

Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity

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Abstract. A plantation of native trees was established in Panama in 2001 to study the relationship between biodiversity and ecosystem functioning. Five years later, mixed-species plots had experienced enhanced tree growth compared with monocultures. Searching for underlying mechanisms, we developed a neighborhood model isolating size and identity effects. We found that the size of neighbors is, by far, the largest source of variation in individual-tree diameter and height. Size-asymmetric competition appears as a structuring factor in the plantation. The relative growth rate of small trees was significantly lower than that of large trees, and their height and basal diameter were most variable. The 50 smallest trees of the plantation suffered a disproportionate amount of death, and the proportion of small trees was highest in monoculture. Increased biomass allocation to branches for trees growing in three-species plots suggests that competition for light might be taking place. Clearly, local neighborhood plays a central role in determining productivity, suggesting that scale needs to be incorporated in the theoretical development and analysis of biodiversity and ecosystem functioning.

Key words: biodiversity and ecosystem functioning; neighborhood; Sardinilla, Panama; size-asymmetric competition; tropical-tree plantations.

INTRODUCTION

While the bulk of experimental evidence on the relationship between biodiversity and ecosystem functioning comes from grassland communities (Srivastava and Vellend 2005, Balvanera et al. 2006), interest for biodiversity is rising in forestry (Bristow et al. 2006). One of the earliest attempts to relate diversity to yield in tropical-tree plantations was made in a study conducted in Costa Rica, where *Cordia alliodora* was grown in monoculture and secondary forest in addition to a system mimicking natural succession (Ewell 1999). The results did not support the hypothesis that species-rich systems were most productive because *C. alliodora* monocultures held nutrients as tightly as natural succession. Differential species performance has been reported in other plantations in Costa Rica, some species growing better in pure stands and others in mixtures (Montagnini and Porras 1998, Stanley and Montagnini 1999, Piotto et al. 2003, Petit and Montagnini 2006, Redondo-Brenes and Montagnini 2006). Results from Australian studies reported positive (Erskine et al. 2006), species-specific (Grant et al. 2006), or negative (Firn et al. 2007) biodiversity effects.

Accordingly, a clear picture of the role of biodiversity in plantations is yet to emerge.

Our study was conducted in a tropical-tree biodiversity plantation designed to test the relationship between biodiversity and ecosystem functioning (Scherer-Lorenzen et al. 2005). Potvin and Gotelli (2008) showed that productivity, estimated by plot basal area, was significantly higher in three-species mixtures than in monocultures. Further increase in diversity, from three to six species, did not affect basal area. Because mortality is an important determinant of biomass and productivity in tree plantations, the effect of diversity and species identity on mortality was partitioned (Potvin and Gotelli 2008). Mortality was species specific, with *C. alliodora* suffering the highest mortality rates, and did not vary significantly with diversity. Increased productivity of mixtures therefore stemmed from growth enhancement of individual trees rather than reduced mortality (Potvin and Gotelli 2008). Assuming that trees interact with each other over small local areas or neighborhoods (Stoll and Weiner 2000), we examined the effects of size and identity of the nearest neighbors on individual-tree growth. Traditionally, the relationship between a plant and its neighbors has been studied following the “mean-field” approach, in which the average performance of individual plants is related to the average competitive environment of the same plot (Pacala 1997). This approach has been increasingly questioned because plants interact at small scale (Stoll and Weiner 2000) and spatial patterns are often

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A) Six-species design

Tr	Co	Ca	Ls	Ae	Hc	Tr	...
Co	Ca	Ls	Ae	Hc	Tr	Co	...
Ca	Ls	Ae	Hc	Tr	Co	Ca	...
Ls	Ae	Hc	Tr	Co	Ca	Ls	...
Ae	Hc	<u>Tr</u>	Co	Ca	Ls	Ae	...
Hc	<u>Tr</u>	<u>Co</u>	<u>Ca</u>	Ls	Ae	Hc	...
Tr	Co	<u>Ca</u>	Ls	Ae	Hc	Tr	...
...

B) Three-species design

Hc	<u>Ca</u>	Co	Hc	...
<u>Ca</u>	<u>Co</u>	<u>Hc</u>	Ca	...
Co	<u>Hc</u>	Ca	Co	...
...

Tr	Ae	Ls	Tr	...
Ae	Ls	Tr	Ae	...
Ls	Tr	Ae	Ls	...
...

Ls	<u>Ae</u>	Co	Ls	...
<u>Ae</u>	<u>Co</u>	<u>Ls</u>	Ae	...
Co	<u>Ls</u>	Ae	Co	...
...

Ls	<u>Hc</u>	Co	Ls	...
<u>Hc</u>	<u>Co</u>	<u>Ls</u>	Hc	...
Co	<u>Ls</u>	Hc	Co	...
...

Tr	Ca	Hc	Tr	...
Ca	Hc	Tr	Ca	...
Hc	Tr	Ca	Hc	...
...

Tr	Ae	Ca	Tr	...
Ae	Ca	Tr	Ae	...
Ca	Tr	Ae	Ca	...
...

FIG. 1. Schematic planting design for (A) six-species and (B) three-species plots, showing the neighborhoods consisting of one focal tree and its four nearest neighbors. Each species was thus grown in four different neighborhoods, as illustrated by the use of bold letters for the neighborhoods of Tr and underlined letters for Co. Species abbreviations are: Ls, *Luehea seemanii*; Ca, *Cordia alliodora*; Ae, *Anacardium excelsum*; Hc, *Hura crepitans*; Co, *Cedrela odorata*; and Tr, *Tabebuia rosea*.

nonrandom (Law and Dieckmann 2000). Neighborhood models linking the performance of an individual plant to some characteristics of its immediate competitors have been proposed as an analytical alternative to overcome these shortcomings (Coomes et al. 2002). A neighborhood approach should allow us to understand tree-to-tree interactions and determine whether the observed growth enhancement is driven by inter- or intra-specific competition or by facilitation (Srivastava and Vellend 2005).

During the gap-formation phase of tropical forests, competition for light is a key determinant of community dynamics (Hubbell et al. 1999). Saplings and seedlings will "race" upward in an attempt to secure access to light. Coomes and Allen (2007) showed that tall neighbors can intercept light before it reaches the focal tree. Thus, size is an important tenet of competitive

interactions between plants (Stoll et al. 2002). Weiner et al. (2001) used the coefficient of variation (CV) of plant biomass as a measure of size inequalities, arguing that the CV will be higher in environments where size-asymmetric competition is a structuring feature. In addition, Coomes and Allen (2007) proposed that, under size-asymmetric competition, small trees should have growth rates lower than those of tall trees until complete growth suppression in small trees. Here, we hypothesize that size-asymmetric competition is a structuring factor of our biodiversity tree plantation.

METHODS

The study was conducted in a tree plantation established in Sardinilla, central Panama, in 2001. This plantation consists of 24 plots (45 × 45 m) with 12 monoculture plots and 6 three- and six-species-mixture plots established with *Luehea seemanii* (Ls), *Cordia alliodora* (Ca), *Anacardium excelsum* (Ae), *Hura crepitans* (Hc), *Cedrela odorata* (Co), and *Tabebuia rosea* (Tr). These six species were chosen because seeds are readily available and known to germinate easily, and because Ca, Ae, Co, and Tr are important native timber species in Panama while Ls and Hc are ecologically important in the Panama Canal Watershed where our experiment is taking place (Potvin and Gotelli 2008). Following standard reforestation practices in Panama, trees were planted at 3 m distance from one another, with 231 individuals per plot, on average.

Each species was planted in two replicated monoculture plots, in three three-species plots and in six six-species plots. Composition of the six three-species plots was defined by randomly choosing between Ca and Ls, Ae and Hc, and Co and Tr. These three groups of species cover the range of relative growth rates in diameter at breast height (dbh) in the nearby forest of Barro Colorado Island. *L. seemanii* is the fastest growing species (9.1% per year), and *C. odorata*, the slowest one (2.3% per year) (Scherer-Lorenzen et al. 2005). Consequently, while species composition differed among the six three-species plots, faster and slower growing species were equally represented in any given plot (Fig. 1). By comparison, the composition of all six six-species plots was identical. Within each plot, trees were planted following a multiple Latin-square design, to ensure that systematic environmental variation did not bias the results (Potvin 2001). It followed that within each three-species or six-species plot, a given species was surrounded by the same two species, thus forming a specific neighborhood (Fig. 1). Because species composition changed over the six three-species plots, individual trees were surrounded, across the plantation, by four different neighborhoods: three from three-species plots and one from six-species plots.

Two key traits of performance, height and diameter, were measured on all individual trees at the end of each growing season (December–January) between 2002 and 2006. In the first four years of the experiment, when

seedlings were <2 m high, basal diameter (BD) was measured at 10 cm from the ground. For saplings of 2 m or taller, dbh was recorded at 1.30 m from the ground. While dbh is often used in forestry studies, it poses difficulties in Sardinilla because many individuals are multi-stemmed and low branches and secondary trunks are easily confounded. Therefore, in 2006, both BD and dbh were measured for each tree.

Our first objective was to determine if the size and identity of the nearest neighbors affected individual tree growth. To do this, we developed two analysis of covariance (ANCOVA) models and analyzed variation in both 2006 height and 2006 BD in relation to the diversity level (Eq. 1) or the neighborhood identity (Eq. 2):

$$X_{ijkl} = \mu + \text{Diversity}_i + \text{Species}(\text{Diversity})_{ji} + \text{Plot}[\text{Species}(\text{Diversity})]_{k|j(i)} + b\text{NN}_{ijkl} + c \times \text{Dead number}_{ijkl} + e_{ijkl} \quad (1)$$

$$X_{ijkl} = \mu + \text{Species}_i + \text{Neighborhood}(\text{Species})_{ji} + \text{Plot}(\text{Species} \times \text{Neighborhood})_{k|(i,j)} + b \times \text{NN}_{ijkl} + c \times \text{Dead number}_{ijkl} + e_{ijkl}. \quad (2)$$

In Eq. 1, “Diversity” represents the number of species (1, 3, or 6 species) planted in any given plot. In Eq. 2, “Neighborhood(Species)_{ji}” represents the four combinations of nearest neighbors corresponding to the three different compositions of three-species plots and the specific neighborhood of six-species plots (Fig. 1). In both models, the first covariate, “NN_{ijkl}” accounts for the linear size effect of neighboring trees and was calculated as the average height, or BD, of nearest neighbors. Trees within a radius of 3 m from a focal tree were considered nearest neighbors. The number of neighbors was four in the absence of death, but was less if mortality had occurred. The second covariate, *Dead number*, was the number of dead nearest neighbors and was scored 1–4 for each individual tree. In the ANCOVA, *Diversity* or *Neighborhood* together with *Species* were fixed effects, and *Plot*, *Nearest Neighbor*, *Dead number*, and the error were treated as random effects. To avoid border effects, trees planted in the first and last rows and columns of each plot were excluded from the analyses. For each model, four ANCOVAs were performed using height or BD as dependent variables and as a measure of neighbor size (NN_{ijkl}). The patterns unveiled by these four analyses were similar (Appendix). Because we are interested in possible competition for light, we will report on individual-tree BD as dependent variable and the average height of nearest neighbors as covariate.

Our second main objective was to test for the presence of size-asymmetric competition in the plantation. To test specifically that, under size-asymmetric competition, small trees grow less than large trees, we analyzed the 2005–2006 relative growth rate in diameter, calculated as $\text{RGR}_{\text{diam}} = (\ln(2006 \text{ diam}) - \ln(2005 \text{ diam})) \times \text{yr}^{-1}$. Diameter was measured in centimeters and RGR is

expressed in percentage following Condit et al. (2006); $\text{RGR} = 0.05 = 5\%$. For trees taller than 2 m in 2005, dbh was used; otherwise, RGR was calculated as a change in BD. For the ANCOVA of RGR_{diam} , individual trees were grouped, within each diversity, into three size categories with equal frequencies based on height: small, medium, and tall. The ANCOVA model used to analyze RGR_{diam} is similar to Eq. 1, but includes the effect of *Size* and its interactions. In this analysis, the covariate NN_{ijkl}, representing the effect of neighboring trees, was provided by the average height of nearest neighbors.

It has been proposed that size-asymmetric competition generates variability in tree size. Therefore, coefficients of variation were computed for height, BD, and dbh across the entire data set, as measures of size inequalities (Weiner et al. 2001). Size-specific survivorship of the 50 smallest and 50 tallest trees in 2005 was estimated by scoring them as alive or dead in 2006. A chi-square test was used to assess differences in frequencies to determine (1) if the proportion of small trees differed among diversity levels and (2) if the proportion of dead small trees differed from the proportion of dead trees in the entire plantation.

Because light competition has been shown to alter biomass allocation to the trunk and branches (Hutchings and de Kroon 1994), 10 trees of each species were harvested from each diversity level in the dry season of 2006. The biomass allocation to the trunk and branches was determined for these 150 trees. For each combination of a species and a diversity level, trees were classified as small, medium, or tall, three trees were randomly chosen from each size category, and an additional one was randomly chosen from the entire data set, resulting in a sample size of 30 harvested trees per species. Trees were cut at the base, as close as possible to the ground, using either a handsaw or a chainsaw, depending on the trunk diameter. Tall trees were lowered with ropes to avoid damaging other trees. If necessary, branches were removed prior to cutting trees, to avoid hitting neighboring trees. For trees with multiple stems, the stem with largest dbh was considered the primary trunk. The primary trunk and all branches were cut and weighed separately using a Salter-AND EK 12-kg scale (Salter Housewares and Taylor Precision Products, Oak Brook, Illinois, USA). Small segments of the primary trunk and branches were cut, dried in an oven and reweighed to determine dry mass. Biomass allocation to the trunk and branches was submitted to a two-way ANCOVA, with *Diversity* and *Species* as main effects and the individual bole length as covariate. Statistical analyses were all conducted with SAS version 9.1 (SAS Institute 2004).

RESULTS

After five years of growth, trees tended to be taller and bigger in three-species plots (height, 497 ± 253 cm; basal diameter [BD], 11.1 ± 4.8 cm) than in monocultures (391 ± 199 cm and 9.1 ± 3.7 cm, respectively) and

TABLE 1. ANCOVA results for (A, B) individual-tree basal diameter in 2006 and (C) 2005–2006 relative growth rate in basal diameter.

Source of variation	df	Type III SS	F	P
A) Diversity†	2	117.4	1.06	0.404
Species(Diversity)†	15	1539.6	1.85	0.230
Plot(Species(Diversity))	6	333.3	4.10	0.001
NNH	1	4482.5	330.60	<0.0001
Dead number	1	154.7	11.40	<0.001
Error	2877	39 005		
B) Species‡	5	428.4	1.32	0.319
Neighborhood(Species)‡	6	563.0	1.45	0.275
Plot(Species × Neighborhood)	12	778.5	5.13	<0.0001
NNH	1	4107.0	324.83	<0.0001
Dead number	1	197.4	15.60	<0.0001
Error	2859	36 148.4		
C) Diversity§	2	0.365	4.50	<0.05
Species(Diversity)§	15	30.77	50.67	<0.0001
Size	2	0.894	11.04	<0.0001
Size × Diversity	4	0.77	0.48	0.752
Size × Species(Diversity)	30	5.829	4.80	<0.0001
NNH	1	0.220	5.45	<0.05
Error	2832	114.66		

Note: The average height of nearest neighbors (NNH) and the number of dead nearest neighbors (Dead number) were used as covariates.

† These effects were tested against Plot(Species(Diversity)).

‡ These effects were tested against Plot(Neighborhood × Species).

§ These effects were tested against the Error because Plot(Species(Diversity)) was found to be nonsignificant.

six-species plots (431 ± 193 cm and 10.4 ± 4.0 cm, respectively) (mean \pm SD). However, the ANCOVAs of individual tree BD failed to detect a significant effect of Diversity (Table 1), and the same pattern was observed for Height (results not shown). The species with largest BD was Hc (*Hura crepitans*; 11.12 cm \pm 5.38), while Ca (*Cordia alliodora*) and Ae (*Anacardium excelsium*) were the thinnest species (BD of 6.9 cm \pm 4.7 and 8.7 cm \pm 3.91, respectively), but these differences were not significant. The most significant terms in both ANCOVA models, diversity- and neighborhood-based, were the covariates Nearest Neighbor Height and Dead number (Table 1). This suggests that tree-to-tree relationships are key to understand growth pattern, and neighbor size is most important.

The ANCOVA performed for RGR_{diam} between 2005 and 2006 unveiled highly significant main effects of Diversity, Species(Diversity) and Size, while the covariate Nearest Neighbor Height exerted a significant effect on RGR_{diam} (Table 1). Across diversity levels, small trees grew significantly more slowly than medium and tall trees (least-squares means of 25.3%, 31.4%, and 30.8%, respectively). A posteriori tests of significance indicated that the RGR_{diam} of three-species plots was significantly smaller, on average, than those of monoculture and six-species plots (Fig. 2). Overall, Ae and Ls (*Luehea seemanii*) show the most consistent increase in RGR_{diam} with tree size, while Tr (*Tabebuia rosea*) shows no sign of size-asymmetric competition.

The presence of size-asymmetric competition was further tested by examining the temporal variation in the CVs (coefficients of variation) of Height, BD, and

dbh (diameter at breast height) from 2002 to 2006. Variation of Height and BD was stable through time (Fig. 3), while the CV of dbh increased continuously and doubled between 2003 and 2006. In 2006, variation in both Height and BD was highest for small trees growing in monoculture (Fig. 4) and smaller trees were consistently more variable than medium and tall trees. The dbh tended to be more variable than Height and BD, possibly because of the difficulty of accounting for

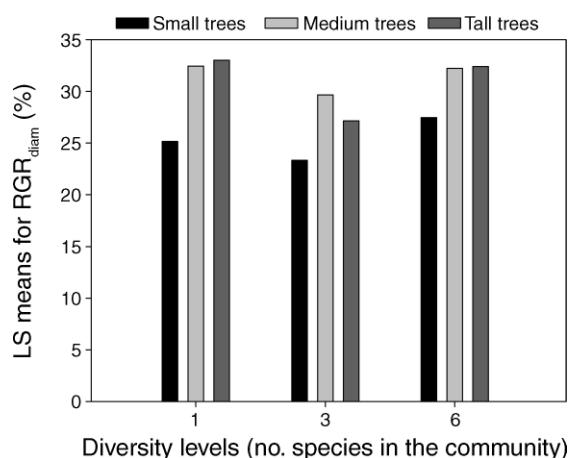


FIG. 2. Least-squares means for relative growth rates in diameter, calculated as $RGR_{diam} = [\ln(\text{diam}_{2006}) - \ln(\text{diam}_{2005})] \times \text{yr}^{-1}$, for trees classified as small, medium, or tall. Diameter was measured in cm and RGR is expressed in % following Condit et al. (2006); $RGR = 0.05 = 5\%$. For trees < 2 m high in 2005, RGR was calculated from basal diameter; for the other trees, it was calculated from diameter at breast height.

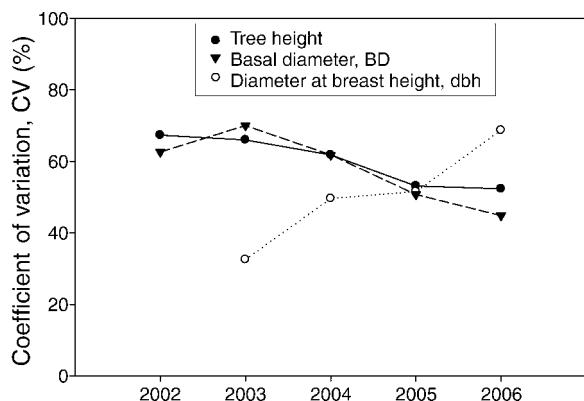


FIG. 3. Temporal trends of the coefficients of variation (CV) for tree height, basal diameter, and diameter at breast height across the data set.

multiple stems (Fig. 4). Pearson's sample correlation coefficients show that the variation in tree Height, BD, and dbh at the plot level in 2006 was not significantly associated with individual-plot biomass (-0.191 , $P = 0.395$ and -0.29 , $P = 0.898$, respectively), suggesting that the increase in variation is not simply a response to increased plot biomass.

Among the 50 smallest trees in the plantation in 2005, 38 (76%) were growing in monoculture plots. This proportion is significantly higher ($\chi^2_2 = 12.15$, $P = 0.002$) than expected, based on the number of trees in monocultures (1992 of 3875 trees). The smallest trees were largely Ls (32%), Ae (28%), and Ca (22%), while 86% of the tallest ones were Co (*Cedrela odorata*). Between 2005 and 2006, 51 trees died in the plantation, which represents 1.2% of the total number of trees ($N_{2005} = 3927$, $N_{2006} = 3876$). Twenty-nine of these dead trees (56%) were among the 50 smallest trees measured in 2005, which is significantly more than expected ($\chi^2_2 = 3067$, $P < 0.0001$). By contrast, no mortality occurred in the 50 tallest trees.

Diversity significantly affected biomass allocation to the trunk and branches ($F_{2,132} = 3.01$, $P = 0.052$). Trees allocated 50% less biomass to branches when growing in monoculture plots (0.636 ± 0.572) than in three-species plots (0.951 ± 0.735) (mean \pm SD). The allocation pattern of trees growing in six-species plots (0.925 ± 0.864) was not statistically different from the two other diversity levels. The statistically significant effect of Species ($F_{4,132} = 2.80$, $P = 0.028$) appears driven by Ae (1.123 ± 0.812) and Ls (0.584 ± 0.499), which respectively allocated the most and the least biomass to branches. Other effects were statistically nonsignificant.

DISCUSSION

We developed a neighborhood model, derived from Wu et al. (1998), taking into account the number, size, and identity of neighbors. Our analytical approach was based on the assumption that local environment matters

for plant productivity (Stoll and Weiner 2000). It has been said that recruitment during the gap formation phase sets the composition of the later mature tropical forest (Hubbell et al. 1999). Our study pertains to the establishment phase of a plantation that exerts long-lasting consequences for the planted forest. In Sardinilla (Panama) the size and number of neighbors were the

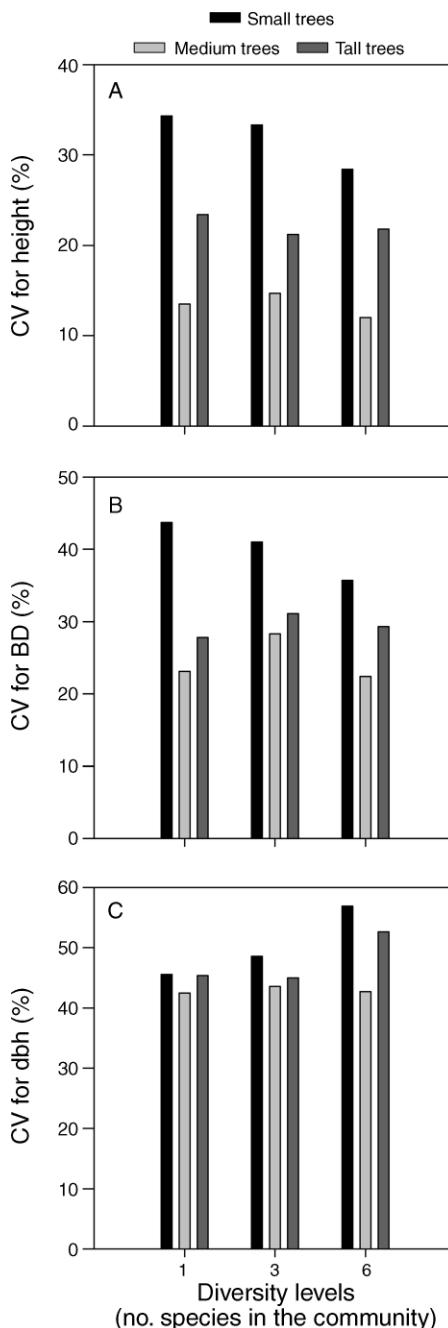


FIG. 4. Coefficient of variation (CV) for height, basal diameter (BD), and diameter at breast height (dbh) for each diversity level in 2006. Within each diversity level, three size classes with equal frequencies were used to classify trees as small, medium, or tall.

overwhelming source of variation in individual-tree basal diameter and height. In the nearby forest of Barro Colorado Island, Urriarte et al. (2004) computed a neighborhood crowding index that accounted for the effects of neighbors' diameter and distance on the focal tree's diameter. While Urriarte et al. (2004) studied neighborhood effects for saplings with dbh between 1 and 4 cm, trees in the Sardinilla plantation had a broader range in diameter (~0.8–20 cm). On Barro Colorado Island, response to crowding was variable among species, with a large number of species exhibiting no growth response (Urriarte et al. 2004). However, a few species were responsive, not only to crowding but also to the identity of specific neighbors. A similar analysis, conducted on mature trees in a Dipterocarpaceae forest of Borneo (Stoll and Newbery 2005), highlighted a differential effect of conspecific vs. heterospecific neighbors. On average over 10 species, the presence of conspecific neighbors reduced the growth of the focal tree substantially more than heterospecific neighbors. Using grassland species, Weigelt et al. (2007) established hexagonal plots in which a target species was surrounded either with itself or with one, two, or three target species. A main conclusion of that study was that competition, by reducing the growth of target species by up to 57% in multi-species communities, was highly dependent on species-specific combinations. Competitive outcome could be predicted from individual species responses in some cases, while competition was nonadditive in other cases. Such unpredictable patterns led the authors to conclude, by quoting Huisman and Weissing (2001:492), that the "outcome of multiple species competition can be as predictable as the throwing of a dice [sic]."

Strong size-asymmetric competition is apparently at the heart of understanding the biodiversity responses in the Sardinilla tree plantation and the dwarfed effects of species identity. This is evidenced by the high variability in height and basal diameter of small trees, the disproportionate proportion of the smallest trees dying, the lowest relative growth rates in diameter of small trees, and the increased variability in diameter at breast height through time. Although plants are sessile, they can modify their growth pattern to minimize light interception by neighbors (Novoplansky et al. 1990, Osada et al. 2004, Clark and Bullock 2007). Reduced intraspecific competition among trees planted in mixtures might allow them to invest more biomass in branches than when growing in monocultures. Increased branch volume could enhance the efficiency of light foraging in mixtures, thus explaining the positive effect of biodiversity on tree growth reported earlier (Potvin and Gotelli 2008). Future experiments in Sardinilla will be designed to test the hypothesis that competition for light is the driving force for competition.

In the biodiversity–ecosystem functioning debate, little attention has been paid to spatial patterns (Schooler 2006). Yet our results and those of Weigelt et al.

(2007) suggest that local neighborhood, defined by the size, number, and identity of immediate neighbors, plays a central role in determining productivity. If, from a tree perspective, the biodiversity effect can be reduced to a neighborhood effect, then the response to biodiversity at the plot level is the aggregate effect of local neighborhoods. While biodiversity is a property of the ecosystem, competition, a main explanatory mechanism of the observed relations between biodiversity and ecosystem functioning, is a phenomenon occurring at the individual scale. Accordingly, issues of scale (Allen and Wyleto 1983, Allen and Hoekstra 1990) need to be incorporated in both the theoretical development and the analysis of biodiversity and ecosystem functioning.

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APPENDIX

ANCOVA results for individual-tree basal diameter in 2006 (*Ecological Archives* E090-023-A1).