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A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter?

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Summary

1 We quantified neighbourhood effects on sapling growth for 60 tree species in the 50-ha plot in Barro Colorado Island, Panama. Additionally, we tested whether target sapling growth responds to taxonomic or functional identity of neighbouring species by comparing four alternate models (that all neighbours have equivalent effects on the target; that conspecific and heterospecific neighbours have distinct effects; that heterospecific neighbours can be divided into confamilials and non-confamilials; and that they can be divided according to their response to light availability).

2 Over half of the species (34 out of 60) analysed were consistent with all neighbours having equivalent effects on the target. This may result from diffuse evolution allowing tolerance of a large number of neighbouring species or could be a statistical artefact of over-clumping species into large neighbour groups (e.g. heterospecific neighbours).

3 Other species supported models that differentiated between conspecific and heterospecific ($n = 6$) or between confamilial vs. non-confamilial ($n = 5$) neighbours and, in general, effects of neighbours were stronger if they were more closely related to the target. Where target species differentiated between neighbours from different light guilds ($n = 15$), effects were stronger if both belonged to the same guild (i.e. both gap requiring or both shade tolerant).

4 Despite the fact that the majority of species did not respond to the identity of neighbours, all differed in their response to the degree of crowding. Our results suggest that the response of target species to crowding, rather than individual species effects on targets, may be subject to selection.

5 Variation among species in response to crowding or to the identity of neighbouring species is likely to contribute to the maintenance of species diversity in tropical forests.

Key-words: Barro Colorado Island, density-dependence, ecological equivalence, neighbourhood effects, neutral theory

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Introduction

Tropical forests contain a staggering diversity of plant species, but the processes that govern the assembly and composition of these communities are poorly understood. The majority of species in these highly diverse forests are locally rare (Whitmore 1984; Richards 1996). The obvious question is whether there are mechanisms that prevent extinction of rare species or restrain the density of numerically dominant species. A large body of theory proposes that density-dependent mechanisms act to equilibrate community composition. A non-exhaustive list of these mechanisms includes compensatory mortality (Janzen 1970; Connell 1971), resource heterogeneity (Tilman 1982), and fluctuations in recruitment (Chesson & Warner 1981). Alternatively, drift theories propose that patterns of species diversity and relative abundance result from a balance of migration, speciation and extinction (MacArthur & Wilson 1967; Hubbell 1979, 1997). Under this scenario, density-dependent processes are weak and ultimately unimportant in explaining patterns of diversity and relative abundance. The relative importance of density-dependent vs. drift mechanisms in determining species diversity and relative abundance remains an open question.

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Spatial autocorrelation of tree recruitment, growth and survival suggests that whatever mechanisms promote coexistence operate at a neighbourhood scale (e.g. Hubbell *et al.* 2001). Both biotic and abiotic factors affect tree growth and survival, and these factors are often spatially autocorrelated (e.g. soil nutrients, treefall gaps). Consequently, quantification of the importance of coexistence mechanisms in determining species diversity and relative abundance requires the use of spatially explicit models to capture the spatial structure of the habitat. Our goal in this paper is to use such a model to assess and quantify one density-dependent mechanism: the effects of local biotic neighbourhoods on sapling growth. We focus on this life-history stage because asymmetry in competition for resources and light implies that neighbourhood effects will have the greatest impact on fitness and, implicitly, on population growth, for relatively small sized trees (Weiner 1990; Goldberg *et al.* 2001).

The present analyses aim to answer three fundamental questions for species coexistence. First, we ask whether neighbourhood interactions are independent of species identity. If all species in a community have equal effects on each other, pairwise species interactions will be unimportant in determining patterns of relative abundance. Secondly, we ask whether common descent increases the strength of neighbourhood interactions between species. Taxonomic proximity might be expected to increase overlap in resource requirements or the likelihood of shared enemies, and evolutionary divergence could have contributed to species coexistence. Thirdly, we ask whether neighbourhood effects of gap-specialist and shade-tolerant species differ. Species with different ecological strategies could have distinct neighbourhood effects, perhaps as a result of morphological or physiological differences, regardless of taxonomic proximity, i.e. membership of an ecological guild may be the prime determinant of the strength of neighbourhood interactions (Gilbert *et al.* 2001). Support for this premise would suggest that divergence into ecological niches may contribute to species coexistence.

We use a likelihood-based regression model to answer these three questions and analyse the effects of the spatial configuration, sizes and species of neighbouring trees on the growth of saplings of 60 tree species at the Barro Colorado Island 50-ha plot (Condit 1998). The model is a phenomenological description of the effects of focal tree size and local biotic neighbourhood interactions on focal sapling growth. Our specific objectives are:

1. To quantify empirically the effects of the spatial configuration, sizes, and species of neighbouring trees on sapling growth of 60 tree species at BCI.

2. To compare models that make different assumptions about the nature of these neighbourhood interactions among trees in the community. Specifically, we test whether target sapling growth responds to taxonomic (conspecific vs. heterospecific or confamilial vs. other) or functional (gap vs. shade tolerant) identity of neighbouring species.

Materials and methods

STUDY AREAS AND FIELD METHODS

We used a spatially explicit model to analyse growth data for 60 species existing in the 50-ha plot in Barro Colorado Island (BCI), Panama. Barro Colorado has a moist, lowland, tropical climate, with 2500 mm per year rain, a strong 3.5-month dry season, and a mean daily temperature year-round of 27 °C (Leigh 1999). The island is covered in tall, high-biomass forest, and most of it, including 48 of the 50 ha in the plot, has been largely undisturbed for over 500 years. Censuses in the plot were first carried out in 1982, and have been repeated every 5 years since 1985. All free-standing woody stems ≥ 1 cm stem diameter were tagged, mapped, identified to species and their bole diameter at 130 cm from the ground recorded to the nearest millimetre: where buttresses or swellings occurred at this height, an alternate height was chosen and recorded for future measurements (for details of census methods see Condit 1998). In the present analyses, we use data from the 1990 and 1995 censuses. Differences in diameter between the two censuses allowed calculation of annual growth rates for individual trees.

A MAXIMUM-LIKELIHOOD MODEL OF NEIGHBOURHOOD EFFECTS

We used growth data for all trees ≤ 4 cm in diameter in the plot to quantify the effects of neighbouring trees on the growth of 60 common tree species (Table 1). In order to have sufficient observations for robust parameter estimation, we selected shade-tolerant species with ≥ 300 live individuals in the selected size class (≤ 4 cm diameter). The rarity of gap species demanded a lower abundance threshold and those with ≥ 200 individuals ≤ 4 cm diameter were included.

Previous studies at BCI found great variation in growth rates among different size classes (Condit *et al.* 1999, 1993a,b). We limited our analyses to saplings (stems ≥ 1 cm and ≤ 4 cm in diameter) because we hypothesized that neighbourhood processes that affect stand development would differ for sapling and adult size classes. Following methods from previous analyses of growth at BCI, we eliminated re-sprouts and trees with extreme growth rates (i.e. diameter increment > 7.5 cm year^{-1}). Individuals with negative growth rates were assumed to have growth of 0 cm year^{-1} because the functional forms of the equations used to predict growth are bounded at zero and these negative rates often reflect erroneous measurements (Condit *et al.* 1993b). Individuals that decreased by more than 7.5 cm year^{-1} were, however, excluded from the analyses. To avoid edge effects, we also excluded target trees that were within 15 m of the edge of the plot.

Our growth model assumes that each target species has an average maximum potential growth rate, which is adjusted to account for the size and taxonomic identity

Table 1 Name, family, light guild, and number of stems = 4 cm in d.b.h. of species included in growth analyses. Growth forms based on maximum size attained (see Hubbell & Foster 1986b). See Condit *et al.* (1996) for criteria used to classify species into light guilds. For full list of species at BCI and nomenclature of species see http://ctfs.si.edu/webatlas/maintreeatlas.html

Genus	Species	Family	Light guild	Growth form	Species code	No. stems
Alseis	*blackiana*, Hemsl.	Rubiaceae	Shade-tolerant	Canopy	ALSEBL	5 511
Aspidosperma	*cruenta*, Woods	Apocynaceae	Shade-tolerant	Canopy	ASPICR	309
Beilschmiedia	*pendula*, SW, Hemsl.	Lauraceae	Shade-tolerant	Canopy	BEILPE	1 691
Brosimum	*alicastrum*, SW.	Moraceae	Shade-tolerant	Canopy	BROSAL	380
Calophyllum	*longifolium*, Willd.	Clusiaceae	Shade-tolerant	Canopy	CALOLO	581
Casearia	*aculeata*, Jacq.	Flacourtiaceae	Gap	Canopy	CASEAC	270
Cassipourea	*elliptica*, SW, Poir.	Rhizophoraceae	Shade-tolerant	Midstorey	CASSEL	674
Chrysophyllum	*argenteum*, Jacq.	Sapotaceae	Shade-tolerant	Canopy	CHR2AR	449
Cordia	*bicolor*, A. DC.	Boraginaceae	Gap	Midstorey	CORDBI	347
Cordia	*lasiocalyx*, Pitt.	Boraginaceae	Shade-tolerant	Midstorey	CORDLA	535
Coussarea	*curvigemmia*, Dwyer.	Rubiaceae	Shade-tolerant	Understorey	COU2CU	1 312
Croton	*billbergianus*, Mull.-Arg.	Euphorbiaceae	Gap	Understorey	CROTBI	218
Cupania	*sylvatica*, Seem.	Sapindaceae	Shade-tolerant	Understorey	CUPASY	787
Desmopsis	*panamensis* (Rob.), Saff.	Annonaceae	Shade-tolerant	Understorey	DES2PA	8 904
Drypetes	*standleyi*, GL Webster	Euphorbiaceae	Shade-tolerant	Canopy	DRYPST	1 284
Eugenia	*colouradensis*, Standl.	Myrtaceae	Shade-tolerant	Canopy	EUGECO	489
Eugenia	*galalonensis*, Standl.	Myrtaceae	Shade-tolerant	Understorey	EUGEGA	1 131
Eugenia	*nesiotica*, Standl.	Myrtaceae	Shade-tolerant	Midstorey	EUGENE	369
Eugenia	*oerstedeana*, Berg.	Myrtaceae	Shade-tolerant	Midstorey	EUGEOE	1 392
Faramea	*occidentalis* (L.) A. Rich.	Rubiaceae	Shade-tolerant	Understorey	FARAOC	15 459
Garcinia	*intermedia* (Pittier) Hammel.	Clusiaceae	Shade-tolerant	Midstorey	GAR2IN	3 303
Guarea	*guidonia* (L.) Sleumer	Meliaceae	Shade-tolerant	Midstorey	GUARGU	1 060
Guarea	*'fuzzy'*	Meliaceae	Shade-tolerant	Midstorey	GUARSP	852
Guatteria	*dumetorum*, R.E.F.	Annonaceae	Shade-tolerant	Canopy	GUATDU	541
Heisteria	*concinna*, Standl.	Olacaceae	Shade-tolerant	Understorey	HEISCO	454
Herrania	*purpurea* (Pittier) RE Schult	Sterculiaceae	Shade-tolerant	Understorey	HERRPU	391
Hirtella	*triandra*, Sw.	Chrysobalanaceae	Shade-tolerant	Midstorey	HIRTTR	3 074
Inga	*marginata*, Willd.	fabaceae:mimos	Gap	Canopy	INGAMA	282
Inga	*nobilis*, Willd.	fabaceae:mimos	Shade-tolerant	Midstorey	INGAQU	388
Inga	*umbellifera*, Vahl.	fabaceae:mimos	Shade-tolerant	Midstorey	INGAUM	626
Lacistema	*aggregatum* (P.J. Berg.) Rusby	Flacourtiaceae	Shade-tolerant	Understorey	LACIAG	1 217
Laetia	*thamnia*, L.	Flacourtiaceae	Shade-tolerant	Understorey	LAETTH	302
Lonchocarpus	*latifolius*, Willd.	Fabaceae:faboid	Shade-tolerant	Canopy	LONCLA	471
Maquira	*costaricana* (Standl.) CC Berg.	Moraceae	Shade-tolerant	Midstorey	MAQUCO	818
Miconia	*affinis* DC	Melastomataceae	Gap	Understorey	MICOAF	235
Miconia	*argentea*, Sw., DC	Melastomataceae	Gap	Midstorey	MICOAR	301
Pentagonia	*macrophylla*, Benth.	Rubiaceae	Shade-tolerant	Understorey	PENTMA	312
Picramnia	*latifolia*, Tul.	Picramniaceae	Shade-tolerant	Understorey	PICRLA	757
Pouteria	*reticulata* (Engl.) Eyma	Sapotaceae	Shade-tolerant	Canopy	POUTRE	1 073
Prioria	*copaifera*, Griseb.	Fabaceae:caesal	Shade-tolerant	Canopy	PRI2CO	716
Protium	*costaricense* (Rose) Engl.	Burseraceae	Shade-tolerant	Midstorey	PROTCO	445
Protium	*panamense* (Rose) I.M. Johnst.	Burseraceae	Shade-tolerant	Midstorey	PROTPA	2 125
Protium	*tenuifolium*, Engl.	Burseraceae	Shade-tolerant	Midstorey	PROTTE	1 857
Pterocarpus	*rohrii*, Vahl	Fabaceae:faboid	Shade-tolerant	Canopy	PTERRO	1 107
Quararibea	*asterolepis*, Pitt.	Bombacaceae	Shade-tolerant	Canopy	QUARAS	937
Randia	*armata* (Sw.) DC	Rubiaceae	Shade-tolerant	Understorey	RANDAR	518
Simarouba	*amara*, Aubl.	Simaroubaceae	Gap	Canopy	SIMAAM	495
Sloanea	*terniflora*, (Sessé & Moc. Ex DC.) Standl.	Elaeocarpaceae	Shade-tolerant	Canopy	SLOATE	335
Swartzia	*simplex_var_grandiflora* (Raddi)	Fabaceae:caesal	Shade-tolerant	Understorey	SWARS1	1 867
Swartzia	*simplex*_var_*ochnacea*	Fabaceae:caesal	Shade-tolerant	Understorey	SWARS2	1 897
Tabernaemontana	*arborea*, Rose	Apocynaceae	Shade-tolerant	Canopy	TAB2AR	772
Tachigalia	*versicolor*, Standl. & L.O. Williams	Fabaceae:caesal	Shade-tolerant	Canopy	TACHVE	2 180
Talisia	*nervosa*, Radlk.	Sapindaceae	Shade-tolerant	Understorey	TALINE	622
Talisia	*princeps*	Sapindaceae	Shade-tolerant	Midstorey	TALIPR	491
Tetragastris	*panamensis* (Engl.) Kuntze	Burseraceae	Shade-tolerant	Canopy	TET2PA	2 802
Trichilia	*pallida*, Sw.	Meliaceae	Shade-tolerant	Midstorey	TRI2PA	309
Trichilia	*tuberculata*, (Tr. & Pl.) C. DC.	Meliaceae	Shade-tolerant	Canopy	TRI2TU	7 819
Unonopsis	*pittieri*, Saff.	Annonaceae	Shade-tolerant	Midstorey	UNONPI	333
Virola	*sebifera*, Aubl.	Myristicaceae	Shade-tolerant	Midstorey	VIROSE	839
Xylopia	*macrantha*, Triana & Planch.	Annonaceae	Shade-tolerant	Midstorey	XYL1MA	617

of the target and the structure and composition of its neighbourhood. Our model takes the form:

$$\text{Predicted growth} = \text{Maximum growth} \times \text{Neighbourhood effects} \qquad \text{eqn 1}$$

Maximum growth

We estimated the average maximum potential growth rate for each target species in the absence of neighbours. We did not include an explicit size-dependent effect on growth because previous studies of sapling growth in tropical rainforests only found weak correlations between sapling size and diameter growth within this size range (1–4 cm diameter) (Clark & Clark 1999).

Neighbourhood effects

Our model relies on traditional distance-dependent analyses of competition, in which tree growth is analysed as a function of the sizes and distances to neighbouring trees (e.g. Bella 1971; Hegyi 1974; Lorimer 1983; Zeide 1993; Wimberly & Bare 1996; Wagner & Radosevich 1998; Vettenranta 1999). The net effect of a neighbouring tree on the growth of a target tree of a given species is assumed to vary as a direct function of the size of the neighbour, and as an inverse function of the distance to the neighbour. In our analysis, the net effect of an individual neighbour is multiplied by a species- or group-specific scalar coefficient λ that ranges from 0 to 1 and allows for differences among species or groups (e.g. conspecific vs. heterospecific neighbour) in their effect on the target tree. Then, for $i = 1 \ldots S$ species or groups of species and $j = 1 \ldots n$ neighbours of a particular species within a maximum radius (R) around the target tree, the neighbourhood crowding index (NCI), an index of net crowding pressure on the focal target tree of species k is given by:

$$NCI_{focal,k} = Diameter_{focal,k}^{\gamma} \sum_{i=1}^{S} \sum_{j=1}^{n_i} \lambda_{ik} \frac{Diameter_j^{\alpha_k}}{Distance_j^{\beta_k}} \qquad \text{eqn 2}$$

where α_k and β_k are estimated by the analyses, and, respectively, determine the shape of the effect of neighbour diameter (α_k) and its distance (β_k) to the target on NCI. The coefficient γ adjusts the effect of NCI when the sensitivity of target saplings to crowding is a function of the size of the target sapling. Our computational procedures standardize the values of λ across species by setting the highest value that λ takes for all neighbours of a given target species equal to 1 and dividing the remaining species-specific values (λ_{ik}) by the maximum value. Our analysis also estimates R, the effective neighbourhood radius, as a fraction of a maximum neighbourhood radius of 15 m. To keep the number of parameters in the model manageable, α and β are assumed to be equal for all neighbouring species or groups of neighbours. Neighbourhood effects are translated into actual growth by using a negative exponential function of the NCI.

$$\text{Neighbourhood effects} = \exp^{-C\left(\frac{NCI_i}{NCI_{\max}}\right)^{D}} \qquad \text{eqn 3}$$

where C and D are species-specific estimated parameters, and NCI_i is the neighbourhood crowding index for target sapling i, and $NCI_{\max}$ is the maximum value of NCI for all saplings of the target species. The use of $NCI_{\max}$ standardizes the neighbourhood effects term and facilitates comparisons across focal species. Parameters C and D are the two inflection points of the function that defines the effect of crowding (i.e. NCI) on growth: parameter C defines the sharpness of the decline in growth due to an increment in NCI whereas parameter D determines whether there is a threshold at which the decline in growth takes effect.

LIKELIHOOD ESTIMATION, HYPOTHESIS TESTING, AND COMPARISON OF ALTERNATE MODELS

Our approach relies on the principles of likelihood estimation (e.g. Hillborn & Mangel 1997) and estimates model parameters that maximize the likelihood of observing the actual overall growth data for the chosen target species, given the model. Data were obtained from the 1990 and 1995 censuses at BCI. For each analysis of the growth of a target tree species, the model described by equation 1 requires estimation of $n + 7$ parameters for n groups of neighbours. Table 2 provides a complete list of all model parameters with initial values and ranges. Parameter ranges were established to provide maximum flexibility while staying within biologically realistic values. For instance, maximum growth was bounded between 0 and 40 mm year^{-1}, as even extreme pioneers are unlikely to exceed this upper bound for the sapling size class (Clark & Clark 1992; Condit *et al.* 1999).

Equation 4, below, provides the likelihood function for observing a given growth in tree i. Our likelihood function assumes that the residuals, i.e. the difference between observed and predicted growth, approximate a normal distribution (Mangel & Clark 1997).

Table 2 List and range of parameters included in growth model. Parameters were estimated for each target species

Parameter name	Range
Maximum growth (Max. Growth)	0–40 mm year^{-1}
Effective neighbourhood radius (R) [0–15]	0–15 m
Coefficients of neighbourhood effects	
C	0–10
D	1–3
Competitive coefficients (λ)	0–1
Size sensitivity of target to crowding (γ)	–2–2
Effect of neighbour size on target growth (α)	0–4
Effects of neighbour distance to target on target growth (β)	0–4

Total number of parameters = $(7 + n)$ for n competitors.

$$\text{Log } Likelihood(Data|Model) = n\left[\log(\sigma) + \frac{1}{2}\log(2\pi)\right] + \sum_{i=1}^{n}\frac{(Observed\ i - Expected\ i)^2}{2\sigma^2} \quad \text{eqn 4}$$

The log likelihood in equation 4 assumes independence among observations (target trees). A preliminary analysis of the data showed that both growth and the residuals of the model were spatially autocorrelated at a scale of approximately 5 m. This strong spatial autocorrelation among observations would produce biased underestimates of parameter variance, but the 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. We used simulated annealing (a global optimization procedure) to determine the most likely parameters (i.e. the parameters that maximize the log likelihood), given our observed data (Goffe *et al*. 1994).

Our motivation for this study was to compare models that make different assumptions about the nature of neighbourhood interactions between trees at BCI. Thus, we explicitly tested four alternate models that made different assumptions about the structure of these interactions. The simplest neighbourhood model (EQUIV) assumed that all neighbours had equivalent effects on the target regardless of taxonomic identity or ecological guild, whereas a second model (INTERCON) differentiated between conspecific and heterospecific neighbours (i.e. calculated separate values of λ for the two classes) and a third (FAMILY) separated heterospecific neighbours into confamilials of the target species and non-confamilials. The final model (LIGHT) separated heterospecific neighbours according to their response to light availability (gap- vs. shade-tolerant species) regardless of taxonomic identity.

Alternate models were compared using Akaike's Information Criterion (AIC_c) corrected for small sample size:

$$AIC_c = -2\log(Likelihood) + 2K\left(\frac{n}{n-K-1}\right) \quad \text{eqn 5}$$

where n is the total number of observations and K is the number of estimated parameters in the model. The best candidate model is the one with the lowest AIC_c.

Although AIC_c values are useful in ranking the fit of alternate models, they do not quantify the strength of evidence for the best model relative to the set of candidate models. To better interpret the strength of evidence for the best model relative to the full set of competing models, we calculated Akaike weights for each model using the following equation:

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{r=1}^{R}\exp(-0.5\Delta_r)} \quad \text{eqn 6}$$

where Δ_i is the difference in AIC_c between the most parsimonious model and model i given a total set of R alternate models (Burnham & Anderson 2002). The best model in this case is the one with the highest Akaike weight. Ratios of Akaike weights for different models provide a measure of the strength of evidence in favour of the most parsimonious model. For instance, if the best model has an evidence ratio of 2 with respect to the next best model, we would conclude strength of evidence for the best model relative to the second best model is weak (2 : 1). At the other extreme, an evidence ratio of 100 would provide extremely strong support for the best model. For the purposes of these analyses we consider evidence ratios greater than 10 as strong support for one of the alternate models. Although the interpretation of these ratios is somewhat arbitrary, they provide an intuitive measure of support for one model relative to the set of models considered (Burnham & Anderson 2002).

Results

LIKELIHOOD AND GOODNESS OF FIT OF GROWTH MODELS

We estimated maximum likelihood parameter values for a series of alternate growth models for the selected target species (Table 3). All of the models produced unbiased estimates of radial growth, with a slope of 1 between predicted and observed, and symmetrically distributed residuals. The percentage of variance (r^2) in individual growth rates explained by the best models ranged from only 1% for *Pentagonia macrophylla* to 23% for *Inga marginata* (Table 3).

EVALUATION OF ALTERNATE MODELS

We compared the four nested models described above using AIC_c. For the majority of target species (34 out of 60 species), the most parsimonious model, i.e. the model with the lowest AIC_c value and the highest Akaike weight, considered all neighbours equivalent (Table 3). A total of six, five and fifteen species, respectively, supported models that differentiated between con- and heterospecific neighbours, confamilial vs. other neighbours and different light guilds (Table 3).

Evidence ratios for 15 out of the 26 species that supported a model that differentiated between neighbours relative to one that considered all neighbours equivalent were greater than 10, indicating fairly strong support for distinct neighbour effects (Table 3). As expected, strong inference was supported for species with large sample sizes, although some species with fewer individuals were included in this group (e.g. *Guarea* spp. and *Miconia argentea*). The relatively weak support (evidence ratio < 10) for the remaining 11 species suggests that we should expect to find variation in the selected best model when using different data sets (e.g. growth data from a different census).

Table 3 Akaike weights and *R*-square values for all models (Equiv = equivalent neighbour model; Intercon = con vs. heterospecific neighbour; Family = conspecific, confamilial and non-confamilial neighbours; Light = conspecific, shade-tolerant, gap and light guild undetermined neighbours), as well as evidence ratios for two best alternative models. Bold lettering indicates most parsimonious model

Species	No.obs.	Equiv.	R^2	Intercon	R^2	Family	R^2	Light	R^2	Evidence ratio between best model and equivalent neighbour model	Evidence ratio between best and second best model
Alseis blackiana	4 863	0.02	0.06	**0.57**	0.06	0.20	0.06	0.21	0.07	32.96	2.89
Aspidosperma cruenta	275	**0.62**	0.06	0.04	0.06	0.02	0.06	0.32	0.08	NA	NA
Beilschmiedia pendula	1 417	0.00	0.05	**0.72**	0.06	0.11	0.06	0.17	0.06	1500.30	4.21
Brosimum alicastrum	355	**0.63**	0.06	0.25	0.07	0.11	0.07	0.01	0.06	NA	NA
Calophyllum longifolium	477	0.19	0.11	0.04	0.11	**0.76**	0.12	0.00	0.11	3.96	3.96
Casearia aculeata	244	**0.85**	0.07	0.10	0.07	0.04	0.07	0.01	0.07	NA	NA
Cassipourea elliptica	633	**0.88**	0.18	0.08	0.18	NA		0.04	0.18	NA	NA
Chrysophyllum argenteum	393	**0.81**	0.03	0.12	0.03	0.04	0.03	0.03	0.03	NA	NA
Cordia bicolor	295	0.45	0.19	0.04	0.19	0.02	0.19	**0.49**	0.21	1.09	1.09
Cordia lasiocalyx	443	**0.59**	0.13	0.24	0.13	0.12	0.13	0.04	0.13	NA	NA
Coussarea curvigemmia	1 199	0.11	0.03	**0.85**	0.04	0.03	0.03	0.02	0.03	8.01	8.01
Croton billbergianus	192	0.04	0.12	0.02	0.13	0.00	0.12	**0.94**	0.19	24.43	24.43
Cupania sylvatica	669	**0.82**	0.05	0.07	0.05	0.04	0.05	0.07	0.05	NA	NA
Desmopsis panamensis	8 173	0.00	0.03	0.00	0.03	0.00	0.05	**1.00**	0.04	> 100 000	> 100 000
Drypetes standleyi	1 170	0.04	0.09	0.20	0.09	0.17	0.10	**0.59**	0.10	14.15	3.46
Eugenia colouradensis	435	**0.85**	0.08	0.10	0.08	0.03	0.09	0.02	0.09	NA	NA
Eugenia galalonensis	1 028	**0.71**	0.05	0.09	0.05	0.05	0.05	0.15	0.05	NA	NA
Eugenia nesiotica	345	**0.83**	0.10	0.08	0.10	0.06	0.10	0.03	0.10	NA	NA
Eugenia oerstedeana	1 296	**0.46**	0.09	0.06	0.09	0.47	0.09	0.01	0.09	NA	NA
Faramea occidentalis	14 229	0.00	0.04	0.00	0.06	0.00	0.06	**1.00**	0.06	> 100 000	> 100 000
Garcinia intermedia	3 029	**0.72**	0.08	0.12	0.08	0.14	0.08	0.01	0.08	NA	NA
Guarea guidonia	889	**0.85**	0.05	0.09	0.05	0.05	0.05	0.01	0.05	NA	NA
Guarea 'fuzzy'	757	0.09	0.07	0.01	0.07	**0.89**	0.08	0.01	0.07	10.44	10.44
Guatteria dumetorum	429	**0.69**	0.04	0.22	0.04	0.08	0.04	0.01	0.03	NA	NA
Heisteria concinna	411	0.19	0.08	**0.67**	0.10	0.11	0.09	0.03	0.09	3.48	3.48
Herrania purpurea	330	**0.80**	0.08	0.14	0.08	0.02	0.08	0.04	0.09	NA	NA
Hirtella triandra	2 643	0.00	0.07	0.43	0.08	0.08	0.08	**0.49**	0.08	4540.15	1.13
Inga marginata	240	0.04	0.18	0.01	0.19	0.00	0.18	**0.95**	0.23	25.94	25.94
Inga nobilis	345	**0.77**	0.06	0.08	0.06	0.10	0.07	0.05	0.07	NA	NA
Inga umbellifera	556	**0.51**	0.06	0.43	0.06	0.04	0.06	0.01	0.06	NA	NA
Lacistema aggregatum	1 109	0.31	0.05	0.05	0.05	0.02	0.05	**0.62**	0.05	1.98	1.98
Laetia thamnia	270	0.36	0.09	**0.59**	0.11	0.03	0.09	0.03	0.09	1.64	1.64
Lonchocarpus latifolius	405	0.18	0.13	0.02	0.13	0.04	0.14	**0.75**	0.16	4.11	4.11
Maquira costaricana	742	**0.51**	0.13	0.08	0.14	0.04	0.14	0.37	0.14	NA	NA
Miconia affinis	219	**0.65**	0.06	0.08	0.06	0.02	0.06	0.25	0.09	NA	NA
Miconia argentea	274	0.07	0.10	0.07	0.11	0.02	0.11	**0.84**	0.16	12.63	12.63
Pentagonia macrophylla	668	**0.85**	0.01	0.08	0.01	0.05	0.02	0.02	0.02	NA	NA0
Picramnia latifolia	260	**0.47**	0.03	0.11	0.03	NA		0.01	0.03	NA	NA
Pouteria reticulata	950	**0.59**	0.09	0.12	0.09	0.17	0.09	0.11	0.09	NA	NA
Prioria copaifera	630	0.06	0.14	0.31	0.15	0.25	0.15	**0.38**	0.16	6.38	1.23
Protium costaricense	374	0.31	0.16	0.05	0.17	**0.64**	0.18	0.00	0.16	2.09	2.09
Protium panamense	1 905	0.00	0.06	0.01	0.06	**0.98**	0.07	0.00	0.07	212.42	113.14
Protium tenuifolium	1 559	0.00	0.08	0.00	0.09	**1.00**	0.11	0.00	0.09	> 100 000	> 100 000
Pterocarpus rohrii	966	**0.86**	0.07	0.08	0.07	0.03	0.07	0.03	0.07	NA	NA
Quararibea asterolepis	848	0.38	0.03	0.10	0.03	0.03	0.03	**0.49**	0.04	1.29	1.29
Randia armata	468	**0.85**	0.13	0.10	0.13	0.04	0.13	0.02	0.13	NA	NA
Simarouba amara	442	**0.76**	0.12	0.10	0.12	0.07	0.12	0.06	0.12	NA	NA
Sloanea terniflora	286	**0.87**	0.03	0.10	0.03	NA		0.03	0.04	NA	NA
*Swartzia simplex*_var_*grand.*	1 763	0.09	0.05	0.01	0.05	0.00	0.05	**0.89**	0.06	9.97	9.97
*Swartzia simplex*_var_*och.*	1 642	**0.65**	0.03	0.11	0.03	0.18	0.03	0.06	0.03	NA	NA
Tabernaemontana arborea	685	**0.85**	0.11	0.08	0.11	0.03	0.11	0.04	0.11	NA	NA
Tachigalia versicolor	1 979	0.02	0.04	0.36	0.05	0.13	0.05	**0.49**	0.05	20.24	3.78
Talisia nervosa	501	**0.79**	0.08	0.08	0.08	0.06	0.09	0.08	0.09	NA	NA
Talisia princeps	434	**0.82**	0.07	0.05	0.07	0.06	0.08	0.07	0.08	NA	NA
Tetragastris panamensis	2 466	0.00	0.05	**0.80**	0.06	0.06	0.06	0.14	0.06	6154.72	5.74
Trichilia pallida	271	**0.86**	0.06	0.09	0.06	0.02	0.05	0.03	0.06	NA	NA
Trichilia tuberculata	6 986	0.00	0.04	0.00	0.05	0.00	0.05	**1.00**	0.05	> 100 000	> 100 000
Unonopsis pittieri	270	**0.82**	0.20	0.07	0.20	0.07	0.20	0.03	0.20	NA	NA
Virola sebifera	725	**0.94**	0.05	0.04	0.05	0.02	0.05	0.00	0.05	NA	NA
Xylopia macrantha	536	**0.76**	0.05	0.10	0.05	0.10	0.06	0.03	0.06	NA	NA

RELATIVE EFFECTS OF CROWDING ON SAPLING GROWTH

We used estimated parameters for the most parsimonious model for each of the 60 species to calculate the decline in growth from a standardized neighbourhood around a 2 cm diameter target sapling. Tables 4 and 5 show the maximum potential annual growth for the most parsimonious model for each of the 60 species (see Appendix S1–S3 in Supplementary Material for full results for the three models that distinguish between neighbouring species). For instance, if we assume that all neighbours have identical effects on target sapling growth, maximum annual growth for *Laetia thamnia* was estimated at 6.50 mm year^{-1} (Table 4) but a 2-cm sapling growing 5 m from a 10-cm neighbour is expected to grow only 5.81 mm year^{-1}. We also estimated the maximum radius at which neighbours have an effect on the growth of target species. For *Laetia thamnia*, only trees within 9.35 m of a target sapling will decrease its growth (Table 4).

Species displayed great variation in the shape of their response to neighbour crowding. For instance, the growth of *Unonopsis pittieri* (Table 4, Fig. 1a) declined very steeply with a small amount of crowding. In contrast, the response of *Eugenia galalonensis* to crowding was fairly flat (Table 4, Fig. 1b). In general, the response of species to neighbour crowding was fairly flat for a large proportion of species that supported the equivalent competitor model (Table 4).

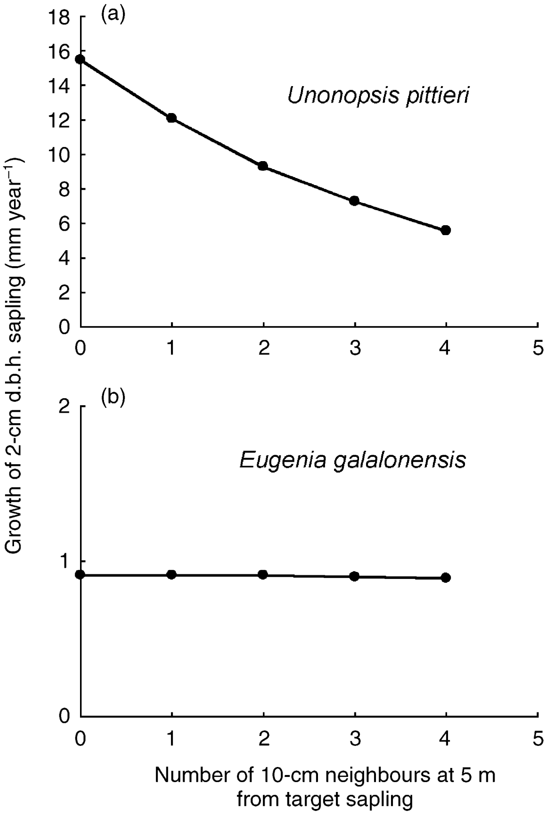

Fig. 1 Effects of neighbours for the most parsimonious model on the growth of *Unonopsis pittieri* and *Eugenia galalonenensis*.

NEIGHBOUR CROWDING COEFFICIENTS

For 26 out of the 60 species included in the analyses, there was striking variation in the effects of crowding, with the value of λ, our species-specific crowding index, depending on the identity of both the target tree and neighbours (Table 5, Appendix S1–S3). For six out of these species, the most parsimonious model differentiated between conspecific and heterospecific neighbours and negative neighbourhood effects were much stronger from conspecifics than from heterospecifics (Table 5, Appendix S1–S3, Fig. 2a,b). A second group of five target species supported a model that differentiated between conspecific, confamilials and non-confamilial neighbours (Table 5), with effects again greater for closer relatives (Table 5, Fig. 2c,d). Even the 15 species that supported a model that differentiated between neighbours on the basis of light strategy tended to show maximum effects from conspecifics (Table 5).

Ecological proximity was also a good predictor of the strength of neighbourhood interactions between species. The growth of shade-tolerant targets (except *Hirtella trianda* and *Lonchocarpus latifolius*), was more affected by other shade-tolerant neighbours than by gap species (Table 5, Fig. 2e), whereas gap species always showed stronger effects of gap neighbours (Table 5, Fig. 2f).

Discussion

EQUIVALENCE OF NEIGHBOURING SPECIES

Over half of the 60 species analysed support the ecological equivalence hypothesis. Consequently, we argue that, for a significant portion of abundant tree species at BCI, species-specific neighbourhood effects on sapling growth are unlikely to be an important explanation for coexistence, although strong negative conspecific effects on seedling recruitment or at other life-history stages are in all likelihood important (Hubbell *et al.* 1990; Harms *et al.* 2000; Peters 2003). These results support previous community-level analyses at BCI and elsewhere, which failed to find distinct conspecific effects on sapling growth for a large proportion of species examined (Connell *et al.* 1984; Hubbell *et al.* 1990; Peters 2003). In fact, the percentage of species that appear to respond to the presence of conspecifics is quite similar (43% in our study vs. 55%) to the figure reported in a recent study of conspecific effects on mortality at the BCI plot (Peters 2003). This congruence is remarkable considering that Peters used mortality from three different census periods, thus increasing the chances of observing conspecific effects by including census intervals with high mortality (e.g. a dramatic drought during the 1982–85 census interval, see Condit *et al.* 1996b).

In contrast, Harms *et al.* (2000) found strong and pervasive conspecific effects on seedling recruitment

Table 4 Maximum growth and effective neighbourhood radius for a 2-cm target sapling. Neighbourhood effects for these saplings are standardized to a 10-cm d.b.h. neighbour at 5 m distance from the target sapling. The model does not differentiate between neighbours. **Indicates this is the most parsimonious model for the target species

	Growth (mm year^{-1})	Radius (m)	Growth (mm year^{-1}) with neighbour
Alseis blackiana	3.35	11.16	2.82
Aspidosperma cruenta	0.69	13.54	0.50***
Beilschmiedia pendula	1.67	13.85	1.65
Brosimum alicastrum	2.50	12.80	2.44***
Calophyllum longifolium	2.49	6.67	1.00
Casearia aculeata	1.86	6.23	1.68***
Cassipourea elliptica	4.98	10.17	4.23***
Chrysophyllum argenteum	0.86	2.91	0.00***
Cordia bicolor	19.91	6.92	17.89
Cordia lasiocalyx	4.92	4.39	4.54***
Coussarea curvigemmia	1.04	2.82	0.78
Croton billbergianus	11.73	14.34	11.53
Cupania sylvatica	2.01	8.16	1.64***
Desmopsis panamensis	1.05	6.66	0.96
Drypetes standleyi	4.42	11.62	4.16
Eugenia colouradensis	2.10	6.46	0.29***
Eugenia galalonensis	0.92	10.00	0.92***
Eugenia nesiotica	2.46	6.31	1.97***
Eugenia oerstedeana	5.55	13.55	5.20***
Faramea occidentalis	1.55	4.55	1.21
Garcinia intermedia	1.22	5.78	0.56***
Guarea guidonia	1.74	14.43	1.73***
Guarea 'fuzzy'	1.79	12.33	1.65
Guatteria dumetorum	4.63	14.89	4.62***
Heisteria concinna	1.93	6.60	1.23
Herrania purpurea	2.73	5.06	2.62***
Hirtella triandra	1.64	4.68	0.46
Inga marginata	20.41	12.99	16.95
Inga nobilis	1.71	15.00	1.46***
Inga umbellifera	1.74	13.21	1.60***
Lacistema aggregatum	1.69	11.18	1.68
Laetia thamnia	6.50	9.35	5.81
Lonchocarpus latifolius	7.99	6.88	7.31
Maquira costaricana	9.83	13.36	9.25***
Miconia affinis	3.52	14.92	3.52***
Miconia argentea	5.50	8.72	5.02
Pentagonia macrophylla	0.84	10.88	0.75***
Picramnia latifolia	2.06	9.00	1.97***
Pouteria reticulata	4.07	12.35	3.66***
Prioria copaifera	8.10	9.75	6.97
Protium costaricense	27.25	14.87	25.32
Protium panamense	4.70	13.72	4.57
Protium tenuifolium	4.57	14.10	4.16
Pterocarpus rohrii	2.88	6.76	2.64***
Quararibea asterolepis	1.06	12.83	1.06
Randia armata	4.80	14.77	4.34***
Simarouba amara	12.94	14.95	12.24***
Sloanea terniflora	0.38	14.17	0.36***
*Swartzia simplex*_var_*grand.*	1.41	11.15	1.27
*Swartzia simplex*_var_*och.*	1.02	11.66	1.00***
Tabernaemontana arborea	12.18	13.12	11.93***
Tachigalia versicolor	3.67	13.86	3.57
Talisia nervosa	0.97	4.99	0.97***
Talisia princeps	4.53	12.26	4.39***
Tetragastris panamensis	1.54	8.49	1.33
Trichilia pallida	1.16	2.99	0.00***
Trichilia tuberculata	2.40	11.99	2.34
Unonopsis pittieri	15.48	5.13	12.02***
Virola sebifera	3.33	14.31	3.13***
Xylopia macrantha	2.01	3.88	0.84***

Table 5 Maximum growth and effective neighbourhood radius for a 2-cm target sapling for the most parsimonious model for the species included in the analyses that responded to the identity of neighbours. Neighbourhood effects for these saplings are standardized to a 10-cm d.b.h. neighbour at 5 m distance from the target sapling. *Other* indicates that the neighbouring species light strategy is not known. ST = shade-tolerant species

			Growth (mm year^{-1}) with neighbour	
Conspecific-vs. heterospecific	Growth (mm year^{-1})	Radius (m)	Conspecific	Heterospecific
Alseis blackiana	3.13	11.16	1.90	2.52
Beilschmiedia pendula	2.19	14.96	1.52	2.06
Coussarea curvigemmia	1.47	5.28	0.64	1.19
Heisteria concinna	1.54	11.85	1.51	1.53
Laetia thamnia	5.66	9.43	4.19	5.53
Tetragastris panamensis	1.56	8.10	0.40	1.25

			Growth (mm year^{-1}) with neighbour			
Conspecific, confamilial and non-confamilial	Growth (mm year^{-1})	Radius (m)	Consp.	Confamilial	Non-confamilial	Family
Calophyllum longifolium	2.77	6.67	0.02	0.00	1.26	Clusiaceae
Guarea 'fuzzy'	1.45	12.12	1.26	1.13	1.36	Meliaceae
Protium copaifera	20.70	14.87	19.56	17.98	19.78	Burseraceae
Protium panamense	4.61	13.72	4.16	4.35	4.50	Burseraceae
Protium tenuifolium	6.81	14.10	4.83	5.09	6.40	Burseraceae

			Growth (mm year^{-1}) with neighbour				
Conspecific., shade-tolerant, gap, other	Growth (mm year^{-1})	Radius (m)	Conspecific	Shade-tolerant	Gap	Other	Light strategy
Cordia bicolor	23.81	6.92	21.78	21.66	20.33	19.07	Gap
Croton billbergianus	31.06	14.60	27.48	30.06	29.56	27.87	Gap
Desmopsis panamensis	0.98	6.13	0.97	0.88	0.97	0.92	ST
Drypetes standleyi	4.17	11.62	3.71	3.91	3.96	4.03	ST
Faramea occidentalis	1.56	4.55	0.72	1.24	1.43	1.51	ST
Hirtella trianda	4.06	14.92	2.50	3.66	3.52	3.79	ST
Inga marginata	30.58	12.37	21.04	25.01	20.66	27.24	Gap
Lacistemia aggregatum	1.88	10.69	1.88	1.86	1.88	1.80	ST
Lonchocarus latifolius	11.77	6.89	10.40	10.96	10.92	9.41	ST
Miconia argentea	15.20	14.16	12.17	14.45	12.90	13.71	Gap
Prioria copaifera	6.70	9.76	4.51	5.65	5.75	6.20	ST
Quararibea asterolepsis	1.21	12.93	1.21	1.20	1.21	1.21	ST
*Swartzia simplex*_var_*grandiflora*	2.23	14.97	2.18	2.06	2.07	2.22	ST
Tachigalia versicolor	3.59	14.54	3.25	3.53	3.50	3.52	ST
Trichilia tuberculata	2.05	12.17	1.94	1.99	2.04	2.04	ST

but these effects appear to weaken or disappear as seedlings are recruited into the larger size classes. Connell *et al*. (1984) and Hubbell *et al*. (1990) also found that strong negative conspecific effects on tree growth became weaker after seedlings or saplings reached larger size classes. Nonetheless, saplings of the selected species at BCI differ in their effective neighbourhood radius, their potential maximum growth in the absence of neighbours and in their *response* to the *magnitude* of neighbourhood crowding (i.e. their ability to grow in the presence of neighbours). However, our findings suggest that these differences did not arise from distinct effects of neighbouring taxa on target species growth but rather from virtue of other neighbourhood effects (e.g. survival) or of other differences established prior to contact.

Previous empirical and theoretical studies have suggested that a plant's response to the presence of neighbours is more likely to be the target of selection than its effect on neighbours (Goldberg 1987; Uriarte *et al*. 2002). Unpredictability of neighbourhood composition over evolutionary time, and similar resource requirements for coexisting species, would favour a generalized response to diffuse competition (Connell 1980; Hubbell & Foster 1986). In addition, spatial aggregation of seedlings around parent trees would hinder selection for strong neighbourhood effects between species and selection for a generalized response to neighbours might also confer a secondary benefit, namely the ability to tolerate pathogen or herbivore damage (Weis & Hochberg 2000; Uriarte *et al*. 2002).

One alternative explanation for the lack of support for alternatives to the equivalent neighbour model is that clumping of neighbouring species has acted to obfuscate true differences in the effects of different neighbouring species on selected target trees. The model presented here has been used to analyse neighbourhood effects on growth and survival for a tropical forest in Puerto Rico (M. U. Uriarte, unpublished data) and for

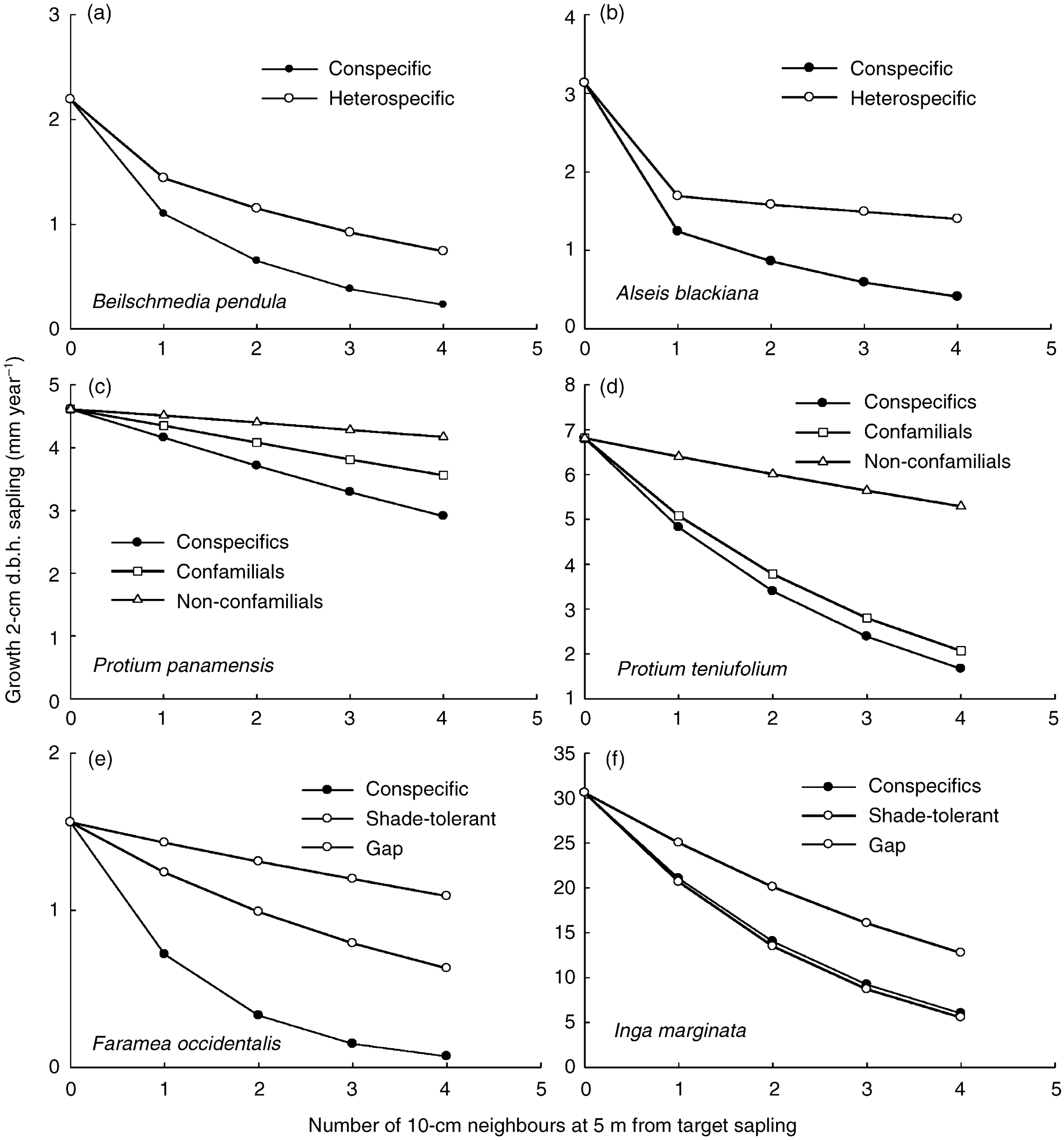

Fig. 2 Effects of neighbours for the most parsimonious model on the growth of various species (*Inga marginata* is a gap species and *Faramea occidentalis* is shade tolerant).

a northern temperate forest (C. D. Canham, unpublished data). The vast majority of target species (*c.* 95%) included in the analyses for these two sites supported models that differentiated between neighbouring species in some fashion. The relatively low diversity in these forests enabled us (sometimes required) to compare the equivalent neighbour model with one that separates neighbours to the level of species. Ongoing analyses at BCI will explore whether the strong support we obtained for the equivalent neighbour model at BCI is an artefact of over-clumping neighbouring species.

NEIGHBOURHOOD EFFECTS AND COMMUNITY STRUCTURE

Nevertheless, almost half of the species at BCI did display variation in their growth response to the identity of neighbours. Despite this variation, some clear messages emerge from our model selection exercise. First, taxonomic proximity augments the strength of interaction between neighbouring species. For species that supported models that differentiated between competitors on the basis of taxonomy, conspecifics and confamilials of target species had on average greater effects on the growth of focal saplings than neighbours unrelated to the target. These results support the idea that species that share a more recent evolutionary history have more similar resource requirements or enemies than those that do not. Three previous studies in tropical forests also found that, for the species that showed distinct responses to conspecifics relative to heterospecifics, the effects of the former were generally stronger (Connell *et al.* 1984; Hubbell *et al.* 1990; Peters 2003). Unfortunately, our findings do not contribute to a deeper understanding of the mechanisms responsible for density dependence. Recent studies at BCI and elsewhere have demonstrated that diet breadth for many tropical herbivores and pathogens encompasses genera and often families, and could easily account for the observed patterns of neighbourhood interactions at the family level (Barone 1998; Novotny *et al*. 2002).

A second conclusion of our model is that families and species differ in the response to neighbour groupings. Thus, for the majority of legumes the taxonomic identity or light guild of the neighbour had distinct effects on sapling growth, whereas the genus *Eugenia* always supported a model that assumed equivalent competitors and three species in the genus *Protium* (family Burseraceae) supported a model that differentiated between confamilial and non-confamilial neighbours. Otherwise, membership of a family or genus was not a good predictor of the response of individual species to the structure of the neighbourhood interactions. These findings have important implications for the development of tropical forest models. The rarity of the majority of species in tropical forests necessitates that species be grouped using criteria that capture their potentially different effects on target species. Historically, forest modellers have chosen from one of several grouping criteria, including taxonomic affinity, ecological guilds, similar growth dynamics and several statistical approaches (see review in VanClay 1991). Our results demonstrate that these groupings differ for individual species and cannot be applied across the board to all species in a community.

GOODNESS OF FIT OF THE MODEL

The usefulness of our analyses rests on two assumptions. The first one is that it provides a reasonable estimate of the effects of neighbourhood crowding on sapling growth. Goodness of fit tests and an understanding of the biological meaning of estimated parameters can aid in this task. The second assumption is that our approach can identify the best model from a set of models that make different assumptions about the nature of neighbourhood interactions. We have relied on information theoretic criteria to determine the strength of inference supported by the data.

The goodness of fit of our growth model (r^2) is slightly lower than that from studies that have examined the relationship of sapling growth to some measure of neighbourhood composition. For instance, Clark & Clark (1999) found partial correlation of a sapling's diameter growth to crown illumination ranging from 0.17 to 0.69 (r^2 range of 0.03–0.46). Growth is a noisy process that reflects both the growth history of individual trees and environmental variation over a range of spatial and temporal scales (Clark *et al*. 2003). Moreover, parameter estimates and the magnitude of the neighbourhood effect generally agree with existing knowledge. For instance, Hubbell *et al*. (1990) found strong negative conspecific effects for *Alseis blackiana* and *Trichillia tuberculata*, similar to the results reported here.

Clearly, a large percentage of individual variation in growth remains unexplained. There are three general classes of variation that need to be considered: physical measurement error (i.e. unavoidable error in the estimation of growth from repeated measurements of tree size); 'process' error, or the inability of the functional forms in our equations to adequately represent neighbourhood interactions; and biological (plant-to-plant) variation in both neighbourhood effects and responses. Of these three sources, the last class is of greatest importance for models of tropical forest dynamics. The scale of spatial autocorrelation of growth (and residuals of our model) at both the individual species and community levels suggests that the most likely candidate may be habitat variation (e.g. soil or water availability) over small patches: the scale of spatial autocorrelation in growth was strongest within 5 m radii from target trees and dropped off dramatically at greater distances. Efforts to understand soil heterogeneity at BCI are underway and will determine whether this factor is an important driver of growth in this forest. Studies of herbaceous plants and some trees (e.g. loblolly pine in Atwood *et al*. 2002) also suggest that genetic makeup is likely to account for a large proportion of variation in growth. Spatially unpredictable effects from herbivores, pathogens or physical damage could also be significant sources of variation in growth. Finally, historical factors, such as a recent change in the structure of the neighbourhoods, may be additional sources of variation. For instance, trees may have experienced a relatively recent release from neighbour crowding but there may be a long delay while they develop the necessary root or crown structures to reach their full growth potential. Studies in temperate forests have shown that these historical lags can account for a large proportion of variation in growth (Wright *et al*. 2000). The recent completion of the fifth tree census at BCI provides an excellent opportunity to test the strength of these historical effects using neighbourhood data from earlier censuses.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC867/JEC867sm.htm

Appendix S1 Maximum growth and effective neighbourhood radius for a 2-cm target sapling. The model differentiates between con- and heterospecific neighbours.

Appendix S2 Maximum growth and effective neighbourhood radius for a 2-cm target sapling. The model differentiates between target, confamilial and non-confamilial neighbours.

Appendix S3 Maximum growth and effective neighbourhood radius for a 2-cm target sapling. The model differentiates between target, gap, shade-tolerant and other neighbours.

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