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Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest

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Abstract. Negative density-dependent mortality can promote species coexistence through a spacing mechanism that prevents species from becoming too locally abundant. Negative density-dependent seedling mortality can be caused by interactions among seedlings or between seedlings and neighboring adults if the density of neighbors affects the strength of competition or facilitates the attack of natural enemies. We investigated the effects of seedling and adult neighborhoods on the survival of newly recruited seedlings for multiple cohorts of known age from 163 species in Yasuní National Park, Ecuador, an ever-wet, hyper-diverse lowland Amazonian rain forest. At local scales, we found a strong negative impact on first-year survival of conspecific seedling densities and adult abundance in multiple neighborhood sizes and a beneficial effect of a local tree neighborhood that is distantly related to the focal seedling. Once seedlings have survived their first year, they also benefit from a more phylogenetically dispersed seedling neighborhood. Across species, we did not find evidence that rare species have an advantage relative to more common species, or a community compensatory trend. These results suggest that the local biotic neighborhood is a strong influence on early seedling survival for species that range widely in their abundance and life history. These patterns in seedling survival demonstrate the role of density-dependent seedling dynamics in promoting and maintaining diversity in understory seedling assemblages. The assemblage-wide impacts of species abundance distributions may multiply with repeated cycles of recruitment and density-dependent seedling mortality and impact forest diversity or the abundance of individual species over longer time scales.

Key words: community compensatory trend; density-dependent mortality; diversity; Janzen-Connell hypothesis; phylogenetic distance; seedling dynamics; tropical forest; Yasuní National Park, Ecuador.

Introduction

Numerous mechanisms have been proposed to explain how high tree species diversity is maintained; these mechanisms include various species interactions, recruitment limitation, environmental fluctuations, and stochasticity, among others (see reviews in Connell 1978, Wright 2002). It has often proved difficult to test their relative importance (Leigh et al. 2004, Carson et al. 2008), in part, because the absolute and relative impacts of different processes change during a tree's ontogeny. Moreover, weak effects at any one life history stage can accumulate over time and influence species' abundances and distributions at later stages. The seed and seedling stages of trees are particularly vulnerable to damage or death by a multitude of biotic and abiotic agents. The very high mortality occurring at these stages can strongly filter the species composition of the seedling bank, i.e., the accumulation over multiple recruitment seasons of shade-tolerant seedlings in the understory "waiting" for a nearby canopy opening, or a series of such openings, to provide the resources necessary for growth and maturation (Hartshorn 1980, Whitmore 1984, Brokaw 1985).

Negative density-dependent mortality is a spacing mechanism that promotes species coexistence by preventing one or a few species from becoming disproportionately abundant at the local scale. Seed dispersal is leptokurtic, so greater densities of conspecific seedlings are typically found near reproductive adults than away. In these aggregations, seedlings experience both the effects of growing at high densities among conspecific neighbors and the positive or negative influence of establishing close to, and often under the crown of, a conspecific adult. Under conditions of high seedling density, resources such as light and soil nutrients could become limiting, resulting in slower average growth rate and higher mortality, compared to areas with lower seedling densities. The resulting self-thinning process would space surviving individuals farther apart, affording opportunity for establishment of other species' seedlings. However, there has been little evidence for interseedling competition in the few studies that have directly examined it (e.g., Paine et al. 2008, Svenning et

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al. 2008). It is generally argued that asymmetric competition with larger individuals and/or competition among individuals in larger size classes is more important than competition among young seedlings (Wright 2002). Suppression of seedling growth or survival by larger neighbors is likely to be independent of conspecific seedling densities, although high seedling densities could compound the effects of larger neighbors. Patterns of negative density dependence based on the seedling neighborhood would therefore be expected to be weak or nonexistent.

High conspecific seedling densities and proximity to an adult of the same species may also lead to enhanced rates of mortality due to specialist natural enemies or pathogens. This form of negative density-dependent mortality is the cornerstone of a prominent hypothesis about plant species coexistence in the tropics, first proposed by Janzen (1970) and Connell (1971) (later labeled the Janzen-Connell hypothesis). It predicts that diversity will be maintained if specialized natural enemies reduce recruitment and survival of plants near conspecific adults or in areas of high conspecific density, effectively increasing the distance between these individuals and freeing space for recruitment of other species. Numerous studies have demonstrated Janzen-Connell effects caused by either seed predation, herbivory on seedlings, or plant pathogens, among other mechanisms (see reviews by Howe and Smallwood 1982, Clark and Clark 1984, Connell et al. 1984, Hammond and Brown 1998, Carson et al. 2008). The "species herd protection" hypothesis (Wills 1996), an extension of the Janzen-Connell model, suggests a heterospecifically diverse neighborhood affords protection by reducing the transmission of species-specific natural enemies. Peters (2003) showed that, at a given density of conspecific neighbors, tree survival increased when surrounded by a more diverse set of neighbors.

The traditional distinction between con- and heterospecifics discards much information on the varying degrees of relatedness among heterospecific neighbors. Considering the evolutionary relationships within a neighborhood extends questions about density-dependent mortality beyond the impacts of two categories of neighbors (conspecifics vs. heterospecifics) to allowing continuous variation in relatedness of neighbors and their influences on each other. Neighbors that are closely related may decrease survival through increased competition if traits are conserved and closely related taxa share traits that determine their response to their environment (Prinzing et al. 2001). Similarly, if it is the interactions with natural enemies, and not competition, that drive patterns of density-dependent mortality, a closely related neighborhood may decrease survival. Host ranges of plant pathogens can have a strong relationship with evolutionary distance among taxa (Gilbert and Webb 2007), and closely related species can act more like conspecifics in interactions with natural enemies than do distantly related species (Webb et al. 2006). Alternatively, closely related taxa may differ greatly in their functional traits, and, thus, a more closely related neighborhood would lead to greater seedling survival. The degree to which evolutionary relationships influence interactions among neighbors will depend on the patterns of trait evolution and whether there is convergence or displacement of the relevant traits among closely related taxa.

At the community level, individuals of species with a higher forest-wide abundance have a greater probability of encountering conspecifics in their neighborhood and may experience stronger negative density dependence because of their frequency relative to other species. Rare species can thus have an advantage in what Connell et al. (1984) called a community compensatory trend (CCT). Webb and Peart (1999) found seedling survival was greater for species that were less abundant at the scale of their 150-ha study area. Similarly, Queenborough et al. (2007) found evidence for a CCT in established tree seedlings of the nutmeg family (*Myristicaceae*) in a lowland Amazon forest in Ecuador.

The spacing mechanisms caused by density-dependent mortality will be most effective at promoting diversity when they are widespread among species. Although the Janzen-Connell hypothesis and related ideas have been widely studied in tropical forests, the majority of studies have focused on the patterns exhibited by one or a few species at a site, or on saplings and older individuals. For example, in a recent review of 53 studies examining density- or distance-dependent mortality, 29 studies included observations or manipulations of seedlings, but only two of these examined more than 10 species (Carson et al. 2008: Table 13.1). In one study, Harms et al. (2000), tracked survival over the seed-to-seedling transition for 53 species on Barro Colorado Island (BCI) in Panama and found widespread negative density dependence, but did not assess whether negative density dependence continued to exert an impact on survival of successfully recruited seedlings. In a second study, Webb and Peart (1999) followed the survival over 19 months of established seedlings (of an unknown age) from 149 species in Gunung Palung, Indonesia. They found seedling survival decreased with increased conspecific seedling density (in 1-m^2 quadrats) and with the basal area of adults (in the surrounding 0.16-ha). A later related analysis at Gunung Palung showed that survival was also enhanced when the neighborhood was more phylogenetically heterogeneous (Webb et al. 2006). More recently at BCI, an assemblage-wide study of established seedlings ($\geq$20 cm in height, age unknown) found negative effects of seedling and adult neighbors on seedling survival and detected a CCT in seedling survival (at the 50-ha scale) when accounting for differences in life history (Comita and Hubbell 2009).

Here we investigate the importance of the seedling and adult neighborhoods in determining the survival of young seedlings, using age- and species-specific seedling dynamics data from an ever-wet, lowland Amazonian rain forest, among the most species-rich forests in the world. We track the survival of multiple cohorts of newly recruited seedlings, to fill the gap between previous studies that look at seedling recruitment and those that examine survival of established seedlings of unknown age. We also account for the importance of evolutionary relationships in these processes by incorporating an estimate of the phylogenetic distance between each of our 163 focal species and the thousand or more species that may be found in their adult and seedling neighborhoods. We examine seedling survival at two spatial scales, the local neighborhood and the community. First, at the local neighborhood scale, we assess whether the density and diversity of nearby conspecific adults or seedlings and the phylogenetic relatedness of neighborhoods determine individual seedling survival. We test the hypotheses that increasing conspecific adult and seedling abundances negatively affect seedling survival, that local seedling neighborhood diversity has a protective effect, and that the phylogenetic distance of local adult and seedling neighbors affects seedling survival. Second, at the community scale, we test whether there is a rare species advantage in seedling survival in accordance with the community compensatory trend of Connell et al. (1984).

METHODS

Study site

This research took place in the environs of the Yasuní Scientific Station, located in the northern section of Yasuní National Park in eastern Ecuador (0°41′ S, 76°24′ W). Yasuní has an aseasonal climate, with a mean maximum temperature of 35°C, mean annual rainfall of 3081 mm and no month with rainfall <100 mm (Valencia et al. 2004*a*). While there are detectable peaks in tree flowering, timed with the period of maximal solar irradiance, adults set fruit and seedlings germinate throughout the year (Persson 2006).

In 1995, a 50-ha forest dynamics plot (FDP) was established at this site by the Pontifical Catholic University of Ecuador and the Smithsonian Tropical Research Institute. The plot is part of the Center for Tropical Forest Science network, and is described in greater detail by Losos and Leigh (2004). As in other plots in the network, every woody stem ≥1 cm dbh (diameter at breast height, 1.3 m) within the Yasuní FDP is marked, mapped, measured and identified in censuses occurring every five years (Valencia et al. 2004*a*). The forest at Yasuní is one of the most species-rich ever studied. There are close to 1200 species of trees ≥1 cm dbh in 50 ha, and the FDP contains, on average, 243 species/ha with dbh ≥10 cm. The plot lies at 230 m above sea level, and contains three large ridges and intervening valleys that include small streams and a small swamp. There is a 33.5 m difference between the plot's highest and lowest points with an average slope of 13% (Valencia et al. 2004*a*).

Within the FDP, a network of 200 seed traps, established in 2000, captures falling flowers and fruit in a study of the forest's phenology. In 2002, we established 600 1-m^2 seedling plots in association with these traps and began annual censuses of all naturally recruiting seedlings of woody tree, shrub, and liana species (see Appendix A for details of seedling plot network design). In each census since the 2002 baseline, we have marked, identified, followed the fate and measured the growth of every seedling recruiting into these seedling plots to quantify species- and age-specific demographic rates. Here, we present analyses following the fate of newly recruited seedlings, for which we have five cohorts of known age (recruited 2003–2007) that have been re-censused at least once (2004–2008).

Study species

We included in our analyses all tree species that recruited seedlings into at least three census stations throughout the study period and that had adults ≥10 cm dbh in the Yasuní FDP. This included 4501 seedling individuals representing 163 species, which had between three and 297 new recruits between 2003 and 2007. The focal species come from 102 genera in 39 families, and represent a variety of tree stature classes, including eight palm species (see Appendix B). Adult abundances range 0.02–65.28 individuals/ha (density = 2.46 ± 5.69 [mean ± SD]) and <0.01–1.78 m^2/ha (basal area = 0.10 ± 0.19). All other censused seedlings (including, for example, lianas, species that do not reach ≥10 cm dbh, or seedlings with recruitment restricted to fewer than three census stations) were included in the seedling neighborhood diversity metrics described below.

Effects of adult and seedling neighborhoods

We examined the factors affecting the survival of individual newly recruited seedlings using generalized linear mixed-effects models (GLMM) and generalized estimating equations (GEE), two methods of analysis that account for the potential spatial autocorrelation inherent when examining seedlings located in close proximity (e.g., at the same census station; Dormann et al. 2007). Both analyses are essentially a logistic regression, using as the dependent variable a logit transformation of seedling fate (survival: yes or no) over the period of interest following a seedling's establishment. The independent predictor variables in the analysis were chosen to follow predictions for patterns of density-dependent mortality based on the species and phylogenetic diversity in the adult and seedling neighborhoods. The GLMM included a linear combination of fixed-effects predictor variables and the random effects of seedling plot nested within census station. The GEE used the same linear combination of predictors, but accounted for spatial autocorrelation among seedling responses by separately calculating a variance–covariance matrix within each census station.

For each seedling, we summed the basal area of conspecific adults $\geq$10 cm dbh within a 5, 10, 15 or 20 m radius of each seedling plot. We included this term in the model to test the hypothesis that increased conspecific adult abundance decreased seedling survival. Previous studies of older seedlings, saplings or trees have used a 10-m neighborhood radius or larger (e.g., Peters 2003, Comita and Hubbell 2009), but young seedlings may be expected to respond differently. Due to the high species richness in this forest, the majority of adult trees surrounding an individual seedling are heterospecifics. We summed the basal area of heterospecific adults ($\geq$10 cm dbh) within the same neighborhood radii and included this in the model as a measure of tree biomass to control for variation in overall tree density and canopy openness across the forest. Although crown size varies greatly among species, life stages, and microsites, basal area from dbh measurements is a useful correlate of tree biomass (O'Brien et al. 1995). The size, location, and species identification of the neighboring adults were taken from census data collected between October 2002 and December 2003 for the western 25 ha of the FDP, and between January 2004 and December 2005 for the eastern 25 ha.

We included in the model the abundance of conspecific and heterospecific seedling neighbors that existed in the seedling plot during the census in which the focal seedling was a new recruit (defined as $\leq$50 cm in height, regardless of age) by summing the number of each. Both of these are, of course, strongly correlated with overall seedling density (conspecific, total $r = 0.55$; heterospecific, total $r = 0.83$). To test whether increased local seedling diversity was beneficial for survival, as predicted by the herd immunity hypothesis, we also included in the model the Shannon-Wiener index of diversity of all seedlings as a predictor (Magurran 1988).

We examined the evolutionary relationships between a seedling and its neighborhood to examine the impact of phylogenetic relatedness of neighbors on seedling survival, beyond the effects of conspecifics alone. We built a phylogenetic tree with all tree species $\geq$10 cm dbh in the Yasuní FDP and all species and morphospecies observed in the seedling study (including lianas and shrubs) using Phylomatic (Webb and Donoghue 2005) and the most recent angiosperm phylogeny hypothesis available at the time of analysis R20081027 (*available online*).[4] We used the age estimates from fossil plants of Wikström et al. (2001) and Phylocom's BLADJ algorithm (Webb et al. 2008) to constrain internal nodes of the tree, and then interpolated the ages of nodes for which age estimates were not available. There are many unresolved polytomies below the family level in this tree, so significant results reflect patterns of trait conservatism or divergence that extend beyond sister taxa to nodes representing genera or families. These polytomies may also serve to make detection of a phylogenetic signal more conservative by introducing noise into the relationships (Webb 2000, but see Kress et al. 2009).

Using this tree, we calculated the mean phylogenetic distance (measured in millions of years) between the focal seedling and all other species in the seedling or adult neighborhood (cf. APd'; Webb et al. 2006) using summed branch lengths. As phylogenetic mean distance varies with the species richness of the sample, we calculated standard effect sizes of observed distances given an expected phylogenetic distance for a specified number of species (Webb 2000, Webb et al. 2006, Kraft et al. 2007). We obtained the expected phylogenetic distances using a null model to generate 10 000 random neighborhoods at a given species richness and calculating the mean and standard deviation of the pairwise phylogenetic distances among species for each neighborhood. Species for the adult or seedling neighborhoods were drawn from, respectively, the pool of tree species $\geq$10 cm dbh in the Yasuní FDP or from the species that have appeared in the seedling censuses in any year, weighted by their abundance in the respective study. Accounting for differences in species relative abundances in the null model is a conservative step (Kembel 2009), although previous analyses have found low phylogenetic signal in species abundances in the Yasuní plot (Kraft and Ackerly 2010). The mean and standard deviation of the distribution of null model distances were combined with our observed mean phylogenetic distance to obtain a standard effect size, indicating whether the focal seedling is more or less related to its neighbors than expected by the null model:

$$\frac{-1(\text{observed distance} - \text{mean}[\text{null distribution distances}])}{\text{standard deviation}[\text{null distribution distances}]}.$$

If this term is positive, then the neighborhood is more closely related to the focal seedling than expected from the null model (phylogenetic clustering), and if the term is negative, the neighbors are more phylogenetically distant (phylogenetic dispersion). It is important to note that the observed phylogenetic distance is the mean distance of all neighbors to the focal seedling (as in APd' by Webb et al. 2006), and is not the mean of all pairwise distances (MPD) as used to calculate NRI, the net relatedness index (Webb et al. 2002). However, the mean phlyogenetic distance used here is standardized in the same way as NRI and other similar measures by using the mean and standard deviation of a null distribution and multiplying by −1 (Webb et al. 2002, Kraft et al. 2007; note, however, that Webb et al. 2006 orient their measures in the opposite way so that greater positive values indicate phylogenetic dispersion, not clustering). We used this effect size in the model as an indicator of phylogenetic distance in the neighborhood. We used phylogenetic distance in the model because it represents the potential for ecological similarity among neighbors. Doing so assumed that traits may be conserved among

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[4] ⟨http://svn.phylodiversity.net/tot/megatrees/⟩

related taxa. Although it is very difficult to quantify trait conservatism for an exhaustive list of the traits involved in plant defenses, species' competitive abilities and habitat use, trait conservatism has been found for many tropical forests, including many functional traits in a forest-wide analysis at Yasuní (Kraft and Ackerly 2010).

Because previous analyses have shown that seedling size is an important predictor of survival, we included each seedling's initial height in the model. We also allowed the height term to interact with the neighborhood density and diversity variables to test whether height mediated or exaggerated the effects of neighborhood characteristics. We included each seedling's recruitment year as a factor in the model to account for the variability among years known to occur in seedling responses (Metz et al. 2008). Seedlings recruiting in the same year or located in close proximity may be affected by similar abiotic factors unrelated to the species identity of neighboring adults.

Both the GEE and the GLMM approach use a logit transformation of the survival probability, p, with binomial errors and a linear relationship with the independent variables. Results consistent with density-dependent mortality would include a negative estimate for the terms representing conspecific adult or seedling abundance, indicating decreases in survival when neighborhoods contain more conspecifics. A protective effect of diversity would be observed with a positive coefficient estimate for the index of local seedling diversity. If the negative effects of conspecifics extend to other closely related species, then a neighborhood with a greater mean phylogenetic distance (more phylogenetic dispersion, represented with a negative standard effect size) should have a beneficial effect on seedling survival, observed with a negative coefficient for the terms representing the phylogenetic relationship of the seedling or adult neighborhood.

After examining survival from recruitment through the first year (age 0 to 1), we further examined whether those variables that had significant impacts on survival through the first year predicted survival from recruitment over longer intervals (age 0 to 2 or 3) or continued survival after the first year (age 1 to 2). Previous community-wide studies of density-dependent seedling mortality have included established seedlings of unknown ages, but the patterns may differ for first year seedling survival. We also repeated our analyses omitting the nine most abundant seedling focal species to confirm that patterns were not driven by relatively few abundant species. These nine species each had $\geq$100 recruits in the study period and together represented approximately one third of the individuals included in the other analyses.

We evaluated our model results using the area under the "receiver operating characteristic" curve (ROC), a standard assessment of model discrimination ability for logistic regressions. The area under the ROC curve captures the model's ability to discriminate between seedling fates, or to correctly classify seedlings that survived or died given predicted probabilities of survival. The ROC curve plots the rate of true positives against the rate of false positives. The area under the curve ranges between 0 and 1, and values $>$0.9 are extremely rare; ROC $\geq$ 0.7 are considered acceptable fits (Hosmer and Lemeshow 2000).

Community compensatory trend

To investigate whether a frequency-dependent CCT in seedling survival favored rare species and hindered common species across our study, as had been found for the *Myristicaceae* family at Yasuní (Queenborough et al. 2007), we used a logistic regression of study-wide seedling survival for each species against species' abundance at the level of the Yasuní FDP. The dependent variable was the number of seedlings surviving their first year out of the total study-wide recruitment for a species. We used the density and basal area of adults ($\geq$10 cm dbh) in the 50-ha FDP as measures of a species' abundance. Each of the 163 species used in the above analyses became one data point in this linear model. A negative relationship between species abundance and seedling survival would indicate the existence of a CCT in the Yasuní forest.

All analyses were performed using the statistical programming language R, version 2.10.1 (R Development Core Team 2007) and the packages ape, geepack, Hmisc, lme4, and vegan.

RESULTS

Effects of adult and seedling neighborhoods on survival

The GLMM and GEE approaches produced qualitatively similar results; we will discuss the results of the GLMM here and include results of the GEE analyses in Appendix C.

Survival of newly recruited seedlings was strongly negatively density dependent (Table 1; Appendix C: Table C1). The abundance of conspecific adults within any radius, 5–20 m, had a significant negative effect on first year seedling survival (Table 1, Fig. 1a). Seedling survival increased when the adults within a 5 m radius were more phylogenetically distant than expected by a null model (Fig. 1b). The impact of height was not statistically significant, but there was a significant interaction between initial seedling height and conspecific adult abundance within a 5 or 10 m radius (Table 1). When examining those neighborhoods, an increase in the height of seedling recruits increased survival, and the negative effect of a high abundance of conspecifics on survival was weakened when seedlings were very large (Fig. 1c).

There was a negative effect on first year survival of the density of conspecific seedling neighbors within the 1-m^2 seedling plot (Fig. 1d), but no negative effect of heterospecific seedling density. There was no evidence that a more diverse local seedling neighborhood reduced the per capita risk of seedling mortality, nor did the

TABLE 1. Effect of seedling and adult neighborhoods (of varying sizes) on individual seedling survival over the first year.

Predictor	Radius (m)			
	5	10	15	20
Conspecific adult basal area	**<0.001**	**0.012**	**0.060**	**0.186**
Heterospecific adult basal area	0.713	0.959	1.247	0.971
Phylogenetic distance (adults)‡	**0.907**	0.936	0.944	0.951
Conspecific seedling density	**0.968**	**0.967**	**0.962**	**0.962**
Heterospecific seedling density	1.000	0.999	0.998	0.999
Phylogenetic distance (seedlings)‡	0.976	0.970	0.961	0.962
Seedling species diversity	0.899	0.897	0.858	0.885
Initial seedling height	1.029	1.032	1.053†	1.006
Height × conspecific adult basal area	**1.382**	**1.166**	1.036	1.034
Height × heterospecific adult basal area	1.041	1.008	0.992	1.010
Height × conspecific seedling density	1.002†	1.002†	**1.002**	1.002†
Height × heterospecific seedling density	1.000	1.000	1.001	1.000
Height × seedling diversity	1.019	1.019	1.021	1.019
Recruit year = 2004§	**0.351**	**0.341**	**0.341**	**0.340**
Recruit year = 2005§	**0.254**	**0.249**	**0.250**	**0.254**
Recruit year = 2006§	**0.218**	**0.213**	**0.209**	**0.210**
Recruit year = 2007§	**0.209**	**0.203**	**0.200**	**0.200**
ROC	0.787	0.789	0.790	0.789

Notes: Values are coefficient estimates, expressed as odds ratios for the fixed-factor predictors in a generalized linear mixed-effects model. Seedling neighbors are found within the same 1-m^2 seedling plot as each focal seedling, and tree neighborhoods contain adults ≥10 cm dbh in circles with the indicated radii surrounding each plot. See *Methods* for a description of the generalized linear mixed-effects model. Significant coefficients are shown in boldface type. Odds ratios >1 have a positive relationship with increased survival, and ratios <1 have a negative relationship with survival. Model receiver operating characteristic (ROC) curve values ≥0.7 indicate acceptable discrimination ability.

† The predictor had $0.5 < P \leq 0.1$; included for heuristic purposes to show changes in the strength of the signal with changes in the size of the adult neighborhood included in the model.

‡ Phylogenetic distance measured as an effect size with values >0 indicating phylogenetic clustering (neighborhood is more closely related than expected by null model) and values <0 indicating phylogenetic dispersion (neighborhood is more distantly related than expected from null model). Positive effects (odds ratios >1) indicate better survival with increased phylogenetic clustering; negative effects (odds ratios <1) indicate survival is decreased when neighbors are more closely related.

§ Change in intercept relative to baseline cohort (recruit year = 2003).

phylogenetic relatedness of the seedling neighborhood significantly affect survival rates (Table 1). Seedling survival varied among recruit cohorts, as expected (Table 1). These models had acceptable discrimination ability (ROC > 0.78). Exclusion of the most abundant nine species (see Appendix B) did not change these results (see Appendix C: Table C4).

Survival from initial recruitment over the first two or three years (age 0 to 2 or 3) was strongly negatively influenced by conspecific adult abundance (Table 2; Appendix C: Tables C2, C3). This effect was likely driven by the strong negative influence of conspecific adults on survival in the first year because the effect of conspecific adults was not significant for survival from age 1 to 2 (Table 2). After surviving the first year, there was a significant beneficial impact of phylogenetic similarity of adult neighbors (within 5–10 m), perhaps indicating shared habitat preferences (Table 2; Appendix C: Tables C2, C3).

There was a significant positive impact on survival beyond the first year of being surrounded by distantly related seedlings, whether survival was examined from recruitment over two to three years, or survival to the second year after already having survived one year (Table 2). Each of these analyses had smaller sample sizes than the analysis of first year survival because not all cohorts were old enough to track across multiple years. Despite the reduction in sample size, the models had good discrimination abilities (0.75 < ROC < 0.83).

Community compensatory trend

Forest-wide, there was little evidence that rare species had a survival advantage compared to common species, whether abundance was measured by adult stem density ($P = 0.47$) or basal area ($P = 0.06$). The basal area model indicated a marginal trend towards increased seedling survival with increased forest-wide abundance, but neither regression fit the data well.

DISCUSSION

Our results clearly show that the composition of the biotic neighborhood in this highly diverse forest influences early seedling survival. Across the 163 species in this study, an increasing abundance of conspecific adults or seedlings in the neighborhood decreased seedling survival over the first few years after initial

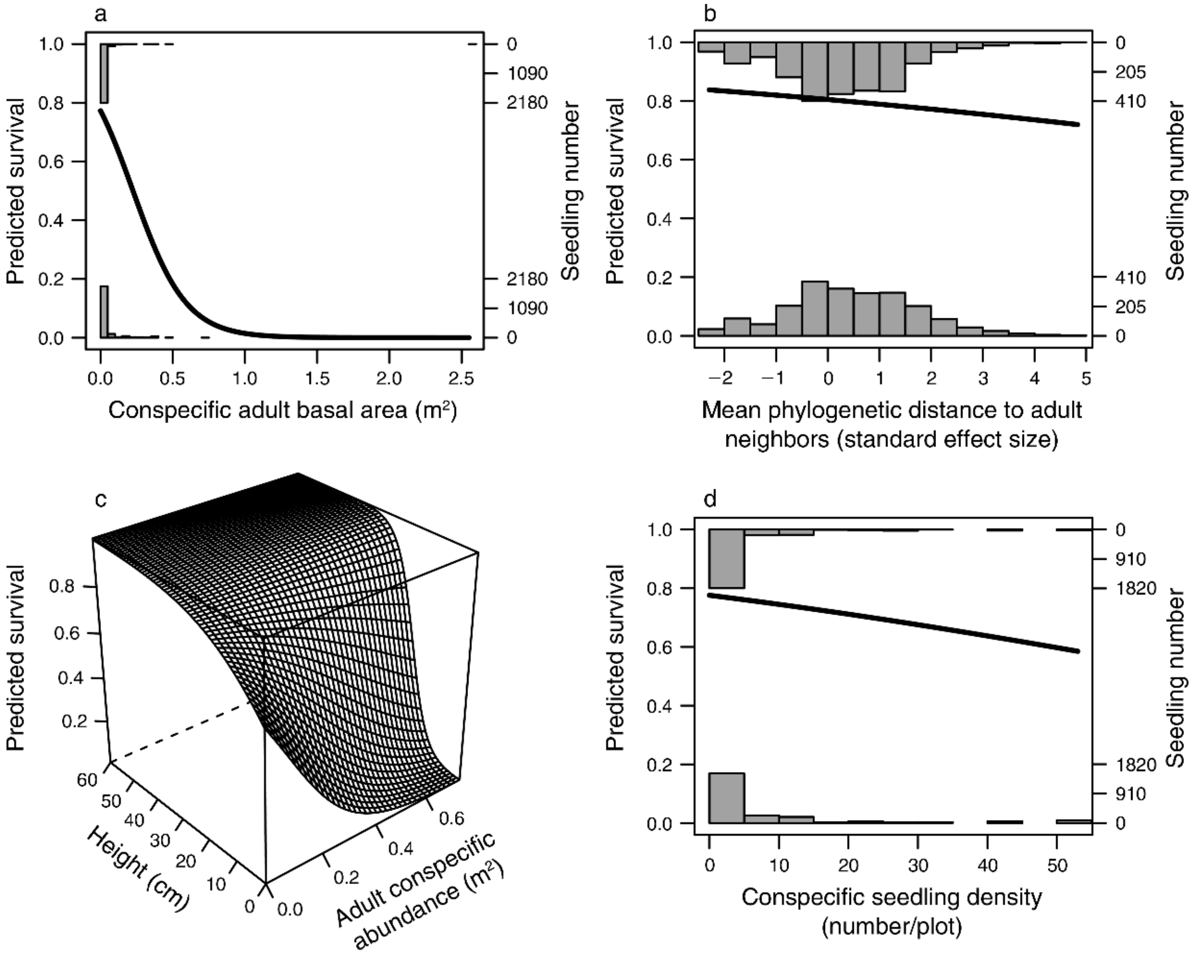

FIG. 1. Neighborhood effects on individual seedling survival. The effects on predicted probabilities of first-year seedling survival of (a) conspecific adult basal area per neighborhood, (b) standard effect size of mean phylogenetic distance between a focal seedling and species in the adult neighborhood, (c) the interaction between seedling height and conspecific abundance (measured as m^2 per neighborhood), and (d) density of heterospecific seedlings. The predicted survival probabilities are from the model results across 163 species presented in Table 1 with an adult neighborhood radius of 5 m. The effects of individual predictors are presented here with the other variables in the model held at their median value. The histograms in panels (a), (b), and (d) represent the distribution of the predictor variable on the x-axis, split by the observed survival of individuals ($y = 1$ indicates survival; $y = 0$ indicates mortality); the right-hand axis gives the number of seedlings in each category in the histogram. See *Methods* for description of the phylogenetic distance effect size; positive values indicate that the neighborhood is more related to the focal seedling than expected from the null model, or that the neighborhood is phylogenetically clustered.

establishment. These effects were not limited to a strict distinction between con- and heterospecifics. Being surrounded by a more distantly related tree neighborhood was beneficial for early seedling survival, as was phylogenetic diversity among close seedling neighbors for survival beyond the first year. We did not detect evidence for a community compensatory trend at this site, as study-wide seedling survival was not significantly associated with adult abundance on the 50-ha FDP. These patterns are discussed in detail below.

Effects of the seedling and adult neighborhoods

The strongest result in these analyses highlighted the important negative effect of conspecific adult abundance on seedling survival. Seedlings that recruited in areas with a greater abundance of adults of the same species had significantly poorer survival than those recruiting elsewhere. This effect would enhance the survival of new seedlings that recruit away from conspecific adults, resulting in a spacing mechanism that frees space near adults for heterospecific seedlings in the seedling bank and promotes species coexistence.

Seedlings also had increased first year survival when their nearby adult neighbors (within a 5-m radius neighborhood) were more distantly related, indicating that similarities among closely related taxa may result in similar affinities for natural enemies or similar competitive traits. Greater phylogenetic dispersion in the seedling neighborhood enhanced survival of established seedlings beyond the first year. Similarly, Webb et al.

TABLE 2. Neighborhood effects on survival beyond the first year.

Predictor	Survival 0 to 2†	Survival 0 to 3‡	Survival 1 to 2§
Conspecific adult basal area	<**0.001**	<**0.001**	0.048
Heterospecific adult basal area	0.677	1.548	0.892
Phylogenetic distance (adults)¶	1.022	1.032	**1.223**
Conspecific seedling density	0.978	0.969	1.011
Heterospecific seedling density	0.996	0.999	0.990
Phylogenetic distance (seedlings)¶	**0.908**	**0.844**	**0.877**
Seedling species diversity	1.165	1.085	1.517
Initial seedling height	1.033	1.028	1.033
Height × conspecific adult basal area	1.161	1.350	0.957
Height × heterospecific adult basal area	1.011	0.971	0.954
Height × conspecific seedling density	1.002	**1.004**	1.000
Height × heterospecific seedling density	**1.001**	1.001	1.002
Height × seedling diversity	1.013	1.023	1.001
Recruit year = 2004#	**0.444**	**0.401**	0.880
Recruit year = 2005#	**0.293**	**0.268**	**0.621**
Recruit year = 2006#	**0.270**		**0.682**
ROC	0.804	0.830	0.744

Notes: The table regression coefficients, expressed as odds ratios for, from left to right, survival of new recruits over the first two years, survival of new recruits over the first three years, and survival of one-year-old seedlings through the second year. See *Methods* for a description of the generalized linear mixed-effects model; the 5-m radius is used for the adult neighborhood in this model. Significant predictor variables are shown in boldface type. Odds ratios >1 have a positive relationship with increased survival, and ratios <1 have a negative relationship with survival. Model ROC values ≥ 0.7 indicate acceptable discrimination ability.

† Analysis included 3690 seedlings from 160 species and four recruit cohorts.

‡ Analysis included 2844 seedlings from 153 species and three recruit cohorts.

§ Analysis included 1950 seedlings from 151 species and four recruit cohorts.

¶ Phylogenetic distance, measured as an effect size, with values >0 indicating phylogenetic clustering (neighborhood is more closely related than expected by null model) and values <0 indicating phylogenetic dispersion (neighborhood is more distantly related than expected from null model). Positive effects (odds ratios >1) indicate better survival with increased phylogenetic clustering; negative effects (odds ratios <1) indicate that survival is decreased when neighbors are more closely related.

Change in intercept relative to baseline cohort (recruit year = 2003).

(2006) found that phylogenetic dispersion affected the survival of seedlings >5 cm high, whose ages are unknown but likely include a greater number of established seedlings older than one year. In that study, seedlings had better survival when the nearest related taxon was more distantly related, but only at spatial scales larger than the size of the seedling neighborhoods in this study. When Webb et al. (2006) examined the average phylogenetic distance (identical to the index used here), they found no benefit of phylogenetically dispersed neighborhoods for seedling survival at small scales, and instead found a closely related neighborhood was beneficial for seedling survival at a much larger scale than the neighborhoods here. In our study, using nearest taxon distance in our model (results not shown) gave qualitatively identical results to those presented here, which use the average neighbor distance. Measuring nearest taxon distance or average neighbor distance captures different aspects of the neighborhood's phylogenetic structure, examining the tips only or the entire phylogenetic tree, respectively. As such, they may easily be expected to have differing relationships with seedling survival, and/or be important at different spatial scales or life stages. Most importantly, our results contribute to the growing body of evidence that the evolutionary relationships among neighbors, and not merely species identity as con- or heterospecific, are important predictors of individual performance.

The negative impact of conspecific seedling density on first year survival indicates the potential for intraspecific seedling interactions to be very important following initial recruitment. Heterospecific seedling abundance was not a significant predictor of survival during the first year, however. These findings contrast with those of Paine et al. (2008), who found no evidence for intraspecific seedling competition in three species from Panama or Peru. The effect of conspecific seedling density on seedling survival was weaker than that of conspecific adult abundance, as we expected from arguments that seedling competition is largely asymmetric with larger size classes (Wright 2002). The negative effect of conspecific seedling density did not continue beyond the first year, suggesting densities had thinned, and subsequent seedling survival benefited from a phylogenetically diverse seedling neighborhood.

While initial seedling height was not an important predictor of survival, it did mediate the negative effects of conspecific adult abundance. This result was not entirely unexpected, as larger seedlings have been found in other studies to persist longer in the shaded understory of tropical forests (Clark and Clark 1985, Whitmore 1996, Gilbert et al. 2001). Larger seedlings may be better able to establish and survive the stresses of the understory, regardless of the adult neighborhood, providing them with a significant head start towards persisting in the understory until a gap opens.

Without further mechanistic studies, we cannot distinguish whether these results arise from competitive interactions or the role of specialized natural enemies. In the first year, a negative effect of conspecific adult abundance and closely related tree neighbors suggests seedlings are vulnerable to the transfer of natural enemies from the adults to the newly recruited seedlings found nearby, and seedling-seedling interactions are more intense among conspecifics than heterospecifics. After seedlings have survived their first year, they are more established and the densities of their conspecific neighbors have decreased. At these lower densities, competition may be of relatively little importance (Wright 2002, Svenning et al. 2008), and seedlings instead benefit from a more phylogenetically diverse seedling neighborhood. This benefit could be due to the protective effect a diverse neighborhood affords for the transmission of natural enemies and pathogens (Wills 1996). The importance of relatedness of the adult neighborhood changes for these older established seedlings. While young-of-the-year seedlings survive more poorly when growing in proximity to closely related adults, such proximity enhances survival of older seedlings. This may indicate that successful sites for adult survival may also be beneficial for the survival of older seedlings because of the habitat preferences (Valencia et al. 2004*b*, Metz 2007) or functional traits that closely related taxa may share.

Community compensatory trend

In our study, rarer species did not have a survival advantage relative to more common species, although another study at the same site found evidence for such a CCT in the nutmeg family (Myristicaceae; Queenborough et al. 2007). Rare nutmeg species (as measured by adult basal area on the 50-ha FDP) had enhanced survival relative to common species at Yasuní (Queenborough et al. 2007), but the basal areas for species included in our community-wide study tended to be greater and spanned a wider range than those of the nutmeg species. Only the most common of the species in the Myristicaceae study had a sample size large enough to be included in our analyses, suggesting our study may not have included enough truly rare species to detect a CCT if present. Further, the Myristicaceae study examined established seedlings of unknown age while the analyses presented here examined several cohorts of newly recruited seedlings in their first year. Because we only used adult trees $\geq$10 cm DBH, some smaller-statured species may appear artificially rare in this analysis if they reach our size cut-off only infrequently. This would have inhibited our ability to detect a rare species advantage. Other attempts to detect CCTs in tropical forests have also not clearly elucidated the importance of this phenomenon to overall forest diversity (see discussions in Wright 2002, Queenborough et al. 2007, Comita and Hubbell 2009).

Consequences of density-dependent mortality

While tropical tree seedling mortality rates can vary greatly year-to-year and among cohorts (Connell and Green 2000), mortality is generally highest in the first year (Clark and Clark 1984) and sharply drops off and then steadily diminishes in subsequent years (De Steven 1994). We found strong impacts of both the adult and seedling neighborhoods on survival of young seedlings, particularly during their first year. These results indicate that the density-dependent mortality common during the transition from seed-to-seedling stages (Harms et al. 2000, Metz 2007) continues from seedling recruitment through a seedling's first years. Many studies may fail to detect this negative density dependence because they focused on the response of established, older seedlings or later life stages and did not observe the earliest stages of seedling establishment and survival.

That the negative effects of conspecific abundance were strongest and most easily detected when examining first year survival emphasizes the value of long-term community-wide studies that include multiple species and track individuals of known age across years. Seedlings at Yasuní and three other tropical forests showed great inter-annual and spatial variation in seedling abundances and vital rates at the community level (Metz et al. 2008). Indeed, there was significant variation among recruit cohorts in the probability of surviving the first year in this study. Recruitment pulses and year-to-year variation in species-specific and assemblage-wide mortality rates can have important consequences for the composition of advanced regeneration and the maintenance of forest diversity (Grubb 1977, Chesson 1985), and the biotic neighborhood plays an important role in determining the composition of the understory seedling assemblage acting as advanced regeneration in canopy turnover.

Previous studies have focused on far fewer species than the 163 species included here, although local spacing dynamics that might promote diversity will only do so if the effect is widespread across species. The species examined in our study comprise a fraction of the almost 1200 species found in Yasuní, yet represent a range of abundances and life forms (see Appendix B), and include some of the most common species at Yasuní and in the western Amazon (Pitman et al. 2001, Valencia et al. 2004*b*, Vormisto et al. 2004). Inclusion of the phylogenetic relationships among species allowed us to extend our inferences beyond our focal species and the differences between hetero- and conspecifics to include the diversity of the entire forest.

The negative density-dependent mortality observed at Yasuní is an important stabilizing mechanism (sensu Chesson 2000) for promoting species coexistence because species will limit themselves more strongly than they will limit other species in their community, regardless of fitness differences among species (Adler et al. 2007). The effects of the biotic neighborhood on survival have the potential to multiply and become stronger when considered on the time scale of forest gap turnover, or on the order of several decades, if not over a century (Denslow 1987). Thus, the biotic neighborhood is an important determinant of local forest diversity and operates without regard to the rarity or commonness of any one species, and the assemblage-wide impacts of species abundance distributions may affect diversity and individual species abundance over longer time scales.

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LITERATURE CITED

Adler, P. B., J. Hille Ris Lambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682–687.

Carson, W. P., J. T. Anderson, E. G. Leigh, Jr., and S. A. Schnitzer. 2008. Challenges associated with testing and falsifying the Janzen–Connell hypothesis: a review and critique. Pages 210–241 *in* W. P. Carson and S. A. Schnitzer, editors. Tropical forest community ecology. Wiley-Blackwell, Oxford, UK.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263–287.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343–366.

Clark, D. A., and D. B. Clark. 1984. Spacing dynamics of a tropical rain-forest tree: evaluation of the Janzen-Connell model. American Naturalist 124:769–788.

Clark, D. B., and D. A. Clark. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. Ecology 66:1884–1892.

Comita, L. S., and S. P. Hubbell. 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. Ecology 90:328–334.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. Pages 298–312 *in* P. J. van der Boer and G. R. Gradell, editors. Dynamics of numbers in populations. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302–1310.

Connell, J. H., and P. T. Green. 2000. Seedling dynamics over thirty-two years in a tropical rain forest tree. Ecology 81:568–584.

Connell, J. H., J. G. Tracey, and L. J. Webb. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain-forest tree diversity. Ecological Monographs 54:141–164.

Denslow, J. S. 1987. Tropical rain forest gaps and tree species diversity. Annual Review of Ecology and Systematics 18: 431–451.

De Steven, D. 1994. Tropical tree seedling dynamics: recruitment patterns and their population consequences for three canopy species in Panama. Journal of Tropical Ecology 10: 369–383.

Dormann, C. F., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628.

Gilbert, G. S., K. E. Harms, D. N. Hamill, and S. P. Hubbell. 2001. Effects of seedling size, El Nino drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panama. Oecologia 127: 509–516.

Gilbert, G. S., and C. O. Webb. 2007. Phylogenetic signal in plant pathogen–host range. Proceedings of the National Academy of Sciences USA 104:4979–4983.

Grubb, P. J. 1977. Maintenance of species richness in plant communities: importance of the regeneration niche. Biological Reviews of the Cambridge Philosophical Society 52:107–145.

Hammond, D. S., and V. K. Brown. 1998. Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. Pages 51–78 *in* D. M. Newbery, H. H. T. Prins, and N. D. Brown, editors. Dynamics of tropical communities. Blackwell, Oxford, UK.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404: 493–495.

Hartshorn, G. S. 1980. Neotropical forest dynamics. Biotropica 12:23–30.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201–228.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Kembel, S. W. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. Ecology Letters 12: 949–960.

Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs 80: 401–421.

Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. American Naturalist 170:271–283.

Kress, W. J., D. L. Erickson, F. A. Jones, N. G. Swenson, R. Perez, O. Sanjur, and E. Bermingham. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. Proceedings of the National Academy of Sciences USA 106:18621–18626.

Leigh, E. G., P. Davidar, C. W. Dick, J. P. Puyravaud, J. Terborgh, H. ter Steege, and S. J. Wright. 2004. Why do some tropical forests have so many species of trees? Biotropica 36:447–473.

Losos, E. C., and E. G. Leigh. 2004. Tropical forest diversity and dynamism: findings from a large-scale plot network. University of Chicago Press, Chicago, Illinois, USA.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

Metz, M. R. 2007. Spatiotemporal variation in seedling dynamics and the maintenance of diversity in an Amazonian forest. Dissertation. University of California, Berkeley, California, USA.

Metz, M. R., L. S. Comita, Y.-Y. Chen, N. Norden, R. Condit, S. P. Hubbell, I.-F. Sun, M. N. N. Supardi, and S. J. Wright. 2008. Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. Journal of Tropical Ecology 24:9–18.

O'Brien, S. T., S. P. Hubbell, P. Spiro, R. Condit, and R. B. Foster. 1995. Diameter, height, crown, and age relationships in eight neotropical tree species. Ecology 76:1926–1939.

Paine, C. E. T., K. E. Harms, S. A. Schnitzer, and W. P. Carson. 2008. Weak competition among tropical tree seedlings: Implications for species coexistence. Biotropica 40:432–440.

Persson, V. 2006. Effects of climatic seasonality on reproductive phenology of tropical forest plants. Dissertation. University of Aberdeen, Aberdeen, UK.

Peters, H. A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. Ecology Letters 6: 757–765.

Pitman, N. C. A., J. W. Terborgh, M. R. Silman, P. Núñez, D. A. Neill, C. E. Ceron, W. A. Palacios, and M. Aulestia. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82:2101–2117.

Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2001. The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society B 268:2383–2389.

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

R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Svenning, J. C., T. Fabbro, and S. J. Wright. 2008. Seedling interactions in a tropical forest in Panama. Oecologia 155: 143–150.

Valencia, R., R. Condit, R. B. Foster, K. Romoleroux, G. Villa Muñoz, J. C. Svenning, E. Magard, M. Bass, E. C. Losos, and H. Balslev. 2004*a*. Yasuni forest dynamics plot, Ecuador. Pages 609–620 *in* E. C. Losos and E. G. Leigh, editors. Tropical forest diversity and dynamism: findings from a large-scale plot network. University of Chicago Press, Chicago, Illinois, USA.

Valencia, R., R. B. Foster, G. Villa, R. Condit, J. C. Svenning, C. Hernandez, K. Romoleroux, E. Losos, E. Magard, and H. Balslev. 2004*b*. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. Journal of Ecology 92:214–229.

Vormisto, J., H. Tuomisto, and J. Oksanen. 2004. Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation? Journal of Vegetation Science 15:485–494.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist 156:145–155.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. Molecular Ecology Notes 5:181–183.

Webb, C. O., G. S. Gilbert, and M. J. Donoghue. 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. Ecology 87(Supplement):S123–S132.

Webb, C. O., and D. R. Peart. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. Ecology 80:2006–2017.

Whitmore, T. C. 1984. Tropical rain forests of the far east. Clarendon, Oxford, UK.

Whitmore, T. C. 1996. A review of some aspects of tropical rain forest seedling ecology with suggestions for further inquiry. Pages 3–39 *in* M. D. Swaine, editor. The ecology of tropical forest tree seedlings. UNESCO, Paris, France.

Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings of the Royal Society B 268:2211–2220.

Wills, C. 1996. Safety in diversity. New Scientist 149:38–42.

Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1–14.

APPENDIX A

Seedling plot network design: description and figures (*Ecological Archives* E091-258-A1).

APPENDIX B

Study species, with adult and seedling abundances and growth form characteristics (*Ecological Archives* E091-258-A2).

APPENDIX C

Results tables for GLMM and GEE models of seedling survival (*Ecological Archives* E091-258-A3).