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# NEIGHBORHOOD AND COMMUNITY INTERACTIONS DETERMINE THE SPATIAL PATTERN OF TROPICAL TREE SEEDLING SURVIVAL

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*Abstract.* Factors affecting survival and recruitment of 3531 individually mapped seedlings of Myristicaceae were examined over three years in a highly diverse neotropical rain forest, at spatial scales of 1–9 m and 25 ha. We found convincing evidence of a community compensatory trend (CCT) in seedling survival (i.e., more abundant species had higher seedling mortality at the 25-ha scale), which suggests that density-dependent mortality may contribute to the spatial dynamics of seedling recruitment. Unlike previous studies, we demonstrate that the CCT was not caused by differences in microhabitat preferences or life history strategy among the study species. In local neighborhood analyses, the spatial autocorrelation of seedling survival was important at small spatial scales (1–5 m) but decayed rapidly with increasing distance. Relative seedling height had the greatest effect on seedling survival. Conspecific seedling density had a more negative effect on survival than heterospecific seedling density and was stronger and extended farther in rare species than in common species. Taken together, the CCT and neighborhood analyses suggest that seedling mortality is coupled more strongly to the landscape-scale abundance of conspecific large trees in common species and the local density of conspecific seedlings in rare species. We conclude that negative density dependence could promote species coexistence in this rain forest community but that the scale dependence of interactions differs between rare and common species.

*Key words: autologistic regression; community compensatory trend (CCT); Ecuador; Myristicaceae; seedling; spatial autocorrelation; species coexistence; tropical forest; Yasuní.*

## INTRODUCTION

The seedling to sapling transition is a critical bottleneck in tree establishment. The spatial pattern of seedling survivorship also influences the long-term distribution patterns of species. The ecological basis of seedling recruitment has therefore become a focus of research on the mechanisms that aid in the maintenance of high species diversity in tropical rain forests (Janzen 1970, Connell 1971, Grubb 1977). Many studies have documented negative density- or distance-dependent effects on survival in one or more species (Augspurger 1984, Harms et al. 2000, Wyatt and Silman 2004). However, these are often limited by a failure to consider explicitly the spatial context of the seedling.

Negative density dependence may be manifested as a community compensatory trend (CCT), defined as an inverse relationship between plant growth, recruitment or survival, and conspecific density (Connell et al. 1984). Coexistence of species may be enhanced by CCTs because rare species achieve a higher rate of population increase than common species. Demonstration of a CCT requires rare species, compared to common species, to exhibit increased performance over a range of abundances.

Four attempts to detect a CCT in tropical forests have yielded equivocal results. For seedlings (<31 cm tall) and saplings (<8 cm diameter at breast height) in Australia, mortality over a period of up to 16 years was unaffected by conspecific density, but recruitment of subcanopy and understory species was affected (Connell et al. 1984). However, this relationship was identified from a regression of per capita recruitment ($y$) on adult density ($x$), of the form $y/x$ vs. $x$, and has been disputed (Wright 2002). Second, at Gunung Palung, Borneo, seedling (5–50 cm tall) survival over 19 months was lower for abundant species, supporting a CCT (Webb and Peart 1999). Third, sapling (1–4 cm dbh) recruitment over three years was greater for rare species in a large forest plot in Panama (Welden et al. 1991). However, survival was positively related to species abundance, contrary to a CCT. Finally, sapling survival also increased with population size for trees $\geq$1 cm dbh at Pasoh, Malaysia (He et al. 1997).

Although testing for density dependence motivated these studies, other mechanisms may give rise to a spurious suggestion of a CCT (Wright 2002). Different microhabitat associations of tree species may affect the detection and apparent direction of a CCT. Webb and

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Peart (1999) monitored seedlings in gaps and in mature forest understory. Pioneer trees are likely to be common in gap plots where high light favors survival, and rare as adults in mature forest (Wright 2002). Conversely, rare pioneers may have survived poorly on the mature forest plot at Pasoh (He et al. 1997). Wright (2002) attributed the suggested CCT for sapling recruitment in Panama to an increase in gaps due to a severe El Niño drought. Here we also use data from a large forest plot, but consider 15 confamilial species, all with shade-tolerant seedlings. Using one ecologically uniform family ensures that variation in ecology and life history will have less of an influence on probabilities of survival of species. We compared the abundance of trees with three-year seedling survival data in nongap plots in mature forest to test for negative density dependence manifested as a CCT. We then support our between-species comparisons with an analysis of factors affecting individual seedling mortality within species.

As well as conspecific density, other factors affect seedling survival to the sapling stage. Biotic factors include seedling predators and pathogens (Janzen 1970, Connell 1971) and the neighboring plant community, which may enhance survival probability via herd immunity (Peters 2003) or reduce it through competition (Gilbert et al. 2001, Uriarte et al. 2005). Effects of abiotic variables on survival are also well documented (Whitmore 1996, Montgomery and Chazdon 2002, Palmiotto et al. 2004). However, most previous work on seedling dynamics is limited by failure to include spatial autocorrelation in these factors in statistical models. Most factors that influence plant survival (e.g., light, nutrients, moisture, herbivory, competition) exhibit spatial autocorrelation at scales larger than an individual plant (Nicotra et al. 1999, Ahumada et al. 2004). Therefore, the fates of plants in close proximity are not statistically independent. Spatial structure has been included in recent analyses of sapling population dynamics (Hubbell et al. 2001, Ahumada et al. 2004, Uriarte et al. 2004, 2005), but the dynamics of tropical tree seedlings have not been considered from this perspective. Previous tests of density dependence also used a quadrat-based approach, which further decreases the information per stem because most individuals may be near a quadrat edge (Peters 2003, Wills et al. 2006). Here we use an individual-based approach to isolate the spatial autocorrelation of mortality and provide a more robust test of whether negative density dependence is responsible for any observed CCT. We use spatially explicit data on the population dynamics of 3531 seedlings of 15 species of Myristicaceae growing on a large forest plot in lowland tropical rain forest in Amazonian Ecuador to address the following specific questions. (1) Is seedling survival negatively density dependent, and is this manifested in a community compensatory trend? (2) Is seedling mortality spatial autocorrelated and, if so, at what spatial scales? (3) Are local spatial autocorrelation and neighborhood interactions influenced by community-level abundance of species?

## Materials and Methods

### *Study site*

Yasuní National Park and Biosphere Reserve and the Huaorani Ethnic Reserve cover $1.6 \times 10^6$ ha of forest in Amazonian Ecuador. There are few roads and most of the park is never logged. The canopy is 10–25 m high, punctuated with emergent trees. The climate is aseasonal (Valencia et al. 2004). Mean annual rainfall is 2800 mm and total monthly rainfall is almost never <100 mm. Mean monthly temperature is 25°–27°C.

A 50-ha permanent forest dynamics plot (FDP) is located inside the park (0°41′ S, 76°24′ W; Valencia et al. 2004; additional information is available on the Center for Tropical Forest Science web site).[5] There are a few indigenous Huaorani settlements north of the station and low-intensity hunting occurs inside the plot. The FDP ranges from 216 to 248 m above sea level. It includes three ridges and an intervening valley that floods for brief periods.

From 1995 to 2000, all freestanding stems ≥1 cm diameter at breast height (dbh at 1.3 m), excluding lianas, in the western 25 ha of the FDP were tagged, mapped, and identified to morphospecies (Valencia et al. 2004). We use data from this initial census. Population properties for the 15 species of Myristicaceae were calculated from plot data, and seeds were collected from beneath parent trees (1–10 seeds for >3 trees) to estimate seed size (Appendix A). Fourteen of these species are dioecious; *Iryanthera juruensis* is andromonoecious (Queenborough et al. 2007).

### *Seedling plots*

Within the western 25 ha of the FDP, 30 plots of 20 × 20 m, each composed of 16 5 × 5 m subplots, were established in February to June 2002 in a stratified random design to sample the three main habitats on the plot with equal intensity (Appendix B). Habitats within the FDP cover the following areas: valley, 7.88 ha; slope, 7.66 ha; ridge, 8.96 ha (Valencia et al. 2004). All plots were under closed canopy in mature forest. We excluded subplots affected by a new gap from subsequent analyses.

The coordinates of all Myristicaceae plants >1 cm in height and <1 cm dbh were mapped according to standard FDP protocols within each 5 × 5 m subplot and tagged with a 10-cm plastic cocktail stick. All stems were identified and measured for height to the apical bud (mm), basal stem diameter (mm), and number of expanded leaves. Species were determined from Estación Cientifica Yasuní (ECY) herbarium material (Persson 2005) and from seedlings grown from shadehouse-germinated seeds collected in 2002–2003. All plots were

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[5] ⟨http://www.ctfs.si.edu⟩

recensused between 28 November 2002 and 31 January 2003, between 5 and 24 November 2003, between 19 June and 13 July 2004, and between 13 June and 3 July 2005. All existing plants were checked and new recruits were enumerated. A total of 2330 seedlings was censused initially and 3531 seedlings were marked over all censuses (see Plate 1). We use data from the initial cohort here. Density of target species stems $\geq$1 cm dbh in 25 ha ranged from 1.76/ha (*Compsoneura sprucei*) to 33.5/ha (*Iryanthera hostmannii*; Queenborough et al. 2007). Density of seedlings ranged from 8/ha (*Virola flexuosa*) to 513/ha (*V. duckei*; Appendix C) and, in total, constitute ~2% of all seedlings at Yasuní (S. Queenborough and M. Metz, *unpublished data*).

In June 2004, a hemispherical canopy photograph was taken from the center of each quarter of each 20 × 20 m plot ($N = 4$ per seedling plot). Photographs were taken 1 m above the ground, in uniformly overcast conditions in the early morning or late afternoon, with a leveled Nikon Coolpix 4500 camera body and Nikon FC-E8 Fisheye Converter lens, saved as black and white JPEG images at size 2272 × 1704 pixels. Images were analyzed using Gap Light Analyzer 2.0 (*available online*).[6] Canopy openness was 5% ± 0.8% (mean ± SD), range 2.8–7.4%. There was no significant difference between habitat types (valley, slope, ridge), but there was significant difference among plots within habitats (nested ANOVA: habitat $F$ value 1.11, $P > 0.05$; habitat(plot) $F$ value 4.47, df = 27, 90, $P < 0.001$).

### Data analysis

*Overview.*—Data were analyzed using the software package R 2.3.1 (R Development Core Team 2005). Species were excluded from a particular analysis if they had <5 individuals, as noted for each analysis. Using randomization approaches detailed later, we examined linear regressions of seedling survival over three years against three measures of tree abundance at the community level, as well as against seedling density. Only trees greater than species-specific minimum reproductive size were included (Queenborough et al. 2007). To assess local density dependence, we used an autologistic regression model to examine spatial autocorrelation in the effects of neighboring conspecific and heterospecific Myristicaceae seedlings and trees on focal seedling survival.

*Seedling survival between species.*—To test for density-dependent effects on seedling survival, we used a linear regression model to examine survival for each species (15 species, 2330 seedlings) as influenced by the following log-transformed measures of abundance: tree absolute basal area, tree relative basal area (basal area of species *i*/total basal area), and tree frequency on the 25-ha FDP, as well as seedling density on the total 1.2 ha of seedling plots. Survival rate variances were not homogeneous, so the slope of each regression was compared to a distribution of 1000 slopes generated by randomly sampling the data set assuming no relationship between seedling survival and each variable (cf. Webb and Peart 1999). If the slope exceeded the 95% confidence intervals of the distribution we inferred a significant relationship between seedling survival and species abundance. Two test distributions were generated; first by randomizing species abundance, and second by randomizing seedling survival. In the first, species abundance values were randomly assigned to species and slopes of observed seedling survival regressed against randomized tree abundance were obtained by standard least squares fitting. In the second test, we generated a binomially distributed random number of survivors for each species based on the observed number of seedlings of each species and the mean survival probability for all species (total number survivors/total number of all seedlings).

We also tested for undersampling of seedlings from rare species occurring at high densities near parents due to random sampling of seedlings in space rather than sampling random individuals. The sex expression of reproductive trees on the FDP was determined (Queenborough et al. 2007). We then excluded all seedlings that had a conspecific reproductive female within 20 m (thus excluding seedlings from potential parents both inside and outside the seedling plot) and repeated the randomization tests as before, on 15 species and 1688 seedlings.

Apparent density dependence in a multiple-aged cohort can be explained if the mean height of seedlings differs between species. Populations of species that recruited every year had lower mean seedling heights than species that recruited less often (Queenborough 2005). Therefore, because seedling survival was significantly related to seedling height (linear regression of a binary response variable with binomial errors: slope = 0.0166, $P < 0.001$) and species had significantly different mean heights (ANOVA: $F = 16.3$, df = 15, 1848, $P < 0.001$) in this initial cohort, we excluded all seedlings $\geq$30 cm tall and repeated the randomization tests on the remaining 11 species and 1387 seedlings. Because two plots had abnormally high seedling densities from large fruiting females, the above analyses were then repeated on a subset of the data excluding these two plots.

Finally, we tested the relationship between observed seedling survival and observed seedling density against a distribution of 1000 slopes of simulated seedling survival against observed seedling abundance. We generated a binomially distributed random number of survivors from initial seedlings of each species with the probability of survival equal to the mean of the observed species-specific survival rates.

In order to examine the generality of the community compensatory trend (CCT) within the FDP and to test whether it was indeed influenced by habitat and light as other authors have suggested (Wright 2002), we repeated the previously described analyses (including those

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[6] ⟨http://www.rem.sfu.ca/forestry/⟩

seedlings >20 m from a female and seedlings <30 cm tall) on further subsets of the full data set. We tested for a CCT for seedlings within each of the three habitats separately, and also within each of the four quartiles of the canopy openness range. We then tested for a CCT at each individual seedling plot, using trees in neighborhood sizes of 1 ha, 4 ha, and 9 ha centered on the seedling plot to define the basal area of species.

*Seedling survival within species.*—Autologistic regression was used to test effects of neighborhood density on individual seedling survival. The response variable was the survival of the focal plant to June 2005, assigned a value of unity (alive) or zero (dead). We fitted autologistic regressions on survival at each of nine contiguous annular rings around focal individuals. Autologistic regression models the spatial autocorrelation in survival. Logistic regression models assume that survival of a plant is independent of that of its neighbors. This is violated if survival is patchy because of such factors as branchfalls, herbivory, and soil nutrient and moisture heterogeneity. Autologistic regression adds a term into the logistic regression model, controlling statistically for the effect of spatial autocorrelation while assessing the effects of the different neighborhood variables. The model was fitted with maximum likelihood estimation. For further discussion see Hubbell et al. (2001) and references therein.

For all seedlings alive in June 2002, we noted confamilial tree and seedling neighbors in concentric annuli of 1 m width to a maximum distance of 9 m. The sample for each annulus varied in order to maximize sample size while not overlapping plot edges. For example, for annulus 0–1 m, focal seedlings were included from the central 18 $m^2$ of each plot, and for annulus 4–5 m, focal seedlings were used only from the central 10 $m^2$ of each plot. Sample sizes of total focal seedling numbers across all species for each annulus are: 1902 (0–1 m), 1508 (1–2 m), 1206 (2–3 m), 926 (3–4 m), 565 (4–5 m), 378 (5–6 m), 220 (6–7 m), 115 (7–8 m), and 45 (8–9 m) seedlings, respectively. Again, we repeated analyses excluding two high-density plots.

Within each annulus, we computed the following independent neighborhood variables: (1) density of conspecific seedlings, (2) density of confamilial seedlings of a different species, (3) relative plant height (fraction of plants shorter than the focal plant), (4) basal area of conspecific trees, and (5) basal area of confamilial trees of a different species. Neither light availability nor habitat was included in this analysis as unique values were not available for each seedling.

The data set was first analyzed on a pooled sample of all species and then grouped according to abundance on the FDP, as either abundant (four species with >0.02 relative basal area in 25 ha) or rare (11 species with <0.02 relative basal area in 25 ha). In the autologistic regression for three annuli, partial or complete separation of the data occurred, whereby conspecific tree basal area correctly allocated all observations to the appropriate response group. Deletion of this parameter did not affect the remaining parameter coefficients. There were insufficient individuals in the 9-m annulus of the rare species group to analyze.

Odds ratios measure the partial effect of each variable on the odds of survival and were calculated by taking the exponential of the estimate of each parameter. Odds ratios >1 indicate positive effects on survival and ratios <1 indicate negative effects.

### *Other factors affecting seedling survival*

*Habitat and light associations.*—Because species may occur in specific rare habitats or light environments, which may generate a spurious CCT without any effect of abundance on survival, we tested for associations of seedlings with these two factors. Habitat associations of trees >1 cm dbh are known on the Yasuní FDP (Valencia et al. 2004, Queenborough 2005). We tested for habitat associations of seedlings using a randomization procedure similar to Webb and Peart (2000). First we calculated the frequency of each species in the 5 × 5 m subplots within each seedling plot (range 0–20). We then randomly shuffled the habitats within which each of the 30 seedling plots occurred and calculated a deviation statistic based on the frequency of each species in each habitat type: $\Sigma$ [(randomized – expected)$^2$/expected]. This was repeated 1000 times per species and we compared the observed deviation value with this randomized distribution of deviation values.

We tested for light associations of species using a logistic regression of the presence or absence of each species in 5 × 5 m subplots (a total of 120 subplots) against $\log_{10}$ canopy openness.

*Light and habitat.*—Because we could not assign unique values of habitat and light availability to each individual seedling, we performed an analysis of deviance on the proportion of seedling survivors for each species in each quarter seedling plot in order to test whether light availability and/or habitat affected species-level survival. It is highly likely that species do differ in their responses to light and habitat; however, for these trends to be manifested as a spurious CCT their responses must scale with abundance. The predictor variables for species were tree relative basal area, canopy openness, and plot nested within habitat. An ANOVA was used to test whether each term in the model produced a significant decrease in residual deviance, using the AIC to select the best-fit model.

*Population parameters.*—A correlation of species abundances with life history traits could also generate an apparent CCT. We tested for a relationship between tree abundance and both seed mass and the seedling : tree ratio to determine whether rare species produced fewer larger seedlings that were more likely to survive well.

## RESULTS

A total of 3531 seedlings were censused over three years. Numbers and percentage survival varied widely

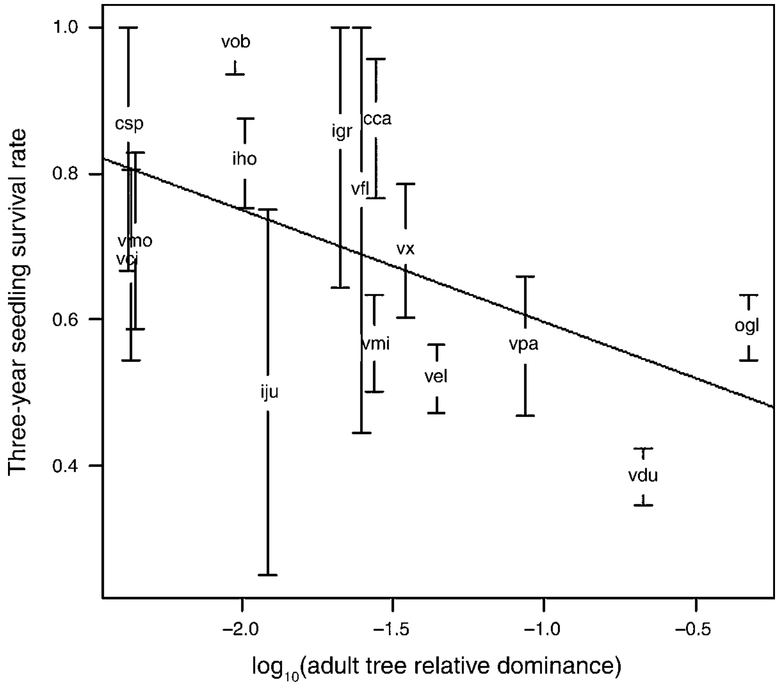

Fig. 1. A test of density dependence among seedlings of 15 species of Myristicaceae on the Yasuní forest dynamics plot, Ecuador. The significance of the slope of the regression of seedling survival over three years against dominance of adult trees, based on log-transformed relative basal area, was tested by comparison of a linear regression model of the observed data with a distribution of liner models generated either by bootstrapping seedling survival or adult relative basal area (see Table 1). The $y$-axis label indicates survival of seedlings of unknown age over a three-year period. Data points are denoted by species codes (for details see Appendix A). Error bars indicate 95% confidence limits of survival rate for each species based on the binomial distribution. Various subsets of the data set were analyzed; this figure illustrates data for all seedlings over the whole forest dynamics plot.

among species (Appendix B). Of the initial seedling cohort (2002), 1025 out of 2330 seedlings of 15 species had died by June 2005. Survival over all seedlings was 0.56, whereas mean survival by species was 0.69.

### *Evidence concerning a community compensatory trend in survival*

The results for relative basal area and seedling density are presented here, and those for basal area and frequency in Appendix C.

Seedling survival was inversely related to the relative basal area of trees (Fig. 1). The observed regression slopes were extreme compared to the distribution of randomized slopes when either tree relative basal area or three-year seedling survival was randomized (Table 1A, B for all seedlings). A 10-fold increase in basal area led to a 5–15% decrease in survival.

When we examined subsamples of the full data set to test the robustness of this result, we found that the significant negative relationship between seedling survival and tree basal area remained in most cases (Table 1A, B). When seedlings $\geq$30 cm tall were excluded in order to remove their inherent survival advantage a significant positive relationship between individual seedling height and survival remained (linear regression of a binary response variable with binomial errors: slope = 0.07, $P < 0.001$). However, seedling survival was independent of mean seedling height per species (weighted regression: $P = 0.93$), and mean seedling height per species was unrelated to adult basal area or density (linear regression, basal area of stems $\geq$10 cm dbh, $P = 0.78$; frequency of stems $\geq$10 cm dbh, $P = 0.51$). When tree abundance was expressed as density, no relationship with seedling survival was apparent (Appendix C).

Seedling survival was significantly negatively related to conspecific seedling abundance, but only in the full data set (Table 1C).

Analysis of the data set stratified according to habitat or light environment also showed significant negative relationships between seedling survival and tree basal area (Appendices D and E). This was also found for four out of 20 seedling plots for which sufficient species were present (with 1 ha of surrounding trees providing the neighborhood), seven of 25 plots (4-ha neighborhood), and three of 25 (9-ha neighborhood). No positive relationships were found (Appendix F).

### *Local neighborhood effects on survival*

The survival of Myristicaceae seedlings was strongly spatially autocorrelated, but this decayed rapidly. At distances >5 m from the focal seedling the spatial term did not differ significantly from zero and therefore survival was not spatially structured beyond this

TABLE 1. Summary of the significance of observed regression slopes of seedling survival on adult tree relative basal area (methods A and B) or seedling density (C), as tested against the distribution of slopes of 1000 simulated regressions randomizing either the predictor (method B) or response variable (methods A and C).

| Randomization method and seedlings included | Seedling data set<br>Full ($N$ = 30 plots) | <br>Partial ($N$ = 28 plots) |
|---|---|---|
| A) Bootstrapped adult relative basal area vs. seedling survival | | |
| All seedlings | * | NS |
| Seedlings >20 m from female | NS | NS |
| Seedlings <30 cm tall | NS | NS |
| Seedlings >20 m from female and <30 cm tall | NS | NS |
| B) Adult relative basal area vs. bootstrapped seedling survival | | |
| All seedlings | *** | *** |
| Seedlings >20 m from female | *** | * |
| Seedlings <30 cm tall | *** | * |
| Seedlings >20 m from female and <30 cm tall | ** | * |
| C) Bootstrapped seedling survival vs. seedling density | | |
| All seedlings | *** | NS |
| Seedlings >20 m from female | ** | NS |
| Seedlings <30 cm tall | ** | NS |
| Seedlings >20 m from female and <30 cm tall | * | * |

*Notes:* The test was conducted on all seedling plots (full) or only those without highly fecund females (partial), and then on subsets of these data (see *Materials and methods*: *Data analysis* for details). See Appendix D for full regression coefficients.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

distance (Fig. 2). There were no significant differences between the full and partial data sets in the spatial autocorrelation term.

Odds ratios for the five neighborhood variables changed with distance from the focal seedling (Table 2). Relative seedling height had a strong positive effect on survival up to 8 m (Table 2A). Conspecific seedling density had a significant negative effect up to 7 m (Table 2A). There was little effect of heterospecific seedling or tree basal area or conspecific tree basal area on focal seedling survival.

*Rare and common species.*—Neighborhood effects on seedling survival varied with tree species abundance. Low statistical power for the rare species subset prevented direct testing of differences between abundant (>0.02 relative basal area) and rare (<0.02 relative basal area) species groups. However, the significance patterns for terms in the respective autologistic regression models are informative. First, the significant positive effects of relative seedling height were similar for both abundant and rare species (Table 2B, C). Second, there were no differences between abundant and rare species in the effects of neighboring heterospecific seedlings and trees (Table 2B, C). Third, both spatial autocorrelation and responses to conspecific neighbors differed substantially depending on species abundance. Among common species, positive spatial autocorrelation was insignificant at >2 m and was negative at 5 m, but rare species exhibited positive spatial autocorrelation to 5 m, and did not become negative (Table 2C, local seedling survival).

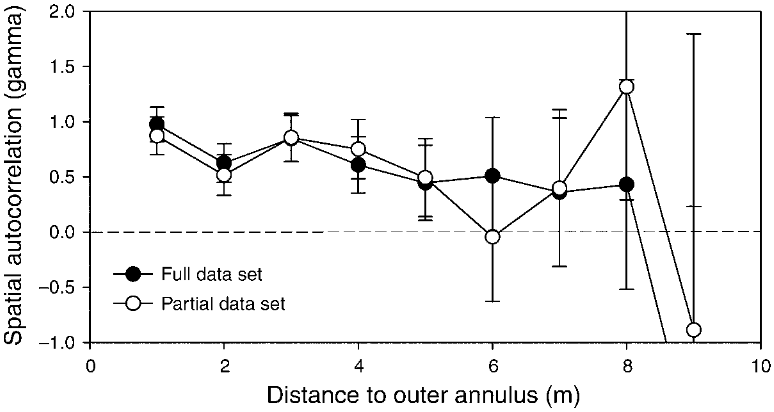

FIG. 2. Decay in the spatial autocorrelation parameter in two autologistic regressions examining the effect of local neighborhood variables on focal seedling survival in 15 species of Myristicaceae on the Yasuní forest dynamics plot. The $x$-axis indicates the distance to the outer edge of each 1-m annular ring. The full data set of all seedling plots is compared to a partial data set in which two high-density plots were excluded. Error bars indicate ±SE.

TABLE 2. Summary of the odds ratios for model parameters from autologistic regression analyses of seedling survival of 15 species of Myristicaceae (four abundant species and 11 rare species).

| Model parameter | Annulus (m) | | | | |
|---|---|---|---|---|---|
| | 0–1 | 1–2 | 2–3 | 3–4 | 4–5 |
| A) All species (*N*) | (1902) | (1508) | (1206) | (926) | (565) |
| Heterospecific seedling density | 0.88 | 0.77 | 0.82 | 0.73 | 0.29 |
| Conspecific seedling density | 0.89*** | 0.81*** | 0.71*** | 0.76* | 0.40** |
| Local seedling survival (spatial term) | 0.97*** | 0.62*** | 0.85*** | 0.61* | 0.45 |
| Relative seedling height | 2.22*** | 3.54*** | 4.28*** | 7.00*** | 6.28*** |
| Heterospecific tree basal area | 0.99 | 0.99 | 0.94 | 0.88* | 1.04 |
| Conspecific tree basal area | <0.01 | 0.98 | 0.99 | 0.78*** | 1.35** |
| B) Abundant species (*N*) | (1023) | (818) | (638) | (460) | (264) |
| Heterospecific seedling density | 0.74 | 0.59 | 0.83 | 0.42 | 0.06 |
| Conspecific seedling density | 0.90*** | 0.85*** | 0.74*** | 0.84 | 0.42** |
| Local seedling survival (spatial term) | 0.84*** | 0.71** | 0.30 | 0.49 | −0.15 |
| Relative seedling height | 2.62*** | 3.99*** | 3.40*** | 7.67*** | 5.33*** |
| Heterospecific tree basal area | 0.98 | 1.04 | 0.99 | 0.98 | 1.03 |
| Conspecific tree basal area | <0.01 | 0.98 | 0.99 | 0.79** | 1.35** |
| C) Rare species (*N*) | (879) | (690) | (568) | (466) | (301) |
| Heterospecific seedling density | 0.88 | 0.69 | 0.69 | 0.62 | 0.19 |
| Conspecific seedling density | 0.50 | 0.06** | 0.03* | <0.01*** | <0.01*** |
| Local seedling survival (spatial term) | 1.11*** | 0.52* | 1.38*** | 0.67 | 0.92* |
| Relative seedling height | 1.85** | 3.90*** | 6.36*** | 7.31*** | 8.93*** |
| Heterospecific tree basal area | 1.00 | 0.98 | 0.92 | 0.87* | 1.11 |
| Conspecific tree basal area | 0.45 | 0.35 | 0.24 | 0.09 | 1.40 |

*Notes:* Odds ratios >1 indicate a positive effect on survival; odds ratios <1 indicate a negative effect on survival. The significance of each parameter within the original autologistic regression model is indicated. We modeled how seedling survival over the three-year period was affected by neighbors in each of nine contiguous annular rings of 1-m width.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Density of conspecific seedlings had a negative effect on survival for both rare and common species, but the odds ratios for this effect were at least an order of magnitude lower for rare species than for common species (Table 2B, C). In parallel, the odds ratios for effects of conspecific trees on rare species were one-third to 1/10 of those for common species (Table 2B, C, for conspecific tree basal area); although this parameter was not significant in the autologistic regression models.

*Seedling habitat and light associations.*—Only two species (*I. paraensis* and *V. flexuosa*) showed significant habitat associations as seedlings (Appendix G). Two other species had significant positive associations with higher light availability (*I. juruensis* and *V. duckei*).

*Light and habitat.*—When we considered the effect of each individual predictor variable (species, relative basal area, habitat, plot, or canopy openness) on the proportion of seedling survivors by species, the model with the lowest AIC value was that with species as the sole term (Appendix H). Due to a lack of all species in all plots and plot quarters, a fully balanced model for all variables could not be examined. However, for less complex models, that of relative basal area + canopy openness + relative basal area × canopy openness + plot nested within habitat had the lowest AIC value. Two points are relevant to the interpretation of this analysis. First, the coefficient for relative basal area was negative, indicating that a community compensatory trend (CCT) was present even after controlling for light availability. Second, there was a significant positive interaction between the relative basal area of species and light availability; more abundant species survived better in higher light environments, which is the reverse of the prediction of Wright (2002) for situations in which rare species in higher light microsites produce a spurious CCT.

*Population and life history parameters.*—No significant relationship was found between tree abundance and either seed mass or seedling : tree ratio.

## DISCUSSION

### *Community compensatory trend (CCT)*

Patterns reported here are consistent with a CCT in seedling survival. Seedlings of rare species had greater survivorship over three years than common species when adult abundance was expressed as relative basal area. This result is unlikely to be biased by higher survival of pioneer seedlings because all plots were in mature forest with <8% canopy openness and all the species have shade-tolerant seedlings.

Factors other than the negative density-dependent effects of established trees on seedling survival may lead to an observed CCT. Intrinsic differences in life histories may correlate with species abundances (Webb and Peart 1999), but it is unlikely in our case that rare species produced fewer, more robust, seedlings than common species. However, relative height did play a major role in seedling survival, and the mean height of common species seedlings was less than that of rare species. When

Table 2. Extended.

| Annulus (m) | | | |
|---|---|---|---|
| 5–6 | 6–7 | 7–8 | 8–9 |
| (378) | (220) | (115) | (45) |
| 0.55 | 0.12 | 0.47 | 19.12 |
| 0.50* | 0.27* | 0.57 | 3.71 |
| 0.51 | 0.36 | 0.28 | −2.46 |
| 11.49*** | 9.04*** | 12.17** | 4.14 |
| 0.98 | 0.95 | 1.09 | 0.48 |
| 0.92 | 1.39 | ··· | ··· |
| (179) | (109) | (60) | (29) |
| 0.23 | 0.01 | 0.00 | 2.90 |
| 0.57 | 0.27* | 0.22 | 7.63 |
| −0.11 | −0.07 | −1.67 | −6.97 |
| 6.78*** | 7.73** | 21.64** | 2.60 |
| 0.93 | 1.01 | 1.02 | 0.00 |
| 0.95 | 1.45 | 130.75 | 42.73 |
| (199) | (111) | (55) | (16) |
| 0.29 | 0.14 | 8.39 | ··· |
| <0.01*** | <0.01** | 0.00 | ··· |
| 0.84 | 0.84 | 2.92 | ··· |
| 23.44*** | 10.53** | 5.21 | ··· |
| 1.13 | 0.92 | 2.09 | ··· |
| 0.46 | 1.38 | ··· | ··· |

we accounted for this difference, a CCT was still apparent.

Variation in survival of species related to habitat preferences may also result in a CCT by artifact (Wright 2002). However, within the forest dynamics plot (FDP) the three major habitats covered equivalent areas, and seedling plots were not placed in rare habitats such as gaps. It is unlikely that rare species gained a survival advantage by preference for a rare habitat or higher light environment, as we found few associations of seedlings with habitat or light, and a CCT was encountered within most habitat and light categories. The results of the logistic analysis of deviance also supported a CCT induced by negative density dependence (Appendix I). Seedling survival was again negatively related to tree relative basal area, as predicted by the CCT. Survival was positively related to light availability, but the significant interaction between basal area and light was also positive, indicating that dominant species had higher survival in high light habitats, which is contrary to the relationship predicted by Wright (2002). A negative interaction between basal area and light availability might lead to a CCT being detected where none existed, but the positive interaction evident from our work is not consistent with such a spurious result.

Evidence is increasing that negative density dependence regulates populations of trees in tropical forests (Harms et al. 2000, Peters 2003, Ahumada et al. 2004, Wills et al. 2006). It has been easier to observe such interactions in early life stages (Augspurger 1984, Connell et al. 1984, Howe 1990, Hammond and Brown 1998, Gilbert et al. 2001, Blundell and Peart 2004, Wyatt and Silman 2004), although contradictory results also exist (e.g., Forget 1993). However, the evidence is difficult to assess rigorously because most studies do not include rare species and/or examine later life history stages (Hille Ris Lambers et al. 2002). In a meta-analysis of 40 studies, Hyatt et al. (2003) concluded that density-dependent effects were not important at the community level. However, to determine effects on community structure one must study multiple species concurrently. We have shown seedlings of rare species to have higher survival than those of common species in this tropical forest community.

### *Local neighborhood effects on survival of tropical forest seedlings*

Seedling survival within species was strongly spatially autocorrelated, but the autocorrelation decayed rapidly, disappearing at distances >6 m. Clumped sibling seedlings may be susceptible to specific strains of pathogen. Fungal diversity in tropical forests is likely to be high (Lodge 1997), as is the potential for fine-scale distribution patterns and host preferences (Ferrer and Gilbert 2003). Controlling for spatial autocorrelation, relative plant height had the only positive effect on the odds of survival. Focal seedlings taller than their neighbors had up to a five-fold increase in their odds of survival compared to plants that were smaller. Taller plants may be less prone to herbivory and pathogens (Clark and Clark 1985, Howe 1990) and can outcompete smaller neighbors for resources (Weiner 1990). Negative correlations between seedling survival and conspecific seedling density were also apparent, potentially affecting spatial distributions of larger individuals (Harms et al. 2000, Uriarte et al. 2005).

Effects of tree basal area on seedling survival were unclear. Neither conspecific nor heterospecific tree basal area was generally significant when all species were lumped, contrary to expectation given a CCT. Few studies have separated the effects of distance (from parent tree) and density (of seedlings or trees). This study appears to agree with Hyatt et al. (2003) in suggesting that distance from conspecific trees has little impact on seedling survival.

In our study, the positive effect of relative seedling size on seedling survival was greater and the negative effects of conspecifics were less than in that of Hubbell et al. (2001). Size differences between plants are relatively greater for seedlings than for trees and this may explain the higher odds ratio for relative plant size in our study. Despite the less negative odds ratio for the effect of conspecific seedling density, density dependence acting in seedling size classes may be important in structuring the community. Negative density dependence is probably more frequent in seedlings than in larger size classes, and survival to 1 cm dbh can take many years (Hubbell 1998).

The greater survival probability for seedlings of rare species compared to common species (the CCT) appears to contradict the finding that effects of conspecific

PLATE 1. (Left) Large *Virola duckei* seedling growing in the understory of Yasuni Forest Dynamics Plot, and (right) greenhouse-grown *Iryanthera hostmannii* seedling. Photo credits: S. A. Queenborough.

seedling density are more negative in rare species than in common species. This inconsistency implies that seedling–seedling interactions may be swamped by seedling–tree interactions in common species. For example, the high abundance of common species may act as a reservoir of natural enemies that overwhelm localized effects of seedling conspecifics. Conversely, seedlings of rare species may be more sensitive to conspecific seedling density, as established trees are too scarce to affect their survival. Seedling dynamics may therefore become uncoupled from tree distributions for rare species. An alternative possibility, that rare species less frequently experience high seedling densities and so overall seedling mortality rates are little influenced even with stronger negative density dependence, can be discounted in this study. This is because there was no significant difference in conspecific seedling density between common and rare species. For comparison of number of conspecific neighbors within 1 m radius of all focal seedlings using Mann-Whitney $U$ test, $U = 32$, $P = 0.23$; common species $= 0.09 \pm 0.03$ (mean ± SD), rare species $= 0.06 \pm 0.06$, excluding two high-density plots. Similar results were obtained for all seedling plots.

In conclusion, it is apparent that strong density-dependent forces are not constrained to the seed-to-seedling transition (Harms et al. 2000), but continue to affect seedling survivorship. Our data provide correlative support for the existence of the CCT in seedling survival. The increase in the survival probability of rare species may help maintain the high diversity found in this tropical forest. Future studies will need to address the consequences of these effects, especially on the little-studied dynamics of rare species.

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## APPENDIX A

Life history characteristics and population parameters of 16 species of Myristicaceae in the 25-ha Yasuní forest dynamics plot (*Ecological Archives* E088-135-A1).

## APPENDIX B

Topographic map of the 25-ha Yasuní forest dynamics plot, showing locations of the 30 nested 20 × 20 m seedling plots (*Ecological Archives* E088-135-A2).

## APPENDIX C

Survival of seedlings of 15 Myristicaceae species in 30 seedling plots within the Yasuní forest dynamics plot over three years (*Ecological Archives* E088-135-A3).

## APPENDIX D

Summary of observed regression slopes of seedling survival on adult tree abundance or seedling density: community test (*Ecological Archives* E088-135-A4).

## APPENDIX E

Summary of observed regression slopes of seedling survival on adult tree abundance or seedling density: habitat test (*Ecological Archives* E088-135-A5).

## APPENDIX F

Summary of observed regression slopes of seedling survival on adult tree abundance or seedling density: light availability test (*Ecological Archives* E088-135-A6).

## APPENDIX G

Community compensatory trend (CCT) analysis for each individual seedling plot and three different areas of surrounding adult trees (*Ecological Archives* E088-135-A7).

## APPENDIX H

Habitat associations of 15 species of Myristicaceae seedlings on the Yasuní forest dynamics plot (*Ecological Archives* E088-135-A8).

## APPENDIX I

Comparison of analysis of deviance models for the proportion of seedling survivors of species in each quarter 20 × 20 m seedling plot (*Ecological Archives* E088-135-A9).