

Density dependence and habitat preference shape seedling survival in a subtropical forest in central China

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Abstract

Aims

Seedlings are vulnerable to many kinds of fatal abiotic and biotic agents, and examining the causes of seedling dynamics can help understand mechanisms of species coexistence. To disentangle the relative importance of neighborhood densities, habitat factors and phylogenetic relatedness on focal seedling survival, we monitored the survival of 5306 seedlings of 104 species >15 months. We address the following questions: (i) How do neighborhood densities, habitat variables and phylogenetic relatedness affect seedling survival? What is the relative importance of conspecific densities, habitat variables and phylogenetic relatedness to seedling survival? (ii) Does the importance of the neighborhood densities, habitat variables and phylogenetic relatedness vary among growth forms, leaf habits or dispersal modes? Specially, does the conspecific negative density dependence inhibit tree and deciduous seedlings more compared with shrub and evergreen species? Does density dependence affect the wind and animal-dispersed species equally?

Methods

We established 135 census stations to monitor seedling dynamics in a 25-ha subtropical forest plot in central China. Conspecific and heterospecific seedling density in the 1-m² seedling plot and adult basal area within a 20-m radius provided neighborhood density variables. Mean elevation, convexity and aspect of every 5- × 5-m grid with seedling plots were used to quantify habitat characteristics. We calculated the relative average phylodiversity between focal seedling and heterospecific neighbors to quantify the species relatedness in the neighborhood. Eight candidate generalized linear mixed models with binominal error distribution were used to compare the

relative importance of these variables to seedling survival. Akaike's information criteria were used to identify the most parsimonious models.

Important Findings

At the community level, both the neighborhood densities and phylogenetic relatedness were important to seedling survival. We found negative effects of increasing conspecific seedlings, which suggested the existence of species-specific density-dependent mortality. Phylodiversity of heterospecific neighbors was negatively related to survival of focal seedlings, indicating similar habitat preference shared among phylogenetically closely related species may drive seedling survival. The relative importance of neighborhood densities, habitat variables and phylogenetic relatedness varied among ecological guilds. Conspecific densities had significant negative effect for deciduous and wind-dispersed species, and marginally significant for tree seedlings >10 cm tall and animal-dispersed species. Habitat variables had limited effects on seedling survival, and only elevation was related to the survival of evergreen species in the best-fit model. We conclude that both negative density-dependent mortality and habitat preference reflected by the phylogenetic relatedness shape the species coexistence at seedling stage in this forest.

Keywords: generalized linear mixed models, negative density dependence, niche partitioning, phylodiversity, seedling dynamics, species coexistence

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INTRODUCTION

Negative density (frequency)-dependent effects (hereafter NDD) and niche partitioning are two of the most important species coexistent mechanisms for maintaining diversity in plant communities (reviewed by [Chesson 2000](#); [Wright 2002](#)). Under the NDD mechanism, a plant's performance decreases when surrounded by higher densities of conspecific neighbors ([Bagchi et al. 2010](#); [Chen et al. 2010](#); [Comita et al. 2010](#); [Janzen 1970](#); [Wang et al. 2012](#)). Numerous studies have reported species distribution and performance is habitat specific, indicating the importance of niche partitioning in plant communities (e.g. [Metz 2012](#); [Zhang et al. 2011](#)). However, in recent years, more and more studies have indicated that these two mechanisms are not mutually exclusive and regulate community composition simultaneously ([Chen et al. 2010](#); [Queenborough et al. 2009](#)).

Former studies of NDD usually divided neighbors into conspecifics and heterospecifics, treating effects of heterospecific species with different phylogenetic relatedness identical on focal plant performance ([Bai et al. 2012](#); [Comita et al. 2010](#); [Johnson et al. 2012](#); [Queenborough et al. 2009](#)). In fact, species are not ecologically identical and species interactions are possibly regulated by species functional traits, which are the result of evolution ([Swenson et al. 2012](#)). Focal plant performance may be inhibited by its phylogenetically similar heterospecific neighbors (e.g. phylogenetic density dependence, [Bagchi et al. 2010](#); [Metz et al. 2010](#)) because shared pathogens and herbivores may infect and transmit among phylogenetically and functionally similar species ([Novotny et al. 2010](#); [Webb et al. 2006](#)). Alternatively, closely related species may share mutualist, possess similar functional traits and tend to react to the abiotic gradients similarly ([Baraloto et al. 2012](#); [Burns and Strauss 2011](#)), therefore positive density dependence related to phylogenetically similar neighbors may reflect a habitat preference or facilitation from shared mutualists, which favors the survival of the focal plant ([Baldeck et al. 2013](#); [Lebrija-Trejos et al. 2014](#)).

Life history strategies may influence the reaction of species to extrinsic factors ([Comita and Hubbell 2009](#)). Trees have larger statures and crowns than understory shrub species and can reach to the canopy of the forest, and therefore gain more energy and produce more seeds ([Terborgh and Petren 1991](#); [Terborgh et al. 2013](#)), thus NDD is usually expected for tree species survival. Leaf habit may affect plant survival. Compared with deciduous species, evergreen species tend to invest a higher proportion of resources to defensive compounds (such as lignin and tannin) and thus are more resistant to biotic and abiotic damages ([Coley and Barone 1996](#); [Villar et al. 2006](#)). In addition, dispersal mode may also affect the plant reactions to the fatal agents and may escape from NDD because of long distance dispersal from conspecific adults by wind or animals ([Bai et al. 2012](#); [Clark et al. 2005](#)). Understanding the complex effects of

life history strategies on seedling survival is important for identifying drivers of species coexistence in the seedling community.

To our knowledge, few studies have examined the relative importance of neighborhood densities, habitat variables and phylogenetic relatedness in driving seedling survival pattern simultaneously. In this study, we address these issues in a species-rich subtropical forest in central China. Particularly, we focus on the two sets of questions:

- (1) How do neighborhood densities, habitat variables and phylogenetic relatedness affect seedling survival? Are the conspecific densities more important than habitat variables or phylogenetic relatedness in influencing seedling survival?
- (2) Does the importance of the neighborhood densities, habitat variables and phylogenetic relatedness vary among growth forms, leaf habits or dispersal modes? Specially, does the conspecific NDD inhibit tree and deciduous seedlings more compared with shrub and evergreen species? Does conspecific NDD affect the wind and animal-dispersed species equally?

MATERIALS AND METHODS

Study site

This study was conducted in a newly established 25-ha forest dynamics plot in the Badagongshan (BDGS) National Nature Reserve in central China (29°46'N, 110°05'E; [Fig. 1](#)). The reserve is located in the northern edge of mid-subtropical zone and the northern part of the Wuling Mountains. The mean rainy days and fog-free days per year are 170 and 220, respectively, and mean annual precipitation is 2105.4 mm. The annual temperature averages 11.5°C, with the hottest month July (mean temperature 23.3°C) and coldest month January (mean temperature 0.1°C). The soil is dominated by typic paleudalfs soil ([Liu 1983](#)). Topographically, the BDGS plot is characterized by steep slopes and flat ridges. Elevations on the plot range from 1355 to 1456 m above mean sea level ([Fig. 1](#)).

In November 2011, a square of 500- × 500-m (horizontal distance) plot was divided into 625 20- × 20-m quadrats (each containing 16 5- × 5-m grids) by total station following the procedures of the Center for Tropical Forest Science ([Condit 1998](#)). All stems of free-standing trees and shrubs with diameter ≥1 cm at breast height (d.b.h.) were tagged, mapped, identified and measured. According to the first census, the plot includes ~187 000 live individuals of 238 species (94 evergreen and 144 deciduous), representing 53 families and 114 genera. The forest is dominated by *Cyclobalanopsis multinervis* and *Fagus lucida*. Other important species include *Cyclobalanopsis gracilis*, *Quercus serrata* var. *brevipetiolata*, *Schima parviflora*, *Carpinus fargesii*, *Sassafras tzumu*, *Litsea elongata* and *Rhododendron stamineum* ([Lu et al. 2013](#)).

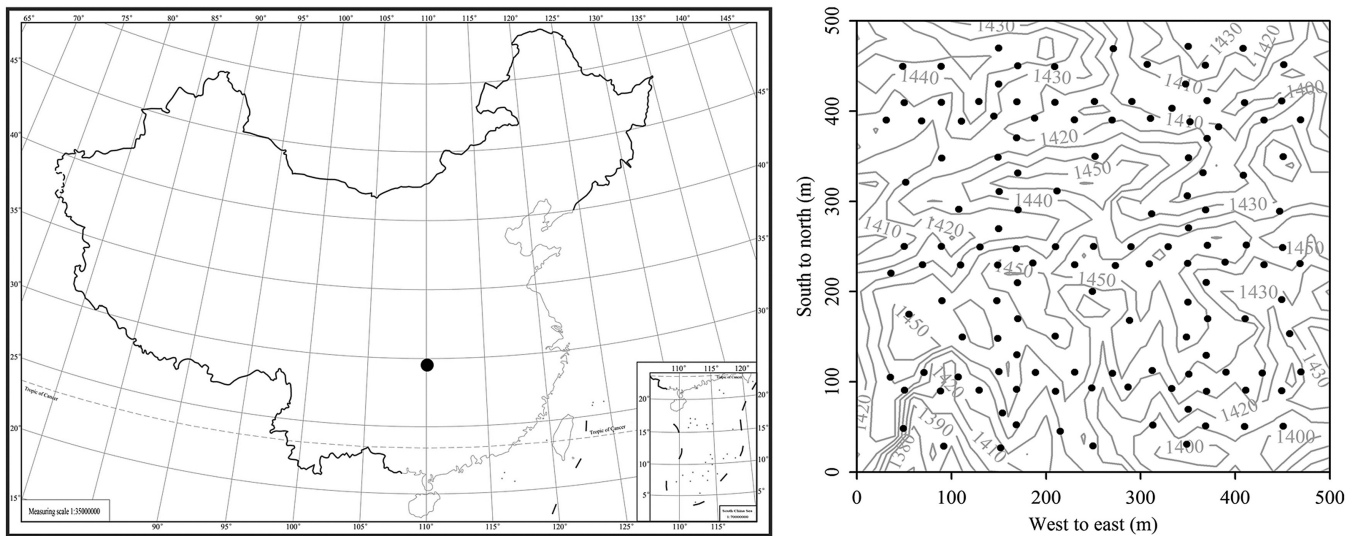


Figure 1: location and contour map of the 25-ha BDGS plot. The number in the contour map is elevation (m) and the solid circles represent the locations of the 135 seed traps.

Seedling census

In April 2012, we established 135 seed traps (0.5 m² each) stratified randomly to monitor seed rain in the BDGS plot (Fig. 1). These seed traps were arrayed on alternating sides of the trails, close to the center of the 20- × 20-m quadrats where they were located. Three 1-m² plots for monitoring seedling dynamics were placed 2 m away from sides of the seed trap and each of them was assigned to a 5- × 5-m grid of the plot (Fig. 2). Every seed trap and its adjacent seedling plots comprise a census station. All of the 135 stations are 5–8 m away from trails with a mean distance of 31.03 ± 6.53 m (SD) between nearest-neighbor stations.

All woody plants <1-cm d.b.h. (defined as seedlings) in each plot were tagged, mapped and measured for height from the ground to the apical bud. The first seedling census was conducted in May–June 2012. Subsequent censuses were conducted in August–September 2012, May–June 2013 and August 2013.

Density parameters

Four density parameters were calculated to quantify local neighborhood effects. For seedling neighbors, we calculated the conspecific (*S*_{con}) and heterospecific (*S*_{het}) seedling density for the focal seedling in the 1-m² seedling plot (Table 1). We calculated total basal area of each conspecific (*A*_{con}) and heterospecific (*A*_{het}) individuals ≥1-cm d.b.h. (hereafter referred to as adults for simplicity) within a 20-m radius, divided by the distance between that tree and the center of the seed trap (Table 1):

$$A = \sum_i^N (BA_i / \text{DISTANCE}_i),$$

where *i* is an individual adult tree. A 20-m radius was selected as it had lowest Akaike's information criteria (AIC) value based on preliminary analyses comparing models with 5-,

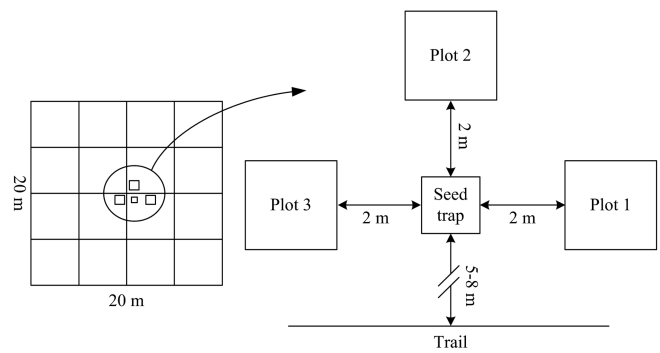


Figure 2: the components of a census station. Each of the three 1-m² seedling plots is 2 m away from the central seed trap and assigned to a 5- × 5-m grid in the 20- × 20-m quadrat. The station is 5–8 m away from the trail.

10-, 15- and 20-m radius. All the stations were at least 20 m away from the 25-ha plot boundary to avoid edge effects.

Habitat parameters

Topography variables of every 5- × 5-m grid with a seedling plot are used as the habitat variables. Values of elevations at the four corners of the 20- × 20-m quadrat were used to interpolate the elevation of the corners of each 5- × 5-m grid. Four topographical variables were calculated for each of the grids. Mean elevation was an average of the elevation of the four corners of each 5- × 5-m grid. Aspect was the direction in which a slope faced. Aspect is a circular variable; cos(Aspect) and sin(Aspect) were computed before data analysis to provide linear predictors (Table 1). Convexity was calculated with elevation of the focal grids minus the mean elevation of its eight surrounding grids. Slope was not included because it was highly correlated with elevation (Spearman rank

Table 1: explanatory variables included in models of seedling survival in the 25-ha BDGS plot

Variable classification	Variables	Data		
		Range	Mean	Median
Individual	Seedling height (log-transformed)	0–2.42	1.04	0.86
Density factors	Seedling factors (density of seedlings per m ²)			
	Conspecific seedling density (Scon)	0–46	7.97	3
	Heterospecific seedling density (Shet)	1–230	14.83	11
	Adult factors (m ² , within 20-m radius)			
	Conspecific adult basal area (Acon)	0–0.39	0.01	0.01
	Heterospecific adult basal area (Ahet)	0.17–0.86	0.50	0.51
Habitat factors	Elevation (m)	1389.25–1450.68	1432.76	1433.46
	Convexity	–2.08 to 4.47	0.07	–0.01
	Aspect (cosine-transformed)	–1 to 1	–0.07	–0.22
	Aspect (sine-transformed)	–1 to 1	0	0.03
Phylogenetic factors	Phylogenetic distance from focal seedling to all other seedling neighbors (sAPd')	–2.51 to 4.01	1.06	1.07
	Phylogenetic distance from focal seedling to all other adult neighbors (aAPd')	–2.02 to 2.85	–0.04	–0.19

Log-transformed seedling height (Log(H)) and cos(Aspect) and sin(Aspect) were computed before data standardization. Other abbreviations can be found in the parentheses following the variable names.

correlation coefficient = 0.99). The summary information of the variables used is listed in Table 1.

Phylogenetic-relatedness parameters

We invoked the relative average phylodiversity (APd') to quantify the species relatedness between the focal seedlings and their heterospecific neighbors (Webb et al. 2006). First, we built a phylogenetic tree for the 238 tree species occurring in the plot using Phylomatic program (Webb and Donoghue 2005) based on APGIII (Angiosperm Phylogeny Group 2009). Branch lengths (Mya) were assigned to the phylogeny using the BLADJ algorithm in Phylocom version 4.2 (Webb et al. 2008) and node ages were estimated from Wikström et al. (2001). Using this tree, we calculated the mean phylogenetic distance from the focal seedling to all other heterospecific seedlings within the plot and heterospecific adult neighbors within 20-m radius. Both observed distances were standardized by the mean and standard deviation of the expected phylogenetic distance generated by a null model for a given number of species and their abundance in the sample to correct for the effect of the sample species richness (sAPd' and aAPd' for phylodiversity between focal seedling and heterospecific seedling neighbors and adult neighbors, respectively, Table 1; Webb et al. 2002).

$$APd' = \frac{\text{observed mean distance} - \text{expected mean distance}}{\text{SD}(\text{expected mean distance})}$$

Note that values of APd' > 0 in this study indicate species in the sample are more phylogenetically distantly related (higher phylodiversity), and <0 indicates species are more

closely related (lower phylodiversity) than expected via the null model.

Data analysis

The survival probability of individual seedlings from May 2012 to August 2013 was modeled as a function of neighborhood densities, habitat variables and phylogenetic relatedness using generalized linear mixed models (GLMMs) with binomial error distribution. The response variable was the state of the focal seedling, assigned 1 (alive) or 0 (dead). All values of continuous explanatory variables as well as log-transformed seedling height were standardized by subtracting the mean value of the variable (covering all individuals in the analysis) and divided by one standard deviation before being added to the model. To control for spatial auto-correlation, we treated every seedling plot and the corresponding station as a nested random effect in the GLMMs. Species identity was also added to the model as a cross random effect to account for the inherent differences in survival probabilities of each species (Table 2). Eight candidate models were developed with different combinations of explanatory variables as fixed effects grouped into density, habitat and phylogenetic categories: (i) a null model only with seedling height; (ii) three models each with one set of the three variable categories added to the null model; (iii) three models each with combinations of two sets of the variables and (iv) a full model with all variables (Table 2). We used the AIC to identify the most parsimonious model, and models with a difference between AIC values <2 were considered equally valid (Burnham and Anderson 2002). Using these models, we first tested the relative contributions

Table 2: variables used as fixed and random effects in the eight candidates GLMMs

Candidate models	Fixed effect	Random effect
Null	Log(H)	(1 SPECIES) +
Density	Log(H) + Scon + Shet + Acon + Ahet	(1 STATION/ PLOT)
Habitat	Log(H) + Elevation + Convexity + cos(Aspect) + sin(Aspect)	
Phylogenetic	Log(H) + sAPd' + aAPd'	
Habitat + Density	Log(H) + Elevation + Convexity + cos(Aspect) + sin(Aspect) + Scon + Shet + Acon + Ahet	
Habitat + phylogenetic	Log(H) + Elevation + Convexity + cos(Aspect) + sin(Aspect) + sAPd' + aAPd'	
Density + phylogenetic	Log(H) + Scon + Shet + Acon + Ahet + sAPd' + aAPd'	
Full	Log(H) + Elevation + Convexity + cos(Aspect) + sin(Aspect) + Scon + Shet + Acon + Ahet + sAPd' + aAPd'	

Species identity as a crossed random effect, and the seedling plots nested in each station as a nested random effect were added in each of the eight models. Abbreviations of fixed effect variables can be found in Table 1.

of all factors on seedling survival at community level. We then compared these effects using the whole set of models for species of different growth form, leaf habit and dispersal mode (Supplementary Table S1).

We obtained odds ratios (OR) by exponentiation of each coefficient to measure the partial effect of each variable on the odds of survival. ORs > 1 indicate positive effects on survival, and ratios < 1 indicate negative effects. All analyses were conducted in R 3.0.3 (R Core Team 2013). Mixed effect models were fitted by glmer() function of lme4 package (Bates et al. 2014) with the recommended Laplace method (Bolker et al. 2009).

RESULTS

Among the censused 5306 seedlings of 104 species tagged in the initial census, 2575 seedlings belonging to 66 species died. Overall, the odds of seedling survival increased with seedling height (OR = 3.20–5.47, $P < 0.001$; Fig. 3). Heterospecific adult basal area was also positively correlated with seedling survival at the community level and in all ecological guilds tested (OR = 1.34–2.07, $P < 0.001$; Fig. 3). The remaining variables in the best-fit models are reported below.

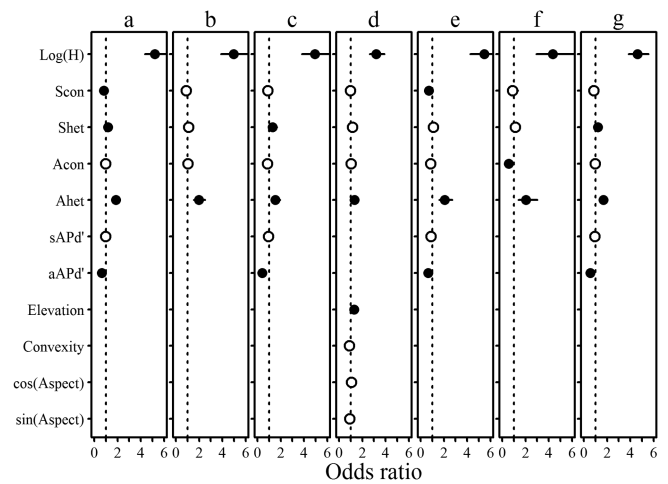


Figure 3: odds ratios of variables on seedling survival for the best-fit models for community and each ecological guild (growth form, leaf habit and dispersal mode). **a**, community; **b**, tree species; **c**, shrub species; **d**, evergreen species; **e**, deciduous species; **f**, wind-dispersed species; **g**, animal-dispersed species. Solid circles indicate variables significantly different from 1 ($P < 0.05$). Values of APd' > 0 indicate neighbors are more phylogenetically distantly related and values < 0 indicates neighbors are more closely related than expected *via* null model. See Table 1 for variable abbreviations.

Community level analysis

At the community level, the most parsimonious model included neighbor density and phylogenetic variables; however, the full model was equally supported (Table 3). The density of conspecific and heterospecific seedling neighbors showed a significant negative and positive effect, respectively, on seedling survival (OR = 0.82, $P = 0.031$; OR = 1.17, $P = 0.041$; Fig. 3a). We found no significant effect from conspecific basal area. We also found that higher phylodiversity between focal seedling and heterospecific adult neighbors significantly inhibited seedling survival (aAPd', OR = 0.64, $P = 0.013$; Fig. 3a). In other words, focal seedlings had greater odds of survival if surrounded by more closely related heterospecific adult neighbors. In the full model, mean elevation was the only significant habitat variables relating to seedling survival (OR = 1.23, $P = 0.013$).

Growth form analysis

Density and density + phylogenetic models were most parsimonious for tree and shrub species, respectively; however, models with habitat variables were also equally valid for both (Table 3). For overall tree seedlings, no significant neighborhood density effects were detected except the heterospecific basal area (OR = 1.97, $P < 0.001$; Fig. 3b). However, we found a marginally negative effect of conspecific seedling density for tree seedlings with height > 10 cm (OR = 0.84, $P = 0.093$; Supplementary Table S2). Although the habitat variables were not included in the best-fit model, in the habitat + density model, elevation also had a significant positive effect on

Table 3: AIC values of GLMMs of seedling survival

Candidate models	Community	Growth form		Leaf habit		Dispersal mode	
		Tree	Shrub	Evergreen	Deciduous	Wind	Animal
Null	2911.06	1643.86	1255.42	1189.68	1665.82	698.10	2212.30
Density	2860.28	1621.17	1238.95	1184.12	1630.36	685.04	2177.72
Habitat	2906.02	1641.29	1253.71	1185.04	1667.16	699.50	2208.24
Phylogenetic	2908.29	1647.61	1241.99	1191.70	1664.66	701.16	2207.13
Habitat + density	2861.00	1622.08	1239.76	1182.74	1633.49	688.94	2178.00
Habitat + phylogenetic	2903.64	1644.98	1241.71	1187.06	1666.31	702.26	2203.57
Density + phylogenetic	2857.17	1624.84	1226.73	1186.53	1627.30	688.05	2173.12
Full	2858.20	1625.67	1228.29	1185.23	1630.77	691.91	2173.72

The best-fit models are shown in bold.

overall tree seedling survival (OR = 1.27, $P = 0.016$). For the shrubs species, seedling survival was positively and negatively associated with the heterospecific seeding density and the phylodiversity between focal seedling and heterospecific adult neighbors (aAPd'), respectively (OR = 1.30, $P = 0.037$; OR = 0.42, $P < 0.001$; Fig. 3c).

Leaf habit analysis

The relative contributions of variables on seedling survival varied between evergreen and deciduous species. For the evergreen species, the most likely model was the habitat + density model; however, the density model was equally valid (Table 3). The mean elevation was the only significant habitat predictor (OR = 1.29, $P = 0.007$; Fig. 3d) and heterospecific basal area was the only significant density variable (OR = 1.34, $P = 0.002$; Fig. 3d). The density + phylogenetic model fit deciduous species the best (Table 3). Both conspecific seedling density and phylodiversity between focal seedling and heterospecific adult neighbors (aAPd') showed significant negative effects on deciduous seedling survival, respectively (OR = 0.70, $P = 0.032$; OR = 0.65, $P = 0.03$; Fig. 3e).

Dispersal-mode analysis

Wind- and animal-dispersed species had different seedling survival patterns. For the wind-dispersed species, the density model was the best fit (Table 3), and the conspecific adults had significantly negative effects on seedling survival (OR = 0.56, $P = 0.038$; Fig. 3f). For the animal-dispersed species, density + phylogenetic model and the full model were equally valid (Table 3). In the best-fit model, ORs of conspecific and heterospecific seedling density showed a marginally negative and a significant positive effect on seedling survival, respectively (OR = 0.85, $P = 0.082$; OR = 1.21, $P = 0.031$; Fig. 3g). The focal seedling survival was also significantly negatively correlated with distantly related heterospecific adult neighbors (aAPd', OR = 0.56, $P = 0.006$; Fig. 3g). Elevation in the full model showed significantly positive relationship with the survival of the animal-dispersed species' seedlings (OR = 1.23, $P = 0.019$).

DISCUSSION

Our results showed that seedling survival did not occur randomly in BDGS plot. Neighborhood densities, habitat variables and phylogenetic relatedness all affected seedling survival. Neighborhood densities were included in all best-fit models of seedling survival. Habitat effects were limited, and mean elevation was the only significant predictor of seedling survival in any of the models tested. Increasing phylodiversity had a negative effect on seedling survival in several analyses, indicating seedling survived better near closely related heterospecific neighbors. The relative importance of each set of variables changed among growth forms, leaf habits and dispersal modes.

Effects of density, habitat and phylogenetic relatedness on seedling survival

The occurrence of NDD at seedling stage is well documented in many types of forests (Bagchi et al. 2010; Chen et al. 2010; Comita and Hubbell 2009; Johnson et al. 2012, 2014). In our analyses, increasing conspecific neighbor density had significant negative effects on seedling survival at community level and for deciduous and wind-dispersed species (Fig. 3a, e and f), and also marginally negatively influenced the survival of tree seedlings with height >10 cm and animal-dispersed species (Fig. 3b and g). Multiple mechanisms could cause this pattern, but NDD induced by natural enemies is emerging as a very likely process (Connell 1971; Janzen 1970; Terborgh 2012). Both field and experimental work have pointed out that host-restricted herbivores and soil-borne pathogens can cause death of conspecific seedlings (Alvarez-Loayza and Terborgh 2011; Comita et al. 2014; Mangan et al. 2010; Packer and Clay 2000). In contrast, heterospecific seedling (Fig. 3a, c and g) and adult neighbors tended to positively affect the focal seedling survival. This pattern was consistent with the 'species herd protection', which suggests that increasing heterospecific neighbors could depress the encounter probability of focal plant and its host-specific enemies and thus enhance focal seedling survival (Peters 2003). There may be alternate explanations for the positive effect of heterospecific adults

on seedling survival but controlled experiments are needed to determine the mechanism. The heterospecific adult basal area is significantly correlated with total adult basal area (Spearman rank correlation coefficient = 0.98); therefore, it mirrors the comprehensive bioenvironmental background of the habitats. When the basal area is high, it implies that the habitat is better for both adult and seedling performance. However, studies have found that heterospecific adults can negatively affect focal seedling survival presumably because of asymmetric competition for light or soil resource (Kobe and Vriesendorp 2011; Lebrija-Trejos *et al.* 2014) or have no significant effect on seedling survival (Comita *et al.* 2010; Johnson *et al.* 2014).

In nearly all cases, the habitat variables were not included in the best-fit models (Fig. 3). Habitat effects might be underestimated in our analyses because of missing variables (such as soil nutrients and light). However, we did find significantly positive effect of elevation on seedling survival in the equally valid models at community level and for trees and animal-dispersed species, and in the best-fit model for evergreen species (Fig. 3e). This could result from the topography in BDGS plot, which is classical valley–slope–ridge pattern. The forest floors of lower elevation slope and valley areas are covered by dense herbs (field observations). Previous studies have demonstrated that herbs can compete with woody species for below-ground resources and light (Rey *et al.* 2003; Vandenberghe *et al.* 2006) and some species of both the herbs and trees can release allelochemicals during growth (Horsley 1977; Wright 2002), which can inhibit the growth and survival of woody seedlings. We also noted soil erosion following rain events in the valleys during vegetation and seedling censuses, which may kill established seedlings and hinder plant colonization (García-Fayos *et al.* 2000). Furthermore, high ridges may contain lower abundance of pathogens infecting seedlings, presumably because of lower humidity at higher elevation (Augsburger 1984), which may enhance seedling survival.

Although the magnitude of effects attributed to habitat variables were limited, we found seedling survival decreased with increasing phylodiversity between focal seedlings and heterospecific adult neighbors (Fig. 3a, c, e and g). Other work has suggested that enhanced seedling survival with closely related neighbors could be an indication of habitat specificity. Webb *et al.* (2006) using APd' also found similar patterns as ours at larger spatial scales (36-m² seedling plot). Using a highly resolved bar code phylogeny, Lebrija-Trejos *et al.* (2014) found seedling survival was enhanced by closely related adult neighbors diverged <15 Mya from the focal seedling. Previous studies have shown that closely related species tended to be functional similar and accordingly preferred the similar habitats or shared mutualists (Baldeck *et al.* 2013; Baraloto *et al.* 2012; Burns and Strauss 2011). The habitats occupied by closely related adults may provide suitable resources and thus enhance seedling survival (Lebrija-Trejos *et al.* 2014). In another study, Metz *et al.* (2010) found closely related adult

neighbors decreased the first-year seedling survival (e.g. phylogenetic NDD), but enhanced the survival beyond the first year. Webb *et al.* (2006) also inferred that habitat preference caused by the effect of abiotic-related mortality is expected more important at later life stages. However, plants might show significant habitat preference at very young age (Metz 2012). When we divided seedlings into groups based on seedling height, negative effects of aAPd' on survival were detected for both of the size classes, although it was only marginally significant for seedling ≤10 cm at community level (OR = 0.70, *P* = 0.077; Table 4). This demonstrates that habitat preference might shape plant performance at all ages but less so at a young age in BDGS plot. The phylogenetic NDD was not found here as previous studies (Bagchi *et al.* 2010; Metz *et al.* 2010). We suspect that the enemies may be more host specialized and thus have limited effect on the survival of closely related species (Lebrija-Trejos *et al.* 2014). One caveat is that the taxonomic resolution provided by APG hypothesis is lower and cannot precisely distinguish the relatedness between very closely related heterospecific neighbors. This lack of resolution might obscure the effects of phylogenetic relatedness. Thus, more resolved phylogenies based on other methods such as DNA barcode sequence could strengthen our results.

Seedling survival of species with different growth form

Compared with shrubs and treelets, large trees tend to produce vastly more seeds and therefore their seedlings were expected to suffer more conspecific NDD (Comita *et al.* 2010; King *et al.* 2006b; Terborgh *et al.* 2013). Surprisingly, no such effects were detected for overall tree seedling survival, although tree seedlings were approximately twice as abundant as shrub seedlings in our plots (Supplementary Table S1). Conspecific NDD might be associated with the seedling age, for example, Bai *et al.* 2012 found significantly negative effect of conspecific adults for 2- to 3-years-old tree seedling survival, not for 1-year-old seedling survival. We did find a marginally significant negative

Table 4: ORs (with 95% confidence interval) of variables on survival of seedlings with height ≤10 cm and height >10 cm for the best-fit models at community level

Variables	Height ≤10	Height >10
Log(H)	2.22 (1.87–2.63)***	1.86 (1.51–2.30)***
Scon	0.75 (0.59–0.96)*	0.91 (0.79–1.04)NS
Shet	1.12 (0.95–1.32)NS	1.34 (1.02–1.75)*
Acon	1.02 (0.83–1.24)NS	0.88 (0.75–1.03)NS
Ahet	2.15 (1.63–2.73)***	1.26 (1.04–1.53)*
sAPd'	0.91 (0.76–1.10)NS	0.98 (0.78–1.24)NS
aAPd'	0.70 (0.47–1.04) [#]	0.57 (0.39–0.82)**

Ten centimeter is selected because most seedlings in BDGS plot beyond this height have successfully established based on field observations. [#]*P* < 0.1; **P* < 0.05; ***P* < 0.01; ****P* < 0.001; NS, not significant. See Table 1 for variable abbreviations.

effect of conspecific seedling density for tree seedlings with height >10 cm (OR = 0.84, $P = 0.093$; [Supplementary Table S2](#)). The mixed-aged seedlings, especially the younger ones in this study, might mask the conspecific effect on seedling survival. We could not exclude the role of competition in causing the NDD for the older tree seedlings ([Wright 2002](#)), although studies from tropical forest suggest that seedling densities in the understory were sparse and hardly competed for resources ([Paine et al. 2008](#); [Svenning et al. 2008](#)). Other studies indicate that shrubs species have slower growth rates than large trees ([King et al. 2006a](#); [Kohyama et al. 2003](#)). In this study, shrub seedlings were much taller on average than tree seedlings (median for shrub and tree species: 14.9–5.8 cm, $W = 2\ 032\ 716$, $P < 0.001$), indicating that they were likely older and therefore robust enough to tolerate natural enemies in the BDGS plot. Furthermore, previous studies showed that habitat factors became more influential to seedling survival as seedlings growing bigger and presumably older ([Bai et al. 2012](#)), which may result in a switch in importance to habitat preference from NDD ([Webb et al. 2006](#)). This might be able to explain the significant habitat preference for shrub seedling survival, not for smaller trees.

Seedling survival of species with different leaf habit

We found no significant effect of conspecific density and phylogenetic relatedness on the survival of evergreen species. In contrast, survival of deciduous species was significantly inhibited by increases in density of conspecifics seedlings and was increased by more closely related adult neighbors. Deciduous species uptake and invest more resources into traits associated with growth, and may lack defensive compounds making seedlings vulnerable to the damages of the natural enemies ([Coley and Barone 1996](#); [Villar et al. 2006](#)), whereas evergreen species tend to be rich in defensive compounds and hence have a higher chance of survival ([Coley 1988](#)). The microhabitats, where the closely related adults established, may have appropriate resources such as soil nutrients or mycorrhizal fungi symbionts for seedling growth, resulting in a significant effect of phylogenetic relatedness on the deciduous seedling survival. We checked the relatedness among evergreens and among deciduous species and found no evidence indicating evergreen species are more closely related than deciduous species. Another study in our plot found that adult distributions of evergreen adults were less explained by the environment variables compared with deciduous species (unpublished data). Together with the results shown here, we considered the survival pattern of evergreen seedling survival was less influenced by the habitat preference, reflected by the absent significant effect of aAPd' ([Fig. 3d](#)).

Seedling survival of species with different dispersal mode

In contrast to our expectations, seedling survival for both of the animal- and wind-dispersed species was inhibited by

conspecifics, but not at the same life-stage. We found a negative effect of neighboring conspecific seedlings for animal-dispersed seedlings, although this effect was only marginally significant (OR = 0.85, $P = 0.082$; [Fig. 3g](#)). Seed distribution of animal-dispersed species can be variable, depending on the plant characters, identity of dispersers and their behaviors ([Schupp 1993](#)). Although dispersing seeds can travel hundred meters away from their mother plants ([Clark et al. 2005](#)), animals often deposited seeds in clumps ([Howe 1989](#); [Muller-Landau et al. 2008](#)), and high density may facilitate location by herbivores and the transmission of pathogens among conspecifics ([Alvarez-Loayza and Terborgh 2011](#); [Comita et al. 2014](#); [Mangan et al. 2010](#); [Packer and Clay 2000](#)). We also found focal seedlings survived better when surrounded by closely related adult neighbors (aAPd', OR = 0.56, $P = 0.006$; [Fig. 3g](#)). This may indicate shared habitat preference by closely related heterospecifics or shared mutualists. Conspecific adult density was detrimental to seedling survival in wind-dispersed species. Wind-dispersed species tend to have very small seeds ([Moles et al. 2005](#)), such as species with dust-like seeds from the families Ericaceae and Saxifragaceae in our plot, which make newly emerging seedlings vulnerable to the damage of biotic and abiotic damages and unable to compete with established vegetation ([Westoby et al. 2002](#)). Landing close to mother plants may result in asymmetric competition between seedlings and conspecific adults for wind-dispersed species in our plot ([Comita et al. 2010](#)) and attract distance-responsive enemies living on or around the mother plant ([Janzen 1970](#)), reflected in the negative effects of conspecific adults on focal seedling survival.

CONCLUSION

We found evidence that neighborhood densities, habitat variables and phylogenetic relatedness exerted effects on the seedling survival pattern in the community, but their relative importance varied among ecological guilds. Neighborhood densities were important for seedling survival and the negative effects of conspecific neighbors, especially for trees, deciduous and both dispersal-mode species, indicate that negative density dependence drove the species coexistence in this forest. Habitat variables had limited effects and were not included in the best-fit models in nearly all cases; however, elevation had a detectable effect on trees, evergreen and animal-dispersed seedling survival. Phylogenetic relatedness was more important for shrubs, deciduous and animal-dispersed species, as the focal seedling derived higher survival rate by being a neighbor of closely related heterospecific adults, suggesting habitat preference shared among closely related species may affect the pattern of seedling survival. Because the effect of habitat preference is indirectly reflected by phylogenetic relatedness, we cannot determine which species coexistent mechanisms are more important at the seedling stage in our plot until more experimental works is done. Overall, our results indicate that both conspecific negative density

dependence and habitat preference are important mechanisms in maintaining species coexistence in this subtropical mountain forest.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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