

## CHAPTER FOUR

# Neighbourhood effects on sapling growth and survival in a neotropical forest and the ecological equivalence hypothesis

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### Introduction

In 1980 S. P. Hubbell and R. B. Foster began a long-term, large-scale study of tropical forest dynamics on Barro Colorado Island (BCI), Panama. The objective of the study was to test competing hypotheses about the maintenance of high tree species richness in the BCI forest, and in tropical moist forests more generally. Hubbell and Foster established a 50-ha permanent plot on the summit plateau of BCI, within which all free-standing woody plants with a stem diameter at breast height (DBH) of a centimetre or larger were tagged, measured, mapped and identified by 1982. Subsequent complete censuses of the BCI plot have been conducted from 1985 to 2000 at 5-year intervals. In setting up the BCI plot, Hubbell and Foster (1983) reasoned that whatever diversity-maintaining mechanisms were important, they would have to operate in a spatially dependent manner in communities of sessile plants such as the BCI tree community, which meant that the trees had to be mapped. A decade earlier, Janzen (1970) and Connell (1971) had independently proposed a spatially explicit ‘enemies hypothesis’, now known as the Janzen–Connell hypothesis. They hypothesized that host-specific seed and seedling predators were responsible for maintaining tropical tree diversity by causing dependence on density and frequency (rare species advantage), through an interaction between seed dispersal and density-dependent seed predation.

In 1980, there were essentially just two principal tropical forest diversity theories to test: the enemies hypothesis and its variants, and the ‘intermediate disturbance’ hypothesis (Connell 1977) and its variants that invoked a role for disturbances associated with opening, growth and closure of light gaps (e.g.

Ricklefs 1978; Hartshorn 1978; Orians 1982; Denslow 1987). These ideas were intellectual descendants of the 'fugitive species' concept (Hutchinson 1961) and  $r$ - $K$  selection (MacArthur & Wilson 1967), which are now embodied in diversity theories that depend on a tradeoff between dispersal ability and competitive ability among species (Tilman 1994; Hurtt & Pacala 1995).

Since the plot was established, a large number of new hypotheses have been put forth to explain tree diversity in tropical forests (see Hubbell 1997, 2001; Terborgh *et al.* 2001; Wright 2002 for reviews). Many of these hypotheses are not mutually exclusive, so the challenge in discriminating among them is not qualitative, but quantitative. One of these newer hypotheses is the 'ecological equivalence' hypothesis. According to this hypothesis many if not all trophically similar species are, to at least a first approximation, demographically and competitively alike on a per capita basis. The ecological equivalence hypothesis arises out of symmetric neutral theory (Hubbell 2001), but has older roots (Hubbell 1979; Goldberg & Werner 1982; Schmidha & Ellner 1985). This hypothesis contrasts with contemporary niche assembly theory (Chase & Leibold 2003), which emphasizes the importance of fundamental asymmetries or differences among species. Symmetric neutral theory fits patterns of relative species abundance remarkably well at the spatial scale of the entire 50-ha BCI plot, as new analytical solutions to the theory show (Volkov *et al.* 2003), contrary to recent assertions (McGill 2003). However, there is strong empirical evidence that symmetry is broken at smaller spatial scales. Ecological dominance deviations – deviations from the expected relative abundances under symmetric neutrality – can be detected in many BCI tree species, especially at the spatial scale of hectares ( $100 \times 100$  m) or smaller. This suggests that species or functional group differences cause symmetry to be broken at small spatial scales and that the approximation of symmetry may apply better on larger scales, possibly because these larger scales average out environmentally driven niche differentiation.

Previously, we examined the effects of local biotic neighbourhood on the survival of focal trees and saplings at the community level (Hubbell *et al.* 2001). We found strong, pervasive, always negative, conspecific density effects, and much weaker effects of relative plant size and neighbourhood species richness. Density dependence per se does not invalidate symmetry, however, so long as all species of equivalent abundance experience the same density effects (Chave *et al.* 2002; Hubbell & Lake 2003). Recently, we have extended the neutral theory to incorporate symmetric density- and frequency-dependence (Banavar *et al.* 2003). However, in the empirical studies, we have found, in fact, that the strength of the conspecific density effects varies among functional groups of BCI species, indicating that symmetry is broken among, if not within, these life-history guilds (Hubbell *et al.* 2001). The reduction in the survival of focal plants due to conspecific neighbours was greater in canopy tree species than in shrub species, and greater in gap species than in shade-tolerant species. We

evaluated the effects of neighbours at different distance intervals: 0–2.5 m, 2.5–5 m, etc., to a distance of 30 m. We found that all effects decayed to mean field (background) within 10–15 m, so the neighbourhood effects were all extremely local.

In this paper we have taken a somewhat different modelling approach to neighbourhood effects, and we analyse both survival and growth for individual species. We assume, as do most current models of such effects, that there is a direct effect of a neighbour's size, and an inverse effect of a neighbour's distance, on the focal plant's growth and survival. The primary question posed here is, to what extent is the ecological equivalence hypothesis supported, and to what extent can it be rejected? Ecological equivalence, for the purpose of these neighbourhood analyses, means that it does not matter to what species or functional group a neighbour belongs, because all of the neighbour's significant effects on focal plant survival and growth are captured by information about the neighbour's size and distance from the focal plant. Whether the ecological equivalence hypothesis can or cannot be rejected is likely to depend on the life-history stage, the species and the functional guild to which the species belongs. Thus, some stages, such as seedlings or small saplings, may be more sensitive to who their neighbours are, and some species and entire functional groups may also be more sensitive than others.

Suppose we assume for the moment that species are indeed ecological equivalents. How could such equivalence arise? The first way to be ecologically equivalent, or nearly so, is through common descent (Federov 1966; van Steenis 1969). This possibility is regarded as sufficiently commonplace to be a major concern for independence assumptions in hypothesis testing in comparative evolutionary biology (Harvey & Pagel 1991). Related species are more likely to respond in the same or similar ways to the mechanisms that are ultimately responsible for diversity. Sister taxa are more likely to have similar resource requirements or share enemies that would keep them in check through Janzen–Connell effects. Tests of community assembly taking phylogenetic relationships into account do tend to show that closely related species occur together more often than expected by chance at a variety of spatial scales (Webb 2000). This finding is generally unexpected from classical niche assembly theory, which predicts greater competition and niche separation among closely related species. A second way that equivalence may arise is through diffuse coevolution in response to a highly unpredictable and diverse neighbourhood (Connell 1980; Hubbell & Foster 1986). If species have unpredictable neighbours over their evolutionary lifespans, which will be especially true in species-rich communities, then species will tend to converge on the same life histories adapted to the long-term statistical average of the neighbourhood conditions that they all experience. If this is the case, we should see minimal if any variation among neighbouring species in their effects on the growth and survival of focal species. If variation among species in these

effects does indeed exist, it will be among functional groups of species with distinct life histories (e.g. gap vs. shade-tolerant species).

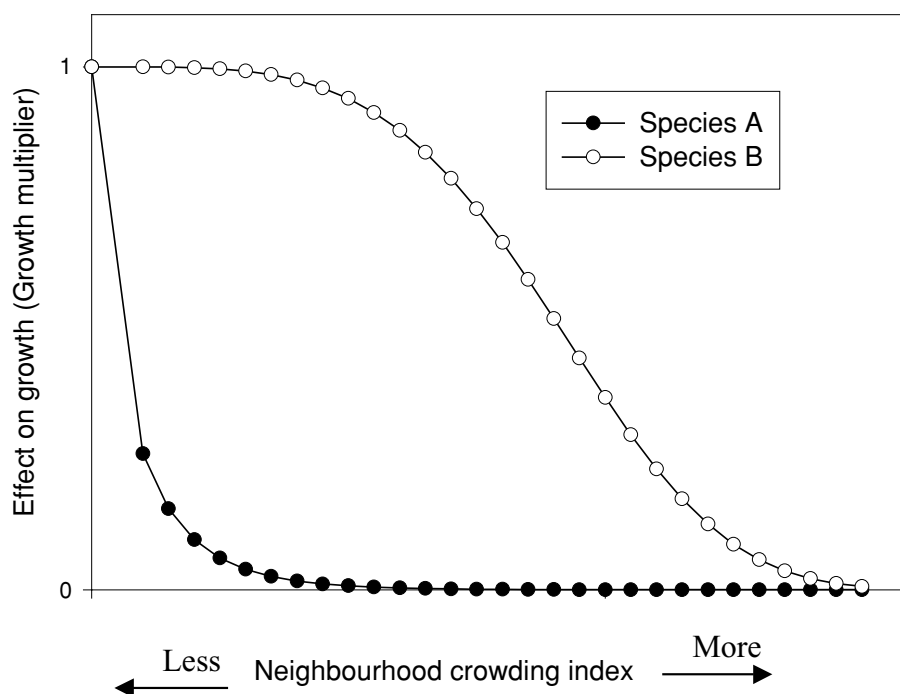
In this paper we address three primary questions. (1) Do all neighbour species have the same effects on focal plant growth and survival? (2) Is common descent a good predictor of the strength of the effects? (3) How does probability of coexistence as adults influence the strength of neighbourhood interactions? We note that these neighbour effects are expected to be generally negative, and they may involve direct competition, or they may be indirect competitive effects, such as density-mediated contagion of pathogens. We address these questions by comparing the ability of different models to explain variation in individual tree growth and survival of focal species. In the first model, neighbours are not identified in terms of species or functional group, but are treated as equivalent. In the second model, neighbours of the same species as the focal individual are separated from neighbours of other species. In the third model, neighbours are classified by degree of relatedness into conspecifics, neighbours belonging to the same plant family (confamilials) but not the same species, and neighbours belonging to other plant families. In the final model, neighbours are classified as conspecifics or other species, and the latter class is divided into gap species and shade-tolerant species. Uriarte *et al.* (2004a) provide a more detailed description of the model and the results for growth.

## Methods

Our modelling approach follows a long tradition in forest ecology, and assumes that each species has a maximum rate of growth and survival, and that the realized growth and survival rates of the focal species are reduced additively by competitive effects, direct and indirect, from neighbours (e.g. Bella 1971; Hegyi 1974; Zeide 1993; Wimberly & Bare 1996; Wagner & Radosovich 1998; Vettenranta 1999). The general formula for growth is:

$$\text{Realized (predicted) growth} = \text{maximum growth} \cdot \exp(-C \cdot \text{NCI}^D) \quad (4.1)$$

The function for survival is strictly analogous, except that in this case we predict the realized probability of survival instead of realized growth rate. In the case of survival, however, the variable is not continuous, but binary, because an individual either lived (1) or died (0). We model neighbour effects using a negative exponential function. First we calculate a combined index of neighbour effects, the neighbourhood crowding index (NCI), and then we fit parameters  $C$  and  $D$  in Eq. (4.1). In our formulation of the effects of crowding on the growth and survival of individual trees we wanted a function that could model species that respond differently to neighbours. We used Eq. (4.1) because it allows for considerable flexibility in the shape of the functional dependence of growth and survival on the NCI. For example, Fig. 4.1 illustrates very different responses by two hypothetical species, one that is very sensitive to neighbourhood competition and



**Figure 4.1** Effects of neighbourhood competition on target growth for two hypothetical species. Species A shows a sharp exponential decline in growth with a small amount of crowding. The growth of species B declines only after a minimum crowding threshold has been reached.

shows a rapid exponential decline in realized growth with increases in NCI, and another species that shows a minimum threshold response. The ratio of parameter  $D$  to parameter  $C$  is small in the first species and larger in the second species.

The neighbourhood crowding index is defined as follows:

$$NCI_{focal,k} = DBH_{focal,k}^{\gamma} \sum_{i=1}^S \sum_{j=1}^{n_i} \lambda_{ik} \frac{DBH_j^{\alpha_k}}{Distance_j^{\beta_k}} \quad (4.2)$$

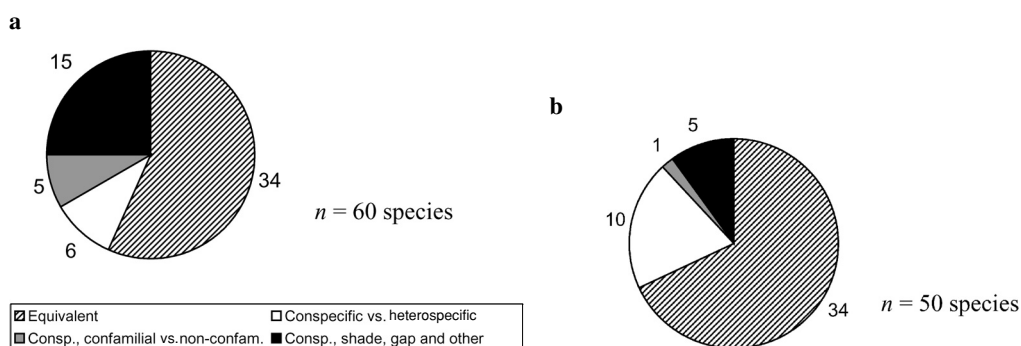
Here  $NCI_{focal,k}$  is the specific value of the neighbourhood crowding index for a given focal individual of species  $k$ , and  $DBH_{focal,k}^{\gamma}$  is the DBH of that focal individual, weighted by an exponent  $\gamma$  that characterizes the sensitivity of individuals of that given DBH of the focal species  $k$  to neighbourhood effects. The double sum is over  $S$  species and the  $n_i$  neighbours of each species  $i$  in the focal individual's neighbourhood of estimated maximum radius  $R$ . The parameter  $\lambda_{ik}$  is a pairwise competition coefficient analogous to Lotka–Volterra competition coefficients, and it estimates the per capita effects of species  $i$  on species  $k$ . Parameters  $\alpha_k$  and  $\beta_k$  allow nonlinear scaling of the effects of neighbour size

(DBH) and distance on focal species  $k$ . The function in Eq. (4.2) leaves unspecified what the effective neighbourhood size of a focal plant is. Based on our previous analyses that showed that neighbourhood effects were undetectable beyond about 12 m, we chose an initial neighbourhood radius of 15 m. The fitting procedure then estimates what neighbourhood radius ( $R$ ) within this 15 m range best explains patterns of growth and survival for each species.

Although Eq. (4.2) is a suitable functional form for  $NCI$  measures in temperate forests that have relatively small numbers of tree species, it is impractical to estimate  $S$  competition coefficients for each species in species-rich tropical tree communities such as BCI. We therefore grouped species into two to four classes or functional groups, and estimated the competition coefficients of these classes with the focal species. There were seven parameters in addition to competition coefficients to estimate for a given focal species: maximum growth (probability of survival) rate, effective neighbourhood radius ( $R$ ),  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $C$  and  $D$ .

We obtained the data for testing the models from the 1990 and 1995 censuses of the BCI 50-ha plot. We adopted maximum likelihood methods and used an optimization procedure to find model parameter values that maximized the likelihood of obtaining the observed overall growth and survival data for each focal species, given the particular model. We used simulated annealing (a global optimization procedure) to determine the most likely parameter values (i.e. the parameter values that maximize the log likelihood), given our observed data (Goffe *et al.* 1994). We then used Akaike's Information Criterion ( $AIC_c$ ) corrected for small sample size to identify the best model among the set of models included in our analyses. The model with the smallest value for  $AIC_c$  is the most parsimonious and therefore the best model among a set of candidate models (Burnham & Anderson 2002). These maximum likelihood methods assume independence of focal individuals, but the growth and survival data are spatially autocorrelated on a spatial scale of about 5 m. Although variances and confidence limits will be slightly underestimated, parameter estimates themselves, and therefore model selection, are generally unaffected by spatial autocorrelation among the observations (Hubbell *et al.* 2001). This is an advantage of likelihood methods over traditional parametric approaches. Further details of the likelihood and fitting methods can be found in Uriarte *et al.* (2004b).

We evaluated the comparative fit of four models of the effects of neighbour groups. Model 1 represented the ecological equivalence hypothesis (species of neighbour unimportant). In Model 2, we distinguished two classes: conspecific neighbours and heterospecific neighbours. In Model 3, we distinguished three classes of neighbours: conspecifics, confamilial but not conspecific neighbours, and other more distantly related neighbours. In Model 4, we included three classes of neighbours, but this time we distinguished conspecifics from heterospecifics divided into gap species and shade-tolerant species. Models 1, 2 and 3 were nested in that order with Model 3 being the largest, while model 4



**Figure 4.2** Number of species included in the analyses supporting alternative growth (a) and survival (b) models. The equivalent neighbours model represented the ecological equivalence hypothesis (species of neighbour unimportant). The second model distinguished between two classes: conspecific and heterospecific neighbours. In model 3, we distinguished three classes of neighbours: conspecifics, confamilial but not conspecific neighbours, and other more distantly related neighbours. In model 4, we included three classes of neighbours, but this time we distinguished conspecifics from heterospecifics divided into gap species and shade-tolerant species.

was distinct. We ran the four growth models on 60 focal species and survival models on 50 species. We analysed shade-tolerant species with >500 individuals and gap species, which are less abundant, with >200 individuals, and the focal individuals had a DBH of 1–4 cm. In the case of survival analyses, we analysed focal individuals of 1–2 cm DBH, the size range at which most mortality occurs. There were fewer total stems in the survival analysis, so we reduced the cutoff abundance for gap species to >100 individuals. Among the species studied for growth, there were seven gap species and 53 shade-tolerant species. Classified by growth form, there were 22 canopy species, 21 midstorey species and 17 understorey treelets. Among the species studied for survival, there were six gap species and 44 shade-tolerant species. By growth form, there were 18 canopy species 20 midstorey species and 12 understorey treelets.

## Results

### Growth

For over half of the focal species (34 out of 60), the growth model best supported (with the lowest  $AIC_c$  value) was Model 1, which treated all neighbours as ecologically equivalent (Table 4.1, Fig. 4.2a). For the remaining 26 out of the 60 species in the analyses, there was striking variation in the effects of crowding (as measured by  $\lambda_s$ , our species-specific crowding index), depending on the identity both of the focal tree and of its neighbours (Table 4.1, Fig. 4.1a). For six out of these 24 focal species, the best supported model was model 2, which differentiated between conspecific and heterospecific neighbours. Conspecific neighbours

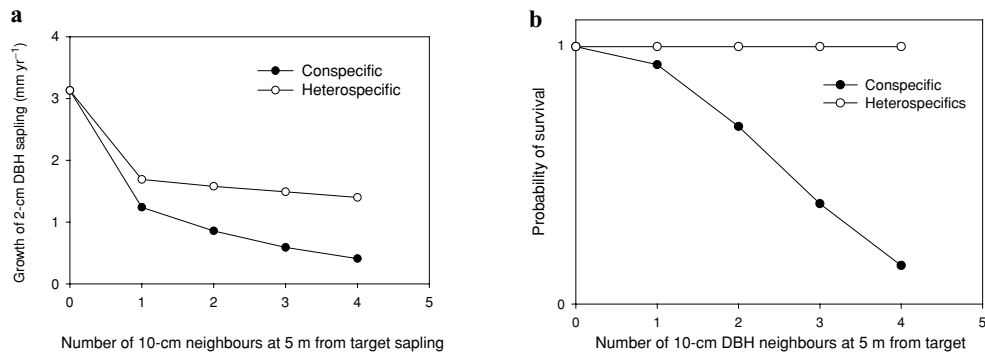
Table 4.1 Best growth and survival models for tree species included in the analyses

Genus	Species	Family	Light guild	Best growth model	Best survival model
<i>Alseis</i>	<i>blackiana</i>	RUBIACEAE	Shade	Conspecific/Heterospecific	Equivalence
<i>Aspidosperma</i>	<i>cruenta</i>	APOCYNACEAE	Shade	Equivalence	NA
<i>Beilschmiedia</i>	<i>pendula</i>	Lauraceae	Shade	Conspecific/Heterospecific	Gap/Shade
<i>Brosimum</i>	<i>alicastrum</i>	MORACEAE	Shade	Equivalence	NA
<i>Catophyllum</i>	<i>longifolium</i>	CLUSIACEAE	Shade	Conspecific/Confamilials/Others	Equivalence
<i>Casearia</i>	<i>aculeata</i>	FLACOURTIACEAE	Gap	Equivalence	NA
<i>Cassipourea</i>	<i>elliptica</i>	RHIZOPHORACEAE	Shade	Equivalence	Equivalence
<i>Chrysophyllum</i>	<i>argenteum</i>	SAPOTACEAE	Shade	Equivalence	Conspecific/Heterospecific
<i>Cordia</i>	<i>bicolor</i>	BORAGINACEAE	Gap	Gap/Shade	Conspecific/Heterospecific
<i>Cordia</i>	<i>lasiocalyx</i>	BORAGINACEAE	Shade	Equivalence	Equivalence
<i>Coussarea</i>	<i>curvigemma</i>	RUBIACEAE	Shade	Conspecific/Heterospecific	Conspecific/Heterospecific
<i>Croton</i>	<i>bilbergianus</i>	EUPHORBIACEAE	Gap	Gap/Shade	Gap/Shade
<i>Cupania</i>	<i>sylvatica</i>	SAPINDACEAE	Shade	Equivalence	Conspecific/Confamilials/Others
<i>Desmopsis</i>	<i>panamensis</i>	ANNONACEAE	Shade	Gap/Shade	Equivalence
<i>Drypetes</i>	<i>standleyi</i>	EUPHORBIACEAE	Shade	Gap/Shade	Conspecific/Heterospecific
<i>Eugenia</i>	<i>coloradensis</i>	MYRTACEAE	Shade	Equivalence	Equivalence
<i>Eugenia</i>	<i>galalonensis</i>	MYRTACEAE	Shade	Equivalence	Equivalence
<i>Eugenia</i>	<i>nesiotica</i>	MYRTACEAE	Shade	Equivalence	Equivalence
<i>Eugenia</i>	<i>oerstediana</i>	MYRTACEAE	Shade	Equivalence	Equivalence
<i>Faramea</i>	<i>occidentalis</i>	RUBIACEAE	Shade	Gap/Shade	Gap/Shade
<i>Garcinia</i>	<i>intermedia</i>	CLUSIACEAE	Shade	Equivalence	Equivalence
<i>Garcinia</i>	<i>madruno</i>	CLUSIACEAE	Shade	NA	Equivalence
<i>Guarea</i>	<i>guidonia</i>	MELIACEAE	Shade	Equivalence	Conspecific/Heterospecific
<i>Guarea</i>	'fuzzy'	MELIACEAE	Shade	Conspecific/Confamilials/Others	Equivalent
<i>Guatteria</i>	<i>dumetorum</i>	ANNONACEAE	Shade	Equivalence	Equivalence
<i>Heisteria</i>	<i>concinna</i>	OLACACEAE	Shade	Conspecific/Heterospecific	NA
<i>Herrania</i>	<i>purpurea</i>	STERCULIACEAE	Shade	Equivalence	NA
<i>Hirtella</i>	<i>triandra</i>	CHRYSOBALANACEAE	Shade	Gap/Shade	Gap/Shade
<i>Inga</i>	<i>marginata</i>	FABACEAE:MIMOS.	Gap	Gap/Shade	Equivalence
<i>Inga</i>	<i>nobilis</i>	FABACEAE:MIMOS.	Shade	Equivalence	Conspecific/Heterospecific



<i>Inga umbellifera</i>	FABACEAE:MIMOS.	Shade	Equivalence	Equivalence
<i>Lacistema aggregatum</i>	FLACOURTIACEAE	Shade	Gap/Shade	Equivalence
<i>Laetia thaminia</i>	FLACOURTIACEAE	Shade	Conspecific/Heterospecific	NA
<i>Lonchocarpus latifolius</i>	FABACEAE:FABOID.	Shade	Gap/Shade	Equivalence
<i>Maquira costaricana</i>	MORACEAE	Shade	Equivalence	Equivalence
<i>Miconia affinis</i>	MELASTOMATACEAE	Gap	Equivalence	Equivalence
<i>Miconia argentea</i>	MELASTOMATACEAE	Gap	Gap/Shade	Equivalence
<i>Pentagonia macrophylla</i>	RUBIACEAE	Shade	Equivalence	NA
<i>Picramnia latifolia</i>	PICRAMNIACEAE	Shade	Equivalence	Equivalence
<i>Pouteria reticulata</i>	SAPOTACEAE	Shade	Equivalence	Equivalence
<i>Prioria copalifera</i>	FABACEAE:CAESAL.	Shade	Gap/Shade	Conspecific/Heterospecific
<i>Protium costaricense</i>	BURSERACEAE	Shade	Conspecifics/Confamilials/Others	Equivalence
<i>Protium panamense</i>	BURSERACEAE	Shade	Conspecifics/Confamilials/Others	Equivalence
<i>Protium tenuifolium</i>	BURSERACEAE	Shade	Conspecifics/Confamilials/Others	Equivalence
<i>Pterocarpus rohrii</i>	FABACEAE:FABOID.	Shade	Gap/Shade	Equivalence
<i>Quararibea asterolepis</i>	BOMBACACEAE	Shade	Equivalence	Equivalence
<i>Randia armata</i>	RUBIACEAE	Shade	Equivalence	Equivalence
<i>Simarouba amara</i>	SIMAROUBACEAE	Gap	Equivalence	Equivalence
<i>Sloanea terniflora</i>	ELAEOCARPACEAE	Shade	Equivalence	NA
<i>Swartzia simplex</i>	FABACEAE:CAESAL.	Shade	Gap/Shade	Equivalence
<i>Swartzia simplex</i>	FABACEAE:CAESAL.	Shade	Gap/Shade	Equivalence
<i>Swartzia simplex</i>	FABACEAE:CAESAL.	Shade	Equivalence	Equivalence
<i>Tabernaemontana arborea</i>	APOCYNACEAE	Shade	Equivalence	Equivalence
<i>Tachigalia versicolor</i>	FABACEAE:CAESAL.	Shade	Gap/Shade	Gap/Shade
<i>Talisia nervosa</i>	SAPINDACEAE	Shade	Equivalence	NA
<i>Talisia princeps</i>	SAPINDACEAE	Shade	Equivalence	Equivalence
<i>Tetragastris panamensis</i>	BURSERACEAE	Shade	Conspecific/Heterospecific	Equivalence
<i>Trichilia pallida</i>	MELIACEAE	Shade	Equivalence	NA
<i>Trichilia tuberculata</i>	MELIACEAE	Shade	Gap/Shade	Conspecific/Heterospecific
<i>Unonopsis pittieri</i>	ANNONACEAE	Shade	Equivalence	NA
<i>Virola sebifera</i>	MYRISTICACEAE	Shade	Equivalence	Conspecific/Heterospecific
<i>Xylopia Macrantha</i>	ANNONACEAE	Shade	Equivalence	Conspecific/Heterospecific

We used data for the 1990–1995 census interval in the BCI 50-ha plot. The best model was determined using Akaike's Information Criterion corrected for small sample size. NA indicates that the species was not included in that set of analyses.

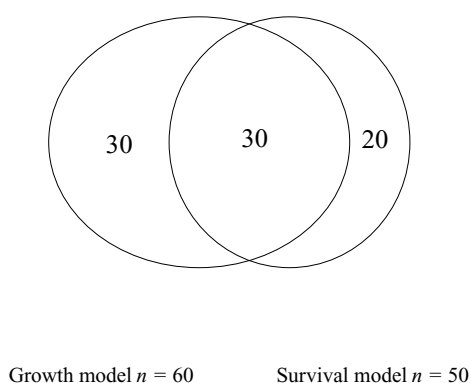


**Figure 4.3** Effects of neighbours for the most parsimonious model of growth of *Alseis blackiana* (a) and survival of *Prioria copaifera* (b). Decrease in growth for *Alseis blackiana* was calculated using the following maximum likelihood parameter values: Max. growth = 3.13,  $C = 9.01$ ,  $D = 1.01$ ,  $\alpha = 1.30$ ,  $\beta = 0.19$ ,  $\gamma = -0.45$ ,  $\lambda$  (conspecific) = 1;  $\lambda$  (heterospecific neighbour) = 0.43.

always had much worse effects on the growth of the focal sapling than did heterospecific neighbours (Fig. 4.3a). A second group of five focal species supported Model 3, the model that distinguished among conspecific, confamilial and non-confamilial neighbours. Conspecific or confamilial effects on sapling growth of all five focal species were greater than the effect of non-confamilial neighbours. Fifteen species supported model 4, which distinguished among conspecifics and heterospecific gap or shade-tolerant neighbours. Once again, conspecifics effects were stronger than the effects of light guild of heterospecifics. Functional group similarity was also a good predictor of the strength of neighbourhood interactions among species. The effect of gap species on the growth of shade-tolerant targets was generally weaker than the effect of other shade-tolerant neighbouring species. In contrast, the effect of gap species on the growth of gap species was always stronger than the effect of shade-tolerant neighbours (see Uriarte *et al.* (2004b) for details).

### Survival

Three-quarters of focal species (34 out of 50) supported survival Model 1, the model in which all neighbours are treated as ecologically equivalent (Fig. 4.2b, Table 4.1). The remaining 16 species in the analyses showed variation in the effects of crowding, depending on the identity both of the focal tree and of its neighbours (Fig. 4.2b, Table 4.1). For 10 of these focal species, the model best supported distinguished between conspecific and heterospecific neighbours. Survival effects were consistent with the results from our growth analyses: negative effects from conspecific neighbours on survival of the focal sapling were always much stronger than heterospecific effects (Fig. 4.3b). Five species supported survival Model 4, the model that distinguished among conspecifics and two



**Figure 4.4** Number of species included in the analyses with similar responses to neighbour groupings for both growth and survival. Intersection shows number of species that supported the equivalent competitor model (model 1) or a distinct neighbour model (models 2–4) for both growth and survival.

categories of heterospecific neighbours, gap species and shade-tolerant species. In general, the negative effect of conspecifics and gap species on target survival was greater than the effect of shade-tolerant neighbours. Only one species supported Model 3, the model that distinguished between confamilial and non-confamilial heterospecific neighbours.

Given the criteria we chose to select focal species, we were able to analyse both growth and survival data for 50 species. For over 60% of this group of species (30 out of 50), data supported similar effects of broad neighbour groupings on both growth and survival (Fig. 4.4). Eleven species that showed distinct conspecific effects on growth also showed distinct effects on survival while 19 species that supported the equivalent competitor model did not show a response to conspecific neighbours in either growth or survival. A list of the species analysed and the best-supported models for growth and survival for each is given in Table 4.1.

## Discussion

We evaluated four models of neighbourhood crowding effects on the growth and survival of 1–4 cm DBH focal saplings of 50–60 species in the BCI 50-ha plot over a 5-year census interval, from 1990 to 1995. The most salient result was that the ecological equivalence model (model 1) was the model best supported by more than half of the species for growth, and three-quarters of the species for survival. The ecological equivalence model treats all neighbours, irrespective of species, as having the same crowding effects, controlling for size and distance from the focal sapling. Of the species that supported one of the three other models, all of which included a separate class for conspecifics neighbours, the strongest effect by far (as measured by the magnitudes of the  $\lambda$  coefficients), was the negative effect of conspecifics neighbours. The dominating importance of conspecifics density in these analyses is congruent with similar findings by Hubbell *et al.* (1990); Hubbell *et al.* (2001); Peters (2003). However, these previous analyses found pervasive density-dependence at the community level (Hubbell

*et al.* 2001) and could have been driven by strong density-dependence in a few dominant species (Hubbell *et al.* 1990).

Common descent also increased the strength of interaction between neighbouring species even at a higher (familial) level of taxonomic separation. Con-familial effects on sapling growth and survival for focal species that supported Model 3 were always greater than effects of neighbours that were not in the same plant family. This is consistent with the idea that related species are more likely to respond in the same or similar ways to the mechanisms that are ultimately responsible for diversity. Nevertheless, support for Model 3 was relatively weak for the group of focal species as a whole.

A few species also supported a model that distinguished between conspecifics and divided heterospecifics into gap species and shade-tolerant species. In the growth analyses, interactions among species belonging to the same light guild were always stronger than those between individuals from different light guilds. This is expected given that species are primarily surrounded by adult trees that belong to the same light guild as the focal sapling. These large neighbouring trees have the strongest effects on the growth of focal saplings. In the survival analyses, we found that heterospecific neighbours that were gap species had a stronger effect than shade-tolerant species. This is probably a correlated response in the focal saplings to being in a gap. Shade-tolerant species have much higher mortality rates in light gaps than in non-gap understorey sites (Hubbell *et al.* 1999). The correlation arises because these are the only sites where gap species occur. Taken together, these results suggest that convergent evolution along broad life-history strategies determine neighbourhood interactions for some species.

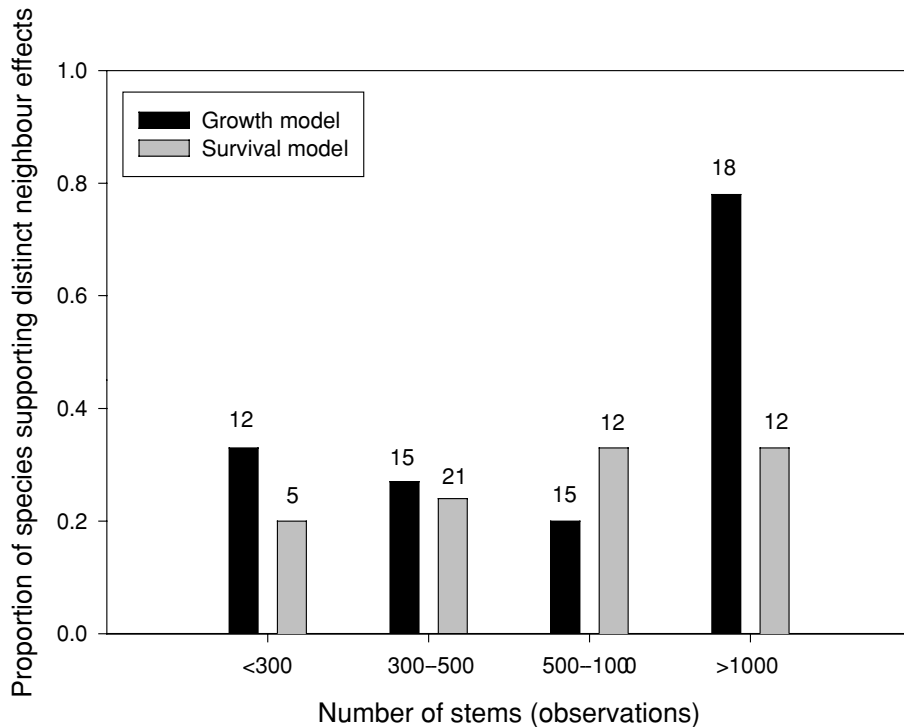
Support for the model of ecological equivalence is stronger and more pervasive than in other studies we have conducted at Luquillo Forest in Puerto Rico (Uriarte *et al.* 2004a) and in temperate forests (Canham *et al.*, in press; C. D. Canham *et al.*, unpublished data). There are several possible explanations for this difference. One is that the difference is real and due to the greater species richness and greater unpredictability of neighbourhoods around saplings of species in the BCI forest. Two individuals of the same BCI species share only about 15% species in common among their 20 nearest neighbours (Hubbell & Foster 1986). In contrast, this percentage is much higher in species-poor temperate forests that have only 15–20 species. The strength and directionality of neighbourhood effects therefore can differ markedly for different individuals of the same species in the BCI forest. Indeed, one might expect the strength of pairwise competitive effects to decline roughly as the square of the number of species in the community.

Nevertheless, none of the models, even those that were supported best and indicated significant differences among neighbour groups, explained much of the variance in growth and survival (see Uriarte *et al.* (2004b) for details). There

could be several reasons for this low explanatory power. First, the models may not be accurately capturing the true effects of neighbours in the BCI forest. Although this is always a possibility, it should be noted that these same spatially explicit neighbourhood models perform well at Luquillo and in temperate forests. Despite this low explanatory power on BCI, it is nevertheless interesting that about 60% of species included in the analyses displayed similar responses in growth and survival to the presence of conspecific neighbours. Species that showed strong conspecific effects on growth also showed strong effects on survival while species that supported the equivalent competitor model did not show a response to conspecific neighbours in either growth or survival. Similarity in the effects of different groups of neighbours on both growth and survival of focal seedlings supports the notion that the processes that determine growth and mortality in forests are tightly linked (Monserud 1976; Kobe *et al.* 1995; Kobe 1996; Wyckoff & Clark 2002). This suggests that the models are indeed capturing reality to some extent. This said, in 40% of the species there was a different best model for growth and survival.

A second possibility for low explanatory power is perhaps that the effects are stronger at a finer level of species discrimination, i.e. at the species level rather than at the functional group or taxonomic pooling levels that we tested here. The argument is that these finer levels of discrimination reflect environmentally driven niche differentiation. Although this is a possibility, we do not think it is likely given that measured heterospecific effects were much weaker than conspecific effects. The third possibility is that once again it is the high diversity and unpredictability of neighbourhoods around individual saplings of each species that obscures neighbourhood effects. These highly diverse and different neighbourhoods may elevate the 'within treatment' variance within our functional groups to the point where the 'between treatment' effects are no longer significant. If this explanation is the right one, it is nevertheless still biologically interesting. It may indicate that species are intrinsically highly variable and overlap broadly in their growth and survival responses to neighbourhood effects. Thus, even in cases where there is a small role for a deterministic 'skeleton', stochastic behaviour in neighbourhood responses remain quantitatively significant. Stochastic effects can clearly overwhelm known neighbourhood effects of light and soil nutrients on tree growth and survival (Beckage & Clark 2003). Thus, the low explanatory power of the models may be further indirect support for ecological equivalence.

The strong showing of the ecological equivalence hypothesis in this study should not be taken as demonstrating that the BCI forest is fully symmetric-neutral. There are several reasons to be cautious of over-interpretation. The most important reason is that we tested neighbourhood models for only one of the life-history stages of tropical trees, saplings of DBH 1–4 cm. We know, for example, that many BCI species differ in the strength of the density-dependent



**Figure 4.5** Proportion of species supporting distinct neighbour effects for growth and survival analyses. Numbers above bars indicate number of species included in the analyses for that sample size class.

mortality they experience in the seed-to-seedling transition (Harms *et al.* 2000), and seedling-to-sapling recruitment (Condit *et al.* 1994a; Wills *et al.* 1997). In general, density-dependent effects appear to weaken or disappear as seedlings are recruited into the larger size classes (Connell *et al.* 1984; Harms *et al.* 2000; but see Condit *et al.* 1994b; Peters 2003). Studies elsewhere have demonstrated that density-dependent effects can range from allelopathic to facilitative through a plant's life history (Goldberg *et al.* 2001). This kind of analysis has not been completed for tropical forests. Also, species differ in their mean growth and survival rates, which will affect their residency times in the forest and the likelihood that they will occupy new sites when these become available (Chesson & Warner 1981).

Finally, detection of ecological equivalence may be a function of the sample size of stems available for different species. If this is the case, the ability to detect interactions should increase with sample size. Figure 4.5 shows the percentage of species supporting the equivalent competitor growth and survival models as a function of sample size class. Although a few species with large sample sizes support the ecological equivalence growth model (e.g. *Garcinia intermedia* and

*Swartzia simplex* var. *ochracea*), the ability to detect distinct neighbour effects on focal sapling growth increases dramatically for sample sizes greater than 1000 stems. Thus, there are likely to be non-symmetrical 'hidden' interactions that cannot be detected with this dataset. Curiously, the probability of detecting distinct neighbour effects on focal sapling survival was fairly constant regardless of sample size. Previous analyses of density dependence in this forest (Hubbell *et al.* 1990) and elsewhere (Uriarte *et al.* submitted) found that being next to a conspecific was more likely to affect growth than survival. Self-thinning and sheer 'crowding' may be the most important drivers of sapling survival regardless of the identity of neighbours, particularly for common species (Hubbell *et al.* 2001). In contrast, the effects of neighbours on focal sapling growth may be more complex (e.g. differentiation in soil resource requirements or neighbour effects on depletion of soil resources). Incorporating these differences into models of tropical forest dynamics should provide insights into the importance of these effects for the maintenance of diversity.

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