

Effects of local biotic neighbors and habitat heterogeneity on tree and shrub seedling survival in an old-growth temperate forest

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Abstract Seedling dynamics play a crucial role in determining species distributions and coexistence. Exploring causes of variation in seedling dynamics can therefore provide key insights into the factors affecting these phenomena. We examined the relative importance of biotic neighborhood processes and habitat heterogeneity using survival data for 5,827 seedlings in 39 tree and shrub species over 2 years from an old-growth temperate forest in northeastern China. We found significant negative density-dependence effects on survival of tree seedlings, and limited effects of habitat

heterogeneity (edaphic and topographic variables) on survival of shrub seedlings. The importance of negative density dependence on young tree seedling survival was replaced by habitat in tree seedlings ≥ 4 years old. As expected, negative density dependence was more apparent in gravity-dispersed species compared to wind-dispersed and animal-dispersed species. Moreover, we found that a community compensatory trend existed for trees. Therefore, although negative density dependence was not as pervasive as in other forest communities, it is an important mechanism for the maintenance of community diversity in this temperate forest. We conclude that both negative density dependence and habitat heterogeneity drive seedling survival, but their relative importance varies with seedling age classes and species traits.

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Introduction

Models of species coexistence in diverse communities generally emphasize density-dependent survival, niche partitioning, or ecological equivalence (Chesson 2000; Nakashizuka 2001; Wright 2002). These three mechanisms have each received some support in studies of tree communities. For example, recent research has identified strong density dependence in temperate forests (HilleRisLambers and Clark 2003; HilleRisLambers et al. 2002). Furthermore, density-dependent mechanisms acting within local biotic neighborhoods can increase the survival of locally rare species in subtropical and tropical forests (Chen et al. 2010; Comita and Hubbell 2009; Hubbell et al. 2001; Queenborough et al. 2007b; Uriarte et al. 2004b).

Similarly, important dimensions of plant trait variation within tree communities are well known (Kraft et al. 2008; Martínez-Vilalta et al. 2010; Wright et al. 2007), and abiotic niche partitioning may be caused by trait-related differential patterns of distribution and demography (Cavender-Bares et al. 2004; Comita et al. 2007b; Harms et al. 2001; McMahon et al. 2011; Queenborough et al. 2007a; Russo et al. 2005; Tateno and Takeda 2003). The null model for evaluating either negative density dependence (NDD) or habitat niche partitioning is the ecological equivalence of coexisting species. In this case, dispersal limitation and stochastic ecological drift therefore govern local community dynamics (Hubbell 2001).

Although researchers are now generally convinced that NDD and niche differentiation are not mutually exclusive (Queenborough et al. 2009), these processes are usually tested separately. For tree communities, studies of seedling survival as a function of the local biotic neighborhood have encountered evidence of NDD (Chen et al. 2010; Comita and Hubbell 2009; Gilbert et al. 2001; Packer and Clay 2000; Queenborough et al. 2007b). Other studies have examined survival and growth as a function of the local abiotic environment (Russo et al. 2005; Tsujino et al. 2006). However, few studies have so far investigated the relative importance of both biotic and abiotic drivers of seedling survival in a single analysis (Comita et al. 2009; Paine et al. 2011; Queenborough et al. 2009; Shibata et al. 2010; Streng et al. 1989). In this study, we aimed to determine the relative importance of biotic and abiotic drivers of seedling survival for a relatively diverse temperate tree community in northeastern China.

As well as individual-level effects, NDD can also have consequences at the community level. The neighbourhoods of common species will be more likely to contain a conspecific, and these species may experience stronger NDD because of their higher frequency relative to less common species. Rare species, therefore, have an advantage in what Connell et al. (1984) termed a community compensatory trend (CCT). This is related to, but contrasts with, recent evidence showing that rare species may be more sensitive to the presence of conspecifics than common species (Comita et al. 2010). A CCT has been found in several tropical and subtropical sites (Chen et al. 2010; Queenborough et al. 2007b; Webb and Peart 1999), although in other sites it has not (He et al. 1997; Welden et al. 1991). No study has yet tested for a CCT in temperate forest.

The current paucity of community-level seedling studies from temperate forests is a major limitation in understanding whether different mechanisms of coexistence operate in temperate compared to tropical forests. Given the incredible difference in diversity between these forest types, exploring potential drivers of this difference is an important ecological question (Kraft et al. 2011). Such data

are critical for understanding the early stages of community assembly that shape temperate forest diversity patterns, and may also reveal similarities or differences between temperate and tropical forest community assembly.

One potential cause of the plethora of hypotheses for mechanisms of species coexistence is that the mechanism may change throughout an organism's life history. Different factors become important at different times and have different effects (Comita et al. 2007a; Grubb 1977). Furthermore, survival generally increases with size (Uriarte et al. 2004a; Winkler et al. 2005), because larger individuals may be more resistant and resilient to biotic and abiotic stresses. In addition, differences among species in terms of functional traits such as dispersal agent will also affect how individuals respond to these pressures (Ramaswami and Sukumar 2011; Streng et al. 1989). For instance, animal-dispersed (especially birds) species may escape from high mortality caused by NDD because some animals, such as frugivorous birds could disperse seeds over several tens or hundreds of meters (Iida and Nakashizuka 1998; Murray 1988). Comparatively, gravity-dispersed species may be more affected by NDD due to high seedling density close to the adults. Understanding the complex effects of this heterogeneity in the forest ecosystem is essential to clarify the potential drivers of species coexistence in the early stages of community assembly.

Our study, therefore, addresses these issues by examining the relative importance of biotic neighbors and habitat heterogeneity for seedling survival over 2 years, using a dataset of 5,827 seedlings in 39 tree and shrub species in an old-growth temperate forest. In particular, we sought to answer the following questions:

1. Do local biotic neighbors or habitat heterogeneity have a greater effect on the survival of tree and shrub seedlings in this temperate forest? Specifically, does an increase in conspecific neighbors decrease the probability of survival to a greater or lesser extent than a decrease in, for example, soil nutrients?
2. Do the effects of biotic neighbors and habitat (edaphic and topographic) variables on survival differ among seedling age classes, dispersal-mode groups or species? Specifically, do older seedlings (>1 year) suffer lower density-dependence than new recruits?
3. Is there evidence of a community compensatory trend, and is this present for both tree and shrub species?

Materials and methods

Study site

The study is located in Changbai Nature Reserve (42°23'N, 128°05'E) in northeastern China. The reserve was

established in 1960 and joined the World Biosphere Reserve Network under the Man and the Biosphere Project in 1980 (Shao et al. 1994; Stone 2006). The reserve is about 200,000 ha with elevation ranging from 740 to 2,691 m. There are five typical vertical vegetation zones: aspen-white birch (*Populus davidiana* and *Betula platyphlla*) forest, broad-leaved Korean pine (*Pinus koraiensis*) mixed forest, spruce-fir (*Picea jezoensis* and *Abies nephrolepis*) forest, subalpine birch (*B. ermanii*) forest, and alpine tundra (Yang et al. 1985).

Our study site is situated in the old-growth broad-leaved Korean pine mixed forest, which is the dominant vegetation type in northeastern China. It has high biodiversity, complex stand structure, and unique species composition (Wang et al. 1980). The climate in the forest region is characterized by low temperatures, high precipitation, and strong winds, with the prevailing direction of west-southwest (Yang et al. 1985). Mean annual temperature is 3.3 °C (−16.5 °C in January and 20.5 °C in August). Mean annual precipitation is 672 mm, most of which occurs between June and September (480–500 mm) (Yang et al. 1985). Mean age of overstory trees is about 300 years.

In 2004, a 25-ha (500 × 500 m) forest plot was established, which was chosen in the core zone of the reserve in order to avoid human disturbances (Hao et al. 2007). Within the plot, all individuals with diameter at breast height (DBH, 1.3 m above the ground) ≥ 1 cm were mapped, tagged, and identified. In the first census in 2004, there were 38,902 living stems, belonging to 52 species, 32 genera, and 18 families. Mean stand density of living trees was 1,556 trees per ha and mean basal area of living trees was 43.2 m² per ha (Hao et al. 2007, 2008).

Seedling census

We set up 150 seed traps within the plot to monitor long-term dynamics of seed production and dispersal (see Zhang et al. 2008). Around each seed trap, we set up four seedling plots (5 × 5 m) in August and September 2006 to monitor long-term seedling dynamics (ESM S1, $n = 600$). All seedling plots were spaced at least 8 m apart. The total sampling area of 600 seedling plots is 1.5 ha. In each seedling plot, all tree seedlings with DBH < 1 cm, shrub and liana seedlings with DBH < 1 cm and height ≥ 30 cm were tagged, mapped and identified. The age of each tree seedling was estimated by counting annual bud scale scars. All seedling plots were recensused in August and September 2007, and August and September 2008.

Biotic neighborhood variables

We calculated the seedling and adult neighbors of each focal seedling. We calculated the density of conspecific

and heterospecific seedling neighbors within 0.5 m of focal seedlings. Seedlings within 0.5 m of the seedling plot edge were not included as focal seedlings to eliminate the boundary effects (ESM S2). The effect of adult neighbors was based on adult size modified by the distance between the neighbor and the focal seedling. Using the 2004 plot census data (trees and shrubs with DBH ≥ 1 cm), we calculated the sum of the basal area (BA) of conspecific and heterospecific adults within 20 m from the focal seedling divided by the distance of each adult from the focal seedling (Canham et al. 2004):

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

where i is an individual adult. To eliminate boundary effects, only those seedlings with a distance greater than or equal to 20 m from the 25-ha plot edges were included in our analyses.

Habitat variables

We defined a seedling's habitat variables in terms of soil properties and topography. For the soil properties, we sampled soils within the plot every 30 m on a regular grid. At each grid point, two additional sample points at 2, 5 n or 15 m were selected in a random compass direction from the grid point. In total, 967 soil samples were sampled in the 25-ha plot (Yuan et al. 2011). Eight soil properties were recorded: pH, organic matter content, available nitrogen (N), total N, available phosphorus (P), total P, available potassium (K) and total K. We interpolated the soil variables to 5 × 5 m grid by kriging, and converted the calculated values for each seedling plot to z scores (John et al. 2007). To reduce multi-collinearity and the number of variables describing soil factors, we performed a principal components analysis (PCA) on these eight soil chemical variables. The first two components produced by the PCA accounted for 86.7 % of the variance in the eight soil variables (ESM S3). PCA axis 1 was associated with high organic matter, available N and total N, P. PCA axis 2 was associated with low available N, P and total N, P.

Three topographic factors were identified: slope, aspect and elevation. Elevation was measured by total station at the four corners of a 20 × 20 m grid in the 25-ha plot. We then calculated the elevation to a 5 × 5 m grid using kriging interpolating methods. Slope, aspect and elevation values were calculated for each seedling plot. Slope was defined as the single average angle from the horizontal of the entire quadrat. Aspect referred to the direction to which the slope faced. Elevation was defined as the mean elevation of the four corners. Plot convexity was not used because it was highly correlated with elevation.

Statistical analysis

We modeled the survival probability of individual seedlings from 2006 to 2008 as a function of biotic neighborhood and habitat variables (Table 1), using generalized linear mixed-effects model (GLMM). The GLMM in this paper was essentially a logistic regression, with the response variable as a logit transformation of seedling state: 1 (alive) or 0 (dead). All the values of the 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.

To test the relative importance of biotic and habitat variables, we compared the following four candidate models: (1) a null model only with random effects, (2) a biotic model in which the fixed effects of seedling and adult neighbors were added to the null model, (3) a habitat model in which the fixed effects of soil and topography were added to the null model, and (4) a biotic + habitat model in which the fixed effects of all variables were added to the null model. Models were compared using Akaike's Information Criterion (AIC), and models with a difference between AIC values of less than 2 were judged equally valid (Burnham and Anderson 2002). We examined four subsets of the data: (1) the community level (all tree and shrub seedlings pooled), (2) different age-classes (tree seedlings only), (3) dispersal mode, and (4) species-level analyses for common species [those that occurred in ≥ 40 seedling plots, and had >100 (trees) or >130 (shrubs) seedlings in 2006].

Finally, we tested whether there was a CCT for both tree and shrub species. We examined the probability of seedling survival as a function of species population size (abundance or basal area of adults ≥ 1 cm DBH in the 25-ha plot) using GLMM (Chen et al. 2010).

Seedlings within the same plot are likely to have more similar probabilities of survival than those of seedlings in different plots, even when considering local biotic and habitat conditions. To account for this spatial autocorrelation in survival, we included seedling plot as a random effect in the GLMMs. We tested for spatial autocorrelation in the residuals of the most likely models by plotting variograms (see ESM S4). Furthermore, because species also have inherently different survival probabilities, in models in which all species were pooled, we also included species as a random effect.

We validated the most likely models and CCT models using the area under the receiver operating characteristic (ROC) curve (a standard assessment of model discrimination ability for logistic regressions) (See ESM S5), and $\text{ROC} \geq 0.7$ are considered acceptable fits (Hosmer and Lemeshow 2000). To measure the partial effect of each variable on the odds of survival, we calculated odds ratios for each coefficient (the exponential of the estimate of each coefficient). Odds ratios >1 indicate positive effects on survival, while ratios <1 indicate negative effects.

All analyses were carried out in the statistical environment R (v.2.13.1), using the 'sqldf' (Grothendieck 2010) and 'lme4' (Bates et al. 2010) packages.

Results

Community level

Of the original 5,827 seedlings in 2006, trees and shrubs accounted for 44.3 and 55.7 % of individuals, respectively. For tree seedlings, 1,385 had died by 2008. For shrub seedlings, 586 had died by 2008.

Table 1 Parameters included in models of seedling survival

Variables	Data		
	Range	Mean	Median
Tree seedling age	1–21	2.47	1
Seedling effect (density of seedlings per m ² within 0.5 m radii)			
Conspecific (Ncon)	0–17.825	0.641	0
Heterospecific (Nhet)	0–20.372	0.729	0
Adult effect (sum of adult basal area m ² divided by distance within 20 m)			
Conspecific (Acon)	0–1.328	0.029	0
Heterospecific (Ahet)	0.148–13.268	0.521	0.500
Soil properties			
Soil PC1	–3.107 to 4.671	–0.113	–1.053
Soil PC2	–3.113 to 2.746	–0.085	–0.110
Topographic variables			
Elevation (m)	794.863–808.812	803.517	804.469
Slope (%)	0.145–19.075	2.977	2.479
Aspect	0.708–359.132	217.073	266.550

There were clear differences in the explanatory power of each of the four models (null, biotic, habitat, biotic + habitat) on seedling survival for trees and shrubs (Table 2). The biotic neighborhood model was the best-fit model for trees, while the null and habitat models were the most likely models for shrubs.

Odds ratios for the parameters of the most likely model for tree seedlings showed a small significant negative effect of neighboring conspecific adults (odds ratio = 0.80, $P = 0.007$; Fig. 1). There was no negative effect of seedling neighbors, but there was a slight significant positive effect of neighboring heterospecific seedlings (odds ratio = 1.20, $P = 0.002$; Fig. 1). In shrubs, while the habitat model (along with the null model) was the most likely, the habitat variables themselves had no significant effect.

Age-class level

The relative importance of biotic neighborhood and habitat varied greatly with the age classes of tree seedlings (Table 2). For 1-year tree seedlings, the best-fit model was

the biotic model. For tree seedlings of 2–3 years old, the equally most likely models were the null, biotic and full ones. However, for seedlings in the ≥ 4 year age class, only the habitat model was the most likely. We present coefficient estimates for the biotic model for 1-year tree seedlings, the fullest model for tree seedlings aged 2–3 years, and the habitat model for tree seedlings ≥ 4 years old (Fig. 2).

For tree seedlings in the 1-year age class, the only significant effect was that of heterospecific neighbors (odds ratio = 1.29, $P = 0.003$; Fig. 2), consistent with the tree community level result (Fig. 1). For tree seedlings in the 2- to 3-year age class, conspecific adult neighborhood and soil PC axis 1 showed a significant negative and positive effect, respectively, on focal seedling survival (odds ratio = 0.74, $P = 0.020$; odds ratio = 2.08, $P = 0.014$; Fig. 2). For tree seedlings in the ≥ 4 year age class, the habitat model showed that soil PC axis 1 and elevation had significant positive effects (odds ratio = 3.79, $P = 0.001$; odds ratio = 4.22, $P = 0.001$; Fig. 2). Tree seedlings in the ≥ 4 year age class had a greater probability of survival in areas of high organic content, available N and total N, P, and at higher elevation.

Table 2 AIC and Δ AIC values of individual-level seedling survival models

Instances	Candidate models							
	Null		Biotic		Habitat		Biotic + habitat	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Community								
Tree seedlings	2,636.654	9.303	2,627.351	0	2,640.811	13.460	2,630.350	2.999
Shrub seedlings	2,912.121	1.095	2,917.487	6.461	2,911.026	0	2,916.515	5.489
Age class (tree seedlings)								
1 year	1,281.274	7.323	1,273.951	0	1,287.720	13.769	1,281.955	8.004
2–3 years	707.808	0.607	707.201	0	710.030	2.829	707.425	0.223
Above 4 years	489.962	13.056	496.770	19.864	476.906	0	483.601	6.695
Dispersal mode								
Wind	3,059.077	1.999	3,061.238	4.160	3,057.078	0	3,058.805	1.727
Gravity	2,368.715	16.197	2,352.518	0	2,370.621	18.103	2,354.378	1.860
Animal	144.242	11.884	132.358	0	148.264	15.906	137.311	4.953
Tree species								
<i>Tilia amurensis</i>	128.546	6.836	121.710	0	134.046	12.336	130.749	9.039
<i>Fraxinus mandshurica</i>	960.703	0	965.680	4.978	969.719	9.016	974.688	13.985
<i>Acer mono</i>	766.449	0	768.009	1.560	771.876	5.427	774.185	7.736
<i>Pinus koraiensis</i>	16.902	0	24.470	7.569	22.495	5.593	26.055	9.153
<i>Acer pseudo-sieboldianum</i>	237.217	0	242.887	5.670	244.156	6.939	249.171	11.954
Shrub species								
<i>Philadelphus schrenkii</i>	1,078.213	0	1,081.080	2.867	1,078.478	0.265	1,081.672	3.459
<i>Sorbaria sorbifolia</i>	358.267	0	365.404	7.137	365.951	7.685	372.953	14.686
<i>Ribes mandschuricum</i>	203.550	0	207.155	3.605	206.956	3.406	210.159	6.609
<i>Spiraea chamaedryfolia</i>	251.911	0	254.888	2.977	256.179	4.268	257.750	5.839
<i>Corylus mandshurica</i>	173.603	0	179.144	5.541	175.814	2.211	180.800	7.197

The most likely models are shown in bold. See Figs. 2, 3, and 4 for odds ratios of the fullest most likely models

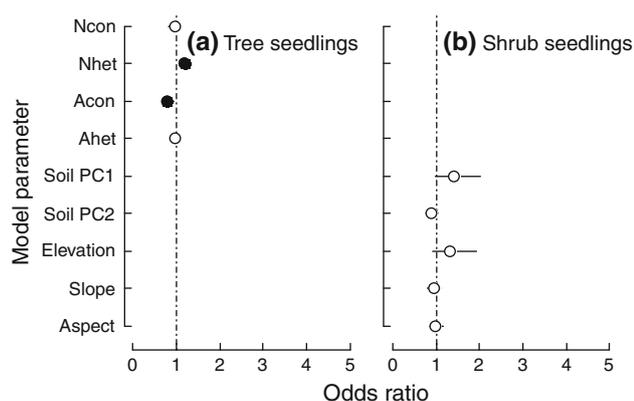


Fig. 1 Odds ratios of **a** tree and **b** shrub seedling survival for the fullest most likely models in Table 2. Circles show odds ratios for each parameter, with 95 % confidence limits (CL) indicated by horizontal lines. Odds ratios significantly different from 1 (95 % CL do not overlap 1) are indicated by filled circles. See Table 1 for variable abbreviations

Dispersal-mode level

The factors driving seedling survival varied with dispersal-mode groups (Table 2). For wind-dispersed species, the best models were the null, habitat, and full ones, with significant positive effects of soil PC axis 1 and elevation (Fig. 3). For gravity-dispersed species, the biotic and full models were the most likely, showing significant negative effects of both neighboring conspecific seedlings and adults. In animal-dispersed species, the best-fit model was the biotic model which included a significant positive effect of heterospecific seedlings (Fig. 3).

Species level

Ten species had sufficient seedlings to be analyzed separately: five tree and five shrub species (Table 3). Seven species (three tree and four shrub) showed no neighborhood effects at all, with the fullest best-fit model being the null model (Table 2). The three remaining species were

consistent with the community-level analyses above. In *Tilia amurensis* and *Acer mono*, both trees, the fullest most likely model included the biotic neighbourhood, and in *Philadelphus schrenkii*, a shrub, the fullest most likely model was the habitat model (Table 2).

However, within these models, the effects of biotic neighborhood and habitat were limited (Fig. 4). There were no significant effects of neighbors on the survival of *Tilia amurensis* seedlings, however, there was a significant negative effect of conspecific neighboring adults on survival of *Acer mono* (odds ratio = 0.75, $P = 0.029$). Soil PC axis 2 showed a significant negative effect on the survival of *Philadelphus schrenkii* seedlings (odds ratio = 0.73, $P = 0.014$).

Community compensatory trend (CCT)

We found a negative relationship between tree seedling survival and basal area (≥ 1 cm DBH) in the 25-ha plot (estimate \pm SD = -1.31 ± 0.17 , $P < 0.001$), indicative of a CCT (Table 4). However, the effect of species abundance on survival was not significant. For shrub seedlings, we found no significant effect on survival for either species abundance or basal area.

Discussion

To test the relative strength of NDD and habitat niche partitioning as mechanisms of species coexistence, we examined the effects of biotic and abiotic neighbourhoods on 2-year survival of 5,827 focal seedlings in 39 species of temperate tree and shrub in an old-growth temperate forest in northeastern China. Overall, we found significant but limited effects of both sets of variables. Trees were more affected by biotic variables than shrubs, and younger tree seedlings more so than older tree seedlings. There were differences in the importance of biotic versus abiotic neighbourhoods depending on the seed dispersal

Fig. 2 Odds ratios of tree seedling survival for three different age classes for the fullest most likely models in Table 2. See Table 1 for variable abbreviations

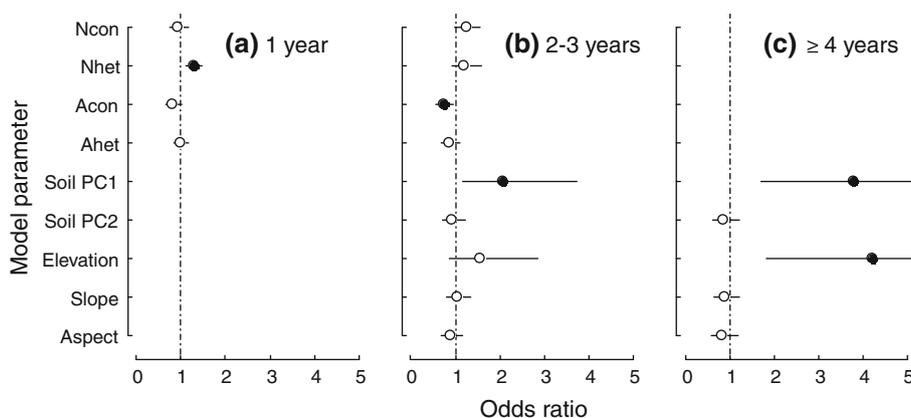


Table 3 Traits for tree species with ≥ 100 focal seedlings and shrub species with ≥ 130 focal seedlings in 2006 in the analysis

Species	Growth form	Canopy layer	Shade tolerance	Dispersal mode	Number of seedlings in 2006	Number of adults
<i>Tilia amurensis</i>	Tree	Overstory	Shade tolerant	Gravity	377	2,644
<i>Fraxinus mandshurica</i>	Tree	Overstory	Midtolerant	Wind	783	694
<i>Acer mono</i>	Tree	Midstory	Shade tolerant	Wind	717	6,569
<i>Pinus koraiensis</i>	Tree	Overstory	Midtolerant	Animal	155	2,450
<i>Acer psedo-sieboldianum</i>	Tree	Midstory	Shade tolerant	Wind	198	4,891
<i>Philadelphus schrenkii</i>	Shrub	Understory	Shade tolerant	Gravity	1,323	466
<i>Sorbaria sorbifolia</i>	Shrub	Understory	Shade tolerant	Wind	313	4
<i>Ribes mandschuricum</i>	Shrub	Understory	Shade tolerant	Gravity	240	1
<i>Spiraea chamaedryfolia</i>	Shrub	Understory	Light demanding	Wind	215	0
<i>Corylus mandshurica</i>	Shrub	Understory	Shade tolerant	Gravity	138	7,700

Fig. 3 Odds ratios of seedling survival for three dispersal-mode groups for the fullest most likely models in Table 2. See Table 1 for variable abbreviations

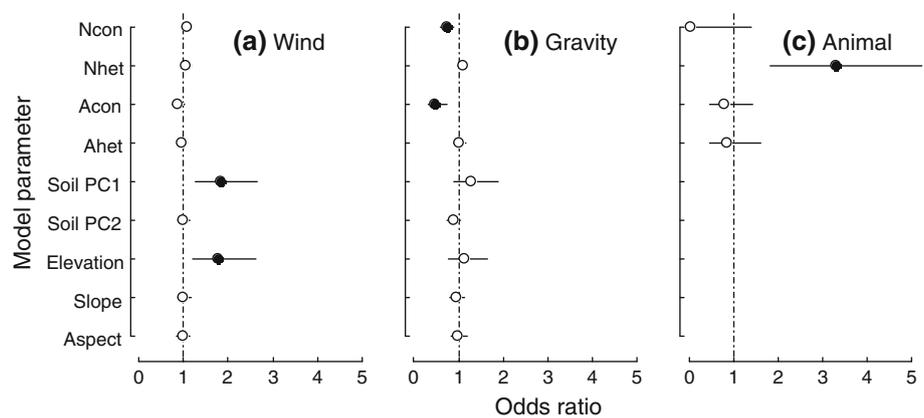


Table 4 Parameter estimates in GLMMs used to test for effects of population size on seedling survival

Categories	Population size (abundance)				Population size (basal area)			
	Estimate	Standard error	Pr(> z)	R ² (%)	Estimate	Standard error	Pr(> z)	R ² (%)
Tree seedlings	-0.212	0.491	0.665	0.3	-1.306	0.169	8.97e-15	84.5
Shrub seedlings	-0.132	0.085	0.12	26.3	-0.050	-0.097	0.604	0.3

Significant estimate at $P = 0.05$ level is shown in bold

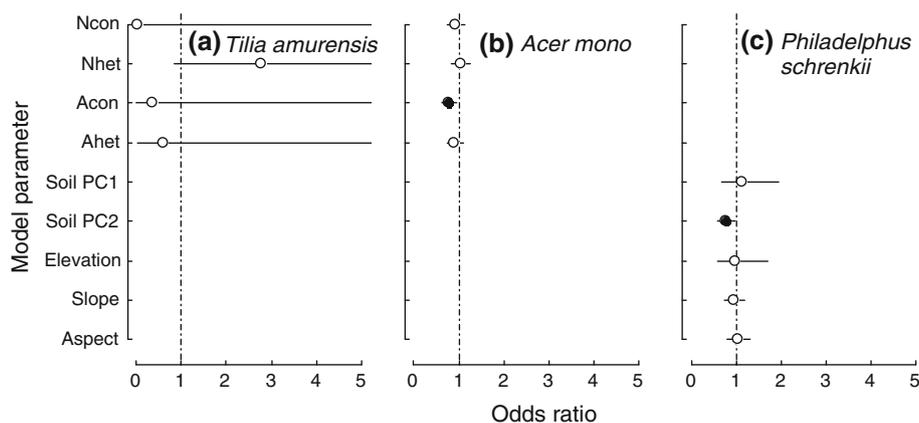
mechanism. Curiously, analyzing the common species individually, most showed no impact of neighborhood variables at all. These results are explored below.

Biotic and habitat drivers of survival of tree and shrub seedlings

A prediction of most mechanisms of coexistence is that performance is limited more by individuals of one’s own species than other species (Chesson 2000; Connell 1971; Janzen 1970; Volkov et al. 2005). We found a significant negative effect of conspecific adults on focal seedling survival for all tree seedlings pooled, young tree seedlings (2–3 years) and gravity-dispersed species. This confirms

previous local-scale findings in temperate forest (HilleRisLambers and Clark 2003; HilleRisLambers et al. 2002), at the larger community-scale, commonly found in subtropical and tropical forests (Chen et al. 2010; Comita and Hubbell 2009; Comita et al. 2009; Metz et al. 2010; Queenborough et al. 2007b). In contrast, we found a positive effect of heterospecific seedlings on survival of all tree seedlings pooled, new recruits (tree seedlings of 1 year old) and animal-dispersed species. These apparently contradictory effects are in line with theory: seedling survival is limited by conspecifics, particularly large adult trees which exert strong asymmetric competition for light and soil nutrients and also a source of enemies (e.g., insects and pathogens) (Wright 2002). However, survival of all

Fig. 4 Odds ratios of seedling survival of three common species for the fullest most likely models in Table 2 (seven species are not shown because their fullest most likely models are null models). See Table 1 for variable abbreviations



seedlings is often elevated in areas that are good for seedling growth and survival (Comita and Hubbell 2009).

Documenting widespread NDD at these scales in this temperate forest may be somewhat surprising, given the much lower densities of seedlings in temperate forest compared to tropical forest. For example, seedling densities in our study are an order of magnitude lower (0.89 ind m^{-2}) than in subtropical and tropical forests [3.2 ind m^{-2} in Gutian (China) (seedlings with DBH $<1 \text{ cm}$; Chen et al. 2010), 2.45 ind m^{-2} in Panama (seedlings with DBH <1 and $\geq 20 \text{ cm}$ tall; Comita and Hubbell 2009) and about 5 ind m^{-2} in Gunung Palung (Indonesian) (seedlings with DBH <1 and $5\text{--}50 \text{ cm}$ tall; Webb et al. 2006)]. Therefore, we might expect that seedling–seedling interactions in temperate forests are weaker than in tropical forests or even nonexistent, and therefore that mechanisms of species coexistence may also be different (Kraft et al. 2011). Indeed, seedling–seedling interactions do seem to be weaker in our study—we found few significant negative effects of conspecific neighboring seedlings, for example, whereas studies from tropical sites frequently report NDD from seedling neighbors (Comita and Hubbell 2009; Comita et al. 2009; Metz et al. 2010; Queenborough et al. 2007b; Webb et al. 2006), although in other sites this NDD is less obvious (Paine et al. 2008; Svenning et al. 2008). However, NDD from large adults still had a significant effect and could further contribute to the maintenance of diversity in this temperate forest.

Shrub seedlings showed no such effects of the biotic neighborhood. This is likely because shrub seedlings were larger and more robust in our seedling plots ($\geq 30 \text{ cm}$ in height, compared to tree seedlings for which there was no minimum cut-off). This interpretation is consistent with results of tree seedling survival for different age classes where the effects of habitat become important as seedlings became older and larger. In contrast to tree seedlings, habitat effects were highlighted in model comparisons for shrub seedlings. However, examination of the coefficients

showed no significant effects of edaphic or topographic variables. This result may be partly due to the small spatial variation in habitat factors in our temperate forest plot. Topography is relatively gentle and the maximum difference in elevation is less than 18 m. Therefore, these habitat factors have low spatial heterogeneity, and their effect on seedling survival may be weak. Furthermore, in order to compensate for low light levels in the understory, many shrub species usually regenerate by vegetative growth (Wilson 1995). Thus, shrub “seedlings” are often supported externally and the effects of competitors from the biotic neighborhood as well as habitat effects that may decrease survival are not so important. Consequently, other factors such as snow cover or physical damage may influence the long-term survival of shrub seedlings.

Tree seedling survival of different age classes

The effects of biotic neighborhood tended to be more important for young tree seedlings of 1 year old and 2–3 years old, and with increasing age classes, habitat became the dominant factor (Fig. 2). This change may be because of improved tolerance to fungal infection (Masaki and Nakashizuka 2002), herbivory, pathogens, or abiotic stressors through lignification of the stems. Consequently, biotic neighbors were less important with increasing age class. Soil PC axis 1 and elevation showed significant positive effect on survival, which demonstrated that larger tree seedlings favored well-drained and suitable soil conditions.

Seedling survival of dispersal-mode groups and common species

For those species dispersed by gravity, we found convincing evidence of NDD: seedlings suffered significant negative effects of both conspecific seedling and adult presence. This is likely because seedling density around

conspecific adults is higher as a result of limited dispersal ability. However, for wind-dispersed species, soil PC axis 1 and elevation showed significant positive effects on seedling survival. This finding indicates that these species can potentially escape from mortality caused by NDD as well as increase the chance of arriving at good recruitment sites (e.g., canopy gaps or suitable soil conditions) where seedling survival is high. Animal-dispersed species were also less affected by NDD and their recruitment sites may be more random, with neighboring heterospecific seedlings as a significant positive predictor of seedling survival.

Most (7/10) of the species for which sample sizes permitted us to examine individually, the null model was the fullest most likely model. This result is more likely because sample sizes were still too small to find any significant effect rather than stochasticity dominating forest dynamics in this system. In three species we did find significant effects of neighborhood.

For the gravity-dispersed species *Tilia amurensis*, we found no significant negative effect of conspecifics. This contradiction with gravity-dispersed seedlings treated as a group may be because the seedling density of *Tilia amurensis* is low (0.04 ind/m²). We found a significant negative effect of conspecific adult trees on the wind-dispersed species *Acer mono*. This may be related to its high tree abundance and wide distribution.

For the shrub species *Philadelphus schrenkii*, habitat effects were more important with a significant negative effect of soil PC axis 2. This result may indicate that *Philadelphus schrenkii* is adapted to suitable soil conditions in the forest understory layer and a signal of niche partitioning.

Community compensatory trend

For tree seedlings, a significant negative correlation between seedling survival and tree species' basal area was found, which explained 84.5 % of the variation among species seedling survival (Table 4). This result indicates that NDD may be occurring at both the local and community levels. However, the CCT was detected with basal area, but not abundance. This means that tree species with larger stems may support more natural enemies or occupy a larger portion of canopy or root space than would smaller stems. Hence, species basal area, a proxy for biomass, may be a better index for examining the existence of a CCT.

Caveats

One major limitation of our study is that it occurred in a single large plot over two census intervals. As such, conclusions from this short-term period of a single study area are tentative.

Conclusion

Our study found evidence of temporal and spatial variation in seedling survival in an old-growth temperate forest, resulting from both local biotic neighborhood and habitat heterogeneity. We found convincing evidence of widespread NDD among tree seedlings. Habitat factors were more important for shrubs. The strength and importance of these processes also varied with dispersal modes and species, lending credence to the ideas that mechanisms of coexistence may vary with ontogeny. Biotic factors were important predictors of seedling survival in young trees whereas habitat factors were significant for older trees and shrubs. It seems likely that both NDD and habitat heterogeneity are important mechanisms that maintain the coexistence of numerous species in both temperate and tropical forests.

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References

- Bates D, Maechler M, Bolker B (2010) lme4: Linear mixed-effects models using Eigen and Eigen. R Package Version: 0.999375-37 edn
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Canham CD, LePage PT, Coates KD (2004) A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can J For Res* 34:778–787
- Cavender-Bares J, Kitajima K, Bazzaz FA (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecol Monogr* 74:635–662
- Chen L, Mi XC, Comita LS, Zhang LW, Ren HB, Ma KP (2010) Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest. *Ecol Lett* 13:695–704
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Comita LS, Hubbell SP (2009) Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology* 90:328–334
- Comita LS, Aguilar S, Perez R, Lao S, Hubbell SP (2007a) Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest. *J Veg Sci* 18:163–174
- Comita LS, Condit R, Hubbell SP (2007b) Developmental changes in habitat associations of tropical trees. *J Ecol* 95:482–492
- Comita LS, Uriarte M, Thompson J, Jonckheere I, Canham CD, Zimmerman JK (2009) Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J Ecol* 97:1346–1359

- Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP (2010) Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) *Dynamics of Populations*. Centre for Agricultural Publishing and Documentation, Wageningen, pp 298–312
- Connell JH, Tracey JG, Webb LJ (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecol Monogr* 54:141–164
- Gilbert GS, Harms KE, Hamill DN, Hubbell SP (2001) Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panama. *Oecologia* 127:509–516
- Grothendieck G (2010) *sqlf: Perform SQL Selects on R Data Frames*. 0.3–5 edn
- Grubb PJ (1977) Maintenance of species-richness in plant communities—importance of regeneration niche. *Biol Rev Camb Philos Soc* 52:107–145
- Hao ZQ, Zhang J, Song B, Ye J, Li BH (2007) Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. *For Ecol Manag* 252:1–11
- Hao ZQ, Li BH, Zhang J, Wang XG, Ye J, Yao XL (2008) Broad-leaved Korean pine (*Pinus koraiensis*) mixed forest plot in Changbaishan (CBS) of China: community composition and structure. *Acta Phytocool Sinica* 32:238–250
- Harms KE, Condit R, Hubbell SP, Foster RB (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J Ecol* 89:947–959
- He FL, Legendre P, LaFrankie JV (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. *J Veg Sci* 8:105–114
- HilleRisLambers J, Clark JS (2003) Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. *Can J For Res* 33:783–795
- HilleRisLambers J, Clark JS, Beckage B (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417:732–735
- Hosmer DW, Lemeshow S (2000) *Applied logistic regression*, 2nd edn. Wiley, New York
- Hubbell SP (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton
- Hubbell SP, Ahumada JA, Condit R, Foster RB (2001) Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecol Res* 16:859–875
- Iida S, Nakashizuka T (1998) Spatial and temporal dispersal of *Kalopanax pictus* seeds in a temperate deciduous forest, central Japan. *Plant Ecol* 135:243–248
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- John R et al (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proc Nat Acad Sci USA* 104:864–869
- Kraft NJB, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580–582
- Kraft NJB et al (2011) Disentangling the drivers of beta diversity along latitudinal and elevational gradients. *Science* 333:1755–1758
- Martínez-Vilalta J, Mencuccini M, Vayreda J, Retana J (2010) Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *J Ecol* 98:1462–1475
- Masaki T, Nakashizuka A (2002) Seedling demography of *Swida controversa*: effect of light and distance to conspecifics. *Ecology* 83:3497–3507
- McMahon SM, Metcalf CJE, Woodall CW (2011) High-dimensional coexistence of temperate tree species: functional traits, demographic rates, life-history stages, and their physical context. *PLoS ONE* 6:e16253
- Metz MR, Sousa WP, Valencia R (2010) Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology* 91:3675–3685
- Murray KG (1988) Avian seed dispersal of 3 Neotropical gap-dependent plants. *Ecol Monogr* 58:271–298
- Nakashizuka T (2001) Species coexistence in temperate, mixed deciduous forests. *Trends Ecol Evol* 16:205–210
- Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281
- Paine CET, Harms KE, Schnitzer SA, Carson WP (2008) Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica* 40:432–440
- Paine CET et al (2011) Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecol Lett* 15:34–41
- Queenborough S, Burslem D, Garwood N, Valencia R (2007a) Habitat niche partitioning by 16 species of Myristicaceae in Amazonian Ecuador. *Plant Ecol* 192:193–207
- Queenborough SA, Burslem D, Garwood NC, Valencia R (2007b) Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology* 88:2248–2258
- Queenborough SA, Burslem DFRP, Garwood NC, Valencia R (2009) Taxonomic scale-dependence of habitat niche partitioning and biotic neighbourhood on survival of tropical tree seedlings. *Proc R Soc Lond B* 276:4197–4205
- Ramaswami G, Sukumar R (2011) Woody plant seedling distribution under invasive *Lantana camara* thickets in a dry-forest plot in Mudumalai, southern India. *J Trop Ecol* 27:365–373
- Russo SE, Davies SJ, King DA, Tan S (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest. *J Ecol* 93:879–889
- Shao GF, Schall P, Weishampel JF (1994) Dynamic simulations of mixed broadleaved-*Pinus koraiensis* forests in the Changbaishan Biosphere Reserve of China. *For Ecol Manag* 70:169–181
- Shibata M et al (2010) Effects of abiotic and biotic factors and stochasticity on tree regeneration in a temperate forest community. *Ecoscience* 17:137–145
- Stone R (2006) Ecology—a threatened nature reserve breaks down Asian borders. *Science* 313:1379–1380
- Streng DR, Glitzenstein JS, Harcombe PA (1989) Woody seedling dynamics in an east Texas floodplain forest. *Ecol Monogr* 59:177–204
- Svenning JC, Fabbro T, Wright SJ (2008) Seedling interactions in a tropical forest in Panama. *Oecologia* 155:143–150
- Tateno R, Takeda H (2003) Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. *Ecol Res* 18:559–571
- Tsujino R, Takafumi H, Agetsuma N, Yumoto T (2006) Variation in tree growth, mortality and recruitment among topographic positions in a warm temperate forest. *J Veg Sci* 17:281–290
- Uriarte M, Canham CD, Thompson J, Zimmerman JK (2004a) A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol Monogr* 74:591–614
- Uriarte M, Condit R, Canham CD, Hubbell SP (2004b) A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *J Ecol* 92:348–360
- Volkov I, Banavar JR, He F, Hubbell SP, Maritan A (2005) Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438:658–661
- Wang Z, Xu ZB, Li X (1980) The main forest types and their features of community structure in northern slope of Changbai Mountain. *Res For Ecosyst* 1:25–42

- Webb CO, Peart DR (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80:2006–2017
- Webb CO, Gilbert GS, Donoghue MJ (2006) Phylodiversity-dependent seedling mortality, size structure, and disease in a bornean rain forest. *Ecology* 87:S123–S131
- Welden CW, Hewett SW, Hubbell SP, Foster RB (1991) sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology* 72:35–50
- Wilson BF (1995) Shrub stems: form and function. In: Gerter BL (ed) *Plant stems: physiology and functional morphology*. Academic, New York, pp 91–102
- Winkler M, Hulber K, Hietz P (2005) Effect of canopy position on germination and seedling survival of epiphytic bromeliads in a Mexican humid montane forest. *Ann Bot* 95:1039–1047
- Wright J (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1–14
- Wright IJ et al (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann Bot* 99:1003–1015
- Yang H, Li D, Wang B, Han J (1985) Distribution patterns of dominant tree species on northern slope of Changbai mountain. *Res For Ecosyst* 5:1–14
- Yuan ZQ et al (2011) Scale specific determinants of tree diversity in an old growth temperate forest in China. *Basic Appl Ecol* 12:488–495
- Zhang J, Hao ZQ, Li BH, Ye J, Wang XG, Yao XL (2008) Composition and seasonal dynamics of seed rain in broad-leaved Korean pine (*Pinus koraiensis*) mixed forest, Changbai Mountain. *Acta Ecol Sinica* 28:2445–2454