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Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank

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Abstract. Accumulating evidence suggests that negative density dependence, particularly at early life stages, is widespread in plant communities. We hypothesized that survival in forest seedling banks declines with increasing density of conspecific neighbors and that local-scale effects cause a negative correlation between seedling survival and tree species abundance in the community. We tested these hypotheses using data on 48 956 established seedlings of 235 species over three years in a 50-ha plot in Panama. For all species combined, we found a significant negative effect of conspecific seedling and adult neighbors within 10 m. In species-level analyses, neighbor density affected survival for 45 of 59 species, with effects of conspecifics different from heterospecifics for 29 species. Despite negative effects of local conspecific neighbors, seedling survival tended to be positively correlated with species abundance at the 50-ha scale. However, when accounting for species' shade tolerance, we found a significant negative relationship between seedling survival and species' basal area, but not density, in the 50-ha plot. Our findings indicate that attempts to quantify the contribution of density dependence to tropical tree species coexistence must integrate effects of neighbors across multiple life stages and should also take into account variation in life history strategy.

Key words: Barro Colorado Island, Panama; community compensatory trend; forest dynamics plot; regeneration; seedling bank; spatial autocorrelation; species coexistence; tropical forest.

Introduction

Understanding the mechanisms maintaining diversity in species rich communities remains a major challenge for ecologists. In diverse tropical forests, biologists have made considerable headway in identifying potential mechanisms for species coexistence (Wright 2002). One of the most discussed hypotheses is the Janzen-Connell hypothesis (Janzen 1970, Connell 1971), which posits that host-specific natural enemies, namely seed predators, pathogens, and herbivores, reduce survival when a species occurs at high local densities, such as when seeds fall close to parent trees. At larger spatial scales, common species will be less likely to escape from their pests compared to less abundant species. This may lead to a decline in seedling survival with increasing species' abundance in the community, resulting in a rare species advantage and community-level compensatory trend (Connell et al. 1984).

Experimental and observational studies have found patterns of distance- and density-dependent seedling recruitment and mortality consistent with the Janzen-Connell hypothesis in both temperate and tropical tree communities (e.g., Augspurger 1983, Webb and Peart 1999, Harms et al. 2000, HilleRisLambers et al. 2002, but see Hyatt et al. 2003). These studies point to density dependence as an important stabilizing force promoting species coexistence in forest systems. Negative density dependence is thought to be strongest for young seedlings, which are highly vulnerable to attack by natural enemies (Clark and Clark 1985). Although more resistant than new seedlings, established seedlings are frequently resource-limited by asymmetric competition with larger individuals (Wright 2002) and may therefore lack adequate resources to tolerate or recover from damage. Thus, established seedlings are also likely to exhibit lower survival rates in areas of high conspecific density.

While previous community-level studies have examined density-dependent mortality of trees at the seed and early seedling stages (Harms et al. 2000, HilleRisLambers et al. 2002) and for larger saplings and adults (Hubbell et al. 2001, Peters 2003, Uriarte et al. 2004*a*, Wills et al. 2006), no study to date has examined density dependence in the seedling bank at the whole-community level. Given that individuals can spend a considerable portion of their life in the seedling bank (Hubbell 1998), slight reductions in annual survival rates can significantly reduce the probability that a seedling reaches maturity. Thus, quantifying density dependence

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during this life stage is critical for assessing the relative importance of local neighborhood interactions for species coexistence in diverse tree communities.

Despite strong evidence for local-scale density dependence, attempts to demonstrate that it produces a community compensatory trend (CCT) have produced mixed results (Wright 2002), with studies reporting negative relationships (Connell et al. 1984, Welden et al. 1991, Webb and Peart 1999, Comita et al. 2007, Queenborough et al. 2007), positive relationships (Welden et al. 1991, He et al. 1997), and no relationship (Connell et al. 1984) between species abundance and various demographic rates in tropical forests. These contradictory findings may result from variation in species' demographic rates driven by differences in life history strategy (Wright 2002). In the seedling bank in particular, species' shade tolerance is likely to have a strong effect on survival, and may decouple the expected relationship between species abundance and seedling survival rates at the community level.

Here we use data on 48 956 seedlings of 235 tree and shrub species to examine the effects of conspecific seedling and adult neighbors on the survival of established seedlings in a diverse forest in central Panama. We test the hypotheses that: (1) survival in the seedling bank declines with increasing local density of conspecific neighbors and (2) the effect of conspecific neighbors is different from that of heterospecific neighbors. We also examine whether negative effects of conspecific neighbors on seedling survival at local scales (<10 m) result in a community compensatory trend at larger spatial scales (50 ha), and whether variation in shade tolerance among species affects correlations between seedling survival and species abundance in the community.

METHODS

Data collection

We conducted the study in the tropical moist forest of the 50-ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama (9°9′ N, 79°51′ W). All trees and shrubs $\geq$1 cm dbh (diameter at breast height) in the plot have been mapped, identified to species, and measured at five-year intervals (Hubbell and Foster 1983, Condit 1998). Here we use data on the location and dbh of saplings and trees $\geq$1 cm dbh in the 2000 census (*available online*).[5] In 2001, we established a permanently marked 1-m^2 seedling plot in the center of each 5×5 m subquadrat of the 50-ha FDP, for a total of ~20 000 plots. All free-standing, woody seedlings and small saplings $\geq$20 cm tall and <1 cm dbh (hereafter referred to simply as seedlings) were tagged, measured, and identified to species within each plot (Comita et al. 2007). We recensused seedling plots in 2002, 2003, and 2004.

Analyses

We used a model selection (Burnham and Anderson 2003), logistic regression approach to estimate the probability of a seedling surviving from 2001 to 2004 as a function of initial seedling height, census interval length, and local conspecific and heterospecific seedling and adult neighbor densities. In the simplest (density-independent) model, seedling survival depended only on the length of the census interval and (log-transformed) initial seedling height (Table 1). To assess the role of conspecific and heterospecific neighbor densities on seedling survival, we compared the density-independent model to models that included seedling and adult neighbor effects. In the full model, seedling survival depended on census interval, initial seedling height, number of conspecific (S_{CON}) and heterospecific (S_{HET}) seedlings in the same 1-m^2 quadrat as the focal seedling in 2001, and an index of conspecific and heterospecific adult influence (Table 1). The influence of neighboring trees is typically modeled as a function of tree size and distance from the focal individual (Canham et al. 2004, and references therein). Preliminary analyses revealed that basal area performed better than stem number or dbh, and that effects of neighbors declined with distance. Adult neighbor influence was therefore quantified as the sum of the basal area (BA) of each conspecific (A_{CON}) or heterospecific (A_{HET}) tree $\geq$1 cm dbh within 10 m, divided by the distance of that tree from the focal seedling:

$$A = \sum_{i}^{N} (\mathrm{BA}_i/\mathrm{DISTANCE}_i).$$

We compared the full model to models in which conspecific and heterospecific neighbor effects were lumped and to models in which only seedling or only adult neighbor effects were included. In total, we fit nine models (Table 1) falling into three classes: (1) the density-independent model, (2) models in which there is an effect of overall seedling density or adult basal area, but the effect of conspecifics is not different from heterospecifics, and (3) models in which the effect of conspecifics differs from heterospecifics for seedling or adult neighbors. Models in the third category are consistent with the Janzen-Connell hypothesis only if conspecific density decreases the probability of survival and has a stronger effect than heterospecific density. Models were compared using Akaike's Information Criterion (AIC; Burnham and Anderson 2003).

We examined the effect of neighbors on seedling survival at three levels. First, we examined survival at the community level by fitting models for all species combined. Second, we categorized species as shade tolerant, intermediate, or light-demanding, based on Comita et al. (2007), and fit models separately for each shade-tolerance guild. We then examined survival on a species-by-species basis for the 59 most abundant species in the seedling census ($N > 99$ seedlings; Appendix A).

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[5] ⟨http://ctfs.si.edu/datasets/bci/⟩

TABLE 1. Nine models compared to determine effects of conspecific and heterospecific neighbor densities on established seedling survival in the Barro Colorado Island (BCI), Panama, plot.

Model class	Model	Log odds of survival	No. species
Density independent	1	$a + b \times \mathrm{INT} + c \times \mathrm{HT}$	14
Effect of conspecific density = effect of heterospecific density	2	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + d \times S_{\mathrm{TOTAL}}$	9
	3	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + d \times S_{\mathrm{TOTAL}} + f \times A_{\mathrm{TOTAL}}$	1
	4	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + f \times A_{\mathrm{TOTAL}}$	6
Effect of conspecific density ≠ effect of heterospecific density	5	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + d_1 \times S_{\mathrm{CON}} + d_2 \times S_{\mathrm{HET}}$	7
	6	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + d_1 \times S_{\mathrm{CON}} + d_2 \times S_{\mathrm{HET}} + f \times A_{\mathrm{TOTAL}}$	3
	7	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + f_1 \times A_{\mathrm{CON}} + f_2 \times A_{\mathrm{HET}}$	7
	8	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + d \times S_{\mathrm{TOTAL}} + f_1 \times A_{\mathrm{CON}} + f_2 \times A_{\mathrm{HET}}$	6
	9	$a + b \times \mathrm{INT} + c \times \mathrm{HT} + d_1 \times S_{\mathrm{CON}} + d_2 \times S_{\mathrm{HET}} + f_1 \times A_{\mathrm{CON}} + f_2 \times A_{\mathrm{HET}}$	6

Notes: The number of species (out of 59 total) for which each model was the most parsimonious was based on comparisons of AIC values. Models include terms for the length of the census interval (INT), log-transformed initial seedling height (HT), number of conspecific (S_{CON}) and heterospecific (S_{HET}) seedlings neighbors, and basal area of conspecific (A_{CON}) and heterospecific (A_{HET}) trees $\geq$1 cm dbh, weighted by distance, within 10 m.

The probability of a seedling surviving is likely to be correlated with the survival of its immediate neighbors, which will not affect estimates of the parameters themselves, but will underestimate parameter variance (Hubbell et al. 2001). To account for this potential bias, we generated 95% confidence intervals around parameters for the best fit models using a modified bootstrapping approach, in which we resampled seedlings in 20 × 20 m blocks (see Appendix B for details).

To determine whether negative effects of local conspecific neighbors result in a community compensatory trend (CCT) at larger spatial scales, we examined seedling survival as a function of species abundance in the BCI 50-ha plot. We examined three measures of abundance: number of individuals $\geq$1 cm dbh, number of reproductive-sized individuals, and basal area of stems $\geq$1 cm dbh in the 2000 census. Number of reproductive-sized individuals was available only for trees, not shrubs, and was based on species-specific estimates of the minimum dbh at which individuals become fully reproductive (Comita et al. 2007; R. Foster, *unpublished data*). We used generalized linear models with quasibinomial errors to test whether the proportion of seedlings surviving was a function of (log-transformed) species abundance. Quasibinomial errors were used because the residual deviance greatly exceeded the residual degrees of freedom for all models, indicating overdispersion (Crawley 2002). We also included shade tolerance in the models to test whether variation in survival among shade-tolerance guilds masked correlations between species abundance and seedling survival rates. For all CCT tests, we excluded *Beilshmedia pendula*, an abundant species that suffered particularly high mortality during the census interval, because model diagnostics revealed that it had a disproportionately large effect on model fits.

RESULTS

Of 48 956 tree and shrub seedlings tagged in the 2001 seedling census, 32 213 were still alive in the 2004 census, indicating mortality of ~13% per year. When analyzing all species together, the probability of seedling survival was best described by the full model (model 9), which included separate conspecific and heterospecific seedling and adult neighbor terms (Table 2). Both conspecific seedling and adult neighbors had a significant, negative effect on seedling survival, as indicated by odds ratios less than one (Table 2). In contrast, the probability of survival significantly increased with increasing heterospecific seedling and adult neighbor densities.

For shade-tolerant and intermediate guilds, seedling survival was also best described by the full model (Appendix C), and effects of conspecific seedling and adult neighbors were again significantly negative. In contrast, the best model for light-demanding species included separate terms for conspecific and heterospecific seedling neighbors, but only one term for adult neighbor effects (model 6). However, the negative effect of conspecific seedling neighbors was stronger for light-demanding species than for shade-tolerant and intermediate species (Appendix C).

Among the 59 focal species, percentage seedling survival between 2001 and 2004 ranged from 14.0% to 96.4% (mean = 70.2). For 14 species, the best-fit model was the density-independent model, indicating that neither seedling nor adult neighbors influenced survival (Table 1). For 16 species, the best-fit model included overall seedling density or adult basal area, with no difference between the effects of conspecifics and heterospecifics. For the remaining 29 species, the best-fit model included parameters for conspecific and heterospecific seedling density or adult basal area, and the effect of conspecifics differed from heterospecifics (Table 1). For the majority of these species, the effect of conspecific neighbors tended to be negative, consistent with predictions of the Janzen-Connell hypothesis (Appendix A). For example, in cases where the best-fit model included separate parameters for conspecific and heterospecific seedling density, the effect of conspecific seedling density was negative for 12 of 16 species (Appendix A). Based on the conservative 95% bootstrapped confidence intervals, the effect of conspecific

TABLE 2. Effects of census interval, seedling height, and neighbor densities on survival of established seedlings of all species combined between 2001 and 2004 in the BCI 50-ha plot.

	Data			Effect on survival	
Parameter	Range	Mean	Median	Odds ratio	95% CI
Census interval (days)	975–1105	1021	1009	0.996	0.995–0.998
Initial height (mm)	200–6000	501.1	320	2.28	2.127–2.464
Seedling density (m^{-2})					
Conspecific	0–130	6.7	0	0.978	0.965–0.988
Heterospecific	0–132	6.7	5	1.02	1.013–1.026
Adult basal area (Σ (BA/dist))					
Conspecific	0–125.3	2.5	0.3	0.936	0.912–0.956
Heterospecific	9–703.8	36.9	33.2	1.007	1.004–1.011

Notes: Odds ratios >1 indicate a positive effect of the independent variable on seedling survival, while values <1 indicate a negative effect. Odds ratios of all parameters are significantly different from one based on modified 95% bootstrapped confidence intervals (see Appendix B).

seedling density on survival was only significantly negative for three of the 12 species. However, for all 12 species, the odds ratio for conspecific seedling density fell below the 95% bootstrapped confidence intervals around the odds ratio for heterospecific seedling density, confirming that the effect of conspecific seedling neighbors is significantly stronger than that of heterospecifics.

In cases where conspecific and heterospecific adult effects were included in the best-fit model, the influence of conspecific adult neighbors was negative in 17 of 19 cases, with 12 species showing significantly negative effects based on conservative 95% confidence intervals. As with seedling neighbors, in all 17 cases the odds ratio for conspecific adult influence fell outside of the 95% confidence intervals for heterospecific adult influence, confirming that effects of conspecifics and heterospecifics are significantly different (Appendix A).

When effects of conspecific and heterospecific neighbors differed, odds ratios for heterospecific seedling and adult effects tended to be >1, suggesting a positive effect (seedlings, 13 of 16 species, eight significant; adults, 14 of 19 species, four significant; Appendix A). Similarly, where best-fit models included terms only for overall seedling or adult influence (i.e., no difference between conspecific and heterospecific effects), the overall effect of neighbors tended to be positive for both seedling density (15 out of 16 species, 11 significant) and adult basal area (10 of 10 species, two significant; Appendix A).

Contrary to expectations, we did not find a CCT, but rather a significant positive relationship between seedling survival and species abundance when abundance was calculated as the number of trees ≥1 cm dbh in the 50-ha plot (slope = 0.29, df = 222, $P < 0.0001$; Fig. 1A) or as the number of reproductive-size individuals in the 50-ha plot (slope = 0.15, df = 186, $P < 0.001$). We found no significant relationship between seedling survival and species total basal area in the plot (slope = −0.03, df = 222, $P = 0.36$). Controlling for shade-tolerance guild did not change the observed relationships between seedling survival and number of reproductive-size or ≥1 cm dbh

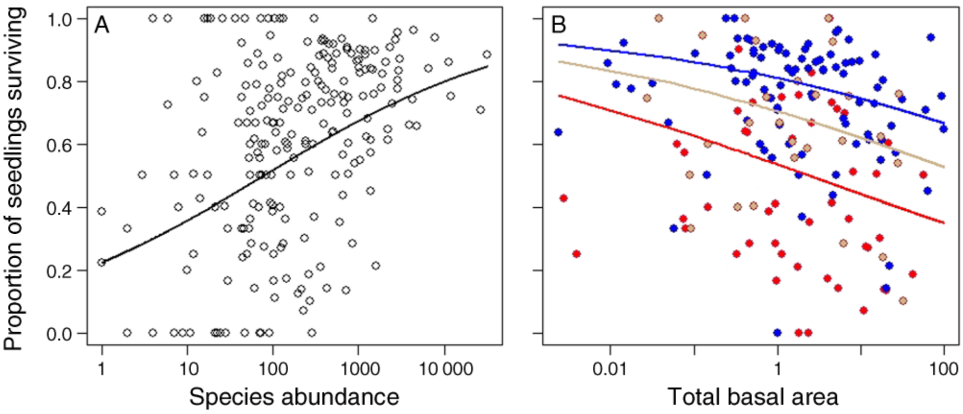

FIG. 1. Relationship between proportion of established seedlings surviving from 2001 to 2004 in the BCI forest and species abundance, measured as (A) the number of individuals ≥1 cm dbh and (B) total basal area (m^2) of shade-tolerant (blue), intermediate (tan), and light-demanding species (red) in the BCI 50-ha plot. Note the different x-axis scales.

trees (Appendix D). However, with shade tolerance included in the model, the relationship between seedling survival and species' total basal area became significantly negative (Fig. 1B; Appendix D), consistent with a CCT. There were no significant interactions between shade-tolerance guild and species abundance (all $P >$ 0.05).

DISCUSSION

Effect of conspecific neighbors on established seedling survival

At the community level, we found a significant negative effect of local conspecific seedling and adult neighbors on established seedling survival, consistent with predictions of the Janzen-Connell hypothesis. Both pathogens and insects have been shown to cause density-dependent mortality in established seedlings and saplings (Wong et al. 1990, Gilbert et al. 2001). Negative effects of conspecific neighbors may also result from intense competition between conspecifics. However, recent studies have shown seedling–seedling competition in tropical forests to be weak (Paine et al. 2008, Svenning et al. 2008).

In species-level analyses, conspecific neighbor density had a negative effect in slightly less than one-half of the species examined. Similarly, in a study of seedling survival in a Bornean forest, Webb and Peart (1999) found a negative effect of local conspecific density in community-level analyses, but in species-level analyses, seedling survival was significantly correlated with local conspecific density for only five of 15 species. This is expected, at least in part, due to decreased power to detect significant effects in species-level analyses because of smaller sample sizes. In our study, however, sample size had only a marginally significantly effect on the probability of detecting significant neighbor effects (logistic regression: $P = 0.07$). The lack of a consistent effect across all species likely also reflects the fact that the strength of density dependence varies considerably among species. In fact, the odds ratios for the effect of conspecific neighbors ranged over an order of magnitude among species (Appendix A). The observed variation among shade-tolerance guilds in the strength of neighbor effects on seedling survival (Appendix C; also see Hubbell et al. 2001) indicates that differences among species in part reflect differences in life history strategies.

In a study of density dependence during the seed-to-seedling transition in the BCI forest, Harms et al. (2000) found significant negative effects of conspecific density for all 53 focal species examined. Our results here, showing negative effects of conspecific density for slightly less than one-half of the species, are more similar to those reported by Peters (2003) and Uriarte et al. (2004*a*, *b*) for saplings and trees $\geq$1 cm dbh on BCI and in other tropical forests. For some species, density dependence during germination and seedling establishment may be sufficiently strong to thin out seedlings to levels below which negative effects of density are not detectable at later life stages, including at the established seedling stage examined here.

Effect of heterospecific neighbors on survival

Many studies of density dependence neglect to differentiate between effects of intra- and inter-specific densities, a key component in assessing the role of density dependence in promoting species coexistence (Freckleton and Lewis 2006). We found a clear difference between conspecific and heterospecific neighbor effects at the community level, and for approximately one-half of the focal species examined. In both community- and species-level analyses, the probability of survival tended to increase with heterospecific neighbor density. This is consistent with the species herd-immunity hypothesis (Wills 1996), which posits that increased heterospecific crowding results in fewer encounters between a host and its species-specific pests and pathogens. Thus, survival should increase with the density of heterospecifics, even when conspecific density remains constant. A simpler explanation for our results is that sites with high rates of seedling survival also support high seedling densities. For example, areas of high resource availability, such as sites with increased light due to canopy openings, will tend to support higher densities. Survival at these sites will also tend to be higher because seedlings are not resource limited. Future studies that simultaneously assess resource availability and neighbor densities are needed to separate out these effects.

Community-level consequences of local density dependence

Although we found negative effects of conspecific density on seedling survival at local scales, this did not translate into a compensatory trend at the community level. In fact, seedling survival rates tended to be positively correlated with species abundance at the scale of the 50-ha plot (Fig. 1A). However, when accounting for variation in species' shade tolerance, we did find a significant negative correlation between seedling survival and species' basal area (Fig. 1B).

Queenborough et al. (2007) also reported a negative relationship between seedling survival and species' basal area (but not species' density) in a study of 15 species in the family Myristicaceae in Ecuador, all of which were shade tolerant. In combination with our results here, this suggests that variation in life history strategy decouples the expected relationship between species abundance and seedling survival rates at the community level. However, even when controlling for differences in shade tolerance, we did not observe a CCT with species' density (i.e., number of reproductive-size or $\geq$1 cm dbh trees). Thus, it remains unclear whether local scale negative density dependence regulates species abundances at landscape scales.

A CCT would also fail to arise if species always experienced high local densities of conspecifics, regardless of their abundance in the community, due to limited seed dispersal (Freckleton and Lewis 2006). Additionally, predator satiation at larger spatial scales could result in a positive relationship between seedling survival and species abundance, even in the face of local-scale negative density dependence (Schupp 1992). Indeed, a community compensatory trend may be "too naive an expectation in real communities" (Freckleton and Lewis 2006), and a failure to observe this pattern does not necessarily indicate that density dependence is unimportant for species coexistence.

Overall, our results demonstrate that conspecific neighbors tend to have a negative effect on survival in the seedling bank and that the effect of conspecific neighbors is significantly different from that of heterospecifics in the BCI forest. Density dependence appears to be less ubiquitous at the established seedling stage compared to earlier life stages (e.g., Harms et al. 2000), but for many species, individuals can spend decades in the seedling bank; and thus weak neighborhood effects may accumulate over time and ultimately have as large an effect as at earlier life stages. In combination with previous community-level analyses, our results indicate that significant negative effects of local conspecific density occur at all life stages from seed to reproductive adult in tropical forests. This suggests an important role for density dependence in tropical tree communities. The challenge now is to integrate the lifetime effects of neighbors across all stages in order to quantify the role of density dependence in limiting species abundances and promoting coexistence in diverse plant communities.

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APPENDIX A

Effects of census interval, seedling height (log-transformed), and conspecific and heterospecific seedling and adult neighbors on three-year survival of established seedlings of 59 tree and shrub species in the BCI 50-ha plot, Panama (*Ecological Archives* E090-024-A1).

APPENDIX B

Explanation of modified bootstrapping approach for calculating 95% confidence intervals (*Ecological Archives* E090-024-A2).

APPENDIX C

Results of survival models for different shade-tolerance guilds (*Ecological Archives* E090-024-A3).

APPENDIX D

Results of models of species' seedling survival rates as a function of shade-tolerance guild (light-demanding, intermediate, or shade tolerant) and species abundance in the BCI 50-ha plot, Panama (*Ecological Archives* E090-024-A4).