# Local neighborhood effects on long-term survival of individual trees in a neotropical forest

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The survival of approximately 235 000 individual tropical trees and saplings in the 50 ha permanent plot on Barro Colorado Island (BCI), Panama was analyzed over a 13-year interval (1982–1995) as a function of four biotic neighborhood variables: (i) total stem density; (ii) conspecific density; (iii) relative plant size; and (iv) relative species richness. These neighborhood variables were measured in annular rings of width 2.5 m, extending 30 m from a given focal plant, and in one more distant annulus at 47.5–50 m. Because survival was spatially autocorrelated, a Gibbs sampler and a Monte Carlo Markov chain method were used for fitting an autologistic regression model to obtain unbiased estimates of parameter variances for hypothesis testing. After pooling all species at the community level, results showed that all four variables had significant and often strong effects on focal plant survival. Three of the four variables had negative effects on focal plant survival; relative plant size was the only variable with a positive effect (18% increase in the survival odds ratio). The variables with a negative effect on the survival odds ratio, in order of their effect strength in the nearest annulus, were: stem density (a 70% reduction in the survival odds ratio), conspecific density (50% reduction) and species richness (13% reduction). A guild-level analysis revealed considerable heterogeneity among guilds in their responses to these variables. For example, survival of gap species showed a much larger positive response to relative plant size than did survival of shade-tolerant species. Survival of shrub species was positively affected by conspecific density, but canopy tree survival was negatively affected. Conspecific density negatively affected survival of rare species much more strongly than survival of common species. The neighborhood effects of conspecific density disappear within approximately 12–15 m of the focal plant. Although locally strong, the rapid spatial decay of these effects raises unanswered questions about their quantitative contribution to the maintenance of tree diversity on landscape scales in the BCI forest.

**Key words:** autologistic regression; Barro Colorado Island; Panama; survival; tropical forests.

## INTRODUCTION

The search for the mechanisms that maintain the extraordinarily high number of tree species in tropical moist forests has a long and rich history. Currently, there are more than a dozen viable candidates for mechanisms but, unfortunately, few of them are mutually exclusive (Hubbell 1998,

2001). The relative importance of these mechanisms is therefore a quantitative question that is still open. Uncertainty remains in part because manipulative experimental tests at the community level are difficult at best because the spatial and temporal scales required for natural experiments (*sensu* Diamond 1986) are large and, not least, because of difficulties imposed by the high species richness itself. These forests can be truly megadiverse. The richest of these forests, which are found in South-East Asia and western Amazonia, reach spectacular levels of local tree diversity. For example, the forests in Lambir Hills National Park in Sarawak, and in Yasuni National Park in

Amazonian Ecuador, contain more than 1200 tree species apiece in 50 ha sample plots. These plots each have approximately twice as many tree species as occur in all of North America, north of Mexico, an area that is 46 million times larger.

For the past 20 years, we have been attempting to identify and quantify the coexistence mechanisms in one particular tropical forest, the old growth, moderately species-rich forest on Barro Colorado Island (BCI), Panama. In 1980, two of us (Hubbell & Foster 1983) and our colleagues established a 50 ha plot on the central plateau of BCI, in which we measured, tagged, mapped and identified to species, all free-standing woody plants with a stem diameter of 1 cm at breast height (d.b.h.) or larger. The BCI plot has now been completely recensused five times, the most recent being in the year 2000. The plot contains a steady-state number of about 242 000 stems of approximately 310 species. We chose BCI for the project because it had the best-known flora of any tropical forest at the time (Croat 1978). The premise of our original approach was that, whatever coexistence mechanisms were operating in the BCI forest, they should leave a spatial signature that could be detected by making explicit maps of individual tree locations in the BCI forest. Because trees are sessile organisms (with the exception of pollen and seed dispersal), we hypothesized that these mechanisms could be deciphered by following the temporal evolution of spatial patterns of tree recruitment, growth, and survival in the forest. Our research strategy would later come to be known generally as the individual-based approach (Pacala & Silander 1990), in which the fate of each individual plant is monitored through time as a function of their explicitly known population and community context.

After two decades, we are now in an excellent position to ascertain whether indeed there are detectable spatial signatures of the mechanisms that regulate tree species diversity in the BCI plot. If the answer to this question is *yes*, then we should ask, what is the spatial scale on which these effects are significant? In the present paper we consider the relatively long-term survival of BCI trees as a function of the local biotic circumstances in which each tree is growing. We analyze the survival of individual trees as a function of their local biotic neighbourhood over a 13-year period, from the first

to the fourth census of the BCI plot. The first census was completed in 1982, and the fourth census in 1995. Results from the year 2000 census were not yet available at the time of preparing this paper. Elsewhere, we demonstrate just how essential having large samples and a long-term study are to detecting these effects, at least in saplings and trees > 1 cm d.b.h. (Hubbell *et al.*, unpubl. data, 2001).

Many abiotic as well as biotic factors affect the chances that a tree will survive, and these factors themselves are often spatially autocorrelated, such as soil nutrients, soil moisture, treefall gaps, etc The role of local biotic neighborhood effects in maintaining tree diversity in tropical forests, and in plant communities in general, has been the subject of theory and debate for decades. The importance of neighborhood competition, particularly for light, has long been recognized (e.g. Horn 1971, 1975), and most mechanistic models of forest successional dynamics, particularly those developed for temperate forests, include explicitly light competition and its effects on tree survival and growth (e.g. Shugart 1984; Botkin 1991; Pacala *et al.* 1996). Species diversity is maintained in these models largely by the differing responses of species to light and light gap disturbances. Similar ideas have been proposed for maintaining tree species diversity in tropical forests (e.g. Connell 1978; Hartshorn 1978; Denslow 1980). However, other aspects of the local biotic environment have seldom been included in forest dynamics models, notably the influence of seed and seedling predators and pathogens (Muller-Landau, Dalling, Harms *et al.* In press; Chave *et al.* In press). In the case of temperate forests, this is partly because the empirical measurements of these effects have seldom been made (Packer & Clay 2000). Theories about the role of enemies in maintaining tree diversity have had greater currency in tropical forests, of which the most prominent theory is the Janzen–Connell hypothesis (Janzen 1970; Connell 1971). The hypothesis is that host-specific seed and seedling predators, interacting with seed dispersal, prevent any given tree species from becoming monodominant in a particular patch of forest by differentially killing more seeds and seedlings near to rather than far from seed-bearing parents. Another rarely considered factor is the effect of local stand species

richness *per se*. Wills *et al.* (1997) hypothesized that plants might enjoy a frequency-dependent advantage when imbedded in more species-rich neighborhoods. The premise of this hypothesis is that host-specific predators and pathogens may not as easily find or spread from one host tree to another if host trees are imbedded in a sea of non-host species. We termed this a 'herd immunity' effect, so named for the observation that only partially immunizing a dairy herd can protect the remaining non-immunized animals from contracting a disease. A higher per capita rate of survival when a tree species is rare would tend to maintain local diversity.

At this stage we are not yet ready to evaluate the consequences of local neighborhood effects for the maintenance of tree diversity in the BCI forest. Our more limited goal here is simply to characterize these effects, assess their relative magnitudes, and measure how far they extend spatially from a given plant. Nevertheless, the approach and analysis we have taken are designed for easy incorporation into an individual-based model of BCI forest dynamics. In a previous paper, we analyzed how the local neighborhood, defined as the 20 nearest neighbors to a given focal plant, affected its probability of survival (Hubbell *et al.* In press). However, this approach is problematic for modeling the spatial extent of neighborhood effects because the 20 nearest neighbors do not occur within the same radius of different focal plants. The present analysis is different in two important ways. First, we now describe neighborhood effects for fixed annular distances. We consider how focal plant survival for the 13-year period is affected by neighbors in each of 12 contiguous annular rings of width 2.5 m, extending to an outermost ring at 30 m, and one far annulus from 47.5 m to 50 m. Second, in the previous analysis we treated neighborhood survival rate among the 20 nearest neighbors as a measure of microsite quality; that is, microsites good for survival, irrespective of plant species (Hubbell *et al.* In press). However, this variable is actually a direct measure of the spatial autocorrelation of survival; that is, the dependent variable of interest. In the present analysis, we incorporate explicitly the spatial autocorrelation function of survival into the model, while simultaneously estimating the partial effects on survival of several biotic neighborhood variables.

The neighborhood variables we measured, and our *a priori* expectations for their effects on focal plant survival, were as follows: (i) stem density; (ii) relative plant size; (iii) number of conspecific neighbors; and (iv) species richness. *Stem density* is the number of neighboring plants in a given annulus at distance *i*. Our *a priori* hypothesis was that as stem crowding increases, irrespective of species, focal plant survival should decrease. We also expected that this effect should weaken with distance because plants progressively farther away from the focal plant should have less and less interaction with and impact on the survival of the focal plant. *Relative plant size* is the fraction of plants in a given annulus at distance *i* that are *smaller* in diameter than the focal plant. In this case, our *a priori* hypothesis was that plants larger than their neighbors would be better competitors, so focal plant survival should monotonically increase as the number of neighbors smaller than the focal plant increases. This result is expected from most theories of asymmetric plant competition for light and other resources (Weiner 1990). *Number of conspecific neighbors* is the number of stems at distance *i* of the same species as the focal plant. In this case, our *a priori* expectation was that focal plants with more conspecific neighbors will suffer greater intraspecific competition and potentially greater enemy depredation and should, therefore, have reduced survival rates. *Relative species richness* is the residual of the observed number of species in the neighborhood of a given focal plant, relative to the mean number of species expected among *x* neighbors of all plants in the 50 ha plot. We chose relative species richness rather than species richness *per se* because it removes the confounding between species richness and number of plants in a given annulus. The number of plants per annulus is not constant, and more species are expected among more stems simply from passive sampling. Our *a priori* hypothesis was that focal plant survival would be higher in relatively species-rich neighborhoods; that is, they were richer in species than expected from the mean number of species for a given stem density.

Whether these are the best and final variables to characterize local biotic neighborhood effects remains to be seen. We regard this analysis as a first-pass exploration of neighborhood effects on long-term focal plant survival in the BCI forest.

Whatever effects these or other variables may ultimately be shown to have, we expect that the magnitude and sign of the effects will depend upon the size class of stems considered to be focal plants (e.g. seedlings, saplings, subadult trees and canopy adults), upon the life history guild of a given tree species (e.g. shade tolerant *vs* pioneer species), and upon the abundance class of the species (e.g. common, occasional, and rare species). For example, for shade-intolerant pioneers, one might expect increasing survival rates with increasing size as the crowns of the plants reach the high-light canopy layer. Conversely, shade-tolerant species should be less dependent on relative plant size for survival. Or, considering differences in abundance class, one of the possible reasons for rarity may be that rare tree species suffer stronger density-dependent, Janzen–Connell effects than do common species.

## STUDY SITE AND MEASUREMENTS

The BCI Forest Dynamics Project (FDP) was established in old-growth forest on Barro Colorado Island, a 15 km$^2$ former hilltop located in artificial Gatun Lake in the Panama Canal. There is paleoecological evidence that the old-growth forest on the island has never been cleared for agriculture, although hunters and gatherers used the forest in pre-Columbian times (Piperno 1992). In 1980, a 50 ha permanent plot was laid out on the central plateau of BCI. By 1982, the first census of all free-standing woody plants ≥ 1 cm d.b.h. (excluding woody climbers) was completed. Data collected included stem diameter (d.b.h.), species identity, *x* and *y* coordinates, and measurements of plant vegetative and reproductive condition (see Condit 1998 for details). Tree height–d.b.h. relationships were determined for 50 tree species (O'Brien *et al.* 1995). These measurements revealed a very tight interspecific relationship between diameter and height, indicating that d.b.h. can be used as a good proxy variable for relative plant size and height.

For every plant alive in 1982, we found its neighbors in concentric annuli of width 2.5 m to a maximum radial distance of 30 m and in one distant annulus, 47.5–50 m. Plants near the edge of the plot with incomplete neighborhoods were not included as focal plants. Within each annulus,

we computed the following independent neighborhood variables, as outlined earlier: (i) the total number of stems in the neighborhood (stem density); (ii) the number of neighbors having smaller stem diameters (d.b.h.) in 1982 (relative plant size); (iii) the number of neighbors that were of the same species as the focal plant (conspecific density); and (iv) the number of different species among the neighboring plants in 1982 minus the mean (plot-wide average) number of species expected from the number of stems in the neighborhood (relative species richness).

With increasing annular distance, all of these variables tend to increase as a result of area effects alone. To normalize for area, we rescaled the variables to a 0–1 range to allow valid comparisons across different distances and variables, with the exception of neighborhood species richness (discussed later). We rescaled by finding the global maximum and minimum values for a given variable and a given annulus, and then applying the transform (Observed value − Minimum value)/ (Maximum value − Minimum value). A special procedure was required for normalizing species richness that does not increase linearly with number of stems (Condit, Hubbell, LaFrankie *et al.* 1996; Hubbell, Foster, O'Brien *et al.* 1999, Hubbell *et al.* 2001). We first fit the mean species accumulation curve for each annulus over all focal plants in the analysis (the expected species richness curve). For example, Fig. 1 illustrates the species accumulation curve for the first annulus, 0–2.5 m. Then we computed the residual species richness (relative species richness), as follows. First, we calculated the number of species expected for the observed number of individuals in a given annulus, which was obtained from the mean species accumulation curve. Then we subtracted this expected number of species from the number actually observed in the annulus. Finally, these residuals were rescaled by dividing by the expected number of species for the observed number of stems, resulting in a 1 : 1 scale (all residuals were less in absolute magnitude than the expected number of species).

The dataset was analyzed at two different levels: (i) at the community level, in which all species were pooled; and (ii) at the guild level, using all species whose guild membership was known. At the community level, we fitted autologistic
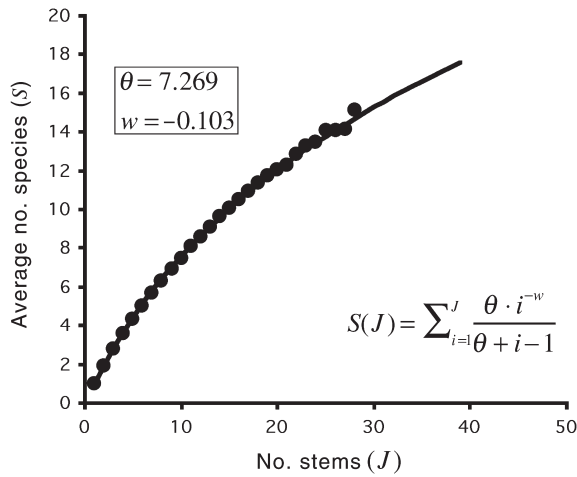
**Fig. 1.** Species–individual curve for the smallest 2.5 m neighborhood annulus. The points are the average number of species observed at a given stem density and the curve is the fitted individual–species model adapted from Hubbell (2001).

regressions on survival at each of 12 concentric annuli 2.5 m in width extending from the focal plant up to a distance of 30 m, and one more distant annulus (47.5–50 m). For the guild level analyses, species were grouped into guilds. In reality there is a continuum of life histories among BCI species (Wright, Korine, Condit *et al.* In press) but, for the purposes of the present analysis, it was convenient to group species into intervals along various axes of life history differentiation.

1. Two extremes of *light guilds* were considered, based on relative shade tolerance: (i) shade-intolerant pioneers (distribution of saplings skewed strongly towards low-height canopy sites); and (ii) shade-tolerant species (distribution of saplings is skewed strongly towards high-height canopy sites). Species were assigned to guilds based on the classification of Welden *et al.* (1991).
2. Four *functional guilds* were created based on the characteristic height of mature plants of member species (shrubs: adults $< 4$ m tall; understorey trees: adults 4–10 m tall; mid-storey trees: adults 10–20 m tall; and canopy trees: adults $> 20$ m tall).
3. Finally, four *abundance classes* were examined, species whose population sizes were in the interval $< 10^2$, $10^2$–$10^3$, $10^3$–$10^4$, or $> 10^4$ individuals, respectively. In addition, we examined

how neighborhood effects differed for small saplings compared with larger plants in the two light guilds.

## STATISTICAL METHODS

The response variable was the survival of the focal plant to 1995. Survival is a binary state variable that was assigned a value of unity if the plant was alive in 1995 and zero if the plant was dead. In logistic regression, the standard method of analysis for binary data, the *odds of survival*, are formally defined as the ratio of the probability of surviving to the probability of dying. Consider, for example, a single independent variable, such as stem density. Let $s_i$ be the probability of survival of a plant $i$ given a given stem density $X_i$. Then, the logistic function for the probability of survival as a function of stem density, and its log odds, are:

$$\Pr(z_i = 1 | \beta_0, \beta_1) = \frac{\exp\{z_i(\beta_0 + \beta_1 X_i)\}}{1 + \exp\{\beta_0 + \beta_1 X_i\}} = S_i \qquad (1)$$

$$\log\left(\frac{S_i}{1 - S_i}\right) = \beta_0 + \beta_1 X_i = \pi_i \qquad (2)$$

The fitted logistic function estimates how the proportion alive or probability of survival changes with stem density. Note that by taking the natural logarithm of the odds, one obtains a linear function of the independent variable, called the *logit transform*, which is symbolized by the Greek letter, pi ($\pi_i$). Note also that $\pi_i$ measures the effect on the logit transform of adding a single stem to stem density.

$$\pi_i[X+1] - \pi_i[X] = \beta_1 \qquad (3)$$

One can generalize the logistic model to accommodate several to many independent variables, and their interactions. However, in the present analysis, we found no significant interactions among the independent variables, so we ignored them. Therefore the generalized logistic model used can be written as:

$$\Pr(z_i | \beta) = \frac{\exp\{z_i(\beta' X_i)\}}{1 + \exp\{\beta' X_i\}} \qquad (4)$$

where $\beta$ is a vector containing $p$ parameters $\beta_0, \beta_1, \ldots \beta_{p-1}$ and $\mathbf{X}_i$ is a vector containing the explanatory variables for plant $i$. An important

tool of logistic regression is the ability to statistically isolate the contribution of each independent variable to a focal plant's survival. This is done using the *odds ratio*, which is not the same as the odds (discussed earlier). The *odds ratio* is defined as $\exp[(\pi_i(X_i+1)-\pi_i(X_i))]$. The most important property of the odds ratio is that it is independent of the particular value of $X_i$; it measures the partial effect of variable $X_i$ on the odds of survival. The numerical value of the odds ratio for variable $X_i$ is $\exp(\beta_i)$. Odds ratios above and below unity indicate positive and negative effects, respectively; and odds ratios of unity indicate no effect.

However, the aforementioned model is insufficient because it assumes that the survival of a focal plant is independent of the survival of its neighbors. It fails to take into account the spatial autocorrelation of survival. This autocorrelation in survival is the potential result of any number of biotic and abiotic factors that may cause survival to be patchy, such as treefall gaps, patchy deep shade, and soil nutrient and soil moisture heterogeneity. Various approaches have been taken to cope with this problem. One approach is to subsample the data, choosing focal plants that are separated far enough so that they share no neighbors, and then to repeat this analysis over and over with a different set of focal plants. However, this approach throws away information, which decreases the resolution and confidence of the model that is being fitted. Also, if the same data are used in the repeated sampling ensembles, the ensemble data are not independent. Another method is to abandon the focal plant approach and use aggregate data on plant survival rates within quadrats. In this approach, one can ask how neighboring quadrats affect survival of plants in the focal quadrat (e.g. Wills *et al.* 1997). However, this approach also does not discard the adjacent quadrats, which themselves are treated as focal quadrats and, once again, there is a non-independence problem.

Spatial statisticians have developed an improved approach, which is actually to model the spatial autocorrelation by an additional term in the logistic regression model (Besag 1974; Cressie 1993). This allows us to weigh the effects of the different neighborhood variables on survival while statistically controlling for the effect of spatial autocorrelation. The simplest conditional

probability expression for such a model for a given plant $i$ is:

$$\Pr(z_i \mid \{z_j : j \neq i\}; \beta, \gamma)$$

$$= \frac{\exp\left\{z_i\left(\beta'X_i + \gamma\sum_{j=1}^{n} a_{ij}z_j\right)\right\}}{1 + \exp\left\{\beta'X_i + \gamma\sum_{j=1}^{n} a_{ij}z_j\right\}} \quad (5)$$

where $a_{ij}=1$ if individuals $i$ and $j$ are neighbors, and is 0 if otherwise, and $\gamma$ is the spatial autocorrelation parameter. The second term in the denominator and numerator is the sum of the number of $j$ neighbors of plant $i$ that survived during the 1982–1995 period. In the present case, we consider those individuals that lay within some distance $r$ of the plant (to 30 m in concentric annuli of width 2.5 m) to be neighbors. In spatial statistics the strength of the spatial autocorrelation is measured by 'gamma' (parameter $\gamma$) which, in the present case, is on survival. The larger the value of $\gamma$, the stronger is the spatial autocorrelation. In the literature, $\gamma$ is called the 'spatial autocorrelation', but it is not a correlation coefficient because its value is not limited to the range $-1$ to $+1$. Note that if $\gamma=0$, the second term in both the numerator and denominator disappear and we recover the original conditional probability logistic regression model (equation 4). This conditional probability model was proposed by Besag (1974), and is dubbed the autologistic regression model.

To find parameters $\beta$ and $\gamma$ that best fit this model for all plants, one needs the likelihood or joint probability function of the model (for all plants in the plot, not just the $i$th plant). For a simple logistic regression model with no spatial autocorrelation, the task is to maximize the product of the conditional probabilities of each plant for the whole plot:

$$\ell(\beta) = \prod_{i=1}^{N} \Pr(z_i \mid \{z_j : j \neq i\}; \beta) \quad (6)$$

However, this likelihood function is not appropriate for the autologistic regression model because equation 6 assumes that the conditional probability of one plant $i$ is independent of the conditional probability of another plant $j$. This might be true if plants $i$ and $j$ were sufficiently far apart, but it will not be true if plants $i$ and $j$ are neighbors.

Using this maximum likelihood estimator will yield unbiased estimates of the parameter values, but the variances of these parameters will be consistently underestimated, hence invalidating hypothesis testing. The correct likelihood function for the autologistic takes into account the lack of independence in survival between plants, and is given by (Besag 1974):

$$\ell(\beta, \gamma) = \frac{\exp\left\{\beta'\sum_{i=1}^{n} x_i z_i + \gamma \sum_{i<j} a_{ij} z_i z_j\right\}}{\sum_{y_1=0}^{1} \sum_{y_2=0}^{1} \cdots \sum_{y_n=0}^{1} \exp\left\{\beta'\sum_{i=1}^{n} x_i z_i + \gamma \sum_{i<j} a_{ij} z_i z_j\right\}}$$

(7)

However, there is a practical problem in computing this likelihood function, which is the vast numbers of terms in the denominator for all possible realizations of the data. Geyer and Thompson (1992) offered a solution to this problem by using a Monte Carlo approach to estimate this likelihood function by using a so-called Gibbs sampler (Geman & Geman 1984). A Gibbs sampler generates a sample of different realizations of the data that can be used to approximate the likelihood function in equation 7. This procedure is called a Monte Carlo Markov Chain (MCMC) simulation because the next estimate depends only on the last data realization (discussed later).

We used a C program to run the Gibbs sampler in a 6-step procedure, as follows:

1. We applied equation 6 to an autologistic model to find initial values of $\beta$ and $\gamma$; this is the so-called pseudo-likelihood estimation (PSE). We implemented the PSE using the freeware GNU version of R for Linux (Ihaka & Gentleman 1996).
2. We started with a realization vector of survival of all the plants (one could start with any arbitrary vector, such as all plants alive, all plants dead or, as we did throughout, the observed survival data).
3. We visited each plant in random order and assigned the condition dead or alive based on the probability of survival calculated from equation 5 with the parameter estimates of $\beta$ and $\gamma$ obtained from PSE.
4. We then stored that value (either 1 or 0) in a new vector which, when complete, became the starting vector for the next iteration.
5. When all plants had been visited, we discarded the starting realization and used the new realization of data for the next iteration.
6. Finally, we went back to step 3 and repeated the operation $N$ times (although there is no hard and fast rule, we typically used 1000 iterations). After a certain number of iterations $M$ (which, in the present case, was often approximately 100), the Gibbs sampler approached an asymptotic stochastic equilibrium. The asymptotic distribution of these realizations approximates the distribution function of the true likelihood (Geman & Geman 1984), thereby allowing one to estimate the likelihood in equation 7.

The mathematical mechanics of the method can be outlined as follows. Equation 7 can be rewritten as follows:

$$\ell(\alpha) = \frac{\exp\{\alpha' T(z)\}}{c(\alpha)}$$

(8)

where the vector $\mathbf{T}_k$, called the 'sufficient statistics' vector, is defined as:

$$\mathbf{T}_k = \begin{bmatrix} \sum_{i=1}^{N} z_i \\ \sum_{i=1}^{N} x_{1i} z_i \\ \sum_{i=1}^{N} x_{2i} z_i \\ \vdots \\ \sum_{i=1}^{N} x_{pi} z_i \\ \sum_{i<j} a_{ij} z_i z_j \end{bmatrix}$$

For a given realization $k$ of the data produced by the Gibbs sampler, $\alpha$ is the vector containing the parameters $\beta$ and spatial autocorrelation $\gamma$: $\alpha = [\beta_0, \beta_1, \beta_2, \ldots \beta_p, \gamma]$ and $c(\alpha)$ is the denominator in equation 7. It can be shown (Geyer & Thompson 1992) that the log of the likelihood function in equation 8 can be approximated by:

$$L^*(\alpha) = \alpha' T(z) - \log\left[\frac{\sum_{t=M}^{N} \exp\{(\alpha' - \varphi) T(z_t)\}}{N - M + 1}\right]$$

(9)

In equation 9, $\varphi$ is a vector containing the initial guesses of parameters $\beta$ and spatial autocorrelation $\gamma$ (which were used to generate the realizations in

the Gibbs sampler), $T(z)$ is the sufficient statistics vector calculated for the observed data, the $T(z_t)$ are each of the sufficient statistics vectors calculated for a given realization $t$ coming from the Gibbs sampler; $N$ is the number of realizations generated by the Gibbs sampler; and $M$ is an adequate number of realizations that are subsequently discarded.

The next step is to estimate the vector $\alpha$ that maximizes the log-likelihood in equation 9 and to obtain estimates of the standard errors of these parameters for hypothesis testing. Although there are many numerical procedures for maximization, the Newton–Rhapson algorithm is the only one that gives estimates both of the parameter values and the standard errors of those parameters (Press *et al.* 1992). To estimate $\alpha$ using the Newton–Rhapson algorithm, update it according to the following equation:

$$\alpha_{i+1} = \alpha_i - \{H(\alpha_i)\}^{-1} g(\alpha_i) \qquad (10)$$

where $g$ and $H$ are the vector and matrix containing the first- and second-order partial derivatives of the likelihood function (equation 9) with respect to parameters $\alpha$. They are also usually known as the gradient vector and the Hessian matrix, respectively. When the second term on the right-hand side becomes negligible, convergence is achieved and the vector $\alpha$ thus obtained contains the estimates of the parameters. The variance–covariance of parameter estimates $\alpha$ is given by:

$$\hat{var}(\hat{\alpha}) = -\{H(\hat{\alpha})\}^{-1} \qquad (11)$$

The standard errors of the estimates can be found by taking the square roots of the diagonal elements of the inverted negative Hessian matrix. As the parameters are normally distributed (Huffer & Wu 1998), it is easy to calculate 95% confidence intervals.

In summary, the steps needed to fit the autologistic regression model are:

1. Using commercial software, fit a logistic regression to the data to obtain initial estimates of the parameters $\beta$ and spatial autocorrelation $\gamma$ (the PSE estimates).
2. Starting with the data as the initial realization, run the Gibbs sampler for $N$ iterations using the parameter estimates obtained from the PSE procedure.
3. Discard the initial $M$ realizations of the data because they represent transient states towards the equilibrium distribution of $T$.
4. Use Newton–Rhapson's algorithm applied to equation 10 to find the asymptotic parameter estimates.
5. Use equation 11 to find the asymptotic standard errors of the parameter values.
6. Finally, construct 95% confidence intervals for the parameter estimates based on a standard normal distribution.

## RESULTS

### Community level results

At the whole community level, the survival of plants in the BCI forest is strongly spatially autocorrelated, but this autocorrelation decays rapidly with increasing distance from focal plants. Figure 2 shows the rapid decline in $\gamma$, the spatial autocorrelation parameter, with increasing distance from the focal plant. Gamma loses approximately half its value within the first 12.5 m, and then declines steadily but more slowly out to the maximal distance examined (50 m), where it becomes indistinguishable from zero. However, it is interesting that the decline in spatial autocorrelation is not monotonic. The maximum spatial autocorrelation is not in the closest annulus, but in the next two annuli, which correspond to the
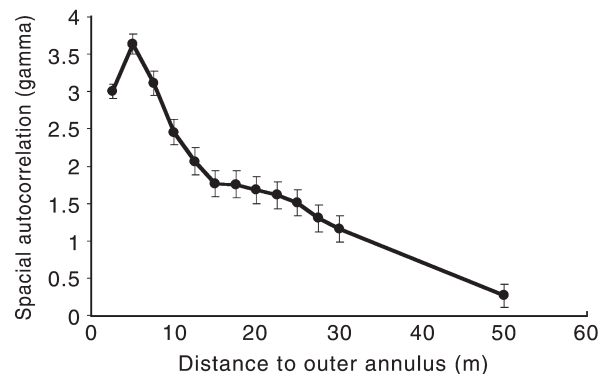
**Fig. 2.** Decay of the spatial autocorrelation in survival ($\gamma$) between 1982 and 1995 as a function of distance (m) as measured in successive annuli of 2.5 m extending from a focal plant to a distance of 50 m. Error bars represent 95% confidence intervals.
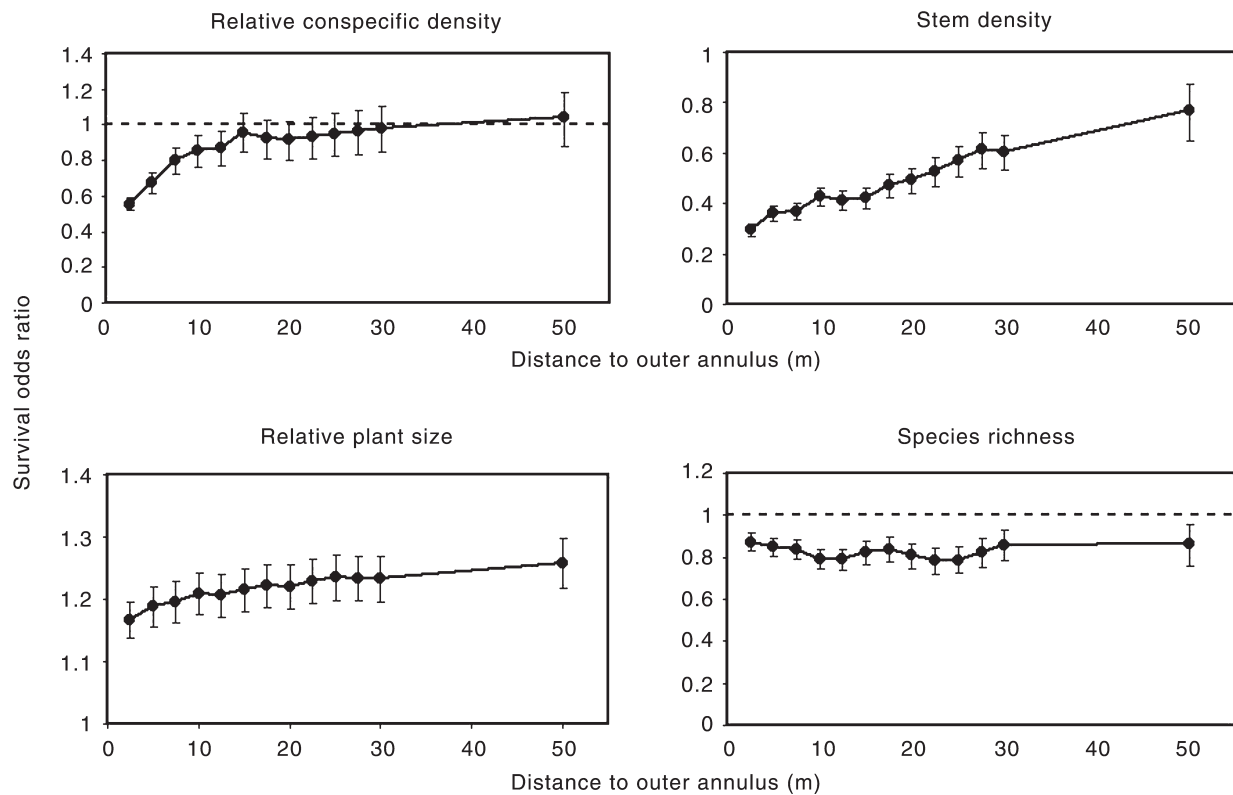
**Fig. 3.** Spatial decay of the effects of four neighborhood variables (odds ratios) as a function of distance (m) in successive 2.5 m annuli extending upto 30 m from focal plants. Error bars represent 95% confidence intervals.

neighborhood ranging from 2.5 m to 7 m from the focal plant.

Figure 3 illustrates how the odds ratios for the four neighborhood variables change as a function of distance from a focal plant in the entire tree community. Odds ratios below unity indicate negative effects on survival, whereas odds ratios greater than unity reflect positive effects on survival. Three of the four variables have significant negative effects on focal plant survival (conspecific density, total stem density and relative species richness); only one variable (relative plant size) has a positive effect on survival. In all cases, the positive or negative effect of a variable remains consistent in sign at all distances.

By far, the variable with the strongest effect on overall plant survival was stem density. The effect of stem density in the innermost annulus was to reduce the odds ratio of survival of the focal plant by nearly 70% (Fig. 3, top right panel). The spatial extent of stem density effects on focal plant survival is quite far, and is still detectable at a distance of 50 m.

The variable with the second strongest effect on overall plant survival was conspecific density. The effect of conspecific density in the innermost annulus (2.5 m) was to reduce the odds ratio of the focal plant by nearly 50% (Fig. 3, top left panel). However, in this case, the strength of this conspecific effect decays spatially very rapidly, becoming undetectable beyond 15 m.

The variable with the third strongest effect was relative plant size (Fig. 3, bottom right panel). Focal plants with larger d.b.h. than their neighbors survived significantly better than smaller plants. The partial effect of relative plant size ranged 17–26%, depending upon the annulus. However, this variable was relatively invariant and uninformative of distance effects, not changing significantly beyond 5 m. In retrospect, we now understand why its effect did not decay with distance (refer to discussion). The only neighborhood annuli that are informative of the effect of relative plant size on focal plant survival are those at very short distances from the focal plant (<5 m).

**Table 1**  Odds ratios and the gamma coefficient of the spatial autocorrelation of survival in the 0–2.5 m annulus, for guilds of shrubs and trees in the Barro Colorado Island forest

| | N | Surv. | Size | Odds ratio Consp. | Richness | Density | Gamma |
|---|---|---|---|---|---|---|---|
| Light guild | | | | | | | |
| Gap | 6 378 | 0.354 | **3.837** | **0.048** | 0.817 | **0.214** | **1.843** |
| Shade tolerant | 213 375 | 0.715 | **1.162** | 0.492 | **0.903** | **0.385** | 1.444 |
| Functional guild | | | | | | | |
| Shrubs | 71 738 | 0.606 | **0.747** | **1.541** | 1.019 | **0.298** | **3.658** |
| Understorey trees | 55 428 | 0.777 | **0.751** | 0.936 | **0.839** | 0.908 | 2.836 |
| Midstorey trees | 41 688 | 0.756 | **1.242** | 1.189 | 1.043 | **0.216** | 2.423 |
| Canopy trees | 59 231 | 0.712 | **1.305** | **0.490** | **0.821** | **0.281** | 2.840 |
| Abundance guild | | | | | | | |
| Very rare ≤100) | 3 975 | 0.639 | **2.109** | **0.179** | 0.709 | **0.114** | **2.660** |
| Rare (>100 and ≤1000) | 42 006 | 0.657 | **1.502** | **0.276** | **0.647** | **0.213** | 2.698 |
| Common (>1000 and ≤10 000) | 96 322 | 0.717 | **1.658** | **0.168** | 1.012 | **0.205** | **2.988** |
| Very common(>10 000) | 85 782 | 0.711 | **0.701** | **0.759** | 0.942 | **0.682** | 2.945 |
| All plants | 228 085 | 0.702 | 1.185 | 0.570 | 0.874 | 0.315 | 3.002 |

N, sample size; Surv., fraction of plants in the guild category that survived between 1982 and 1995; Size, relative plant size; Consp., conspecific density; Richness, relative species richness; Density, total stem density; Gamma, gamma coefficient. Bold-face indicates odds ratios are significant by pseudo-likelihood estimation (PSE) at $P < 0.05$.

The fourth neighborhood variable in strength was relative species richness, which was also largely invariant with distance (Fig. 3, bottom left panel). This variable, contrary to our expectations, had a weak but significantly negative effect on focal plant survival. In the innermost annulus, this variable reduced the odds ratio of survival by approximately 14%, independently of the other neighborhood variables.

## Guild level results

Because neighborhood effects were strongest in the annulus closest to the focal plant, we limit the present report to the guild level results for the odds ratios in only the 2.5 m annulus. At greater distances, the effects are the same qualitatively, but weaker. Table 1 presents the odds ratios for the four neighborhood variables for each guild category tested in the 0–2.5 m annulus. Boldface odds ratios are significant at $P < 0.05$. The guild level analyses indicate that there were sometimes large among-guild differences in the response of survival to the neighborhood variables, differences that are hidden by the community level analyses.

The two light guilds differed strongly in their survival responses, as measured by the odds ratios

(OR). Not surprisingly, gap species respond extremely strongly to being taller than their neighbors (OR = 3.837), much more than shade-tolerant species which, nevertheless, also respond positively (OR = 1.162). Gap species are more vulnerable to competition from neighbors (OR = 0.214 *vs* OR = 0.385 for stem density) and they are more sensitive to conspecifics in their neighborhood (OR = 0.048 *vs* OR = 0.492), but they are more likely to die than shade-tolerant species when their neighborhoods are species-rich (OR = 0.817 *vs* OR = 0.903). Gap pioneers also exhibited larger γ values (stronger spatial autocorrelation) in survival than did shade-tolerant species.

Turning to the four functional guilds, we again found contrasting survival responses to the neighborhood variables, particularly between the functional extremes of shrubs and canopy trees. Shrubs survive worse when they are taller than their neighbors (OR = 0.747), but canopy trees survive better when they are taller (OR = 1.305). Note the monotonic increase in the odds ratio for relative plant size moving from small to large plant growth forms. Conversely, canopy trees survive much worse when they are near conspecifics (OR = 0.490), but shrubs actually survive better with conspecific

neighbors than without them (OR = 1.541). Shrub survival is unaffected by species richness in the neighborhood (OR = 1.019), but canopy tree survival is lower in species-rich neighborhoods (OR = 0.821). All functional guilds, with the possible exception of understorey trees, are similarly negatively affected by neighborhood stem density. The spatial autocorrelation of survival ($\gamma$) is higher in shrubs than in midstorey or canopy trees.

In the case of species grouped into powers-of-10 abundance classes, there were also interesting differences in survival responses to the neighborhood variables. Perhaps the most interesting difference is that the survival of rare species was negatively impacted much more by conspecific density (OR = 0.129) and by stem density (OR = 0.114) than was the survival of the very common species (OR = 0.759 and OR = 0.682, respectively). Rare species were also more likely to survive if they were taller than their neighbors (OR = 2.109), whereas the opposite was true for very common species (OR = 0.701).

Figures 4 and 5 illustrate in greater detail the univariate responses of survival in some of these guilds in the 2.5 m annulus. Figure 4 examines responses to relative plant size. Figure 4a shows the contrasting response of survival in canopy trees compared with understorey shrubs to relative plant size. Shrubs show a 30% decrease in survival from the extreme of having no neighbors that are smaller to having all neighbors that are smaller. Conversely, trees show an approximate 10% increase in survival over the same range of relative plant size. When a comparison is made between gap and shade-tolerant species, gap species show a survival increase of 159% when they are taller than all of their neighbors, whereas shade-tolerant species show only a survival increase of 4% (Fig. 4b). Common and rare species also differ in their responses to relative plant size; rare species show a much larger response (22%) than common species (2%) (Fig. 4c).

Figure 5 illustrates guild responses to neighborhood conspecific density. Figure 5a contrasts the responses of tree and shrub survival to the proportion of neighbors in the 2.5 m annulus that are of the same species. Canopy trees show a strong decrease in survival with an increasing proportion of conspecifics in the neighborhood, exhibiting a 20% decline in survival if they are surrounded
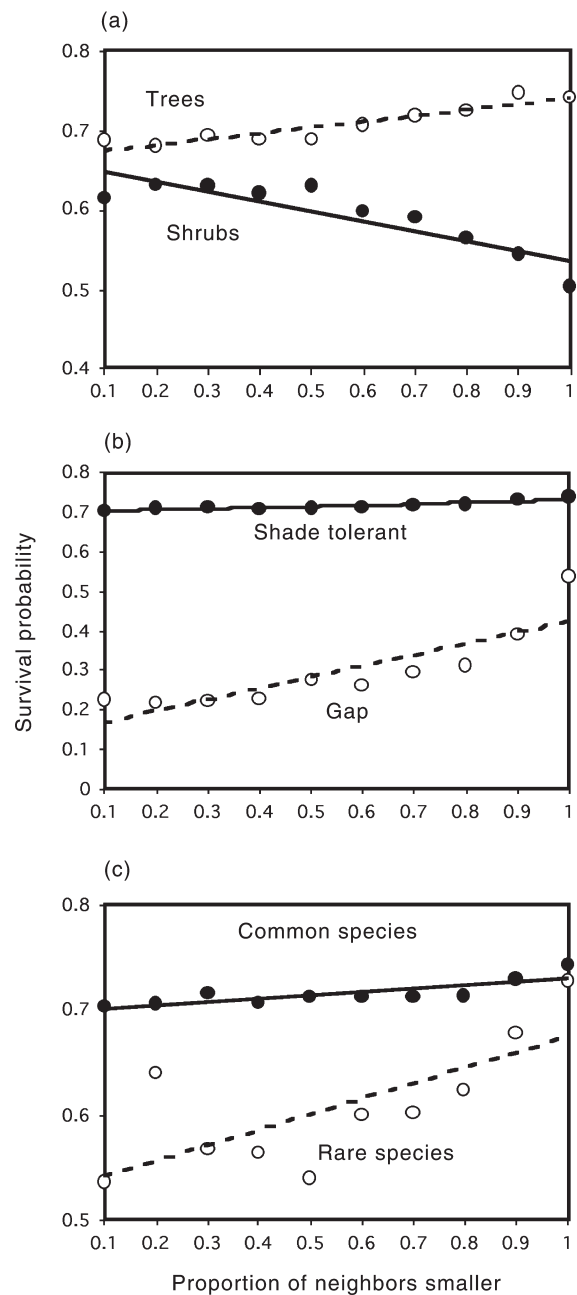


Fig. 4. Comparative effects of relative plant size on the survival of plants (from 1982 to 1995) from different light and functional guilds. (a) Comparison between gap and shade-tolerant species. (b) Comparison between canopy trees and shrubs. (c) Comparison between very abundant (> 10 000 stems) and very rare (< 100 stems) species. Fitted curves are the best line fit through the points (for illustrative purposes only) and do not correspond to the best logistic fits.
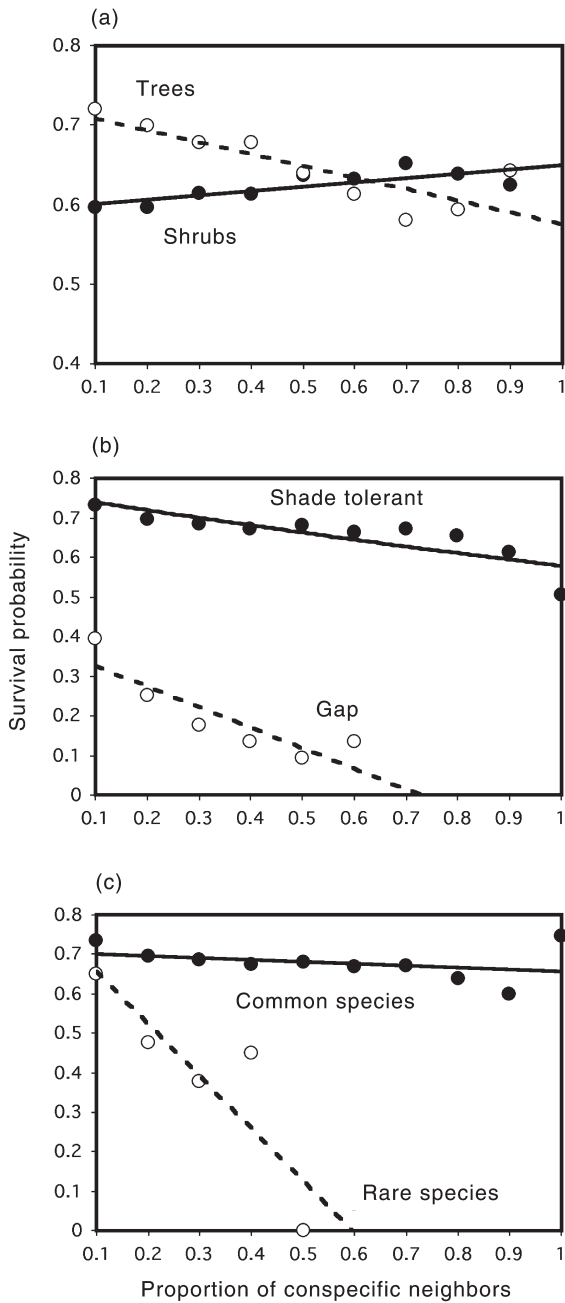
**Fig. 5.** Comparative effects of proportion of conspecifics on the survival of plants (from 1982 to 1995) from different light and functional guilds. Points represent the actual data grouped into ten 0.1 categories. (a) Comparison between gap and shade-tolerant species. (b) Comparison between canopy trees and shrubs. (c) Comparison between very abundant (> 10 000 stems) and very rare (< 100 stems) species. Fitted curves are the best line fit through the points (for visualization purposes only) and do not necessarily correspond to the best logistic fits.
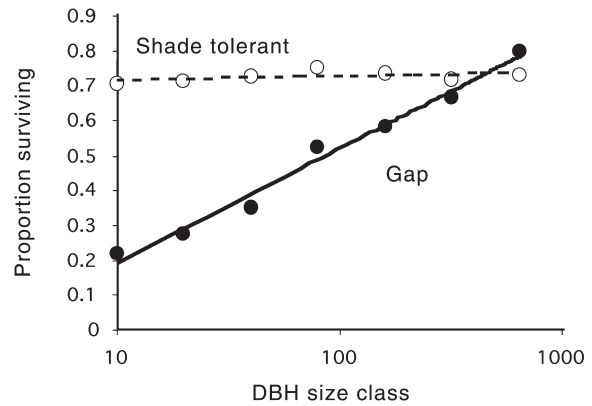


**Fig. 6.** Relationship between stem size [diameter at breast height (d.b.h.), mm] and the probability of survival from 1982 to 1995 for gap and shade-tolerant species.

completely by conspecifics compared with no conspecific neighbors. Surprisingly, as mentioned earlier, shrubs actually do better when they have more conspecific neighbors, increasing in survival by 10% over the same range of conspecific densities. Gap species are very strongly impacted by conspecific neighbors, declining to 0% survival by the point at which 70% of their neighbors are conspecifics (Fig. 5b). This is a far stronger effect than the response of gap species to simple stem density (Table 1). Shade-tolerant species are also affected negatively by conspecific density, but are much less sensitive to neighbors of the same species, declining only 22% in survival. However, the greatest contrast in response to conspecific density is between common and rare species (Fig. 5c). Rare species are extremely sensitive to conspecific density, dropping from 65% survival when there are no conspecific neighbors in the 2.5 m annulus, to 0% survival when 60% of the neighboring plants are of the same species. In contrast, commons species decline much less in survival (6%).

As a final test, we examined how survival was affected by the initial size of a plant, irrespective of its relative size in its local neighborhood (Fig. 6). We show only one relationship in this case: contrasting gap and shade-tolerant species. Gap species show a very strong increase in survival as they grow larger, whereas shade-tolerant species show only a very slight increase in percent survival, which is already high in saplings. It is quite

interesting that when gap species are as large as the shade-tolerant species, their long-term (13 years) survival rates are no different from the shade-tolerant species.

## DISCUSSION

### Interpretation of the odds ratios

Before discussing the results, it should be noted that because the neighborhood variables were expressed as proportions in the present analysis, the odds ratios have a non-standard interpretation. They represent the partial (i.e. controlling for the other variables) proportional effects after normalizing for the number of neighbors. For example, in Table 1, gap species have an odds ratio of 3.84 for relative plant size. This means that the odds of surviving for a gap plant (probability of surviving/probability of dying) are almost four times larger when all neighboring plants are smaller than when none of them are. An overview of the results in Table 1 shows that stem density had the strongest effect on focal plant survival, and was significant in eight out of 10 guild tests. Conspecific density was next in strength, and was significant in seven out of 10 guild tests. Relative plant size was third strongest, yet it was significant in all 10 guild tests. The variable with the weakest effect was species richness, which was significant in only four of 10 guild tests.

### Community wide analysis

The large γ values indicate that spatial autocorrelation in survival was very high in the BCI plot. If all neighbors of a given focal plant were still alive in 1995, its odds of survival were 15–20 times greater than those of a plant whose neighbors were all dead in 1995. Controlling for spatial autocorrelation, the variables that most affected the odds of survival at the community level were relative stem density and relative conspecific density (Table 1). A plant with the highest proportional stem density showed a 70% reduction in the odds of survival relative to a plant with the smallest possible neighborhood stem density. Focal plants with the most conspecific neighbors had an approximately 44% smaller survival odds ratio than plants

with the least conspecific neighbors. The effect of relative species richness was also negative on the survival odds ratio but smaller (13% reduction, respectively). In contrast, plants which were taller than all their neighbors enjoyed a 19% increase in their survival odds compared to plants that were smaller than all their neighbors.

### Guild level analyses

Results in Table 1 and Figs 4 and 5 reveal strong differences in the way that neighborhood variables affected the survival of plants in different light, functional and abundance guilds. In general, gap species had a higher mortality than shade-tolerant species. Relative plant size had a much larger effect on gap species than on shade-tolerant species. Gap species displayed an almost fourfold increase in their odds of survival when they were larger than all their neighbors compared with when they were smaller than all of them. This effect was still positive although smaller for shade-tolerant species (Fig. 4b). The effects of relative plant size were opposite in shrubs and canopy trees (Fig. 5a). While not surprising, to our knowledge, this is the first long-term demographic demonstration of the understorey specialization of shrubs. Understorey and midstorey trees were intermediate between canopy trees and shrubs. Rare species also exhibited a larger advantage when they were taller than all of their neighbors compared with common species (Fig. 4c). However, this is expected because many rare species are also gap species. The effects of conspecific density were also radically different among guilds. Gap species suffered the effects of relative conspecific density much more strongly than did shade-tolerant species (Fig. 5b). Again, the effects of relative conspecific density were opposite in canopy trees and shrubs. Shrubs showed an increase in the odds of survival when imbedded in patches of conspecifics, whereas trees suffered a reduction in the odds of survival when their neighbors were conspecific (Fig. 5a). Finally, rare species suffered much more from conspecific density than common species (Fig. 5c). Relative species richness had a larger negative effect on trees than on shrubs, while relative total density had a stronger negative effect on rare species than on common species. Relative species richness was not significant in gap species, shrubs, midstorey trees,

rare and common species. Total density had negative but similar effects along the remaining guilds.

## Expectations and distance decay of the neighborhood variables

How well did our qualitative expectations match the results? Our expectations were met for three of the four neighborhood variables: stem density, conspecific density and relative plant size. We expected negative effects on survival for the first two of these variables, and positive effects for the third, and this was confirmed. However, we also expected positive effects of neighborhood species richness on focal plant survival, and this expectation was soundly rejected; in every case having statistical significance, the effects were negative. We were surprised by the strength of the neighborhood effects on the 13 years' survival of focal plants. We were impressed by how fast the strength of the conspecific density variable decayed with increasing distance from the focal plant. However, the effects of the other neighborhood variables did not decay as fast (stem density) or did not decay at all (relative plant size and species richness).

The lack of distance decay on the effect of relative plant size can be explained as follows. The relative size of the focal plant was calculated from the proportion of plants that were smaller than the focal plant at each distance. As the annular area increases, they contain more stems, and this proportion becomes more constant as larger annuli approach which have the average distribution of plant sizes in the BCI forest. At larger distances, relative plant size become less and less informative because we are comparing the focal plant's fixed d.b.h. to an increasingly invariant distribution of plant sizes. Therefore, the only informative distances for relative plant size are those close to the focal plant (< 5 m).

The lack of distance decay in relative species richness has a similar explanation. We took into account the effects of increasing stem density on expected numbers of species. Therefore, the variable of relative species richness used in the present study measures the effects of the residual variance in species richness at each distance. Because tree species are remarkably well mixed in the BCI forest, these residuals, expressed as proportions of

maximal values, are therefore quite constant with distance. Hence, once, again the inormative distances for relative species richness are those close to the focal plant.

More remarkable is the quite slow decay of the effects of stem density with distance, which are still causing a significant 20% decline in the odds ratio of survival at 50 m. This suggests that crowding in the forest may have effects that propagate far beyond the crown radii of individual focal plants. It is not entirely clear what these effects might be but one can speculate the possibilities. We know that root systems can radiate much farther from tree boles than their aboveground canopy crown edges; hence, there may be more spatially extensive belowground competition for nutrients and water than might have been anticipated. During droughts, soil water potentials might be drawn over larger areas in dense stands than in sparse ones. Whatever the mechanisms by which stem density reduces focal plant survival, these stem density effects are partial effects; they are not due to variation in conspecific stem densities.

## Significance

To the best of our knowledge, the present study is the first long-term spatially explicit approach to neighborhood survival in any plant community. The results are important in a number of contexts. First of all, the results strongly validate the individual-based, spatially explicit approach that was an assumption of the project from its inception. There is, indeed, a clear and strong signature of spatial dependence in the survival of tropical trees and shrubs in the BCI forests. Second, the results show that several neighborhood variables that are not measured traditionally are important to individual tree survival. In particular, most of the current forest simulators based on temperate forests do not account for the effects of conspecific density ( Muller-Landau, Dalling, Harms *et al.* In press), although many consider stem densities and thinning mortality. Of interest is the fact that conspecific density is quantitatively approximately three times as strong as relative plant size, but the latter variable is what drives survival (competition for light) in most of the current models. The importance of density dependence is often

overlooked in models of forest dynamics, yet it may play a large role in regulating local diversity.

Third, in contrast with our earlier quadrat-based findings (Wills *et al.* 1997), neighborhood species richness had a negative effect on focal plant survival. This finding is important in view of current interest in the potential self-stabilizing effects of diversity because the results of the present study indicate that BCI tree species actually do worse when they are in species-rich areas, independent of conspecific density. The analysis presented here is of very local neighborhood effects. Nevertheless, we could find no positive effects of species richness upto 50 m from the focal plant. Our previous results were not corrected for spatial autocorrelation, and there were other potential colinearity problems with the manner in which density dependence and species richness were modeled and interpreted (Wills *et al.* 1997). The present findings are more definitive in that these effects are well separated in the survival analysis, and the spatial autocorrelation of survival is now modeled properly to yield unbiased estimates of the parameters and their variances.

Finally, a very significant finding is that in the case of the main neighborhood effect postulated to regulate tree diversity in tropical forests, conspecific density dependent mortality, the effects are quite local. The influence of conspecific density on focal plant survival over a 13-year period did not reach farther than about 1–2 canopy tree crown radii (10–50 m). Neighborhood species richness, also postulated to be a mechanism maintaining divrsity, did not result in a frequency-dependent, rare species advantage, but if fact had the opposite effect. The other two variables, total stem density and relative plant size, although they had strong effects on focal plant survival, are unlikely to be important coexistence mechanisms.

These findings raise questions about whether such local biotic neighborhood effects can be responsible for regulating tree diversity in the BCI forest. One result supporting such a role was the finding that the survival of rare species is more susceptible to a given level of conspecific density than common species. This suggests that one reason for their rarity may be that they suffer greater mortality for a given local density of conspecifics than common species. More generally, however, If the actions of density- and frequency-dependent neighborhood variables are limited to a few meters beyond the edge of focal tree crowns, then how can these effects regulate adult abundances of tree species on much larger spatial scales? How do we explain the larger landscape spatial heterogeneity in tropical tree populations and species diversity observed in the BCI plot (Hubbell, Foster, O'Brien *et al.* 1999; Condit, Ashton, Baker *et al.* 2000)? It may be that very subtle and long-term effects are involved that are simply too weak to be detected over a 13-year period. This is not unreasonable because even 13 years represents < 10% of the lifespan of most canopy tree species in the BCI forest. A second possibility is that the processes that regulate species diversity in the BCI forest are already finished by the time saplings have reached 1 cm d.b.h. and have entered the primary census. Recently, results of a 14-year study of seed rain and seedling germination in the BCI 50 ha plot have found very strong and community-wide evidence of species-specific density dependence in the seed-to-seedling transition (Harms *et al.* 2000). Saplings that are 1 cm in d.b.h. have an estimated median age of 17 years (Hubbell 1998), providing a long time for density dependent processes to work their effects on survival before plants are recruited into our main census. A third possibility is that the larger spatial patterns of tropical tree species and diversity in the BCI plot are driven by seed dispersal and dispersal limitation (Hubbell, Foster, O'Brien *et al.* 1999). Each of these possibilities will become more amenable to study as the long-term research on the BCI forest continues, and we look forward to the challenge of their resolution.

## ACKNOWLEDGEMENTS

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