplots with seedling quadrats located at the centers of these subplots. The elevation of each seedling quadrat was taken as the mean of values at each of the four corners of the 20×20 m subplots. The convexity of each seedling quadrat was calculated by subtracting the mean of the four corner elevations of the surround-

ing 20×20 m subplots from the elevation at its center. The slope was calculated as the mean angular deviation from horizontal of each of the four triangular planes of the 20×20 m subplot formed by connecting three of its corners. Aspect was calculated as

$$\text{Aspect} = 180 - \arctan\left(\frac{fy}{fx}\right) \times \left(\frac{180}{\pi}\right) + 90 \times \left(\frac{fy}{|fx|}\right)$$

where fx was the elevation difference from east to west in the 20×20 m subplot while fy was that from north to south.

To reduce the colinearity of habitat variables in our models, we used a principal components analysis (PCA) in the Vegan package (Dixon 2003) of the R software (v. 3.0.2; R Development Core Team 2014) on the 14 habitat variables (soil pH, C, TN, TP, TK, AN, AP, AK, soil bulk density, soil moisture, elevation, slope, aspect, and convexity). Canopy openness was not included in the PCA and was inserted into models directly. The first two principal components, accounting for 56.96% variation of these 14 habitat variables, were used in the later analysis. The first principal component was associated with high elevation and convexity, and low TN, TP, TK, AN, AP, AK, C, pH, and soil moisture. The second principal component was associated with high TN, AN, C, elevation, and convexity, and low AK, pH, soil bulk density, and soil moisture (Appendix S1: Table S2).

Statistical analysis

We conducted analyses separately for all living seedlings in each census interval (2010–2011, 2011–2012, 2012–2013, and 2013–2014). Living seedlings at any one census included survivors from the previous census and new recruits from the most recent census interval.

Generalized linear mixed models (GLMMs) were constructed using the lme4 package (Bates et al. 2014) in R software (v. 3.0.2; R Development Core Team 2014) to model the probability of seedling survival as a function of explanatory variables, with binomial errors (Bolker et al. 2009). Due to the unknown age of seedlings in this study, we included seedling height as a covariate in our models to account for the fact that larger seedlings have higher survival, and therefore to approximately exclude effects of age on survival. The focal seedling height was log-transformed, and all continuous explanatory variables were standardized by subtracting the mean value of the variable (across all individuals in the analysis) and dividing by 1 standard deviation before analyses. This allowed us to directly compare the relative importance of these explanatory variables (Gelman and Hill 2006). The means and ranges of all continuous explanatory variables used in the analysis are listed in Table S3.

It is possible that spatial autocorrelation exists in seedling survival due to unexplored habitat and other factors. However, previous studies have found that spatial autocorrelation in tropical seedling survival is negligible at

distances > 5 m (Queenborough et al. 2007), and seedling quadrats in this study were spaced 20 m apart. Therefore, we added random seedling quadrat effects to our models to exclude any effect of spatial autocorrelation within quadrats on our results. Previous studies suggest that this should be sufficient to account for autocorrelation (Comita et al. 2009, Chen et al. 2010). Furthermore, we included species identity as a random effect, because seedlings of different species were expected to respond differently to local neighborhood variables (Lin et al. 2012).

In the simplest, density-independent model, seedling survival depended only on the initial heights of focal seedlings (Table 1, Appendix S1). This model was grounded in evidence that the probability of seedling survival increases with increasing seedling stature (Paine et al. 2012). Given the importance of habitat filtering on seedling survival, we then built a habitat-only model, including habitat variables in addition to initial seedling height (Table 1, Appendix S1). To assess the role of neighbor densities on seedling survival, we then built models in which conspecific and heterospecific neighbor effects were included together and separately. In these density-dependent models, seedling survival depended on initial seedling height, the total seedling neighbor density or conspecific and heterospecific seedling neighbor densities, and the total adult neighbor density or conspecific and

heterospecific adult neighbor densities (Table 1, Appendix S1). To assess the importance of evolutionary relationships in the survival model, we finally constructed phylogenetic density-dependent models in which heterospecific neighbor densities were replaced by the phylogenetic diversity indices described above (Table 1, Appendix S1).

Akaike's information criterion (AIC) was used to compare models, with ΔAIC calculated by subtracting the overall minimum value of AIC from each of the models' AIC values. We selected the most parsimonious models among those with ΔAIC less than 2, which are thought to be the equally best-fitting models (Burnham and Anderson 2002). We identified the best-fitting density-dependent model (Appendix S1: Table S4) and the best-fitting phylogenetic density-dependent model (Appendix S1: Table S5).

To explore the influence of habitat filtering on the detection of CNDD and PNDD, we compared the best-fitting density-dependent model to the equivalent model in which habitat variables were included (density + habitat model; Table 1, Appendix S1). We also compared the best-fitting phylogenetic density-dependent model with its equivalent phylogenetic + habitat model (Table 1, Appendix S1). We also included interactions between habitat variables and neighborhood variables and used AIC scores to identify the best interaction terms combination in both the density

TABLE 1. Akaike information criterion (AIC) values for the six classes of model for each of the four one-year census intervals.

Candidate model	AIC			
	2010–2011	2011–2012	2012–2013	2013–2014
Density-independent model				
<i>H</i>	3463.1	3213.7	4227.3	4997.7
Habitat-only model				
<i>H</i> + light + PCA1 + PCA2	3448.3	3203.9	4225.2	4998.8
Density-dependent model†				
<i>H</i> + cons + hets + CA + HA	3462.6	3214.8	4230.2	5003.1
Density + habitat model‡				
<i>H</i> + cons + hets + CA + HA + light + PCA1 + PCA2 + cons × PCA1 + cons × PCA2 + CA × PCA1 + CA × PCA2	3442.0	3201.9	4234.0	4998.2
Phylogenetic density-dependent model§				
<i>H</i> + cons + s_NTPd' + CA + a_NTPd'	3466.0	3211.4	4230.1	5000.4
Phylogenetic + habitat model¶				
<i>H</i> + cons + s_NTPd' + CA + a_NTPd' + light + PCA1 + PCA2 + cons × PCA1 + cons × PCA2 + CA × PCA1 + CA × PCA2 + s_NTPd' × PCA1 + s_NTPd' × PCA2 + a_NTPd' × PCA1 + a_NTPd' × PCA2	3449.1	3196.9	4234.7	4996.6

Notes: *H* is the height of focal seedlings. Neighborhood variables included the density of conspecific seedling neighbors (cons), the density of heterospecific seedling neighbors (hets), sum of conspecific adults' basal areas weighted by the distance between the focal seedling and the adult neighbors at distances up to 20 m (CA), sum of heterospecific adults' basal areas weighted by the distance between the focal seedling and the adult neighbors at distances up to 20 m (HA), and two phylogenetic diversity indices: relative nearest taxon phylogenetic diversity between heterospecific seedling neighbors and focal seedlings (s_NTPd') and relative nearest taxon phylogenetic diversity between heterospecific adult neighbors and focal seedlings (a_NTPd'). Habitat variables included percentage of canopy openness (light) and the first two principal components (PCA1 and PCA2) of soil properties and topography. ΔAIC is calculated by subtracting the minimum AIC value from each of AIC values of the models. We selected the most parsimonious models among the models with $\Delta\text{AIC} \leq 2$ (AIC in boldface type) (Appendix S1: Table S2).

†The model comparison for density-dependent models is shown in Appendix S1: Table S4.

‡The model comparison for density + habitat models with different interaction term combinations is shown in Appendix S1: Table S6.

§The model comparison for phylogenetic density-dependent models is shown in Appendix S1: Table S5.

¶The model comparison for phylogenetic + habitat models with different interaction combinations is shown in Appendix S1: Table S7.

+ habitat model (Appendix S1: Table S6) and the phylogenetic + habitat model (Appendix S1: Table S7). In total, we ran six classes of model: (1) density independent, (2) habitat-only, (3) density dependent, (4) density + habitat, (5) phylogenetic density dependent, and (6) phylogenetic + habitat. Equations defining these models can be found in Appendix S1.

We analyzed the above six model classes for each of the four one-year census intervals (Table 1). To explore the effects of habitat filtering on the detection of CNDD and PNDD, we compared the estimated coefficients of neighborhood variables in four of our models: the best-fitting density-dependent model (Model I in Table 2), the density + habitat model with the same neighborhood variables as in the best-fitting density-dependent model (Model II in Table 2), the best-fitting phylogenetic density-dependent model (Model III in Table 2) and the phylogenetic + habitat model with the same neighborhood variables as in the best-fitting phylogenetic density-dependent model (Model IV in Table 2). We labeled Models I and II as density models, and Models III and IV as phylogenetic models. The estimated coefficients represent the relative strength of the variables' effects, and coefficients > 0 indicate positive effects on seedling survival while coefficients < 0 indicate negative effects. Specifically, a positive estimated coefficient for phylogenetic diversity indices indicates a negative relationship between the phylogenetic similarity of heterospecific neighbors and seedling survival (and vice versa). We calculated the variance for each of the models' fixed effects, random effects and for the residuals in each of the above four models (Appendix S1: Table S8).

To determine whether and how habitat filtering affects the detectability of CNDD and PNDD among species, we added species-specific random slopes for each neighborhood variable in the above four models. Differences between these slopes within a model, and across models with and without habitat variables, were used to capture species-specific responses to neighbor densities and the extent to which habitat filtering might obscure these responses. We used likelihood ratio tests to assess the significance of added species-specific random slopes (Appendix S1: Table S9). If P values were less than 0.05, we inferred that the coefficients of neighborhood variables did vary across species. We also used two-sample Kolmogorov–Smirnov tests to compare the distributions of the species-specific coefficients of neighborhood variables between the varying-slope models with and without habitat variables.

RESULTS

CNDD, PNDD, and habitat filtering for seedling survival in the best-fitting model

In the 414 target seedling quadrats, there were 8324, 7868, 7680, and 8156 living seedlings of 238, 237, 240, and 262 focal woody plant species in the 2010, 2011, 2012, and 2013 censuses, respectively.

Of the six survival models we built, the phylogenetic + habitat model had the best-fit for the 2011–2012 and 2013–2014 census intervals, while the density + habitat model and habitat-only model had the best-fit for 2010–2011 and 2012–2013 respectively (Table 1). Across all four census intervals, seedling survival was mainly influenced by fixed effects for habitat variables, followed by the density of conspecific seedling and adult neighbors and NTPd' of heterospecific seedling and adult neighbors (Fig. 1). The effects of the first principal component of topographic and edaphic variables were significantly positively correlated with seedling survival for three census intervals (2010–2011, 2011–2012, and 2013–2014), whereas canopy openness was significantly negatively related for the 2012–2013 census interval. Conspecific adult neighbors had significantly negative effects on survival for the first three census intervals (Table 2). Across all four census intervals, seedling and adult NTPd' generally had insignificant negative effects.

How does habitat filtering affect the detection of CNDD?

Across all four census intervals, the coefficients of conspecific seedling and adult neighbor densities were smaller in Models I and III (without habitat variables) than in Models II and IV (with habitat variables) (Table 2). There were also significant positive interactions between habitat variables and conspecific seedling and adult neighbor densities in Models II and IV (Table 2). Furthermore, we found that adding habitat variables increased the variance explained by the densities of conspecific seedling and adult neighbors, while variances explained by random effects remained almost constant (Appendix S1: Table S8). Together, these results indicate that the true extent of CNDD was obscured when not accounting for habitat variables.

Because adult CNDD was significant in the best-fit models for 2010–2011 and 2011–2012 (Table 2), we added species-specific random slopes for conspecific adult neighbor density to these models. The distribution of these species-specific coefficients changed significantly between models with and without habitat variables (Models II and IV vs. I and III; two-sample Kolmogorov–Smirnov test, $P < 0.05$, Fig. 2). When taking into account habitat variables in Model II, we found that 97.90% and 97.47% of the focal species in the 2010–2011 and 2011–2012 census intervals suffered stronger negative effects of conspecific adult neighbor densities than those in equivalent non-habitat-informed models (Model I). Similarly, 98.32% and 92.83% of the focal species in Model IV (with habitat variables) suffered stronger negative effects than those in Model III (without habitat variables).

How does habitat filtering affect the detection of PNDD?

Across all four census intervals, the coefficients of seedling NTPd' and adult NTPd' were generally negative in both Models III (without habitat variables) and IV (with habitat variables; Table 2), indicating that seedlings

TABLE 2. Coefficient estimates for all explanatory variables in the density-dependent model (Model I), the density + habitat model with the same neighborhood variables as that in the density-dependent model (Model II), the phylogenetic density-dependent model (Model III), and the phylogenetic + habitat model with the same neighborhood variables as that in the phylogenetic density-dependent model (Model IV), for each of the four one-year census intervals.

Explanatory variables	2010–2011				2011–2012				2012–2013				2013–2014			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Intercept	3.686***	3.640***	3.663***	3.601***	3.616***	3.581***	3.584***	3.514***	2.849***	2.830***	2.827***	2.811***	2.691***	2.633***	2.644***	2.599***
Height	0.698***	0.678***	0.696***	0.678***	0.783***	0.779***	0.783***	0.748***	0.323***	0.318***	0.322***	0.314***	–0.037NS	–0.037NS	–0.037NS	–0.038NS
cons	0.095NS	0.006NS	0.042NS	–0.019NS	0.076NS	–0.038NS	0.075NS	–0.022NS	0.071NS	0.042NS	0.052NS	0.034NS	–0.010NS	–0.115NS	–0.029NS	–0.125NS
hets	0.159NS	0.088NS			0.002NS	–0.059NS			0.054NS	0.050NS			0.047NS	0.026NS		
CA	–0.110*	–0.169**	–0.116*	–0.187**	–0.127*	–0.166**	–0.125*	–0.185**	–0.091*	–0.113NS	–0.090*	–0.117*	–0.055NS	–0.095NS	–0.052NS	–0.093NS
HA	0.002NS	0.035NS			0.003NS	0.020NS			–0.026NS	–0.010NS			–0.061NS	–0.045NS		
s_NTPd'			–0.029NS	–0.025NS			–0.100NS	–0.137*			–0.016NS	–0.055NS			–0.016NS	–0.024NS
a_NTPd'			–0.034NS	0.001NS			–0.083NS	–0.028NS			–0.071NS	–0.059NS			–0.157NS	–0.140NS
Light		–0.084NS		–0.076NS		–0.025NS		–0.020NS		–0.177**		–0.170*		–0.059NS		–0.065NS
PCA1		0.328***		0.314***		0.299***		0.272***		0.117NS		0.106NS		0.197**		0.201**
PCA2		0.261**		0.245**		0.202**		0.143NS		0.103NS		0.106NS		0.025NS		0.038NS
cons × PCA1		0.103NS		0.084NS		0.056NS		0.053NS		0.069NS		0.056NS		0.118NS		0.121NS
cons × PCA2		0.029NS		0.011NS		0.167*		0.138NS		–0.001NS		–0.015NS		0.004NS		0.011NS
CA × PCA1		0.150*		0.133NS		0.072NS		0.088NS		0.041NS		0.035NS		0.164**		0.165**
CA × PCA2		0.224**		0.212**		0.052NS		0.055NS		0.021NS		0.022NS		0.089NS		0.083NS
s_NTPd' × PCA1				0.059NS				0.032NS				0.020NS				–0.082NS
s_NTPd' × PCA2				0.016NS				0.128*				0.115*				0.063NS
a_NTPd' × PCA1				0.017NS				0.073NS				0.044NS				0.011NS
a_NTPd' × PCA2				0.051NS				0.093NS				–0.041NS				–0.086NS

Note: See Table 1 for variable abbreviations.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

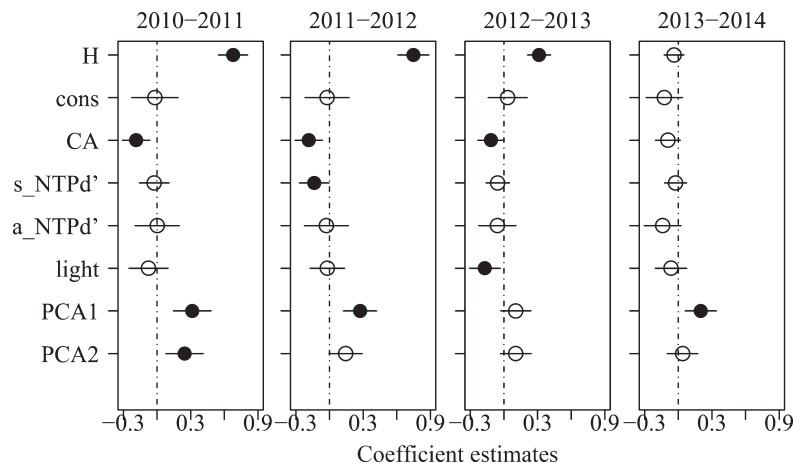


FIG. 1. Estimated effects (mean $\pm$ 2SE) of neighborhood variables and habitat variables on seedling survival for each of the four one-year census intervals in phylogenetic + habitat model (model IV in Table 2). Solid circles indicate significant effects ($P < 0.05$). The interactions of neighborhood variables and habitat variables were not shown here and can be found in Table 2. See Table 1 for variable abbreviations. Dash-dot lines mark 0 on the x-axis scale.

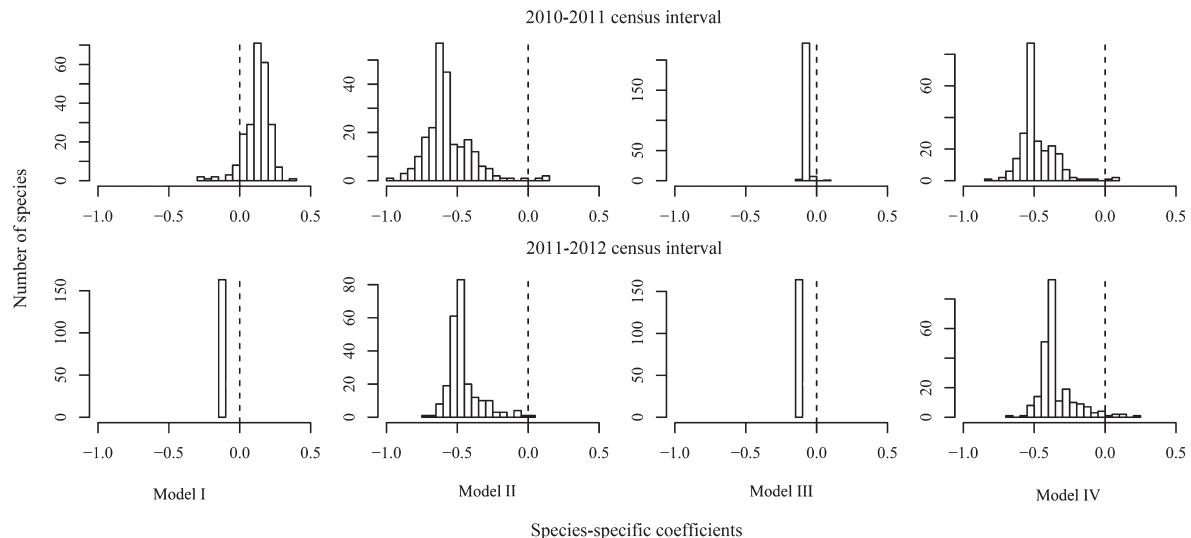


FIG. 2. A comparison of the frequency distribution of species-specific coefficients of conspecific adult neighbor density between Model I (density model without habitat variables) and Model II (density model with habitat variables), and between Model III (phylogenetic model without habitat variables) and model IV (phylogenetic model with habitat variables) for 2010–2011 and 2011–2012 census intervals. Bars to the left of the dashed zero line indicate species whose survival is reduced by increasing neighborhood variables.

survived significantly better when growing among closely related heterospecific neighbors. In contrast to conspecific neighbor densities, adding habitat variables into the survival models did not substantially affect the coefficients of the phylogenetic diversity indices, and the interactions between habitat variables and s_NTPd' and a_NTPd' were insignificant (Table 2). The inclusion of species-specific random slopes for seedling $NTPd'$ and adult $NTPd'$ did not significantly increase the variation explained (Appendix S1: Table S9). Thus, we did not conduct further analyses into how habitat filtering affected the variation of PNDD among species.

DISCUSSION

Conspecific negative density dependence (CNDD), phylogenetic negative density dependence (PNDD), and habitat filtering are often cited as prominent mechanisms maintaining the composition and diversity of communities. Some studies have discussed a potentially confounding influence of habitat filtering when attempting to quantify negative density dependence (Comita et al. 2009, Chen et al. 2010, Bai et al. 2012, Piao et al. 2013), but this has not previously been well documented. Our results show that CNDD and habitat filtering

simultaneously influence seedling survival. Taking habitat variables into account elucidated more clearly the negative impacts of conspecific neighbors (seedlings + adults) on seedling survival, and made the species-specific negative effects of conspecific neighbor densities generally stronger. Our study system showed the opposite effect with respect to PNDD. In the following, we discuss these results in more detail.

Local neighborhood and habitat effects

Seedling–seedling and seedling–adult interactions may be stronger in tropical forests than in subtropical forests (e.g., Chen et al. 2010) or temperate forests (e.g., Bai et al. 2012). We found these interactions, at the scales we considered, were a significant driver of seedling survival. These results are in line with evidence from other tropical forests (e.g., Queenborough et al. 2007, Comita et al. 2009, 2010, Metz et al. 2010, Kobe and Vriesendorp 2011, Johnson et al. 2012, Lebrija-Trejos et al. 2014). The negative effects of conspecific neighbors on seedling survival are consistent with intraspecific competition and the Janzen–Connell hypothesis (Janzen 1970, Connell 1971). Our results show that seedling survival was significantly influenced by densities of conspecific seedling and adult neighbors, which may be involved in intraspecific competition for shared resources and/or as a source for specialized natural enemies (herbivore and pathogen; e.g., Augspurger 1984, Packer and Clay 2000, 2003, Bell et al. 2006, Freckleton and Lewis 2006, McCarthy-Neumann and Kobe 2008). Another possible explanation for the negative impact of conspecific adult neighbors is that their presence implies that there may be many more conspecific seedling neighbors over the wider area (beyond our seedling quadrats), making competition and mortality due to pests and pathogens even greater than we expect from measured seedling densities.

Recently, several studies focusing on NDD for seedling survival have scaled the effects of heterospecific neighbors by phylogenetic relatedness. For example, Liu et al. (2012) found a phylogenetic Janzen–Connell effect, which might be caused by associated host-specific fungal pathogens in a subtropical forest. Metz et al. (2010) found that seedling survival increased where nearby adult neighbors were more distantly related to focal seedlings. The critical factors affecting a pathogen's infection of a host plant are morphological and biochemical, which are often phylogenetically conserved (Mitter et al. 1991). Further, empirical evidence has shown that closely related species are more likely to share the same or similar pests and pathogens (e.g., Novotny et al. 2006, Gilbert and Webb 2007, Gilbert et al. 2012, Liu et al. 2012), and to have several similar key functional traits (Yang et al. 2014). Thus, the effects of neighbors on a focal plant should depend upon phylogenetic similarities, and should be less negative for less related plants. However, we found a negative effect of phylogenetic diversity, indicating that increased

phylogenetic similarities between heterospecific neighbors and focal seedlings increased seedling survival. Our results therefore do not support PNDD. While these findings are in contrast to those of the studies cited above, they are consistent with several other studies that have shown that plants perform better when heterospecific neighbors are relatively closely related (summarized in Lebrija-Trejos et al. 2014). Our results also suggest that this phylogenetic positive density dependence (PPDD) is a more important determinant of seedling survival than PNDD (see below).

The edaphic and topographic variables in our study had important effects on seedling survival. Specifically, the positive effect of the first principal component of edaphic and topographic variables on seedling survival demonstrated that the availability of belowground resources is also an important driver of tree seedling survival (Comita et al. 2009, Bai et al. 2012, Piao et al. 2013). Many works have also shown that light availability has a strong effect on the performance of shade-tolerant seedlings in tropical forests (e.g., Paz and Martínez-Ramos 2003, Comita et al. 2009, Queenborough et al. 2009). However, light availability had a slight negative effect on seedling survival in our study, even though the range of canopy openness we found was sufficient to produce positive effects (with approximately 90% of seedling quadrats within a range of canopy openness between 0.29% and 3%). This unexpected relationship may indicate a widespread problem with the use of canopy photographs in studies of this kind (e.g., Comita et al. 2009, Lin et al. 2014).

Habitat filtering and CNDD

The increase in survival driven by favorable habitat may offset the thinning of conspecific trees due to CNDD (Wright 2002). A positive relationship with conspecific densities would therefore be found when host-specific natural enemies or intraspecific competition do not offset the advantages of occurring in a preferred habitat (at least until the population size becomes too large). A few studies have shown such an interaction between habitat variables and negative density dependence. For example, Piao et al. (2013) suggested that a failure to take into account the confounding effect of habitat heterogeneity may lead to mischaracterization of the role of density dependence in shaping plant communities. Zhu et al. (2010) found that factoring out habitat heterogeneity made most tree species show negative density dependence in a subtropical forest, but did not explore in detail exactly how habitat variables affected density dependence.

Our work clearly shows that taking habitat variables into consideration made the effects of conspecific neighbors appear more negative in both the density models and the phylogenetic models (Table 2). The significant positive interactions between habitat variables and conspecific seedling and adult neighbor

densities (Table 2) implied changes in CNDD across different habitat conditions. This is why the variance explained by the densities of conspecific seedling and adult neighbors increased in models with habitat variables (Appendix S1: Table S8).

The impact of habitat filtering on the detection of CNDD can also be seen in the prevalence of species-habitat associations at both seedling and adult stages in the XSBN plot (Appendix S1: Table S10). Of the species with more than 20 surveyed seedlings, 41.77% and 60.76% showed significant habitat preferences at the seedling stage and the adult stage, respectively. Our results therefore suggest that conspecific negative density dependence is evident at lower densities in marginal habitats and only at higher densities in optimal habitats. Further, the inclusion of habitat variables led to an increase in apparent strength of species-specific negative effects of conspecific neighbors, especially conspecific adult neighbors. In sum, CNDD and habitat filtering both had vital influences on seedling dynamics and the observed effects of conspecific neighbors were the result of an interaction between them.

Lack of evidence for PNDD

Though more and more ecologists have concluded that phylogenetic density dependence is an important mechanism for seedling dynamics and coexistence (e.g., Webb et al. 2006, Metz et al. 2010, Zhu et al. 2015), the influence of habitat filtering on the detection of phylogenetic density dependence had not been taken into account. As with conspecifics, the impact of natural enemies and the stronger competition for similar resources among closely related neighboring plants should lead to a negative effect of phylogenetic similarity on seedling survival. An apparently positive relationship between phylogenetic similarity and seedling survival might be caused by habitat filtering, because closely related plants may often have similar habitat requirements (Vamossi et al. 2009, Baldeck et al. 2013). We expected that habitat filtering could therefore affect the detection of the negative effect of phylogenetic similarity on seedling survival in the same way that it affected CNDD detectability. However, this expectation was not met in this study. While we did find that the inclusion of phylogenetic relatedness of heterospecific neighbors improved model accuracy, we found no evidence of PNDD. Furthermore, differences in the effects of phylogenetic relatedness between survival models without and with habitat variables were relatively slight. Instead, we found evidence of phylogenetic positive density dependence (PPDD). There appears to be an emerging consensus about the existence of this effect, perhaps due to the shared habitat preferences between closely related individuals (Lebrija-Trejos et al. 2014). However, our results showed that seedling survival was greater among closely related heterospecific neighbors even when habitat variation was controlled (Model IV in Table 2). While it is possible that unobserved habitat factors had

a confounding effect on this analysis, it is not clear what these factors might be, and it seems unlikely that they could be strong enough to reverse the apparent direction of relationships between seedling survival and neighbor relatedness. We therefore suggest that PPDD, as detected here, may be a real and independent effect of some as-yet unrecognized mechanism.

CONCLUSIONS

To the best of our knowledge, our study is the first to explore the joint effects of conspecific negative density dependence (CNDD), phylogenetic negative density dependence (PNDD), and habitat filtering and their relative importance for tropical tree seedling survival. Our results demonstrate that replacing heterospecific neighbor densities with phylogenetic diversity indices improved survival models, which is in line with an increasing awareness of the importance of evolutionary relationships in neighborhood dynamics. However, the effect of phylogenetic diversity indices in our study system was opposite to that expected under PNDD, even when we controlled for the effects of habitat. CNDD and habitat filtering played important roles in seedling survival simultaneously. The observed effect of conspecific neighbor densities is primarily a result of an interaction between habitat filtering and conspecific neighbor densities, making CNDD detectable at lower densities in marginal habitats than in preferred habitats. Therefore, adding habitat variables into survival models strengthens the measured negative effects of conspecific neighbors on seedling survival. We conclude that future studies of neighborhood density dependence must take habitat filtering and phylogenetic relationships into account in order to properly assess the effects of conspecific and heterospecific neighbors, and the occurrence and cause of phylogenetic positive density dependence.

ACKNOWLEDGEMENTS

This study was supported by National Key Basic Research Program of China (Grant No. 2014CB954104), the National Natural Science Foundation of China (31370445), the West Light Foundation of Chinese Academy of Sciences and the Applied Fundamental Research Foundation of Yunnan Province (2014GA003). N. G. Swenson was funded by NSF Dimensions of Biodiversity US-China grants (DEB-1241136; DEB-1046113). We thank David L. Erickson and W. John Kress for their assistance on the construction of the molecular phylogenetic tree and Lang Ma, Yongzhen Shen, Jiu Ma, Zhenhua Sun, Shishun Zhou, Wenfu Zhang, Xiaofei Yang, and Xiaobao Deng for their assistance in seedling censuses and species identification. Special thanks to all the people who have contributed to the establishment of the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot. Logistical support was provided by Xishuangbanna Station of Tropical Rainforest Ecosystem Studies (National Forest Ecosystem Research Station at Xishuangbanna), Chinese Academy of Sciences. We thank S. Joseph Wright and one anonymous reviewer for their critical comments on the manuscript.

LITERATURE CITED

- Augsburger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712.
- Bai, X., S. A. Queenborough, X. Wang, J. Zhang, B. Li, Z. Yuan, D. Xing, F. Lin, J. Ye, and Z. Hao. 2012. Effects of local biotic neighbors and habitat heterogeneity on tree and shrub seedling survival in an old-growth temperate forest. *Oecologia* 170:755–765.
- Baldeck, C. A., S. W. Kembel, K. E. Harms, J. B. Yavitt, R. John, B. L. Turner, G. B. Chuyong, D. Kenfack, D. W. Thomas, and S. Madawala. 2013. A taxonomic comparison of local habitat niches of tropical trees. *Oecologia* 173:1491–1498.
- Bates, D., M. Maechler, B. Bolker and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- Beaudet, M., and C. Messier. 2002. Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. *Agricultural and Forest Meteorology* 110:217–228.
- Bell, T., R. P. Freckleton, and O. T. Lewis. 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters* 9:569–574.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34:778–787.
- Cao, M., X. M. Zou, M. Warren, and H. Zhu. 2006. Tropical forests of Xishuangbanna, China. *Biotropica* 38:306–309.
- Cao, M., H. Zhu, H. Wang, G. Lan, Y. Hu, S. Zhou, X. Deng, and J. Cui. 2008. Xishuangbanna tropical seasonal rainforest dynamics plot: tree distribution maps, diameter tables and species documentation. Yunnan Science and Technology Press, Kunming, Yunnan, China.
- Chen, L., X. Mi, L. S. Comita, L. Zhang, H. Ren, and K. Ma. 2010. Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest. *Ecology Letters* 13:695–704.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Comita, L. S., and B. M. J. Engelbrecht. 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology* 90:2755–2765.
- Comita, L. S., and S. P. Hubbell. 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology* 90:328–334.
- Comita, L. S., R. Condit, and S. P. Hubbell. 2007. Developmental changes in habitat associations of tropical trees. *Journal of Ecology* 95:482–492.
- Comita, L. S., M. Uriarte, J. Thompson, I. Jonckheere, C. D. Canham, and J. K. Zimmerman. 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology* 97:1346–1359.
- Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332.
- Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, and Y. Zhu. 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology* 102:845–856.
- Condit, R. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer, Berlin, Germany.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. J. den Boer, and G. R. Gradwell, editors. *Dynamics of populations. Proceedings of the advanced study institute on dynamics of numbers in populations*. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands.
- Dixon, P. 2003. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* 14:927–930.
- Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York, USA.
- Freckleton, R. P., and O. T. Lewis. 2006. Pathogens, density dependence and the coexistence of tropical trees. *Proceedings of the Royal Society B* 273:2909–2916.
- Gelman, A., and J. Hill. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.
- Gilbert, G. S., and C. O. Webb. 2007. Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences USA* 104:4979–4983.
- Gilbert, G. S., R. Magarey, K. Suiter, and C. O. Webb. 2012. Evolutionary tools for phytosanitary risk analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens. *Evolutionary Applications* 5:869–878.
- Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495.
- Hu, Y. H., L. Q. Sha, F. G. Blanchet, J. L. Zhang, Y. Tang, G. Y. Lan, and M. Cao. 2012. Dominant species and dispersal limitation regulate tree species distributions in a 20-ha plot in Xishuangbanna, southwest China. *Oikos* 121:952–960.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, R. Valencia, H. Navarrete, and M. Vallejo. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences USA* 104:864–869.
- Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific negative density dependence and forest diversity. *Science* 336:904–907.
- Johnson, D. J., N. A. Bourg, R. Howe, W. J. McShea, A. T. Wolf, and K. Clay. 2014. Conspecific negative density-dependent mortality and the structure of temperate forests. *Ecology* 95:2493–2503.
- Kobe, R. K., and C. F. Vriesendorp. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters* 14:503–510.
- Lan, G., S. Getzin, T. Wiegand, Y. Hu, G. Xie, H. Zhu, and M. Cao. 2012. Spatial distribution and interspecific associations of tree species in a tropical seasonal rain forest of China. *PLoS ONE* 7:e46074.

- Lebrija-Trejos, E., S. J. Wright, A. Hernández, and P. B. Reich. 2014. Does relatedness matter? Phylogenetic density dependent survival of seedlings in a tropical forest. *Ecology* 95:940–951.
- Lin, L., L. S. Comita, Z. Zheng, and M. Cao. 2012. Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *Journal of Ecology* 100:905–914.
- Lin, F., L. S. Comita, X. Wang, X. Bai, Z. Yuan, D. Xing, and Z. Hao. 2014. The contribution of understory light availability and biotic neighborhood to seedling survival in secondary versus old-growth temperate forest. *Plant Ecology* 215:795–807.
- Liu, X., M. Liang, R. S. Etienne, Y. Wang, C. Staehelin, and S. Yu. 2012. Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. *Ecology Letters* 15:111–118.
- McCarthy-Neumann, S., and R. K. Kobe. 2008. Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. *Ecology* 89:1883–1892.
- Metz, M. R. 2012. Does habitat specialization by seedlings contribute to the high diversity of a lowland rain forest? *Journal of Ecology* 100:969–979.
- Metz, M. R., W. P. Sousa, and R. Valencia. 2010. Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology* 91:3675–3685.
- Mitter, C., B. Farrell, and D. J. Futuyma. 1991. Phylogenetic studies of insect-plant interactions: insights into the genesis of diversity. *Trends in Ecology & Evolution* 6:290–293.
- Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why are there so many species of herbivorous insects in tropical rainforests? *Science* 313:1115–1118.
- Packer, A., and K. Clay. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281.
- Packer, A., and K. Clay. 2003. Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. *Ecology* 84:108–119.
- Paine, C. E. T., K. E. Harms, S. A. Schnitzer, and W. P. Carson. 2008. Weak competition among tropical tree seedlings: Implications for species coexistence. *Biotropica* 40:432–440.
- Paine, C., N. Norden, J. Chave, P. M. Forget, C. Fortunel, K. G. Dexter, and C. Baraloto. 2012. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters* 15:34–41.
- Paradis, E. 2006. Analysis of phylogenetics and evolution with R. Springer, New York, New York, USA.
- Parker, I. M., and G. S. Gilbert. 2004. The evolutionary ecology of novel plant-pathogen interactions. *Annual Review of Ecology Evolution and Systematics* 35:675–700.
- Paz, H., and M. Martínez-Ramos. 2003. Seed mass and seedling performance within eight species of *Psychotria* (Rubiaceae). *Ecology* 84:439–450.
- Pebesma, E. J. 2004. Multivariable geostatistics in S: the gstat package. *Computers & Geosciences* 30:683–691.
- Peters, H. A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* 6:757–765.
- Piao, T., L. S. Comita, G. Jin, and J. H. Kim. 2013. Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia* 172:207–217.
- Queenborough, S. A., D. F. R. P. Burslem, N. C. Garwood, and R. Valencia. 2007. Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology* 88:2248–2258.
- Queenborough, S. A., D. F. Burslem, N. C. Garwood, and R. Valencia. 2009. Taxonomic scale-dependence of habitat niche partitioning and biotic neighbourhood on survival of tropical tree seedlings. *Proceedings of the Royal Society B* 276:4197–4205.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rüger, N., A. Huth, S. P. Hubbell, and R. Condit. 2009. Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology* 97:1360–1368.
- Song, Q. H., Z. H. Tan, Y. P. Zhang, M. Cao, L. Q. Sha, Y. Tang, N. S. Liang, D. Schaefer, J. F. Zhao and J. B. Zhao. 2013. Spatial heterogeneity of soil respiration in a seasonal rainforest with complex terrain. *iForest-Biogeosciences and Forestry* 6:65–72.
- Svenning, J. C., T. Fabbro, and S. J. Wright. 2008. Seedling interactions in a tropical forest in Panama. *Oecologia* 155:143–150.
- Swamy, V., J. Terborgh, K. G. Dexter, B. D. Best, P. Alvarez, and F. Cornejo. 2011. Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecology Letters* 14:195–201.
- Vamosi, S. M., S. B. Heard, J. C. Vamosi, and C. O. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* 18:572–592.
- Volkov, I., J. R. Banavar, F. He, S. P. Hubbell, and A. Maritan. 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438:658–661.
- Webb, C. O., and D. R. Peart. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80:2006–2017.
- Webb, C. O., and D. R. Peart. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88:464–478.
- Webb, C. O., G. S. Gilbert, and M. J. Donoghue. 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* 87:S123–S131.
- Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences USA* 94:1252–1257.
- Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1–14.
- Yang, J., G. C. Zhang, X. Q. Ci, N. G. Swenson, M. Cao, L. Q. Sha, J. Li, C. C. Baskin, J. W. F. Slik, and L. X. Lin. 2014. Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. *Functional Ecology* 28:520–529.
- Zhu, Y., X. Mi, H. Ren, and K. Ma. 2010. Density dependence is prevalent in a heterogeneous subtropical forest. *Oikos* 119:109–119.
- Zhu, Y., L. S. Comita, S. P. Hubbell, and K. Ma. 2015. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. *Journal of Ecology* 103:957–966. doi:10.1111/1365-2745.12414.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/14-2465.1/supinfo>