EVIDENCE OF SPECIES-SPECIFIC NEIGHBORHOOD EFFECTS IN THE DIPTEROCARPACEAE OF A BORNEAN RAIN FOREST

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Abstract. Although accumulating evidence indicates that local intraspecific density-dependent effects are not as rare in species-rich communities as previously suspected, there are still very few detailed and systematic neighborhood analyses of species-rich communities. Here, we provide such an analysis with the overall goal of quantifying the relative importance of inter- and intraspecific interaction strength in a primary, lowland dipterocarp forest located at Danum, Sabah, Malaysia. Using data on 10 abundant overstory dipterocarp species from two 4-ha permanent plots, we evaluated the effects of neighbors on the absolute growth rate of focal trees (from 1986 to 1996) over increasing neighborhood radii (from 1 to 20 m) with multiple regressions. Only trees 10 cm to 100 cm girth at breast height in 1986 were considered as focal trees. Among neighborhood models with one neighbor term, models including only conspecific larger trees performed best in five out of 10 species. Negative effects of conspecific larger neighbors were most apparent in large overstory species such as those of the genus Shorea. However, neighborhood models with separate terms and radii for heterospecific and conspecific neighbors accounted for more variability in absolute growth rates than did neighborhood models with one neighbor term. The conspecific term was significant for nine out of 10 species. Moreover, in five out of 10 species, trees without conspecific neighbors had significantly higher absolute growth rates than trees with conspecific neighbors. Averaged over the 10 species, trees without conspecific neighbors grew 32.4 cm² in basal area from 1986 to 1996, whereas trees with conspecific neighbors only grew 14.7 cm² in basal area, although there was no difference in initial basal area between trees in the two groups. Averaged across the six species of the genus Shorea, negative effects of conspecific larger trees were significantly stronger than for heterospecific larger neighbors. Thus, high local densities within neighborhoods of 20 m may lead to strong intraspecific negative and, hence, density-dependent, effects even in species-rich communities with low overall densities at larger spatial scales. We conjecture that the strength of conspecific effects may be correlated with the degree of host specificity of ectomycorrhizae.

Key words: density dependence; Dipterocarpaceae; ectomycorrhizae; growth increment; host specificity; individual-based models; interspecific vs. conspecific neighborhood effects; Sabah, Borneo, Malaysia; Shorea spp.; tropical rain forest.

INTRODUCTION

The competitive exclusion principle states that, given a suite of species, interspecific competition will result in the exclusion of all but one species. This is particularly true if there is little or no temporal and spatial variation in the environment and the species are ecologically similar. Yet, the number of similar plant species coexisting in tropical forests may reach extraordinarily high levels. Explaining how hundreds of species can coexist within a single hectare in the face of potential competitive exclusion remains challenging and has generated many hypotheses. Among them, negative density dependence receives strong support as judged in a recent review (Wright 2002). Negative density-dependent effects occur when nearby conspecifics decrease individual performance (i.e., recruitment, survival, or growth). For example, recruitment for abundant species (Hubbell et al. 1990, Condit et al. 1992), and more generally at the community level (Wills et al. 1997, Wills and Condit 1999, Harms et al. 2000), has been shown to be negatively density dependent. Similarly, long-term survival (Hubbell et al. 2001) and mortality (Peters 2003) have been shown to be negatively density dependent for some species. Finally, growth of seedlings (<8 cm girth at breast height) and saplings (<4 cm diameter) has also been shown to be negatively density dependent (Connell et al. 1984, Uriarte et al. 2004b). There is, however, comparatively little empirical evidence of density-dependent effects on the growth of medium-sized trees and the question arises whether or not such density-dependent effects on growth exist and may contribute to the maintenance of tree species diversity. Moreover, if such species...
specific effects exist and can be detected, they will challenge neutral theories on biodiversity (e.g., Hubbell 2001), which assume that hetero- and conspecific neighbors have equivalent, or at least similar, effects on individual performance.

Interactions among plants and other sessile organisms are local processes that usually extend over limited distances. Therefore, the spatial pattern of individuals within and among species is central in ecological theory (Huston et al. 1988, Pacala 1997, Dieckmann et al. 2000) because the frequency with which individuals have other individuals of the same or different species as neighbors depends less on the relative abundance than on the particular spatial pattern. However, pattern analyses of fully mapped tree census plots at six different sites in tropical forests, including dry deciduous to wet evergreen forests on two continents, showed that nearly every species was more aggregated than a random distribution (Condit et al. 2000). Intraspecific encounters, therefore, may be much more frequent than interspecific encounters because of aggregated spatial patterns. Although overall densities of most species in very diverse communities are necessarily low (Whitmore 1984, Huston 1994, Richards 1996), local densities can nevertheless reach very high levels. These local densities are most relevant for performance of individual plants (Harper 1977). This implies that analysis and models to address ecological questions such as density dependence need to focus on individuals and adopt a spatially explicit neighborhood approach.

The neighborhood view of plant interactions has received much attention in population ecology of single species (Stoll and Weiner 2000). However, in very species-rich communities such as tropical forests, we cannot yet generalize about the spatial scales over which neighbors influence different plant population processes (Hubbell et al. 1990). Several factors may explain why. For example, different approaches and competition indices have been applied (Liu and Ashton 1998, Gourlet-Fleury and Houllier 2000). The growth component of the single-tree, distance-dependent model took the annual diameter increment to variables describing tree neighbors’ diameters at breast height, yielded the most efficient statistical model for diameter increments of V. indic a. Again, generalization to other species remains to be demonstrated.

Another individual diameter growth model relating annual diameter increment to variables describing tree size and instantaneous competition, as well as recent past evolution of competition, was developed by Gourlet-Fleury and Houllier (2000). The growth component of the single-tree, distance-dependent model took the number of neighbors located ≤30 m from the focal tree into consideration. Social status was accounted for by including neighbors with diameters at breast height (dbh) greater than or equal to the dbh of the subject tree. They concluded that competition indices needed to be asymmetric (one-sided), particularly for shade-intolerant species. In their discussion, Gourlet-Fleury and Houllier (2000) argued that the neighborhood radius should be flexible and not fixed at 30 m.

Survival and mortality have been modeled with neighborhood approaches in Neotropical forests (Hubbell et al. 2001) and the results have been compared with those in Paleotropic forests (Peters 2003). Both studies found strong density-dependent effects, i.e., survival of focal trees at the centers of circular neighborhoods generally decreased with the density of conspecific neighbors. Although Peters (2003) used 5-, 10-, 15-, and 20-m neighborhood radii, Hubbell et al. (2001) considered those individuals to be neighbors that lay within some fixed distance (up to 30 m in concentric annuli of width 2.5 m) of the focal individuals. However, both studies did not explicitly ask at which distance negative effects of conspecifics on focal trees survival were strongest and did not include growth in their analysis. More recently, Uriarte et al. (2004b) found differences between conspecific and heterospecific neighborhood effects on sapling growth for only six of 60 species tested at Barro Colorado Island.
Panama. In most cases, increased crowding around a sapling generally suppressed its growth, largely irrespective of the identity of the neighbors. Finally, Phillips et al. (2003) modeled mortality and recruitment with various approaches, and tree growth with fixed neighborhood radii of 5 and 30 m. Their diameter increment model used a shade index, a distance-dependent competition index that took relative size differences between neighbor and focal trees into account, but no differentiation was made between heterospecific and conspecific neighbors. This last assumption needs to be explored further.

Models must make some simplifying assumptions such as applying fixed neighborhood radii or lumping species and neighbors into functional types (e.g., Köhler et al. 2000, Phillips et al. 2002). However, empirical tests of these assumptions are rare. In this paper, we focus on testing direct empirical evidence of interactions among conspecific and heterospecific neighbors at various distances on individual tree growth in a species-rich lowland dipterocarp forest.

The main overstory of lowland dipterocarp rain forest, which is the most important and extensive vegetation type of Borneo, is formed by trees of the Dipterocarpaceae (Ashton 1982, Whitmore 1984; see Plate 1). Many species of this family are of the genus Shorea, and also belong to the most important timber trees in Southeast Asia (Ashton 1982) and especially in Sabah, Borneo (Meijer and Wood 1964, Newman et al. 1996, 1998). Many dipterocarp species (Condit et al. 2000), particularly species in the genus Shorea, show striking spatial aggregation (Ashton 1988, Okuda et al. 1997), which is usually explained by limited seed dispersal or the fact that all dipterocarp species examined so far have been found to be ectomycorrhizal (Malloch et al. 1980, Alexander and Högberg 1986, Ducousso et al. 2004). Small-scale habitat specificity may be less important than limited seed dispersal as an explanation for spatial aggregation (Newbery et al. 1996, Plotkin et al. 2000, Webb and Peart 2000). However, habitat preferences may very well explain the distribution of some species (Newbery and Proctor 1984, Newbery et al. 1986, Harms et al. 2001, Potts et al. 2002) and therefore may interact with density-dependent effects (Palmiotto et al. 2004) in creating spatial patterns.

Using a completely mapped data set from a lowland dipterocarp forest and a detailed, systematic, individual-based, and spatially explicit neighborhood ap-
proach, we addressed four main questions. (1) Is there
evidence for interference? If yes, (2) what is the relative
importance of intra- and interspecific interference? (3)
What are the distances over which neighborhood in-
teractions can be detected? (4) Can neighbor effects be
interpreted with specific spatial patterns (e.g., degree
of clumping)?

To address the first question, we regressed absolute
growth rate (AGR) from 1986 to 1996 in basal area on
basal area (BA) in 1986, and asked whether trees in
the neighborhood accounted for additional variation in
absolute growth. Size is only one determinant of plant
growth (Stoll et al. 1994, Duncan 1995); especially in
dense and closed vegetation, there is usually intense
interference among neighboring trees. Therefore, some
of the individual variation around the size model may
be explained by the presence or absence of neighboring
trees. The neighborhood was evaluated over several
neighborhood radii (from 1 to 20 m in steps of 1 m)
to see whether there was an optimal neighborhood ra-
dius or whether different categories of neighbors in-
fluenced the growth of focal trees at different distances.

The second question was addressed by asking which
category of neighbors, if any, yielded the best-®tting
model. We used the following categories: all neighbors
regardless of species; only heterospeci®cs; and only
conspeci®cs. Each of these categories was tested using
all trees (regardless of size) in the corresponding cat-
egory or only trees larger than focal trees at the centers
of circular and ®lexible neighborhoods of 1±20 m ra-
dius. The reason for contrasting all vs. only larger
neighbors was to test for asymmetric competition. Be-
cause competition for light is often asymmetric, i.e.,
larger neighbors may have an overproportional effect
compared to smaller ones (Thomas and Weiner 1989,
Schwinning and Weiner 1998, Brown et al. 1999), the
question was whether or not conspeci®c or hetero-
speci®c larger trees, compared to all neighbors in the
 correspondingly smaller trees, were also excluded from the analysis. Six of the remaining 10 species were in the genus Shorea (S. argentifolia Sym., S. fallax Meijer, S. johorensis Foxw., S. parvifolia Dyer, S. pauciflora King, and S. pilosa Ashton), and all of
them ranked within the 10 most abundant species in
terms of mean basal area (Table 1). The other species,
were Dipterocarpus kerrii King, Hopea nervosa King,
Parashorea malaanonan (Blanco) Merr., and Vatica
dulitensis Sym.

**Species selection**

For the present analysis, we selected all 12 overstory
dipterocarp species (Table 1) out of the 40 most abun-
dant species in terms of basal area (cf. Newbery et al.
1996: Table 1). Analyses on the other mainly under-
story species will be presented elsewhere. Two dip-
terocarp species with densities <8 trees/ha (Shorea le-
prosula Miq, and Anisoptera costata Korth.) were also
excluded from the analysis. Six of the remaining 10
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**Evaluating the neighborhood**

Circular areas with radii up to 20 m around each
individual tree were searched for neighbors in steps of
1 m. A 20-m border along each side of the two plots
was imposed so that the neighborhoods of all focal trees
were completely evaluated. Within these neighbor-
hoods of increasing radius, two competition indices
(number of neighbors and sum of basal area) were cal-
culated. However, the sum of basal area was better

<table>
<thead>
<tr>
<th>Species</th>
<th>BA (m²/ha)</th>
<th>Rank</th>
<th>Contribution to total BA (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shorea johorensis</td>
<td>3.17</td>
<td>1</td>
<td>10.3</td>
</tr>
<tr>
<td>Shorea argentinifolia</td>
<td>2.40</td>
<td>2</td>
<td>7.8</td>
</tr>
<tr>
<td>Shorea parvifolia</td>
<td>3.22</td>
<td>3</td>
<td>7.5</td>
</tr>
<tr>
<td>Shorea pauciflora</td>
<td>1.74</td>
<td>4</td>
<td>3.8</td>
</tr>
<tr>
<td>Shorea pilosa</td>
<td>0.98</td>
<td>5</td>
<td>3.2</td>
</tr>
<tr>
<td>Shorea fallax</td>
<td>0.94</td>
<td>6</td>
<td>3.1</td>
</tr>
<tr>
<td>Parashorea malaanonan</td>
<td>0.71</td>
<td>7</td>
<td>2.3</td>
</tr>
<tr>
<td>Shorea leprosula</td>
<td>0.35</td>
<td>14</td>
<td>1.1</td>
</tr>
<tr>
<td>Vatica dulitensis</td>
<td>0.29</td>
<td>22</td>
<td>&lt;1.0</td>
</tr>
<tr>
<td>Dipterocarpus kerrii</td>
<td>0.24</td>
<td>29</td>
<td>&lt;1.0</td>
</tr>
<tr>
<td>Hopea nervosa</td>
<td>0.17</td>
<td>34</td>
<td>&lt;1.0</td>
</tr>
<tr>
<td>Anisoptera costata</td>
<td>0.12</td>
<td>39</td>
<td>&lt;1.0</td>
</tr>
</tbody>
</table>

**Table 1.** Basal area (BA; in 1986), rank, and contribution to total basal area of trees (≥10 cm girth at breast height) of all 12 overstory dipterocarp species out of the 40 most abundant species in two 4-ha plots of a Bornean rain forest.

Note: Only the 10 species with densities of more than eight individuals were included in subsequent neighborhood analyses.

**Material and Methods**

**Study site**

Two 4-ha permanent plots, each 100 m wide (W–E)
and 400 m long (S–N), were set up in a lowland dip-
terocarp forest at Danum Valley Conservation Area,
Sabah, Malaysia (4°58' N, 117°48' E) from 1985 to
1987 (Newbery et al. 1992). All living trees ≥10 cm
girth at breast height (gbh at 1.3 m) were tagged, iden-
ti®ed, mapped to the nearest 0.1 m, and measured. The
~18 000 trees in the 8 ha were completely re-enumer-
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plicity, the two sampling periods subsequently will be
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correlated than the number of neighbors with the residuals from relationships of absolute growth rate and size. That is, number of neighbors did not account for as much variability as the sum of basal area. Therefore, number was not considered further. The sum of basal area of neighbors within a given radius was evaluated for six different categories of neighbors. Data from the two 4-ha plots were combined, not only to have sufficient sample sizes, but also because five species (D. kerrii, H. nervosa, S. pauciflora, S. pilosa, and V. daulisensis) occurred in only one or other of the plots.

**Regression models**

Absolute growth rate in basal area from 1986 to 1996 (AGR in square centimeters) was modeled with various regressions of increasing complexity (Table 2). First, AGR was modeled as a function of basal area (BA) in 1986, i.e., size at the beginning of the growth interval (model A). Second, one neighbor term was added to the size term. The neighbor term took into account all neighbors regardless of species and relative size differences (model B1); only heterospecific neighbors (B2); or only conspecific neighbors (B3) (both B2 and B3 regardless of relative size differences). Each of these terms was also tested using only trees that were larger than the focal trees (corresponding models B4, B5, and B6). Finally, to compare effect sizes of heterospecifics and conspecifics more directly, and because the corresponding terms could be correlated, the single-neighbor-term models were extended to models of size and two neighbor terms (C1-C4), i.e., one for heterospecific and the other for conspecific neighbors. Two-term models allowed the radii that maximize the fit to be different for conspecific and heterospecific neighbors. Note that results of models C1 and C2 were generally very similar to those of C3 or C4. Therefore, they are not presented in the Results section or in the figures, but are included in the electronic appendices. Finally, to meet the assumptions of least squares linear regression, AGR, BA, and the neighbor terms (ΣBA of neighbors) were log10-transformed. Only trees <100 cm girth were used as focal trees because including the largest trees as focals resulted in skewed residuals.

The different regression models were then fitted for each species and all neighborhood radii. The regression statistics were stored such that the radius yielding the highest $R^2$ value (adjusted for the number of parameters, i.e., $1 - \text{residual mean squares/total mean squares}$) could be found for each neighborhood model with one neighbor term. Similarly, for the neighborhood models including two neighbor terms (C1-C4), the combination of heterospecific and conspecific radii yielding the highest (adjusted) $R^2$ values were found. The adjusted $R^2$ values or Akaike’s information criterion (Sakamoto et al. 1986) were used because both take the number of parameters into account; this is important if models with different numbers of parameters are compared (cf. Hilborn and Mangel 1997). Because the criteria selected identical models, with very few exceptions, we report only the more familiar adjusted $R^2$ values as a function of neighborhood radius.

In addition to assessing significance, we also investigated the magnitude of effects by calculating variance components and effect sizes (Cohen 1977). Effect sizes

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**Table 2. Overview of the different regression models and neighbor terms used to model absolute growth rate in basal area (AGR) from 1986 to 1996.**

<table>
<thead>
<tr>
<th>Model label</th>
<th>Dependent variable, absolute growth</th>
<th>+ one neighbor term</th>
<th>+ second neighbor term</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>log$_{10}$(AGR)</td>
<td>log$_{10}$(BA)</td>
<td></td>
</tr>
<tr>
<td>B1</td>
<td>all</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B2</td>
<td>ALL</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B3</td>
<td>het</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B4</td>
<td>HET</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B5</td>
<td>con</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B6</td>
<td>CON</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C1</td>
<td>het</td>
<td>HET</td>
<td>CON</td>
</tr>
<tr>
<td>C2</td>
<td></td>
<td>HET</td>
<td>CON</td>
</tr>
<tr>
<td>C3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C4</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** The model label is used to refer to a particular regression model. Model A included only size; models B1-B6 included size plus one neighbor term; and models C1-C4 included size plus two neighbor terms. Capital letters in neighbor terms are used to refer to neighbor terms that only included larger neighbors relative to the focal tree in the center of the circle. The neighbor terms were calculated as the sum of basal area (BA) in 1986 (calculated from girth at breast height in 1986 and log$_{10}$-transformed) of neighbors in different categories and evaluated in 1-m steps within circular neighborhoods from 1 to 20 m. Independent variables to the right of the ‘‘+’’ sign in the column head, were used as additive (‘‘+’’) terms in multiple regressions. Abbreviations: all, neighbor terms included all neighbors independent of species; het, neighbor terms included only heterospecific neighbors; con, neighbor terms included only conspecific neighbors.
Model predictions and bootstrap

To compare the predictive accuracy of the various models, the following randomization procedure was applied. For each species, we randomly divided the available focal trees into two halves. One half was used to estimate the parameters of the statistical model and the other half was used to test the predictions made by the statistical model. This resampling was repeated 20 times. The neighborhood information on conspecific neighbors was used to divide focal trees into one group with and one group without conspecific neighbors. The neighborhood radius dividing the trees into the two groups was taken as the first maximum adjusted $R^2$ of model B$_5$ ("con," all trees) with a minimum of 5 m in order to have sufficient individuals in the group with conspecific neighbors. This grouping allowed not only a comparison of the predictions of competing models, but also a comparison between the performances of groups of trees with and without conspecific neighbors.

Pattern analysis

The results from standard pattern analysis, i.e., a combined count–distance analysis (Ripley 1977, Haase 1995), together with a short explanation of their interpretation, may be found in Appendix B.

Results

Regression models

The profiles of the adjusted $R^2$ values showed considerable variation among the species, models, and radii (Fig. 1).

Shorea johorensis.—The neighbor term of model B$_1$ (i.e., including all neighbors, irrespective of species and relative size differences) was significant ($P < 0.05$) from 6 to 17 m, and that of B$_2$ (i.e., all neighbors, irrespective of species but larger than focal trees) was significant at neighborhood radii from 4 to 17 m. The maximum adjusted $R^2$ of model B$_1$ was 43% at 5 m; that of B$_2$ was 38% at 12 m. Model B$_1$ (heterospecific neighbors) had significant ($P < 0.05$) neighbor terms from 11 to 15 m and maximum adjusted $R^2$ of 31% at 11 m. Model B$_2$ (heterospecific larger neighbors) had significant neighbor terms at 6 m and from 11 to 17 m and a maximum adjusted $R^2$ of 29% at 12 m. Models B$_3$ (conspecific neighbors) and B$_6$ (conspecific larger neighbors) were significant at neighborhood radii from 4 to 14 m and 3 to 16 m, respectively. Model B$_5$ had a maximum adjusted $R^2$ of 38% at 6 m; B$_8$ had one of 43% at 5 m. Models C$_1$ and C$_2$ (i.e., two-neighbor terms with different radii for heterospecific and conspecific (C$_1$) or heterospecific larger and conspecific larger (C$_2$) neighbors) had maximum adjusted $R^2$ of 57% and 56%, respectively, at heterospecific radii of 11 m and conspecific radii of 9 m for C$_1$ and heterospecific radii of 15 m and conspecific radii of 6 m for C$_2$.

Shorea argentifolia.—Models B$_1$–B$_4$ were never significant. By contrast, model B$_5$ was significant from 17 to 20 m and model B$_6$ was significant at 19 and 20 m with an $R^2 > 60\%$. Models C$_1$ and C$_2$ had highest $R^2$ values at conspecific radii of 19 m and heterospecific radii of 18 m.

Shorea parvifolia.—Models B$_1$ and B$_2$ had highest $R^2$ values at 5 and 4 m. Model B$_3$ was never significant and B$_4$ was only significant at 1 m. Model B$_5$ was significant at 4, 16, and 17 m, and model B$_6$ showed additional significances from 8 to 15 m. The two-neighbor-term model C$_2$ had considerably higher $R^2$ values and a maximum of almost 50% at heterospecific radii of 1 m and conspecific radii of 14 m.

Shorea pauciflora.—Model B$_1$ was significant from 7 to 15 m and B$_2$ at 4 m and from 8 to 15 m. Moreover, model B$_2$ always had higher $R^2$ values than model B$_1$. Maximum adjusted $R^2$ values were $\sim 40\%$ and 44% at 9 m. Models B$_1$ and B$_2$ showed a similar pattern with a maximum of 41% at 9 m for B$_1$. Model B$_3$ was not significant at any of the neighborhood radii. In contrast, model B$_4$ was significant at 7 and 10 m but the $R^2$ values were well below those of any of the other models with a single neighborhood term. The models with two neighbor terms reached $R^2$ values of 44% and 53% at heterospecific and conspecific radii of 10 m.

Shorea pilosa.—Models B$_1$ and B$_2$ were significant at 6 m and both peaked in terms of adjusted $R^2$ at 6 m. Models B$_3$ and B$_4$ were not significant at any of the neighborhood radii. Models B$_5$ and B$_6$ again showed a similar pattern with the highest $R^2$ value of 38% for model B$_5$ at 5 m. Model C$_1$ had maximal $R^2$ values higher than any of the models with one neighbor term only. The maximum $R^2$ value for model C$_1$ (45%) was at a heterospecific radius of 6 m and conspecific radius of 5 m.

Shorea fallax.—Model B$_1$ was significant at neighborhood radii of 3 and 4 m and peaked at 3 m. Model B$_2$ was only significant at 3 m. Model B$_3$ was only significant at a neighborhood radii of 3 m, whereas model B$_4$ was never significant. In contrast, models B$_5$ and B$_6$ again were very similar and significant over almost all of the neighborhood radii. Both reached maximum $R^2$ values over 45% and peaked at 4 and 6 m, respectively. Models C$_1$ and C$_2$ reached $R^2$ values around 50%. The peak for C$_1$ was at a heterospecific radius of 3 m and conspecific radius of 4 m. On the other hand, model C$_2$ peaked at a heterospecific radius of 3 m and conspecific radius of 6 m.

Among the other dipterocarp species, Parasorella malacanan showed little, and Dipterocarpus
Fig. 1. Variance accounted for (adjusted $R^2$) in size and neighborhood models over neighborhood radii (m) of six *Shorea* species and four other dipterocarp overstory species at Danum (Sabah, Malaysia). Absolute growth rate (AGR) in basal area (1986–1996) was modeled as function of size, i.e., basal area (BA) in 1986, and size plus one or two neighbor terms ($\Sigma$BA of neighbors in 1986). All terms were log$_{10}$-transformed. The adjusted $R^2$ of the size-alone model (A) is independent of the neighborhood radius and is represented by the horizontal red line. Neighborhood models with one neighbor term are represented by thin lines and small symbols if relative size differences of the corresponding neighbor category and focal trees were ignored (models B$_1$, B$_3$, and B$_5$). Thick lines and large symbols are used for neighborhood models with one neighbor term that only considered neighbors larger than the focal trees (models B$_2$, B$_4$, B$_6$). If the corresponding neighbor terms were significant ($P < 0.05$), symbols were used as follows: stars (•, *) for neighborhood models including all neighbors (models B$_1$, B$_2$, black lines), diamonds (○, ○) for neighborhood models including only heterospecific neighbors (models B$_3$, B$_4$, blue lines), and circles (◦, ○) for neighborhood models including only conspecific neighbors (models B$_5$, B$_6$, green lines). Adjusted $R^2$ values of the neighborhood models with two neighbor terms (C$_1$ and C$_2$) are presented. Note the different axis scaling for different species; in particular, the $y$-axis starts at zero only for *S. johorensis* and *S. argentifolia*. 
kerrii showed no significance for the models with a single neighborhood term. Nevertheless, model C1 had significant conspecific terms for P. malaanonan, with an $R^2$ of 64%. In Vatica dulitensis, no model showed significances beyond a neighborhood radius of 2 m. Model C2 reached an $R^2$ of 74% at a heterospecific radius of 20 m and a conspecific radius of 2 m. Finally, in Hopea nervosa, models B1–B4 showed significance at small and large neighborhood radii. By contrast, model B5 was significant at neighborhood radii > 14 m. Model B6 was only significant at 18 m. Both had maximum $R^2$ values of >65% at 20 and 18 m, respectively. Model C2 reached the highest $R^2$ (76%) at a heterospecific radius of 7 m and a conspecific radius of 18 m.

Correlations between the $R^2$ values for models A and B1–B6 (Table 3) across the 10 species were all significant ($r_s = 0.663–0.993$, $P < 0.05$); those between A and B1–B6 were highly so ($P < 0.001$). $R^2$ values for models A and B1–B6 were poorly correlated with those of models C1 and C2 ($r_s = 0.435–0.572$, $P = 0.084–0.209$). However, correlations for models B5, B6, C1, and C2 were again much higher ($r_s = 0.825–0.974$, $P < 0.003$).

In summary, in all species except Dipterocarpus kerrii, at least one neighborhood model explained significantly more variation in AGR than did model A. The size term of model A was significant in all species and accounted for 15–64% of variability in absolute growth rate (Table 3). The adjusted $R^2$ values for model A were generally higher for dipterocarp species not belonging to the genus Shorea. For six out of 10 species, the neighbor term of model B1 and B2 was significant ($P < 0.05$). For model B3, eight of 10 species had significant neighbor terms; for model B6, all species except Dipterocarpus kerrii and Parashorea malaanonan had significant neighbor terms. Among the models with two neighbor terms, the conspecific term of model C1 was significant for nine species and the average adjusted $R^2$ across these species was 58%. It increased slightly to 59%, on average, for model C2, which thus performed best among all models in terms of adjusted $R^2$.

We used the radius at which model B5 reached the first maximum value of adjusted $R^2$ to partition the individual trees into groups with and without conspecific neighbors. For each species, the border was decreased from 20 m to the particular radius that increased the number of available individuals. Average basal area (BA) and absolute growth rate (AGR) of trees in both groups showed considerable differences for AGR (up to more than sixfold), but not for BA (Table 4). Only one of the species (S. pilosa) showed

**Fig. 1.** Continued.
a significant difference in BA. Averaged over the 10 species, mean BA was 49.3 cm² in the group without conspecific neighbors and 40.5 cm² in the group with conspecific neighbors. These means were not significantly different (t = 1.47, P = 0.176). In contrast, AGR was significantly higher for four of the six Shorea species in the group without conspecific neighbors than in the group with conspecific neighbors. For another species, Hopea nervosa, this difference was marginally significant. Averaged over the 10 species, AGR was 32.4 cm² for trees without conspecific neighbors and 40.5 cm² in the group with conspecific neighbors. This twofold difference in AGR was significant (t = 2.58, P = 0.049).

The effect sizes of the neighborhood models with two terms (C₁ and C₂) generally showed stronger effects of conspecific compared to heterospecific neighbors (Table 5a). In Dipterocarpus kerrii, however, heterospecific effects were significantly stronger than conspecific effects. Averaged across the 10 species, the effect size of model C₁ for heterospecific neighbors was −0.076; for conspecifics, the average effect size was −0.251. This difference was marginally significant (t = 2.25, P = 0.051, tested with absolute effect sizes). The effects of conspecific larger neighbors were stronger than effects of heterospecific larger neighbors in four out of 10 species. (Table 5b). For the other three species (Shorea parvifolia, S. pauciflora, and S. pilosa) heterospecific larger neighbors had effects very similar to those of conspecific larger neighbors. For model C₂, the average effect size was −0.095 for heterospecific larger neighbors and −0.296 for conspecific larger neighbors. This difference was marginally significant across all 10 species (t = 2.14, P = 0.061, tested with absolute effect sizes). Across the six species of the genus Shorea, effects of conspecific larger neighbors (−0.329) were significantly stronger (t = 3.06, P = 0.028, tested with absolute effect sizes) than effects of heterospecific larger neighbors (−0.033).

Model predictions
To test predictions from the various models, 20 random samples were drawn per species. Half of the trees in each sample were used to fit the regression model at the neighborhood radius with the highest adjusted $R^2$. These estimates were then used to predict the AGR of the other half of the trees, which again were grouped into trees with and without conspecific neighbors (Fig. 2). In Shorea johorensis, S. argentifolia, S. pilosa, and S. fallax, focal trees without conspecific neighbors, on average, had much higher AGR than did focal trees with conspecific neighbors. Thus the randomizations supported the results presented earlier (cf. Table 4). Moreover, the size model underestimated AGR for focal trees without conspecific neighbors in all four species. In contrast, for trees with conspecific neighbors, the size model predicted higher AGR than that actually measured. If all neighbors were included in a single-neighbor-term model, the predictions did not differ much compared to predictions from the size-alone model. However, single-neighbor-term models taking only conspecific neighbors into account yielded much
better predictions than did either of the previous models. Models with two neighbor terms (not shown), yielded predictions very similar to those of the single-neighbor-term models with conspecific neighbors.

**Pattern and size analysis**

There was variation in the degree of clumping among the 10 species, but also within species among plots. (Maps of each species’ distribution in the plots, and graphs of L vs. t, are found in Appendix B.) *Shorea fallax* and *S. pilosa* showed the most clumped patterns among the *Shorea* species. *Shorea parvifolia* (especially in plot 1) and *S. pauciflora* were the least clumped. *S. johorensis* was not more clumped than either *S. parvifolia* or *S. pauciflora*. For *S. argentifolia*, there were few individuals per plot, so that pattern analysis must be interpreted with caution. *Parashorea malaanonan* in plot 1 was almost random, but in plot 2 it was clumped. The remaining three species all showed strikingly clumped spatial patterns. Comparing the five strongly clumped species (*S. pilosa*, *S. fallax*, *V. dulitensis*, *D. kerrii*, and *H. nervosa*) with those species with no or little evidence of clumping (the other five in Table 3), $R^2$ values for models $B_5$, $B_6$, $C_1$, and $C_2$ (Table 3) were not significantly different ($t_{0.005,0.01,0.05,0.10} = -1.34$ to $-0.11$, $P = 0.221-0.918$).

Using the numbers of trees of each species in both plots together, the proportions of trees with girth < 100 cm (of those ≥10 cm) ranged from 0.046 to 0.304. This ratio was strongly negatively correlated with the $R^2$ values in Table 3 for models A and $B_5$, $B_6$ ($r_8 = -0.732$ to $-0.760$, $P = 0.011-0.016$), but for $B_5$ and $B_6$ the correlations were much weaker ($r_8 = -0.318$ and $-0.281$, $P = 0.370$ and 0.432, respectively), and for $C_1$ and $C_2$ the correlations were near zero ($r_8 = 0.026$ and $-0.039$, $P = 0.942$ and 0.914, respectively). Thus, species with strong conspecific effects were not those with greater proportions of larger, or smaller, trees.

**DISCUSSION**

Using individual-based and spatially explicit neighborhood models, we found strong negative effects of neighbors on absolute basal area increment in 10 abundant dipterocarp overstory species of a lowland dipterocarp forest on Borneo. For most of the 10 species, these negative effects were primarily due to conspecific (larger) neighbors. That is, trees with many conspecific neighbors showed markedly reduced basal area increments compared to trees with few or no conspecific neighbors. Averaged over all 10 species, trees without conspecific neighbors grew about twice as fast as those with conspecific neighbors. However, significant negative conspecific effects were only found in four of the six *Shorea* species. In the other two species (*S. pauciflora* and *S. parvifolia*), there were no differences in absolute growth rate between trees with or without conspecific neighbors. *S. argentifolia* was very different in that its conspecific larger neighbors’ effect was at distances ≥19 m, whereas for *S. fallax*, *S. johorensis*, and *S. pilosa*, the effect was over the whole range of 5–20 m (Fig. 1). Differences in the strength of the conspecific effect were not explainable by the degree of spatial clumping or by relative size distributions. From the results of our phenomenological neighborhood approach, we can only speculate about the mechanisms that lead to the strong intraspecific negative effects. However, that models with all or heterospecific larger trees as neighbors did not generally perform better than the models with conspecific neighbors suggests that suppression of the focus trees was not due to shading.
Our analysis underlined the importance of intraspecific density-dependent effects on growth are only strong enough to regulate populations of common species (Hubbell et al. 1990, Wright 2002), whereas most species show no species-specific effects. However, our results, together with results from a hurricane-driven tropical forest (Uriarte et al. 2004a, 2005), suggest that intraspecific density dependence may be strong. Therefore, we conclude that not all neighbors are equivalent, as is supposed in the neutral model of Hubbell (2001). In the tropical forest that we studied, conspecific vs. heterospecific interference effects probably play an important role in forest dynamics and community structure.

In tropical forests, decreased performance of individuals around conspecifics has more often been explained by species-specific herbivores and pathogens (Janzen 1970, Connell 1971) rather than resource competition. On the other hand, the many tests of the Janzen-Connell hypothesis have yielded mixed results. For example, Blundell and Peart (1998) found distance-displacement responses that were not consistent with the Janzen-Connell hypothesis. Our results, together with results from a hurricane-driven tropical forest (Uriarte et al. 2004a, 2005), suggest that intraspecific density dependence may be strong. Therefore, we conclude that not all neighbors are equivalent, as is supposed in the neutral model of Hubbell (2001). In the tropical forest that we studied, conspecific vs. heterospecific interference effects probably play an important role in forest dynamics and community structure.

Table 5. Effect sizes ($t^2$/residual df + $r^2$; the sign of $t$ indicates the direction of the effects) for neighbor models with size and two neighbor terms: (a) for model $C_1$, and (b) for model $C_2$.}

<table>
<thead>
<tr>
<th>Species</th>
<th>$r_h$</th>
<th>$r_c$</th>
<th>$r_{het}$</th>
<th>$r_{con}$</th>
<th>$t$</th>
<th>df</th>
<th>$P$</th>
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<tr>
<td><strong>a) Model $C_1$</strong></td>
<td></td>
<td></td>
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</tr>
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<td>-0.11</td>
<td>8.1</td>
<td>19</td>
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</tr>
<tr>
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<td>-0.41</td>
<td>2.2</td>
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<td><strong>b) Model $C_2$</strong></td>
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<td>-0.36</td>
<td>-0.3</td>
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Notes: The neighborhood radius is designated ‘‘$r_h$’’ for heterospecific neighbors and ‘‘$r_c$’’ for conspecific neighbors. Values are averages over 20 randomizations randomly selecting half of the available focal trees (the other half was used to test the predictions of the models). The last three columns give the results of paired $t$ tests comparing the effect size of the two neighbor terms among the 20 randomizations. For some species, df are <19 because the regression models could not be fitted: for example, if there were no focal trees with conspecific neighbors. Boldface values indicate significance at $P < 0.05$. The effects that we found for growth can be linked to survival and reproduction and are therefore relevant for population and community dynamics. It is well established that small plants have higher probabilities of dying than large plants, and that small plants produce fewer seeds than large plants. Moreover, plants must reach a threshold size (Weiner 1988, Schmid et al. 1994) in order to start flowering and reproduction, and tropical trees are no exception, as has recently been shown (Uriarte et al. 2005). Hence, any effects on growth and therefore size will have similar effects on survival and reproduction and, ultimately, on population dynamics.

Before we formulate a new hypothesis about possible mechanisms underlying the observed species-specific effects, we will briefly discuss some implications of our results for population and community dynamics of tropical forests. These implications are also relevant for management strategies and simulation models of tropical forests.

Our individual-based neighborhood analysis revealed differences in the spatial extent of conspecific vs. heterospecific effects of neighbors. Spatially explicit competition models have shown that such differences promote coexistence if conspecific interactions occur over larger distances than heterospecific interactions (Murrell and Law 2003). Our analysis uncovered intraspecific negative density-dependent effects at various distances. However, most earlier analyses (reviewed in Wright 2002) only considered effects of conspecifics (not heterospecifics) and plot-based or fixed (rather than flexible) neighborhoods. Taken together, the general conclusion seems to be that intraspecific density-dependent effects on growth are only strong enough to regulate populations of common species (Hubbell et al. 1990, Wright 2002), whereas most species show no species-specific effects. However, our results, together with results from a hurricane-driven tropical forest (Uriarte et al. 2004a, 2005), suggest that intraspecific density dependence may be strong. Therefore, we conclude that not all neighbors are equivalent, as is supposed in the neutral model of Hubbell (2001). In the tropical forest that we studied, conspecific vs. heterospecific interference effects probably play an important role in forest dynamics and community structure.
FIG. 2. Comparison of measured absolute growth rate (AGR in cm\(^2\)) of basal area from 1986 to 1996 with predicted AGR from multiple regressions including size only, size plus all neighbors (B\(_1\)), and size plus conspecific neighbors (B\(_3\)). Random samples (n = 20) were drawn for each of four Shorea species (S. johorensis, S. argentifolia, S. pilosa, and S. fallax). Half of the trees of each sample were used to fit the regression model and the other half were grouped into trees with (solid circles) and without (open circles) conspecific neighbors. Large crosses indicate the means (±2 se) over 20 samples in each group. Predicted group means within ±2 se of the measured AGR are highlighted with thick crosses.
dependent effects of herbivores for two out of four Shorea species and cautioned against generalizations regarding distance-dependent effects in diverse forests. Indeed, a recent meta-analysis found no general support for the distance-dependent predictions of the Janzen-Connell hypothesis and concluded that further testing to explore this hypothesis as a diversity-maintaining mechanism is unnecessary (Hyatt et al. 2003). Moreover, local species-specific density dependence, mediated through specialist enemies of offspring such as fungal pathogens and insect seed predators, only facilitates coexistence in spatially explicit simulations when both offspring and enemies disperse over short distances (Adler and Muller-Landau 2005).

We hypothesize that the varying conspecific neighborhood effect might be a function of the degree of host specificity of the ectomycorrhizae. Those species with very strong conspecific effects are postulated to have highly specific fungal symbionts. The ectomycorrhizal status of the Dipterocarpaceae is well established (Malloch et al. 1980, Alexander and Högberg 1986, Ducousso et al. 2004), but the degree of host specificity appears to be variable. Studies to date on Shorea species show that they may have roughly 10–30 fungal types (or species) on their roots, but one or two species frequently dominate (Becker 1983, Smits 1983, Lee and Alexander 1996, Ingelby et al. 1998). Nevertheless, some species of fungi are specialists and others are broad generalists (Janos 1983, Alexander 1989). Across sites, the same tree species may have a different composition of ectomycorrhizae (Lee and Alexander 1996). Finally, ectomycorrhizal associations of dipterocarps have been shown to influence the accessibility of organic nutrients from leaf litter (Brearley et al. 2003).

Our results show that small trees (10 to <100 cm dbh) are suppressed in their growth when they have adults of the same species as neighbors. Because most of the large dipterocarps are still growing fast (the forest has not yet reached its expected maximum basal area for the site; Newbery et al. 1992), we propose that they drain resources from the smaller trees via mycelial networks. Although carbon is probably at a premium for small trees in the understory, and they gain it partly from the larger trees, large trees may take phosphorus from the smaller ones and thus slow their growth. To acquire phosphorus, mycorrhizae allow the large trees to expand their root systems by connecting with and using the smaller trees. We predict that S. johorensis, S. argentifolia, S. pilosa, S. fallax, V. dalitensis, and H. nervosa might have highly specific ectomycorrhizae, whereas S. parvifolia, S. pauciflora, P. melaanonan, and D. kerrii have less species-specific or no ectomycorrhizae. This is a completely new way of looking at conspecific neighbor interactions between trees.

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APPENDIX A

Supplementary tables with adjusted $R^2$ values, best-fitting radii, estimates, standard errors, and $t$ and $P$ values of the regression coefficients are available in ESA’s Electronic Data Archive: Ecological Archives E086-166-A1.

APPENDIX B

Spatial patterns and combined count–distance ($L_m$ vs. distance $t$ in meters) of dipterocarp species in the two 4-ha plots at Danum are available in ESA’s Electronic Data Archive: Ecological Archives E086-166-A2.