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Published paper

Queenborough, S.A., Burslem, D.F.R.P., Garwood, N.C. and Valencia, R. (2007)
Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival, *Ecology*, Volume 88 (9), 2248 - 2258.

1 **Neighborhood seedling interactions**

2

3

4 **NEIGHBORHOOD AND COMMUNITY INTERACTIONS DETERMINE THE**

5 **SPATIAL PATTERN OF TROPICAL TREE SEEDLING SURVIVAL**

6

7

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

20

21 *Key-words:* autologistic regression, Myristicaceae, seedling, spatial autocorrelation,
22 species coexistence, tropical forest, Yasuni.

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INTRODUCTION

3

The seedling-sapling transition is a critical bottleneck in tree establishment.

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The spatial pattern of seedling survivorship also influences the long-term distribution

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patterns of species. The ecological basis of seedling recruitment has therefore become

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a focus of research on the mechanisms that aid in the maintenance of high species

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diversity in tropical rain forests (Janzen 1970, Connell 1971, Grubb 1977). Many

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studies have documented negative density- or distance-dependent effects on survival

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in one or more species (Augspurger 1984, Harms et al. 2000, Wyatt and Silman

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2004). However, these are often limited by a failure to consider explicitly the spatial

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context of the seedling

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Negative density dependence may be manifested as a community

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compensatory trend (CCT), defined as an inverse relationship between plant growth,

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recruitment or survival, and conspecific density (Connell et al. 1984). Coexistence of

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species may be enhanced by CCTs because rare species achieve a higher rate of

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population increase than common species. Demonstration of a CCT requires rare

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species to exhibit increased performance compared to common species, over a range

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of abundances.

19

Four attempts to detect a CCT in tropical forests have yielded equivocal

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results. For seedlings (<31 cm tall) and saplings (<8 cm girth at breast height) in

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Australia, mortality over up to 16 yrs was unaffected by conspecific density, but

22

recruitment of subcanopy and understorey species was (Connell et al. 1984).

23

However, this relationship was identified from a regression of per capita recruitment

24

(y) on adult density (x), of the form y/x versus x , and has been disputed (Wright 2002).

25

Second, at Gunung Palung, Borneo, seedling (5-50 cm tall) survival over 19 mo was

1 lower for abundant species, supporting a CCT (Webb and Peart 1999). Thirdly,
2 sapling (1-4 cm diameter at breast height) recruitment over 3 yrs was greater for rare
3 species in a large forest plot in Panamá (Welden et al. 1991). However, survival was
4 positively related to species abundance, contrary to a CCT. Finally, sapling survival
5 also increased with population size for trees ≥ 1 cm dbh at Pasoh, Malaysia (He et al.
6 1997).

7 Although testing for density dependence motivated these studies, other
8 mechanisms may give rise to a spurious suggestions of a CCT (Wright 2002).
9 Different microhabitat associations of tree species may affect the detection and
10 apparent direction of a CCT. Webb & Peart (1999) monitored seedlings in gaps and in
11 mature forest understorey. Pioneer trees are likely to be common in gap plots where
12 high light favors survival, and rare as adults in mature forest (Wright 2002).
13 Conversely, rare pioneers may have survived poorly on the mature forest plot at Pasoh
14 (He et al. 1997). Wright (2002) attributed the suggested CCT for sapling recruitment
15 in Panamá to an increase in gaps due to a severe El Niño drought. Here we also use
16 data from a large forest plot, but consider 15 confamilial species, all with shade-
17 tolerant seedlings. Using one ecologically uniform family ensures that variation in
18 ecology and life history will have less of an influence on species' probabilities of
19 survival. We compared the abundance of trees with 3-yr seedling survival data in non-
20 gap plots in mature forest to test for negative density dependence manifested as a
21 CCT. We then support our between-species comparisons with an analysis of factors
22 affecting individual seedling mortality within species.

23 As well as conspecific density, other factors affect seedling survival to the
24 sapling stage. Biotic factors include seedling predators and pathogens (Janzen 1970,
25 Connell 1971) and the neighboring plant community, which may enhance survival

1 probability via herd immunity (Peters 2003) or reduce it through competition (Gilbert
2 et al. 2001, Uriarte et al. 2005). Effects of abiotic variables on survival are also well
3 documented (Whitmore 1996, Montgomery and Chazdon 2002, Palmiotto et al.
4 2004). However most previous work on seedling dynamics is limited by failure to
5 include spatial autocorrelation in these factors in statistical models. Most factors that
6 influence plant survival (e.g. light, nutrients, moisture, herbivory, competition) exhibit
7 spatial autocorrelation at scales larger than an individual plant (Nicotra et al. 1999,
8 Ahumada et al. 2004). Therefore, the fates of plants in close proximity are not
9 statistically independent. Spatial structure has been included in recent analyses of
10 sapling population dynamics (Hubbell et al. 2001, Ahumada et al. 2004, Uriarte et al.
11 2004, 2005), but the dynamics of tropical tree seedlings have not been considered
12 from this perspective. Previous tests of density dependence also used a quadrat-based
13 approach, which further decreases the information per stem because most individuals
14 may be near a quadrat edge (Peters 2003, Wills et al. 2006). Here we use an
15 individual-based approach to isolate the spatial autocorrelation of mortality and
16 provide a more robust test of whether negative density dependence is responsible for
17 any observed CCT. We use spatially explicit data on the population dynamics of 3531
18 seedlings of 15 species of Myristicaceae growing on a large forest plot in lowland
19 tropical rain forest in Amazonian Ecuador to address the following specific questions:

- 20 1. Is seedling survival negatively density dependent, and is this manifested in a
21 community compensatory trend?
- 22 2. Is seedling mortality spatial autocorrelated and, if so, at what spatial scales?
- 23 3. Are local spatial autocorrelation and neighborhood interactions influenced by
24 species' community-level abundance?

25

1 MATERIALS AND METHODS

2 *Study site*

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

9 A 50-ha permanent forest dynamics plot (FDP; www.ctfs.si.edu) is located
10 inside the park (0°41'S, 76°24'W, Valencia et al. 2004). There are a few indigenous
11 Huaorani settlements north of the station and low-intensity hunting occurs inside the
12 plot. The FDP ranges from 216 to 248 m a.s.l: it includes three ridges and an
13 intervening valley that floods for brief periods.

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

21
22 *Seedling plots*

23 Within the western 25 ha of the FDP, 30 plots of 20 x 20 m, each composed of
24 sixteen 5 x 5 m subplots, were established in February to June 2002 in a stratified
25 random design to sample the three main habitats on the plot with equal intensity

1 (Appendix B). Habitats within the FDP cover the following areas: valley, 7.88 ha;
2 slope, 7.66 ha; ridge, 8.96 ha (Valencia et al. 2004). All plots were under closed
3 canopy in mature forest. We excluded subplots affected by a new gap from
4 subsequent analyses.

5 The coordinates of all Myristicaceae plants >1 cm in height and <1 cm dbh
6 were mapped according to standard FDP protocols within each 5 x 5 m subplot and
7 tagged with a 10 cm plastic cocktail stick. All stems were identified and measured for
8 height to the apical bud (mm), basal stem diameter (mm), and number of expanded
9 leaves. Species were determined from ECY herbarium material (Persson 2005) and
10 from seedlings grown from shadehouse-germinated seeds collected in 2002-2003. All
11 plots were recensused during 28 Nov 2002 – 31 Jan 2003, 5 - 24 Nov 2003, 19 June –
12 13 July 2004 and 13 June – 3 July 2005. All existing plants were checked and new
13 recruits were enumerated. A total of 2330 seedlings was censused initially and 3531
14 seedlings were marked over all censuses. We use data from the initial cohort here.
15 Density of target species stems ≥ 1 cm dbh in 25 ha ranged from 1.76 ha^{-1}
16 (*Compsonaura sprucei*) to 33.5 ha^{-1} (*Iryanthera hostmannii*) (Queenborough et al.
17 2007). Density of seedlings ranged from 8 ha^{-1} (*Virola flexuosa*) to 513 ha^{-1} (*V.*
18 *duckei*) (Appendix C) and, in total, constitute c.2 % of all seedlings at Yasuní (S.
19 Queenborough and M. Metz, *unpublished data*).

20 In June 2004, a hemispherical canopy photograph was taken from the center of
21 each quarter of each 20 x 20 m plot ($n = 4$ per seedling plot). Photographs were taken
22 1 m above the ground, in uniformly overcast conditions in the early morning or late
23 afternoon, with a leveled Nikon Coolpix 4500 camera body and Nikon FC-E8 Fisheye
24 Converter lens, saved as black and white JPEGs at size 2272 x 1704 pixels. Images
25 were analyzed using Gap Light Analyzer 2.0 (<http://www.rem.sfu.ca/forestry/>). Mean

1 canopy openness was $5\% \pm 0.8$ (SD), range 2.8% - 7.4%. There was no significant
2 difference between habitat types (valley, slope, ridge), but there was among plots
3 within habitats (nested ANOVA: Habitat F -value 1.11, $P > 0.05$; Habitat:plot F -value
4 4.47, $P < 0.001$).

5

6 *Data analysis*

7 *Overview.*—Data were analyzed using the software package R 2.3.1 ([www.R-](http://www.R-project.org)
8 project.org). Species were excluded from a particular analysis if they had <5
9 individuals, as noted below. Using randomization approaches detailed later, we
10 examined linear regressions of seedling survival over three yrs against three measures
11 of tree abundance at the community level, as well as against seedling density. Only
12 trees greater than species-specific minimum reproductive size were included
13 (Queenborough et al. 2007). To assess local density dependence, we used an
14 autologistic regression model to examine spatial autocorrelation in the effects of
15 neighboring conspecific and heterospecific Myristicaceae seedlings and trees on focal
16 seedling survival.

17

18 *Seedling survival between species.*—To test for density dependent effects on
19 seedling survival, we used a linear regression model to examine survival for each
20 species (15 species, 2330 seedlings) as influenced by the following log-transformed
21 measures of abundance: tree absolute basal area, tree relative basal area (= basal area
22 of species i / total basal area) and tree frequency on the 25 ha FDP, as well as seedling
23 density on the total 1.2 ha of seedling plots. Survival rate variances were not
24 homogeneous, so the slope of each regression was compared to a distribution of 1000
25 slopes generated by randomly sampling the dataset assuming no relationship between

1 seedling survival and each variable (cf. Webb and Peart 1999). If the slope exceeded
2 the 95% confidence intervals of the distribution we inferred a significant relationship
3 between seedling survival and species abundance. Two test distributions were
4 generated, firstly randomizing species abundance, and secondly randomizing seedling
5 survival. In the first, species abundance values were randomly assigned to species and
6 slopes of observed seedling survival regressed against randomized tree abundance
7 were obtained by standard least squares fitting. In the second test, we generated a
8 binomially-distributed random number of survivors for each species based on the
9 observed number of seedlings of each species and the mean survival probability for all
10 species (total number survivors/total number of all seedlings).

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

18 Apparent density dependence in a multi-aged cohort can be explained if the
19 mean height of seedlings differs between species. Populations of species that recruited
20 every yr had lower mean seedling heights than species that recruited less often
21 (Queenborough 2005). Therefore, because seedling survival was significantly related
22 to seedling height (linear regression of a binary response variable with binomial
23 errors: slope = 0.0166, $P < 0.001$) and species had significantly different mean heights
24 (ANOVA: $F = 16.3$, $P < 0.001$) in this initial cohort, we excluded all seedlings ≥ 30
25 cm tall and repeated the randomization tests on the remaining 11 species and 1387

1 seedlings. Because two plots had abnormally high seedling densities from large
2 fruiting females, the above analyses were then repeated on a subset of the data
3 excluding these two plots.

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

9 In order to examine the generality of the CCT within the FDP and test whether
10 it was indeed influenced by habitat and light as other authors have suggested (Wright
11 2002), we repeated the analyses described above (including those seedlings >20 m
12 from a female and seedlings <30 cm tall) on further subsets of the full dataset. We
13 tested for a CCT for seedlings within each of the three habitats separately, and also
14 within each of the four quartiles of the canopy openness range. We then tested for a
15 CCT at each individual seedling plot, using trees in neighborhood sizes of 1 ha, 4 ha
16 and 9 ha centered on the seedling plot to define species' basal area.

17

18 *Seedling survival within species.*—Autologistic regression was used to test
19 effects of neighborhood density on individual seedling survival. The response variable
20 was the survival of the focal plant to June 2005, assigned a value of unity (alive) or
21 zero (dead). We fitted autologistic regressions on survival at each of nine concentric
22 annuli around focal individuals. Autologistic regression models the spatial
23 autocorrelation in survival. Logistic regression models assume that survival of a plant
24 is independent of that of its neighbors. This is violated if survival is patchy because of
25 such factors as branchfalls, herbivory, and soil nutrient and moisture heterogeneity.

1 Autologistic regression adds a term into the logistic regression model, controlling
2 statistically for the effect of spatial autocorrelation while assessing the effects of the
3 different neighborhood variables. The model was fitted with maximum likelihood
4 estimation. For further discussion see Hubbell et al. (2001) and references therein.

5 For all seedlings alive in June 2002, we noted confamilial tree and seedling
6 neighbors in concentric annuli of width 1 m to a maximum distance of 9 m. The
7 sample for each annulus varied in order to maximize sample size whilst not
8 overlapping plot edges. For example, for annulus 0-1m, focal seedlings were included
9 from the central 18 m² of each plot, and for annulus 4-5 m, focal seedlings were used
10 only from the central 10 m² of each plot. Sample sizes of total focal seedling numbers
11 across all species for each annulus are: 1902 (0-1 m), 1508 (1-2 m), 1206 (2-3 m), 926
12 (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
13 respectively. Again, we repeated analyses excluding two high-density plots.

14 Within each annulus, we computed the following independent neighborhood
15 variables: (i) density of conspecific seedlings, (ii) density of confamilial seedlings of a
16 different species, (iii) relative plant height (fraction of plants shorter than the focal
17 plant), (iv) basal area of conspecific trees, and (v) basal area of confamilial trees of a
18 different species. Neither light availability nor habitat were included in this analysis as
19 unique values were not available for each seedling.

20 The dataset was first analyzed on a pooled sample of all species and then
21 grouped according to abundance on the FDP, as either abundant (four species with
22 >0.02 relative basal area in 25ha) or rare (11 species with <0.02 relative basal area in
23 25ha). In the autologistic regression for three annuli, partial or complete separation of
24 the data occurred, whereby conspecific tree basal area correctly allocated all
25 observations to the appropriate response group. Deletion of this parameter did not

1 affect the remaining parameter coefficients. There were insufficient individuals in the
2 9-m annulus of the rare species group to analyze.

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

6

7 *Other factors affecting seedling survival*

8 *Habitat and light associations.*—Because species may occur in specific rare
9 habitats or light environments, which may generate a spurious CCT without any effect
10 of abundance on survival, we tested for associations of seedlings with these two
11 factors. Habitat associations of trees >1 cm dbh are known on the Yasuní FDP
12 (Valencia et al. 2004, Queenborough 2005). We tested for habitat associations of
13 seedlings using a randomization procedure similar to Webb and Peart (2000). Firstly
14 we calculated the frequency of each species in the 5 x 5 m subplots within each
15 seedling plot (range 0-20). We then randomly shuffled the habitats within which each
16 of the 30 seedling plots occurred and calculated a deviation statistic based on the
17 frequency of each species in each habitat type: $\sum[(\text{Randomized} - \text{Expected})^2 /$
18 $\text{Expected}]$. This was repeated 1000 times per species and we compared the observed
19 deviation value with this randomized distribution of deviation values.

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

23 *Light and habitat.*—Because we could not assign unique values of habitat and
24 light availability to each individual seedling, we performed an analysis of deviance on
25 the proportion of each species' seedling survivors in each quarter seedling plot in

1 order to test whether light availability and/or habitat affected species-level survival. It
2 is highly likely that species do differ in their responses to light and habitat; however,
3 for these trends to be manifested as a spurious CCT their responses must scale with
4 abundance. The predictor variables were species' tree relative basal area, canopy
5 openness and plot nested within habitat. An ANOVA was used to test whether each
6 term in the model produced a significant decrease in residual deviance, using the AIC
7 to select the best-fit model.

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

12

13

RESULTS

14 A total of 3531 seedlings was censused over three yrs. Numbers and percent
15 survival varied widely among species (Appendix B). Of the initial seedling cohort
16 (2002), 1025 out of 2330 seedlings of 15 species had died by June 2005. Survival
17 over all seedlings was 0.56, whereas mean survival by species was 0.69.

18

19 *Evidence concerning a community compensatory trend in survival*

20 The results for relative basal area and seedling density are presented here, and
21 those for basal area and frequency in online Ecological Archives Appendix C.

22 Seedling survival was inversely related to the relative basal area of trees
23 (Figure 1). The observed regression slopes were extreme compared to the distribution
24 of randomized slopes when either tree relative basal area or 3-yr seedling survival was

1 randomized (Table 1: A.i, B.i). A ten-fold increase in basal area led to a 5-15%
2 decrease in survival.

3 When we examined subsamples of the full dataset to test the robustness of this
4 result, we found that the significant negative relationship between seedling survival
5 and tree basal area remained in most cases (Table 1 A and B). When seedlings ≥ 30 cm
6 tall were excluded in order to remove their inherent survival advantage a significant
7 positive relationship between individual seedling height and survival remained (linear
8 regression of a binary response variable with binomial errors: slope = 0.07, $P <$
9 0.001). However, seedling survival was independent of mean seedling height per
10 species (weighted regression: $P = 0.93$), and mean seedling height per species was
11 unrelated to adult basal area or density (linear regression, basal area of stems ≥ 10 cm
12 dbh: $P = 0.78$; frequency of stems ≥ 10 cm dbh: $P = 0.51$). When tree abundance was
13 expressed as density, no relationship with seedling survival was apparent (see online
14 Ecological Archives Appendix C).

15 Seedling survival was significantly negatively related to conspecific seedling
16 abundance, but only in the full dataset (Table 1: C).

17 Analysis of the dataset stratified according to habitat or light environment also
18 showed significant negative relationships between seedling survival and tree basal
19 area (see online Ecological Archives Appendices D and E). This was also found for
20 four out of 20 seedling plots for which sufficient species were present (with 1 ha of
21 surrounding trees providing the neighborhood), 7 of 25 plots (4 ha neighborhood), and
22 3 of 25 (9 ha neighborhood). No positive relationships were found (see Ecological
23 Archives Appendix F).

24

Local neighborhood effects on survival

1
2 The survival of Myristicaceae seedlings was strongly spatially autocorrelated,
3 but this decayed rapidly. At distances >5 m from the focal seedling the spatial term
4 did not differ significantly from zero and therefore survival was not spatially
5 structured beyond this distance (Figure 2). There were no significant differences
6 between the full and partial datasets in the spatial autocorrelation term.

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

12
13 *Rare and common species.*— Neighborhood effects on seedling survival varied with
14 tree species abundance. Low statistical power for the rare species subset prevented
15 direct testing of differences between abundant (>0.02 relative basal area) and rare
16 (<0.02 relative basal area) species groups. However, the significance patterns for
17 terms in the respective autologistic regression models are informative. First, the
18 significant positive effects of relative seedling height were similar for both abundant
19 and rare species (Table 2: B.iv, C.iv). Second, there were no differences between
20 abundant and rare species in the effects of neighboring heterospecific seedlings and
21 trees (Table 2: B.i, C.i). Third, both spatial autocorrelation and responses to
22 conspecific neighbors differed substantially depending on species abundance. Among
23 common species, positive spatial autocorrelation was insignificant at >2 m and was
24 negative at 5 m (Table 2: B.iii), but rare species exhibited positive spatial
25 autocorrelation to 5 m, and did not become negative (Table 2: C.iii). Conspecifics had

1 a negative effect on survival for both rare and common species, but the odds ratios for
2 this effect were at least an order of magnitude lower for rare species than for common
3 species (Table 2: B.ii, C.ii). In parallel, the odds ratios for effects of conspecific trees
4 on rare species were one-third to one-tenth of those for common species (Table 2:
5 B.vi, C.vi; although this parameter was not significant in the autologistic regression
6 models).

7
8 *Seedling habitat and light associations.*—Only two species (*I. paraensis* and
9 *V. flexuosa*) showed significant habitat associations as seedlings (Ecological Archives
10 Appendix G). Two other species had significant positive associations with higher light
11 availability (*I. juruensis* and *V. duckei*).

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

1 induced by negative density dependence. Seedling survival was again negatively
2 related to tree relative basal area, as predicted by the CCT. Survival was positively
3 related to light availability, but the significant interaction between basal area and light
4 was also positive, indicating that dominant species had higher survival in high light
5 habitats, which is contrary to the relationship predicted by Wright (2002). A negative
6 interaction between basal area and light availability might lead to a CCT being
7 detected where none existed, but the positive interaction evident from our work is not
8 consistent with such a spurious result.

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

22

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

24 Seedling survival within species was strongly spatially autocorrelated, but the
25 autocorrelation decayed rapidly, disappearing at distances >6 m. Clumped sibling

1 seedlings may be susceptible to specific strains of pathogen. Fungal diversity in
2 tropical forests is likely to be high (Lodge 1997), as is the potential for fine-scale
3 distribution patterns and host preferences (Ferrer and Gilbert 2003). Controlling for
4 spatial autocorrelation, relative plant height had the only positive effect on the odds of
5 survival. Focal seedlings taller than their neighbors had up to a five-fold increase in
6 their odds of survival compared to plants that were smaller. Taller plants may be less
7 prone to herbivory and pathogens (Clark and Clark 1985, Howe 1990) and can out-
8 compete smaller neighbors for resources (Weiner 1990). Negative correlations
9 between seedling survival and conspecific seedling density were also apparent,
10 potentially affecting spatial distributions of larger individuals (Harms et al. 2000,
11 Uriarte et al. 2005).

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

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

1 The greater survival probability for seedlings of rare species compared to
2 common species (the CCT) appears to contradict the finding that effects of
3 conspecific seedling density are more negative in rare species than common species.
4 This inconsistency implies that seedling-seedling interactions may be swamped by
5 seedling-tree interactions in common species. For example, the high abundance of
6 common species may act as a reservoir of natural enemies that overwhelm localized
7 effects of seedling conspecifics. Conversely, rare species' seedlings may be more
8 sensitive to conspecific seedling density, as established trees are too scarce to affect
9 their survival. Seedling dynamics may therefore become uncoupled from tree
10 distributions for rare species. An alternative possibility, that rare species less
11 frequently experience high seedling densities and so overall seedling mortality rates
12 are little influenced even with stronger negative density-dependence, can be
13 discounted in this study. This is because there was no significant difference in
14 conspecific seedling density between common and rare species (comparison of
15 number of conspecific neighbors within 1-m radius of all focal seedlings: Mann
16 Whitney test, $W = 32$, $P = 0.23$, common species mean = 0.09 ± 0.03 standard
17 deviation, rare species = 0.06 ± 0.06 , excluding two high-density plots. Similar results
18 were obtained for all seedling plots).

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

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ACKNOWLEDGEMENTS

We thank the Ministerio del Ambiente for authorization to work in Yasuní National Park and R. Condit for permission to work within the Yasuní FDP. We thank the plot census team of P. Alvia, G. Grefa, A. Loor, W. Loor, J. Suarez, J. Zambrano and M. Zambrano. Fieldwork was aided by A. Humphries, S. Koelen, S. Spehar, M. Zambrano, and especially G. Bramley. Indefatigable support was provided by P. Barriga, M. Metz, S. and B. Queenborough, and tremendously by G. Bramley. K. Woods and two anonymous reviewers offered insightful comments on the text, and R. Freckleton, J. Illian and T. Marthews confirmed statistical analyses. The first author was funded by a Study Abroad Studentship from The Leverhulme Trust and a grant from the Center for Tropical Forest Science. The Forest Dynamics Plot of Yasuní National Park has been made possible through generous support of the US National Science Foundation, the Andrew W. Mellon Foundation, the Pontificia Universidad Católica del Ecuador, the Smithsonian Tropical Research Institute, and the University of Aarhus, Denmark. The Yasuní Forest Dynamics Plot is part of the Center for Tropical Forest Science, a global network of large-scale demographic tree plots.

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1 TABLE 1. Summary of the significance of observed regression slopes of seedling survival on adult tree relative basal area (methods A and B) or
 2 seedling density (C), as tested against the distribution of slopes of 1000 simulated regressions randomising either the predictor (B) or response
 3 (A and C) variable. The test was conducted on all seedling plots (Full) or only those without highly fecund females (Partial), and then on subsets
 4 of these data (see text for details), (* $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$). See Ecological Archives for full regression coefficients.

Randomisation method	Seedling dataset	
	Full (n = 30 plots)	Partial (n = 28 plots)
A: bootstrapped adult relative basal area		
Seedlings included: i) all	*	NS
ii) > 20 m from ♀	NS	NS
iii) < 30 cm tall	NS	NS
iv) ii and iii	NS	NS
B: bootstrapped seedling survival		
Seedlings included: i) all	***	***
ii) > 20 m from ♀	***	*

iii) < 30 cm tall	***	*
iv) ii and iii	**	*

C: bootstrapped seedling survival vs seedling density

Seedlings included: i) all	***	NS
ii) > 20 m from ♀	**	NS
iii) < 30 cm tall	**	NS
iv) ii and iii	*	*

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3 TABLE 2. Summary of the odds ratios for model parameters from autologistic regression analyses of seedling survival of 15 species of
 4 Myristicaceae. Odds ratios >1 indicate a positive effect on survival; odds ratios <1 indicate a negative effect on survival. The significance of
 5 each parameter within the original autologistic regression model is indicated by asterisks (* $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$).

Model parameter	Annulus (m)								
A. All species	1	2	3	4	5	6	7	8	9
N	1902	1508	1206	926	565	378	220	115	45
i. Heterospecific seedling density	0.88	0.77	0.82	0.73	0.29	0.55	0.12	0.47	19.12
ii. Conspecific seedling density	0.89 ***	0.81 ***	0.71 ***	0.76 *	0.40 **	0.50 *	0.27 *	0.57	3.71
iii. Local seedling survival (spatial term)	0.97 ***	0.62 ***	0.85 ***	0.61 *	0.45	0.51	0.36	0.28	-2.46
iv. Relative seedling height	2.22 ***	3.54 ***	4.28 ***	7.00 ***	6.28 ***	11.49 ***	9.04 ***	12.17 **	4.14
v. Heterospecific tree basal area	0.99	0.99	0.94	0.88 *	1.04	0.98	0.95	1.09	0.48
vi. Conspecific tree basal area	<0.01	0.98	0.99	0.78 ***	1.35 **	0.92	1.39	NA	NA
B. Abundant species									

N	1023	818	638	460	264	179	109	60	29
i. Heterospecific seedling density	0.74	0.59	0.83	0.42	0.06	0.23	0.01	0.00	2.90
ii. Conspecific seedling density	0.90 ***	0.85 ***	0.74 ***	0.84	0.42 **	0.57	0.27 *	0.22	7.63
iii. Local seedling survival (spatial term)	0.84 ***	0.71 **	0.30	0.49	-0.15	-0.11	-0.07	-1.67	-6.97
iv. Relative seedling height	2.62 ***	3.99 ***	3.40 ***	7.67 ***	5.33 ***	6.78 ***	7.73 **	21.64 **	2.60
v. Heterospecific tree basal area	0.98	1.04	0.99	0.98	1.03	0.93	1.01	1.02	0.00
vi. Conspecific tree basal area	<0.01	0.98	0.99	0.79 **	1.35 **	0.95	1.45	130.75	42.73

C. Rare species

N	879	690	568	466	301	199	111	55	16
i. Heterospecific seedling density	0.88	0.69	0.69	0.62	0.19	0.29	0.14	8.39	NA
ii. Conspecific seedling density	0.50	0.06 **	0.03 *	<0.01 ***	<0.01 ***	<0.01 ***	<0.01 **	0.00	NA
iii. Local seedling survival (spatial term)	1.11 ***	0.52 *	1.38 ***	0.67	0.92 *	0.84	0.84	2.92	NA
iv. Relative seedling height	1.85 **	3.90 ***	6.36 ***	7.31 ***	8.93 ***	23.44 ***	10.53 **	5.21	NA
v. Heterospecific tree basal area	1.00	0.98	0.92	0.87 *	1.11	1.13	0.92	2.09	NA
vi. Conspecific tree basal area	0.45	0.35	0.24	0.09	1.40	0.46	1.38	NA	NA

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2 FIG. 1. A test of density dependence among seedlings of 15 species of Myristicaceae
3 on the Yasuní FDP. The significance of the slope of the regression of seedling
4 survival over three years against adult relative basal area was tested by comparison of
5 a linear regression model of the observed data with a distribution of linear models
6 generated either by bootstrapping seedling survival or adult relative basal area (see
7 Table 1). Data points are denoted by species codes (for details see the online
8 Appendix A). Error bars indicate 95% confidence limits of each species' survival rate
9 based on the binomial distribution. Various subsets of the dataset were analysed; this
10 figure illustrates data for all seedlings over the whole FDP.

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12 FIG. 2. Decay in the spatial autocorrelation parameter in two autologistic regressions
13 examining the effect of local neighborhood variables on focal seedling survival in 15
14 species of Myristicaceae on the Yasuní FDP. The full dataset of all seedling plots is
15 compared to a partial dataset in which two high-density plots were excluded.

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APPENDIX A

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[Life history characteristics and population parameters of 16 species of](#)

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[Myristicaceae in the 25 ha Yasuní FDP are available in ESA's Ecological Data](#)

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[Archive: Ecological Archives A/E/M000-000-A#.](#)

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APPENDIX B

1 [A topographic map of the 25ha Yasuni FDP, showing locations of the 30 nested](#)
 2 [20x20 m seedling plots, is available in ESA's Ecological Data Archive:](#)
 3 [*Ecological Archives A/E/M000-000-A#.*](#)

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 5 **APPENDIX C**

6 [Data on the survival of seedlings of 15 Myristicaceae species in 30 seedling](#)
 7 [plots within the Yasuni FDP over three years is available from ESA's Ecological](#)
 8 [Data Archive: *Ecological Archives A/E/M000-000-A#.*](#)

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 10 **APPENDIX D**

11 [A summary of the observed regression slopes of seedling survival on adult tree](#)
 12 [abundance or seedling density at the level of the community is available from](#)
 13 [ESA's Ecological Data Archive: *Ecological Archives A/E/M000-000-A#.*](#)

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 15 **APPENDIX E**

16 [A summary of the observed regression slopes of seedling survival on adult tree](#)
 17 [abundance or seedling density, examining each habitat is available from ESA's](#)
 18 [Ecological Data Archive: *Ecological Archives A/E/M000-000-A#.*](#)

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 20 **APPENDIX F**

21 [A summary of the observed regression slopes of seedling survival on adult tree](#)
 22 [abundance or seedling density for different levels of light availability is](#)

1 [available from ESA's Ecological Data Archive: *Ecological Archives* A/E/M000-](#)
2 [000-A#.](#)

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4 **APPENDIX G**

5 [A CCT analyses for each individual seedling plot and three different areas of](#)
6 [surrounding adult trees is available from ESA's Ecological Data Archive:](#)
7 [*Ecological Archives* A/E/M000-000-A#.](#)

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9 **APPENDIX H**

10 [Habitat associations of 15 species Myristicaceae seedling on the Yasuní FDP](#)
11 [are available from ESA's Ecological Data Archive: *Ecological Archives*](#)
12 [A/E/M000-000-A#](#)

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14 **APPENDIX I**

15 [Comparison of analysis of deviance models for the proportion of species' seedling](#)
16 [survivors in each quarter 20x20 m seedling plot are available from ESA's Ecological](#)
17 [Data Archive: *Ecological Archives* A/E/M000-000-A#.](#)

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