

LETTER

Biodiversity enhances individual performance but does not affect survivorship in tropical trees

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Abstract

We developed an analytical method that quantifies the relative contributions of mortality and individual growth to ecosystem function and analysed the results from the first biodiversity experiment conducted in a tropical tree plantation. In Sardinilla, central Panama, over 5000 tree seedlings were planted in monoculture and mixed-species plots. After 5 years of growth, mixed-species plots yielded, on average, 30–58% higher summed tree basal area than did monocultures. Simulation models revealed that the increased yield of mixed-species plots was due mostly to enhancement of individual tree growth. Although *c.* 1500 trees died during the experiment, mortality was highly species-specific and did not differ consistently between biodiversity treatments. Our results show that the effects of biodiversity on growth and mortality are uncoupled and that biodiversity affects total biomass and potentially self-thinning. The Sardinilla experiment suggests that mixed-species plantings may be a viable strategy for increasing timber yields and preserving biodiversity in tropical tree plantations.

Keywords

Basal area, biodiversity and ecosystem function, mortality, tropical trees.

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INTRODUCTION

Rapidly shrinking biodiversity levels have raised the concern that species loss could eventually lead to ecosystem collapse (Naeem 2002), and ecologists are intensely studying the relationship between biodiversity and ecosystem function (BEF). A decade of research has highlighted a generally positive relationship (Hooper *et al.* 2005; Balvanera *et al.* 2006), but the magnitude of biodiversity effects may depend on species composition and potential sampling artefacts (Cardinale *et al.* 2006). Most BEF experiments have been conducted in microcosms or in north-temperate grassland ecosystems, raising the concern that this bias might have shaped researchers' perception of the BEF relationship (Srivastava & Vellend 2005). At a time of heightened concern over the impact of tropical deforestation on global climate (Gullison *et al.* 2007), we assessed the effect of tropical tree biodiversity on ecosystem function.

According to the Food and Agriculture Organization, tree plantations cover 272 million hectares worldwide, and their extent is continuously increasing (FRA 2005). Nevertheless, over 99% of tree plantations consist of monocultures of a small number of exotic species (Nichols *et al.* 2006).

Understanding the potential role of biodiversity in tree plantations is therefore of great importance for the efficient management of ecosystem services (Erskine *et al.* 2006; Vila *et al.* 2007). We analysed data from the first experiment applying the BEF methodology to a tree plantation (Scherer-Lorenzen *et al.* 2005).

Biodiversity and ecosystem function experiments established with trees differ in some crucial aspects from those conducted in grasslands (Scherer-Lorenzen *et al.* 2005). First, BEF tree plantations require large plots, e.g. >20 × 20 m, containing enough individual trees for analysis, to allow the presence of buffer rows between plots of different diversity and to stabilize microclimate. Large forest plots will be more environmentally heterogeneous than small grassland quadrats, and this environmental heterogeneity could either diminish or magnify biodiversity effects. Second, clonal growth is common in herbaceous plants but is rare in tropical trees. Therefore, the patterns of spatial occupancy and resource acquisition in tree stands and in herbaceous grasslands may be very different.

Most importantly in the context of this paper, ecosystem function in grasslands is usually measured as a bulk property of an entire plot while productivity in forests is usually

assessed on an individual tree basis. Individual tree growth, mortality and recruitment determine forest population dynamics (Botkin 1993), although in tree plantations recruitment is controlled through initial plantings. However, tree mortality, by affecting stem density, is an important determinant of yield and performance (Paquette *et al.* 2006; Vila *et al.* 2007). Total plot yield thus reflects the combined effects of mortality and individual performance of surviving trees. A positive effect of biodiversity on tree plantations should result from either a reduction in per capita mortality and/or an increase in per capita growth. Building on the knowledge accumulated from key BEF experiments (Naem & Li 1997; Loreau & Hector 2001; Tilman *et al.* 2001; Hector *et al.* 2002), we developed statistical simulation models to quantify the per capita contributions of mortality and individual tree growth to ecosystem function. This distinction is critical in the context of tree plantations, where self-thinning (Weller 1987) could influence the outcome of biodiversity experiments (Scherer-Lorenzen *et al.* 2005).

MATERIALS AND METHODS

In July 2001, we planted a total of 5566 tree seedlings, <6-months old, in a pasture of *c.* 5 ha in Sardinilla, central Panama. Native tree species were planted in 24 contiguous 45 m by 45 m plots with either one, three or six species per plot. The layout of the experiment was a substitutive randomized block design, with the diversity levels randomly allocated within the site. Planting distance between individual trees was 3 m, following standard reforestation practices in Panama.

Half the plots received 225 seedlings each. Because we had enough seedlings of some species to plant additional trees, nine plots received 240 seedlings and one plot received 256 seedlings (mean 231.9 ± 8.93 seedlings per plot). The six tree species planted (*Cordia alliodora* (Ca), *Luebea seemannii* (Ls), *Anacardium excelsum* (Ae), *Hura crepitans* (Hc), *Cedrela odorata* (Co) and *Tabebuia rosea* (Tr)) are all native to Panama. They grow on nearby Barro Colorado Island, where they span a range of relative growth rates (Condit *et al.* 1993). *Cordia*, *Anacardium*, *Cedrela* and *Tabebuia* are important timber species in Panama, and *Hura* and *Luebea* are very common in lowland semi-dry forests.

Six plots each received all six species, six plots each received a unique three species combination, and 12 plots received the six monoculture plantings, with two replicate plots per monoculture. All species planted in mixed-species plots were represented in monoculture, allowing to properly control for sampling effects in the analyses. The three-species plots were established using random combinations of either: Ca or Ls, Ae or Hc and Co or Tr to ensure representation of fastest and slowest growing species in each block. Seedlings were fertilized three times during the first

growing season (2001) and the grass around them was cut to the ground to avoid competition with herbaceous vegetation. Thereafter, the plantation was cleaned of undergrowth three times per year. All cleaning was manual, and no herbicides were used.

Individual tree height and basal diameter (10 cm from the ground) were measured every year at the onset of the dry season starting in 2001. Data from the fifth dry season (January 2006) were used to calculate stem basal area (BA) as $\pi * r^2$, where *r* is the radius of each individual tree, and plot BA ($\text{m}^2 \text{ ha}^{-1}$) as the sum of individual trees' BA. At the plot level, we estimated the instantaneous mortality rate *m* for each species over the 5-year interval as: $N_{2006} = N_{2001} \exp^{(m*5)}$. We then converted this rate *m* to an annual instantaneous percentage mortality. Nested ANOVA with Diversity, Species (nested within Diversity) and Plot (nested within Diversity) was used to examine variation in instantaneous mortality percentages. To determine if the plots were undergoing self-thinning and shed light on the relationship between tree density and productivity we regressed individual tree BA (m^2), averaged for each plot, on tree density measured in the same plot (# individuals ha^{-1}). Data were log-transformed prior to the analysis, and regressions were fit separately for the 12 monocultures and the 12 mixed-species plots. Statistical tests were conducted with SYSTAT (version 10.1).

We used bootstrapping to isolate the effects of individual growth and mortality on BA using separate tests for three-species plots and six-species plots. For each simulation model, we created 1000 null mixed-species assemblages, sampling with replacement from the pool of monoculture trees. Species-specific growth rates and probabilities of mortality were preserved in these simulations. For each null assemblage, we calculated summed BA, then determined the mean and true 95% CI for the set of null assemblages. The BA in the observed mixed-species plots was compared to the simulated histogram by calculating the exact one-tailed probability of the observed result. As in other meta-analyses of simulation model results (Gotelli & McCabe 2002), we used the observed mean and variance of the simulated distribution to calculate a standardized effect size (SES) as:

$$\text{SES} = (\text{Observed basal area} - \text{Mean simulated basal area}) / (\text{Standard deviation of simulated basal area})$$

This transformation converts the tail probability from the simulation into a standardized normal deviate, with an approximate 95% CI of [-2.0, 2.0]. If $\text{SES} > 2.0$, the mixed-species plots over-yielded compared to the monocultures, whereas if $\text{SES} < -2.0$, the mixed-species plots under-yielded. If $\text{SES} < |2.0|$, the observed BA is approximately within the range predicted by the simulation model. These analyses assume that the observed error distributions

in the simulation model follow a normal distribution, and we have confirmed by a goodness-of-fit test that the simulated distributions do not differ significantly from a normal distribution ($P > 0.05$). Although the simulations generated P -values for individual plots, we tested hypotheses across sets of plots by comparing replicate SES values with one-sample t -tests. All simulation models were written in S-PLUS, version 6.2.

We tested each mixed-species plot against three separate models to quantify the contributions of mortality, individual growth, and their net effect to BA. As in two-species relative yield analyses (Trenbath 1974), the yield of mixed species plots is measured relative to the yield of comparable monocultures. The bootstrap models that we developed have some similarities to the model used by Crutsinger *et al.* (2006) to isolate sampling effects of plant genotypic diversity on insect diversity. Loreau & Hector (2001) also partitioned biodiversity effects into components of selection and complementarity. But neither of these approaches isolates the per capita effects of tree mortality and individual growth processes on ecosystem function. We developed three bootstrapping models to quantify the contributions of growth, mortality and growth plus mortality effects of individual trees to the BA of mixed-species plots (Fig. 1). In these simulation models, the null hypothesis is that the BA measured in the mixed-species plots is no different than would be expected from random sampling that occurred in the monoculture plots.

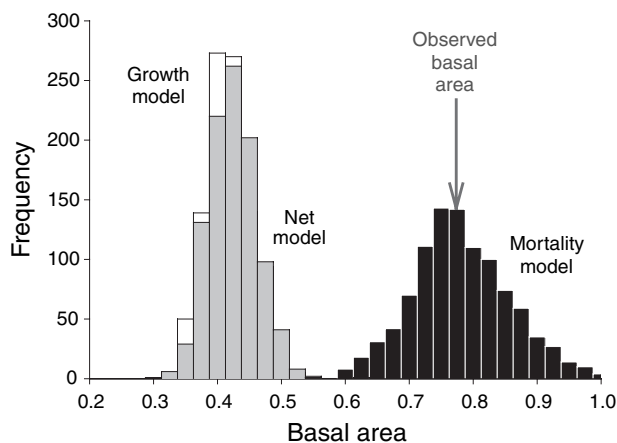


Figure 1 Example of simulation model results for partitioning growth and mortality effects on ecosystem function. The summed basal area (BA) of trees for one of the three-species plots is shown as a red arrow. The three stochastic models estimate the effects of mortality (black histogram bars) growth model (white histogram bars), and mortality + growth (grey histogram bars) on BA in mixed species plots vs. monocultures.

Growth model

For the growth model, we used the observed mortality probabilities for each species in the mixed-species plots, sampled individual trees from the monoculture plots, and summed their BAs. Any differences between the observed BA and simulated data would therefore reflect differences in the growth of individual trees in mixed-species plots vs. monoculture plots.

Mortality model

For the mortality model, we used the observed mortality probabilities for each species in the monoculture plots, sampled individual trees from the mixed-species plots, and summed their BAs. Any differences between the observed BA and simulated data would therefore reflect differences in the mortality probability of trees in mixed-species plots vs. monoculture plots.

Net model (growth + mortality)

For the net model, we used the observed growth rates and mortality probabilities of each species in the monoculture plots, sampled individual trees from the monoculture plots, and summed their BAs. Any difference between the observed BA and the simulated data would therefore reflect the combined effects of mortality and growth differences in mixed species plots vs. monoculture plots.

Species-specific effects

We were careful in the simulation models to preserve species identity when calculating mortality probabilities and randomly sampling individual trees. The design of the Sardinilla experiment ensured that all species grown in mixture-plots were also represented in monoculture plots, and that each three-species block had a randomly chosen species with a fast, slow, and intermediate growth rate. These precautions ensured that the results are not confounded by sampling artefacts. The species-specific models use identical species sets in the monocultures and mixtures, and maintain all species-specific mortality and individual growth rates. To test for the generality of the observed patterns, all simulations were repeated with generic models that draw individuals randomly from all monocultures, and do not retain species identity or species-specific mortality probabilities and growth rates.

RESULTS

After 5 years, tree height across the entire plantation averaged $4.21 \text{ m} \pm 2.15$; the tallest trees were over 14 m

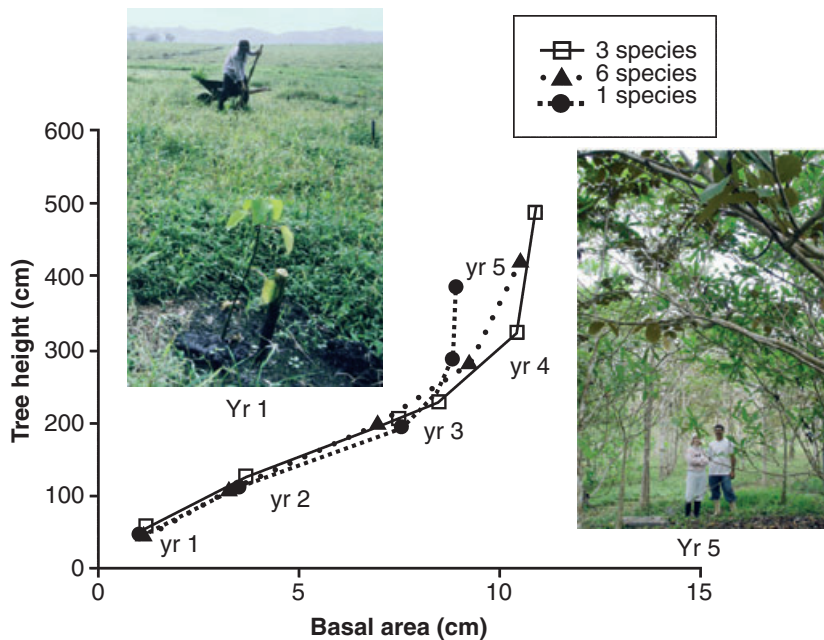


Figure 2 Temporal trajectory of biodiversity effects. Each point represents the average tree height (cm) and basal diameter (cm) of all surviving trees in monoculture (●), three-species (■), and six-species plots (▲) during the first five years of the Sardinilla experiment (2001–2006). The sample size for the first year of growth (2001–2002) was $n = 5160$ trees. In year 5 (2005–2006), $n = 3843$ trees.

and average annual growth rate was $0.98 \text{ cm year}^{-1}$ for diameter at breast height. Differences in size among diversity treatments were first noticeable in the third year of growth and have become more pronounced since then (Fig. 2). For 5-year-old trees, the overall enhancement of individual tree height ranged between 25% and 11% respectively for three- and six-species plots compared with monocultures. We used the summed BA of all the trees in a plot as a measure of ecosystem function that can be additively scaled from individual trees to the plot level. Average BA in monoculture plots was $2.39 \pm 1.68 \text{ m}^2 \text{ ha}^{-1}$, $3.77 \pm 1.69 \text{ m}^2 \text{ ha}^{-1}$ in three- and $3.09 \pm 1.56 \text{ m}^2 \text{ ha}^{-1}$ in six-species plots.

In the Sardinilla experiment, instantaneous mortality rates did not vary significantly among diversity treatments ($F_{2,37} = 0.873$, $P = 0.426$) but showed a significant effect of species identity (nested within diversity; $F_{15,37} = 20.98$, $P < 0.001$). Clearly, the main effect of species identity explained most of the variation in mortality. Instantaneous mortality rates ranged from 0.8%/year for *T. rosea* in monoculture to 57%/year for *C. alliodora* in the six-species plots (Fig. 3). A spatial analysis of Moran's I statistic (Rangel *et al.* 2006) indicates that both mortality and BA data were spatially independent among the 24 contiguous plots (bootstrap $P > 0.05$ for all distance classes), so each plot could be considered an independent replicate for analysis. Regressions of average individual tree BA on tree density had positive slopes [$\log_{10}(\text{BA}) = -10.7 + 0.721 \cdot \log_{10}(\text{density})$; $\log_{10}(\text{BA}) = -12.7 + 1.112 \cdot \log_{10}(\text{density})$ respectively for monocultures and mixed-species] indicating that overall the plantation has not reached the point of self-thinning.

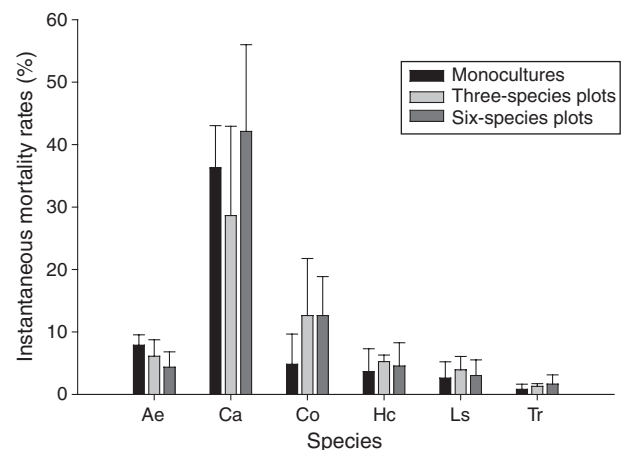


Figure 3 Annual instantaneous mortality rates (%/year) over the period 2001 and 2006. Species are abbreviated as follow: *Anacardium excelsum* (Ae), *Cordia alliodora* (Ca), *Cedrela odorata* (Co), *Hura crepitans* (Hc), *Lubea seemanii* (Ls) and *Tabebuia rosea* (Tr). Each bar is the average mortality rates among plots within each of the three diversity treatments. The vertical line represents one SD.

However tree BA is less responsive to density in mixed-species plots ($r^2 = 0.210$) than in monocultures ($r^2 = 0.828$).

A combined analysis of results from all mixed-species plots showed significant net overyielding compared to monocultures [Average Standardized Effect Size (ASES) = 5.55; one-sample t -test, $P < 0.01$]. The pattern was strongest for three-species plots (ASES = 7.40, $P < 0.05$). Six-species plots also showed positive effects of biodiversity, but the pattern was non-significant when they

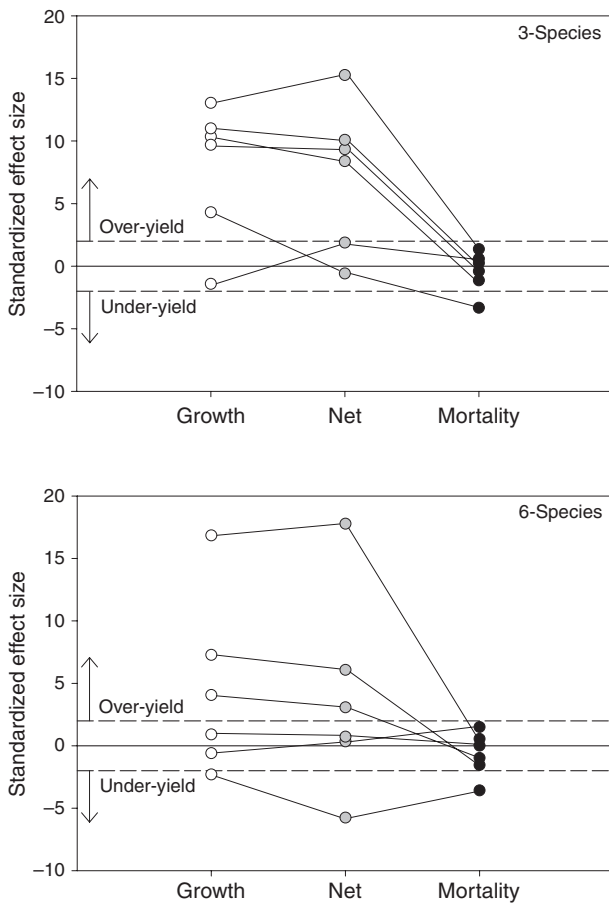


Figure 4 Effects of growth and mortality on summed basal area (BA) of trees in mixed-species tree plots of the Sardinilla experiment. Each point represents a block planted with three or six tree species. The SES represents the deviation of observed tree BA from the predictions of a stochastic model that incorporates growth effects (white symbols), mortality effects (black symbols), or both growth and mortality (grey symbols). $SES < |2.0|$ indicates effects that are within the range predicted by the simulation model. Lines join the simulation results for the same plot. Upper panel = three-species plots; lower panel = six species plots.

were analysed separately ($ASES = 3.71, P > 0.05$). The same pattern emerged for the growth effect (Fig. 4): per capita tree growth contributed to significant over-yielding of all mixed-species plots ($ASES = 6.10, P < 0.01$) and of three-species plots ($ASES = 7.82, P < 0.05$). Conversely, modeling shows that mortality effects were close to 0.0 in all treatments, and were non-significant ($P > 0.05$; one-sample *t*-test) for all mixed-species plots combined ($ASES = -0.56$), three-species plots ($ASES = -0.44$), and six-species plots ($ASES = -0.67$).

To further explore the consequences of using species-specific mortality probabilities, we conducted a parallel set of model simulations, in this case ignoring species identity. We used overall mortality probabilities of all trees grown in monoculture and mixed-species plots, and we randomly sampled trees from monoculture or mixed-species plots without regard to species identity. Table 1 summarizes the average SES and their statistical significance for models that did and did not preserve species identity. The only difference between the species-specific and general models was that the net effect for the three-species model was marginally non-significant ($P = 0.096$) when species identities were ignored.

DISCUSSION

Measures of tree size, mortality and growth rates achieved in our tree plantation are comparable to data from forests on nearby Barro Colorado Island (Condit *et al.* 1993, 1995), as well as data from mixed-species or monoculture plantations of tropical trees established with native species (Stansley & Montagnini 1999; Wightman *et al.* 2001; Cole & Ewel 2006; Grant *et al.* 2006).

Loreau & Hector (2001) suggested that future progress in BEF research will require studies that address underlying mechanisms. They proposed that positive BEF relationships might be caused by complementarity – more efficient resource allocation among species due to niche partitioning, and by selection – increased productivity due to the presence

Table 1 One-sample *t*-tests of standardized effect sizes (SES) from simulation models of growth, mortality and growth + mortality effects on total tree biomass. Each entry is the average SES from the simulation models for each block. Positive values indicate over-yielding with respect to monocultures, negative values indicate under-yielding

	Generic			Species-specific		
	G + M	Growth	Mortality	G + M	Growth	Mortality
3 species ($n = 6$)	7.07 (n.s.)	7.18*	-0.20 (n.s.)	7.40*	7.82*	-0.44 (n.s.)
6 species ($n = 6$)	3.38 (n.s.)	4.09 (n.s.)	-0.62 (n.s.)	3.71 (n.s.)	4.36 (n.s.)	-0.67 (n.s.)
All mixtures ($n = 12$)	5.23*	5.64**	-0.42 (n.s.)	5.55*	6.10**	-0.56 (n.s.)

* $P < 0.05$; ** $P < 0.01$; NS = $P > 0.05$. n.s., not significant.

of an highly performing species. In Sardinilla, enhanced yield can be attributed almost entirely to increases in growth of individual trees in mixed-species plots. We speculate that the mechanism underlying enhanced growth relates to competition for light which is apparently stronger in monocultures than in mixtures (C. Potvin and P. Dutilleul, McGill University, Montreal, unpublished results). The modeling results also suggest that the pattern of enhanced growth of trees in mixed-species plots is a quite general phenomenon of monocultures vs. mixed-species plots, and does not depend, in this case, on preserving species identity in the simulation models. However, consistent with the results of a recent meta-analysis (Cardinale *et al.* 2006), we found no evidence that the BEF relationship is linear or even increasing. Thus, tree growth is not affected by plot-level species richness (three vs. six species), but rather is sensitive to local neighborhoods of heterospecific vs. conspecific individuals, as reported for intact tropical forests (Uriarte *et al.* 2004; Stoll & Newbery 2005).

The positive per capita growth effects were, on average, an order of magnitude greater in size than mortality effects and more than compensated for tree losses. Most of the variation in mortality was species-specific, but mortality rates can also vary by site and local abiotic conditions. For example, the survival rate after 5 years for *Cordia* in the Sardinilla experiment was *c.* 20% in mixed-species plantings, and has been as high as 49% in plantations in Costa Rica (Wightman *et al.* 2001). According to Bergman *et al.* (1994), *Cordia* is sensitive to soil compaction and requires highly fertile and well drained sites for establishment. On the other hand, *C. odorata* seedlings and small trees (5–8 m) are susceptible to attacks by the mahogany shoot borer, *Hypsipyla grandella* (Zeller) (Cole & Ewel 2006). These sources of variation in mortality and establishment seem to be more important than local biodiversity levels.

Because mortality did not differ consistently between diversity treatments, it contributed relatively little to the BEF relationship. Clearly different mechanisms underlie growth and mortality responses; just as in the case of complementarity and selection (Loreau & Hector 2001), they can act in opposite ways to determine the net biodiversity effect. In the Sardinilla experiment, the biodiversity effects on mortality and growth are uncoupled: individual tree growth is stimulated by biodiversity, whereas mortality is unaffected. With average canopy opening ranging between $60\% \pm 19.6\%$ for monocultures and $43.0\% \pm 19.5\%$ for three-species plots, our plantation has not yet reached self-thinning densities. However our results suggest that biodiversity has already begun to alter the growth-density relationship. Possible biodiversity effect on self-thinning could have large consequences for aggregate productivity and ecosystem function at later time (Weller 1987).

The interest of ecologists in the BEF relationship was originally motivated by a concern for the ecosystem consequences of biodiversity loss (Naeem 2002; Hooper *et al.* 2005). However, questions have been raised regarding the relevance of BEF studies to biodiversity conservation (Srivastava & Vellend 2005). Our focus on tropical tree diversity—a key component of terrestrial carbon sequestration and land-use planning—addresses this concern directly. The demonstration that diversity enhances yield through an increase in per-capita growth builds on previous studies of tree plantations reporting positive species-specific growth responses in mixtures (Piotto *et al.* 2003; Brislow *et al.* 2006; Erskine *et al.* 2006; Grant *et al.* 2006). Assuming that the observed diversity effect will persist or even increase over the plantation life time, our results provide a scientific rationale for a strategy of mixed-species plantations as an integrated part of land-use planning in tropical countries struggling to conserve forest resources and biodiversity while meeting the demand for timber (Cyranoski 2007).

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