Ecology, 94(4), 2013, pp. 941–952

Beyond shading: Litter production by neighbors contributes to overyielding in tropical trees

JURGIS SAPIJANSKAS,[1,2,5] CATHERINE POTVIN,[1,3] AND MICHEL LOREAU[1,4]

[1]*Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec H3A 1B1 Canada*
[2]*AgroParisTech ENGREF (L'École Nationale du Génie Rural, des Eaux et des Forêts), Direction Scientifique, 19 Avenue du Maine, 75015, Paris, France*
[3]*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama*
[4]*Centre for Biodiversity Theory and Modelling, Experimental Ecology Station, Centre National de la Recherche Scientifique, 09200 Moulis, France*

Abstract. The influence of biodiversity on ecosystem functioning is now well established. However, our ability to predict the ecological consequences of biodiversity changes remains limited by our poor understanding of the mechanisms underlying biodiversity effects. We disentangled the contributions of light competition and residual neighborhood interactions in a 10-year-old biodiversity experiment with tropical trees that display overyielding, i.e., higher community-level yields in mixtures compared with monocultures. We developed models of individual tree growth that partition the effects of neighboring trees into shading and residual effects assumed to reflect primarily belowground interactions. These models reject the hypothesis that reduced light competition in mixtures is the only mechanism driving overyielding. After factoring out the effects of shading, litter production by neighbors was a far better predictor of tree growth than traditional crowding indices; it contributed to overyielding by producing pairwise interactions that ranged from competitive to facilitative, but which, on average, concentrated competition within species. Consistent with litter-mediated biodiversity effects, the magnitude of overyielding increased over time. Our results provide evidence for diversity effects extending beyond that of light and reveal the neglected role of litter-mediated interactions among trees.

Key words: belowground interactions; biodiversity and ecosystem functioning; facilitation; forest stand dynamics; interspecific interactions; light competition; litter; mixed-species forests; neighborhood; overyielding; Sardinilla Project, Panama; tree plantation.

INTRODUCTION

Forest ecosystems cover 30% of the global land area, hold more than twice the amount of carbon as the atmosphere, and half of terrestrial carbon (FAO 2006). As such, they are of particular interest for climate change mitigation initiatives promoting carbon sequestration in the biosphere as a way to stabilize atmospheric CO_2 and methane levels. Forests also hold about two-thirds of terrestrial biodiversity (Millenium Ecosystem Assessment 2005) and, although there are many reasons to believe that biodiversity affects the amount, rate, and persistence of carbon in the biosphere (Catovsky et al. 2002), it is still considered at best as a side benefit in mechanisms such as the Clean Development Mechanism or the proposed REDD (Reduced Emissions from Deforestation and forest Degradation) (Díaz et al. 2009). In order to provide integrated ways of dealing with the dual environmental challenges of carbon sequestration and biodiversity protection, an increasing body of research is devoted to examining how the protection and manipulation of biodiversity can enhance carbon sequestration (e.g., Bunker et al. 2005, Potvin and Gotelli 2008).

Understanding the relationship between biodiversity and ecosystem functioning (BEF hereafter) has emerged as a central issue in ecological and environmental sciences during the past 15 years (Loreau 2010). Hundreds of experimental and theoretical studies have revealed that biological diversity influences numerous ecosystem processes through overyielding, i.e., an increased community-level performance in mixture compared to that expected from the average of the component species' monocultures (Balvanera et al. 2006, Cardinale et al. 2007, 2011). Some observations even support the hypothesis that diverse communities may outperform their most efficient species (Cardinale et al. 2011). Nonetheless, the balance of evidence is that it is two times more likely for mixtures to produce less biomass, sequester fewer nutrients, and decompose litter more slowly than their best monoculture (Cardinale et al. 2011). Although the interpretation of early BEF experiments stimulated considerable scientific debate,

Manuscript received 28 February 2012; revised 29 October 2012; accepted 1 November 2012. Corresponding Editor: B. J. Cardinale.

[5] Present address: AgroParisTech ENGREF, 19 Avenue du Maine, 75015, Paris, France.
E-mail: jurgis.sapijanskas@polytechnique.org

the central BEF question has now moved from the discussion of whether diversity matters to the identification of the biological mechanisms underlying its effects on ecosystem functioning (Loreau and Hector 2001, Reiss et al. 2009)

Because trees simultaneously compete aboveground for light and belowground for water and nutrients, disentangling the effects of above- and belowground competition is a prerequisite for making BEF research more predictive. Light competition is widely acknowledged as the most fundamental process driving forest dynamics (Oliver and Larson 1996), is central to virtual forest models (Bugmann 2001), and is responsible for the very growth form of trees (Purves and Pacala 2008). Accordingly, architectural complementarity among crown shapes and a better multilayered exploitation of light are frequently proposed to explain growth enhancement in mixtures (Kelty 1989, Erskine et al. 2006, Yachi and Loreau 2007, Pretzsch and Schutze 2009). However, successful forestry mixtures often involve N-fixing trees, which have a significantly positive effect on the growth of non-fixing trees (Rothe and Binkley 2001, Piotto 2008). Root trenching results in increased growth rates in many forest types, especially under high light conditions (Coomes and Grubb 2000). Neighborhood models show that although competition for light has a strong influence on the growth of small trees (Coomes and Allen 2007), crowding, which supposedly reflects belowground interactions, affects all trees (Canham et al. 2004, Coomes and Allen 2007) and can have stronger effects than shading (Canham et al. 2004, Coates et al. 2009). Moreover, complementary rooting depths are commonly invoked to account for biodiversity effects (Loreau 1998, Ewel and Hiremath 2005, Pretzsch and Schutze 2009).

Here, we disentangle the factors contributing to overyielding in an experimental tree plantation designed to study the links between carbon cycling and biodiversity. In 2001, a synthetic gradient of tree diversity was established by planting more than 5000 trees of native species in Sardinilla, central Panama. Five years after planting, tree growth was significantly enhanced in mixtures compared to monocultures while diversity had little effect on mortality (Potvin and Gotelli 2008). Potvin and Dutilleul (2009) reported that the size of neighbors was the largest source of variation in individual tree diameter. Together with the increased allocation to branches in mixtures, this finding was interpreted as evidence that reduced competition for light in mixtures was driving the positive effect of biodiversity on tree growth. Our first objective was therefore to test whether light alone could explain overyielding. Second, we explicitly partitioned the effects of neighboring trees on individual tree growth into the effects of shading (aboveground competition) vs. "residual" interactions, which are usually assumed to reflect primarily belowground interactions (Canham et al. 2004, Coates et al. 2009). A detailed analysis of tree transpiration concluded that water was most likely not constraining interspecific interactions in our site, which receives >200 mm of precipitation per month during the wet season (Kunert et al. 2012). Tropical forests are thought to rely prominently on nutrient recycling. Moreover, litter inputs occur directly on the root mat layer, where biological demand is the highest and mycorrhizal activity is adapted to take advantage of intermittent inputs (Lodge et al. 1994). We therefore hypothesized that overyielding in Sardinilla was in good part explained by litter-mediated interactions. More specifically, we predicted that the relationship between growth and litter production by neighboring trees would be less negative (or become positive), i.e., would produce less competitive residual interactions in mixtures than in monocultures. Such a relationship may result from complementarity in belowground resource uptake (e.g., use of different forms of the same nutrient, complementary rooting volumes) or redistribution of resources among trees limited by different nutrients.

To reach these objectives, we first compared the magnitude of overyielding between canopy and smaller, shaded trees. If overyielding were fully explained by less intense competition for light in mixtures, we would expect canopy trees to benefit less from growing in mixtures because they respond less than shaded trees to increases in light availability. Next, we developed linear mixed models of individual tree growth that partition the effects of neighbors into the effect of shading and the residual effect of litter production. These models were designed (1) to infer the effects of litter production by neighboring trees while controlling for light availability and environmental heterogeneity; (2) to test whether residual interactions contributed to overyielding; and (3) to test for differences in residual interactions among species. Finally, because biodiversity effects mediated by positive litter-mediated interactions should develop over time as trees grow and litter production increases, we tested whether these effects built up between year 5 and 10 after planting.

METHODS

Experimental design

The study was conducted in Sardinilla, ~50 km north of Panama City (Panama, Central America; see Plate 1). A synthetic gradient of species richness was established in July 2001 by planting 5566 seedlings of six native species: *Luehea seemanii* (Ls), *Cordia alliodora* (Ca), *Anacardium excelsium* (Ae), *Hura crepitans* (Hc), *Cedrela odorata* (Co), and *Tabebuia rosea* (Tr) (Scherer-Lorenzen et al. 2007). These species were chosen to cover the range of relative growth rates in diameter at breast height (dbh) found in the nearby forest of Barro Colorado Island and because Ca, Ae, Co, and Tr are important native timber species in Panama, whereas Ls and Hc are ecologically important in the Panama Canal watershed. Species Ca failed to establish: of the 900 initially planted, only 54 individuals were still alive in

2011, all in mixtures. At year 10 after planting, there were thus 22 plots of interest: 10 monocultures (two per species), 6 three-species mixtures, and 6 six-species mixtures.

Following standard reforestation practices in Panama, seedlings were planted at 3 m distance from each other in our 45 × 45 m plots. Each species was planted in 2 replicated monoculture plots, in 3 three-species plots, and in 6 six-species plots. Within each plot, trees were planted following a multiple Latin-square design to ensure that systematic environmental variation did not bias the results. Thus, the species identity of neighbors around trees of a given species remained the same within a plot, thereby forming a specific neighborhood (Appendix A: Fig. A1). Because species composition changes over the three-species plots while the six-species plots are perfect replicates, trees from any given species will experience, across the plantation, five different neighborhoods: one in monoculture, three from three-species plots, and one from six-species plots.

Overyielding and canopy status

We built on Potvin and Gotelli's (2008) bootstrap method to detect differences in diversity effects depending on canopy status by comparing the magnitude of overyielding between canopy trees and smaller, shaded trees. Canopy status was determined based on yearly height measurements on each tree between 2006 and 2011. We considered a tree to be a canopy tree if it had been taller than its eight direct neighbors since 2006. Trees located at the plots' edges were excluded from analysis to avoid edge effects. We computed null expectations for the summed basal area ($\mathrm{SBA} = \sum \pi\,(\mathrm{dbh})^2/4$) of canopy trees in mixtures based on the basal area of monoculture canopy trees. Null assemblages were created by sampling trees from the monoculture canopy trees with replacement while keeping the total number of individuals and the composition as observed in the mixture. We constructed 5000 replicate null assemblages per diversity treatment (three- or six-species mixtures). SBA was computed for each null assemblage so that the replicate simulations yielded a bootstrap SBA distribution.

The same type of analysis was carried out with small trees, defined as those that had been smaller in height than at least four out of their eight direct neighbors since 2006. As in other meta-analyses (Gotelli and McCabe 2002), we computed standardized effect sizes from the observed and expected SBA as: SES = (observed SBA − mean simulated SBA)/standard deviation of simulated SBA. SES has an approximate 95% CI of [–2.0, 2.0], provided that the simulated SBAs follow a normal distribution. For $\mathrm{SES} > 2.0$ and $\mathrm{SES} < -2.0$, the mixtures significantly over- and underyielded compared to the monocultures at the 5% confidence level. For $|\mathrm{SES}| < 2$, there was no detectable diversity effect. Standardized measures allowed us to compare among diversity treatments and canopy statuses despite unbalanced sample sizes. We used 2006 as the reference year because trees were small enough to avoid substantial shading before then. We grouped plots in either three- or six-species mixtures to ensure sufficient sample size ($\geq$41 trees per year × diversity treatment × canopy status). R code (R Development Core Team 2011) for the bootstrapping procedure is provided in the Supplement.

Neighbor effects on growth

We developed a hierarchy of linear mixed models of individual tree growth to test for the existence of, as well as differences in, residual interactions beyond the effects of shading among species. Inspired by the diversity interaction framework proposed by Kirwan et al. (2009), we built models corresponding to five classes of model complexity (Table 1, Fig. 1). Because BEF experiments with trees require an individual-based approach (Potvin and Gotelli 2008, Potvin and Dutilleul 2009), our goal was not to decompose the net plot-level diversity effect in a mixture, but rather to identify (if any) the patterns of interspecific interactions contributing to diversity effects on individual tree growth. Therefore, although the overall approach is similar, we formulated different models than that of Kirwan et al. (2009). We first considered a null model (M_0) with neither residual neighborhood interactions nor diversity effects, but only abiotic, size, and shading effects. All of the other models explicitly partitioned the effects of neighboring trees into the effects of shading and residual effects assumed to primarily reflect belowground interactions (Canham et al. 2004, Coates et al. 2009). Each model class corresponded to different underlying assumptions about how tree diversity may alter residual neighborhood interactions. Precisely, these four other classes were composed of models (M_{nb}) further including a residual effect of neighbors on growth independent of neighbor identity; models (M_{div}) where the diversity treatment entered as a factor and modified both the intercept and the residual effects of neighbors; models (M_{het}) distinguishing conspecific from heterospecific residual interactions and, finally, models (M_{full}) incorporating species-specific pairwise interactions. By successively comparing the relative support for models in this hierarchy with an information criterion, we can test the following questions: (1) Do neighboring trees have an effect on growth besides shading (M_{nb} against M_0)? (2) Are there diversity effects that are not captured by light, size, environmental heterogenity, and crowding (M_{div} against M_{nb})? (3) Are diversity effects explained by a consistent difference between interspecific and intraspecific interactions among species (M_{het} against M_{div})? (4) Or, do diversity effects stem from pairwise interactions that differ in magnitude and/or direction (M_{full} against M_{div} and M_{het})?

All models included controls for species-specific light, species-specific size, and environmental heterogeneity effects. To capture the effects of shading by neighbors, light, measured by exposed crown area (ECA), entered

TABLE 1. Linear mixed models of individual tree growth.

Model class	Model specification	δAIC
M_0	Terms included in all models: $y_{ijkl} = a_i + \text{light}_{ij} + b_i \log \text{BA}_{ijkl} + \text{subplot}_k + \varepsilon_{ijkl}$	115
Basal area-based		
M_{nb}	$M_0 + c_i \sum_{n=1}^{N_{ijkl}} \text{BA}_n$	62.8
M_{div}	$M_0 + (c_i + d_{ih(k)}) \sum_{n=1}^{N_{ijkl}} \text{BA}_n + \text{div}_{ih(k)}$	30.4
M_{het}	$M_0 + c_i \sum_{n/\text{sp}(n)=i} \text{BA}_n + d_i \sum_{n/\text{sp}(n)\neq i} \text{BA}_n$	36.2
M_{full}	$M_0 + \sum_{n=1}^{N'_{ijkl}} c_{i,\text{sp}(n)} \text{BA}_n + d\text{BACa}_{ijkl}$	15.5
Litter-based		
M_{nb}	$M_0 + c_i \sum_{n=1}^{N'_{ijkl}} \text{LP}_n + d\text{BACa}_{ijkl}$	23.8
M_{div}	$M_0 + (c_i + d_{ih(k)}) \sum_{n=1}^{N'_{ijkl}} \text{LP}_n + e\text{BACa}_{ijkl}$	12.8
M_{het}	$M_0 + c_i \sum_{n/\text{sp}(n)=i} \text{LP}_n + d_i \sum_{n/\text{sp}(n)\neq i} \text{LP}_n + e\text{BACa}_{ijkl}$	21.2
M_{full}	$M_0 + \sum_{n=1}^{N'_{ijkl}} c_{i,\text{sp}(n)} \text{LP}_n + d\text{BACa}_{ijkl}$	0

Notes: Growth models are for the log(basal area increment) of a tree *ijkl* of species *i* perceiving a light level *j* in subplot *k* corresponding to the diversity treatment *h*(*k*) (monoculture, three-, or six-species mixture) and surrounded by neighbors $n = 1, \ldots, N_{ijkl}$. Model subscripts are 0, no residual neighborhood interactions; nb, residual neighborhood interactions; div, diversity effects beyond shading; het, heterospecific vs. conspecific residual interactions; full, species-specific pairwise residual interactions. Neighbors are trees located within a 5-m radius from the focal tree. Subplot was treated as a random effect such that $\text{subplot}_k \sim \mathcal{N}(0, \tau^2)$ i.i.d. and $\varepsilon_{ijkl} \sim \mathcal{N}(0, \sigma^2)$ i.i.d. (independent and identically distributed). Log-transformed basal area of the focal tree is log BA. BA_n, LP_n, and sp(*n*) designate, respectively, the basal area, litter production, and species identity of neighbor *n*; $\text{div}_{ih(k)}$ are the species-specific effects of diversity treatments coded as three-level factors. Because *Cordia alliodora* failed to establish, it had to be treated separately in all litter-based and M_{full} models (see *Methods*). In these models, $n = 1, \ldots, N'_{ijkl}$ designate all neighbors that are not *Cordia alliodora*, and BACa is the summed basal area of *Cordia alliodora* neighbors. For the rightmost column, δAIC are differences in AIC relative to the best (smallest AIC) model.

as a four-level-factor in every model. In September 2010, the ECA of all trees was scored as being <25%, in [25%, 50%], in [50%, 75%], or ≥75% of total crown area. Environmental heterogeneity was treated as a random subplot effect to parallel the experimental design and allow for correlation among trees within a 12 × 12 m subplot.

At each level of model complexity except M_0, two alternative models were tested, with neighborhood indices based on either basal area (BA), which is standard practice (e.g., Canham et al. 2004), or litter production by neighboring trees (LP). We considered a tree's total leaf dry mass to be a good proxy for its litter production and established species-specific allometric relationships of total leaf dry mass (see Appendix B). Individual trees influence soil properties primarily within the radius of the canopy (Zinke 1962), whereas litterfall may influence nutritional interactions up to a radius of one tree height (Ferrari and Sugita 1996). A neighborhood approach of litter-mediated interactions is thus fully justified (Rothe and Binkley 2001). We did not develop allometric relationships for the litter production of the species that failed to establish (Ca, *Cordia alliodora*). Yet, despite being rare in the plantation, Ca trees might have an impact on the growth of their neighbors. In litter-based models, the effect of Ca neighbors was thus treated separately by including their summed BA as an additional covariate (Table 1). With only 54 Ca individuals, however, we did not attempt to detect species-specific responses to Ca neighbors.

Individual tree growth was measured as mean yearly basal increment between 2009 and 2011 to average out measurement error while ensuring that the 2010 ECA was a valid proxy for light availability. Increments $y =$

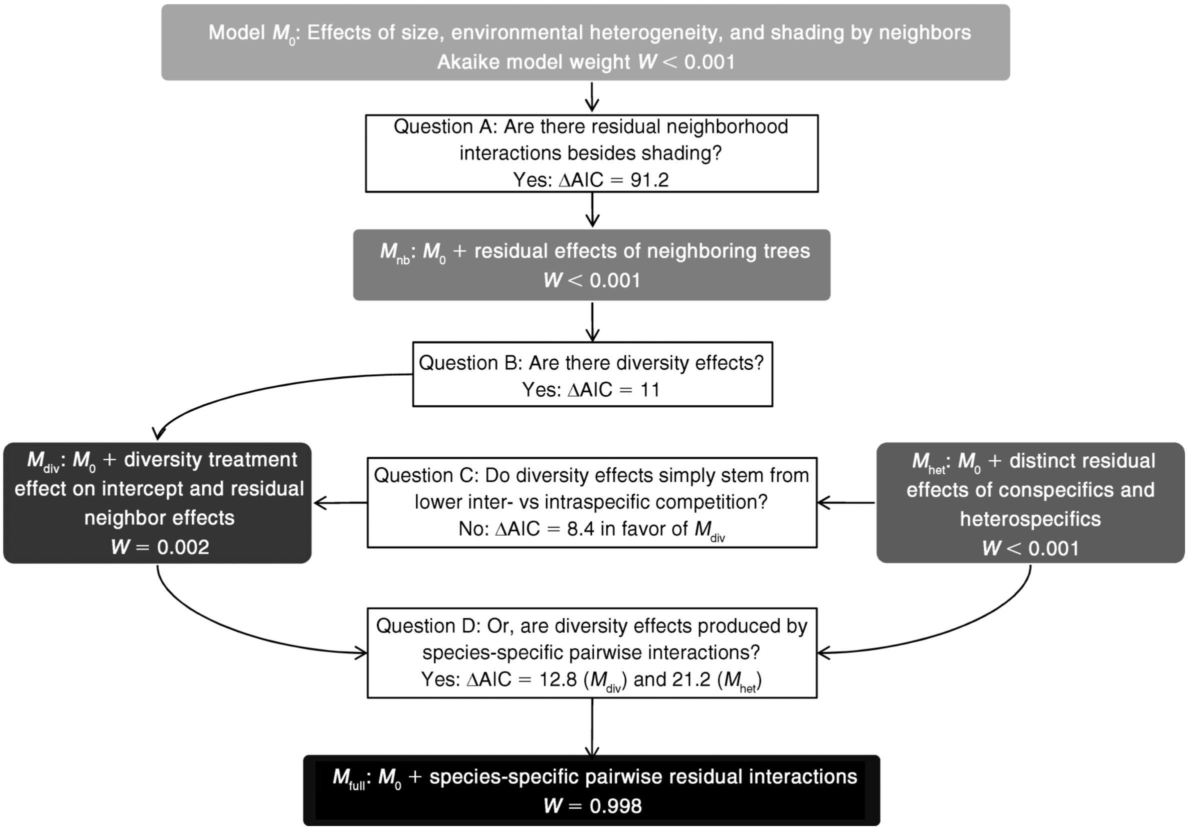

FIG. 1. Relative strength of evidence for competing models of individual tree growth (solid boxes) organized in a hierarchy to test specific biological hypotheses (open boxes). Biological questions A, B, C, and D are answered by comparing the relative support for the models they link. Pairwise comparisons among models, thanks to differences in AIC (ΔAIC), are here reported for litter-based models. Results were similar for BA-based models (Table 1). The darker the shaded box, the more support there is for the model as measured by Akaike weights, W, the probability of selecting a model as being the best if analyses were repeated using independent samples from the same population (Burnham and Anderson 2002). Explicitly, $W = e^{-0.5\delta\mathrm{AIC}_i} / \sum_{m=1}^{M} e^{-0.5\delta\mathrm{AIC}_m}$ where $\delta\mathrm{AIC}_i$ is the AIC difference between the best (smallest AIC) and the ith model and the sum is across all models m considered, i.e., across $M = 9$ total models, including both BA-based and litter-based models. With $W = 0.998$, the litter-based M_{full} model is by far the "best" model in the candidate set.

$\log(\mathrm{BA}_{2011} - \mathrm{BA}_{2009})/2$ were log-transformed to meet the assumptions of Gaussian residuals. The total sample size was 2557, with more than 439 observations per species. Neighborhood interaction radii from 3 to 9 m were compared. However, because they provided the best fit, only results based on neighbors located within a 5 m radius are presented. Mixed models were fit using the lme4 package of R and were compared using Akaike's Information Criterion (AIC). Supplementary details on model development are given in Appendix C, with R code in the Supplement.

Temporal changes in diversity effects

To test whether diversity effects had developed over time, we built, for each year between 2006 and 2011, null expectations for stand-level yields from mortality and growth rates observed in monocultures. Plots were aggregated by diversity treatment i.e., three- and six-species mixtures. For each species i, we first computed p_i, the observed survival probability to year 10 of individual trees grown in monoculture. For each diversity treatment, initially planted with N_i trees of species i, 5000 null mixed-species assemblages were constructed by sampling with replacement, for each species i, $N_i^* \sim \mathrm{Binomial}(N_i, p_i)$ trees from its monoculture pool. Summed basal area (SBA) was calculated for each replicate assemblage, yielding a bootstrap SBA distribution based on species-specific growth and mortality rates in monoculture. Compared to Potvin and Gotelli (2008), we added the binomial draw of N_i^* to propagate uncertainty due to the stochastic nature of mortality. We computed standardized effect sizes (SES, see *Overyielding and canopy status*) from the observed and expected SBA to compare among years and diversity treatments. SES values were submitted to an analysis of covariance to detect effects of the covariate "time," the factor "diversity treatment" (either three or six species), and their interaction. R code for the bootstrapping procedure is provided in the Supplement.

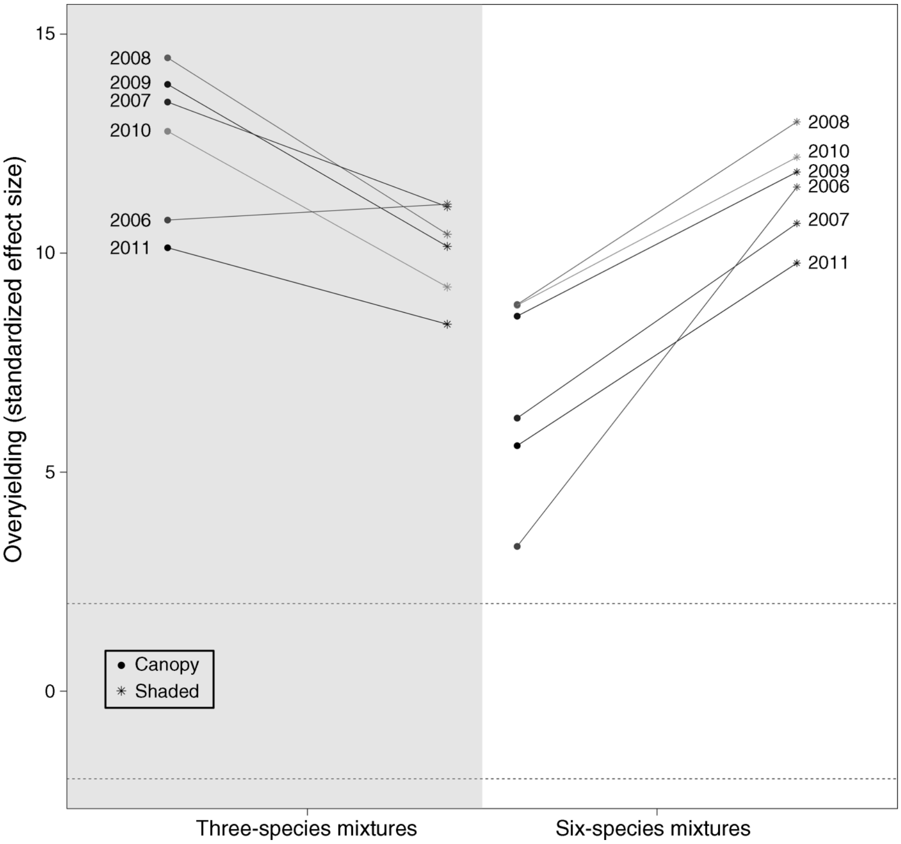

FIG. 2. Overyielding (higher community-level yields in mixtures compared with monocultures), depending on canopy status. Dots and stars show the magnitude of the diversity effect on the growth of canopy trees and small shaded trees, respectively. Diversity effects are measured for each subset of trees (canopy or shaded) by the standardized deviation (SES) of their summed basal area in mixtures from null expectations based on their observed basal area in monocultures. Different shades of gray depict different years, and lines connect symbols corresponding to the same year. Horizontal lines show the $|SES| = 2$ limits, with $SES > 2$ corresponding to significant overyielding at a 5% confidence level. Canopy trees were defined as the subset of trees that had been taller than their eight direct neighbors since 2006. Small trees were individuals that had been smaller than at least four of their eight direct neighbors since 2006.

RESULTS

Overyielding and canopy status

Fig. 2 shows that both canopy and small, shaded trees had a significantly higher basal area in mixture than expected based on monoculture yields. The effect sizes were overall of the same magnitude for both canopy statuses and indicate general overyielding of the mixtures. Nevertheless, shaded trees appeared to benefit a little more from diversity effects than canopy trees in the six-species mixtures, whereas the reverse was true in three-species mixtures.

Neighbor effects on growth

Within a type of neighborhood measure, either BA-based or litter-based, the relative strength of evidence for models were similar (Table 1). There was a strong effect of neighboring trees besides shading; with more than 91 (litter-based) and 52 (BA-based) AIC units difference, there was no support for the null model (M_0) compared to models incorporating a residual effect of neighbors (Fig. 1). Diversity effects were detected on growth, because the M_{div} model was substantially more supported than the M_{nb} model ($\Delta\text{AIC} = 11$ and 32.4 for litter- and BA-based models, respectively). Given the low support for M_{het} compared to M_{div} and M_{full} models ($\Delta\text{AIC} = 12.8$ and 21.2 for litter-based, 5.8 and 20.7 for BA-based), we can reject the hypothesis that diversity effects are simply explained by a consistent difference between intra- and interspecific interactions. At any given level of model complexity, litter-based models were more supported than their BA-based counterparts, with ΔAIC ranging between 8 and 28 (Table 1). There was a difference of >15 AIC units between the best litter-based and BA-based models. Because we controlled for light availability, we conclude that litter-mediated interactions influenced growth in the plantation and produced pairwise belowground interactions differing at least in magnitude, if not in direction, among species.

TABLE 2. For five tree species native to Panama, (a) species-specific effect of litter production (LP) by neighbors on individual tree growth and (b) resulting differences among inter- and intraspecific interactions, with inference based on the M_{full} litter model (see Table 1).

LP by neighbor trees	Effect on growth of species									
	Ae, *Anacardium excelsium*		Co, *Cedrela odorata*		Hc, *Hura crepitans*		Ls, *Luehea seemanii*		Tr, *Tabebuia rosea*	
	Coeff.	95% CI	Coeff.	95% CI	Coeff.	95% CI	Coeff.	95% CI	Coeff.	95% CI
a) Species-specific effect of litter production by neighbors										
LPAe	**−0.43**	*0.64, −0.28*	−0.58	*−1.43, 0.05*	**−0.65**	*−0.90,−0.40*	**−0.57**	*−0.77, −0.32*	−0.24	*−0.51, 0.21*
LPCo	2.38	*−1.28, 5.63*	**−0.71**	*−1.02, −0.43*	−0.06	*−0.46, 0.45*	−0.40	*−0.67, 0.40*	0.08	*−0.41, 0.46*
LPHc	1.41	*−0.82, 2.73*	0.33	*−1.34, 2.34*	*−0.53*	*−1.01, 0.01*	0.87	*−1.61, 3.96*	0.20	*−1.59, 1.31*
LPLs	**−0.42**	*−0.72, −0.03*	−0.26	*−0.54, 0.44*	**−0.98**	*−1.40, −0.25*	**−0.54**	*−0.76, −0.35*	**−0.63**	*−0.93, −0.17*
LPTr	−0.18	*−0.56, 0.26*	−0.11	*−0.43, 0.16*	0.07	*−0.26, 0.31*	**0.66**	*0.17, 2.26*	**−0.31**	*−0.46, −0.22*
b) Differences among inter- and intraspecific litter-mediated interactions										
LPAe			0.12	*−0.72, 0.80*	−0.13	*−0.71, 0.42*	−0.03	*−0.25, 0.27*	0.07	*−0.17, 0.53*
LPCo	*2.72*	*−0.93, 6.15*			0.47	*−0.11, 1.14*	*0.15*	*−0.12, 0.82*	*0.39*	*−0.07, 0.82*
LPHc	*1.84*	*−0.33, 3.31*	1.09	*−0.60, 3.17*			1.46	*−0.97, 4.72*	0.51	*−1.31, 1.65*
LPLs	0.03	*−0.24, 0.47*	**0.46**	*0.14, 1.15*	−0.46	*−1.00, 0.36*			−0.31	*−0.55, 0.22*
LPTr	*0.25*	*−0.11, 0.76*	**0.61**	*0.21, 1.01*	**0.59**	*0.03, 1.05*	**1.27**	*0.77, 3.06*		

Notes: Table entries are interaction coefficients and their 95% confidence intervals, given as lower and upper confidence limits. In panel (a), negative coefficients correspond to reductions in yearly basal area log-increment per 10 kg of litter dry mass produced by neighbors; positive coefficients correspond to increases. In panel (b), positive coefficients correspond to species pairs for which competition is more intense within the focal species (columns) than with trees of the other species (rows). Coefficients in bold and italic, respectively, differ from zero at $\alpha = 0.05$ and $\alpha = 0.1$. A semiparametric bootstrapping approach was used to propagate uncertainty due to environmental heterogeneity in the confidence intervals (see Appendix C).

Because a best model was clearly identified (litter-based M_{full}; Fig. 1 and Appendix C), we based inference on this model only (Burnham and Anderson 2002). Species-specific effects of neighbor litter production are reported in Table 2a. Litter production by conspecifics had a significantly negative effect at $\alpha = 0.05$ for four species and at $\alpha = 0.1$ for the fifth (Hc). For all species, litter production by heterospecifics had either a less negative effect than litter production by conspecifics or an effect that was not significantly different from the latter (Table 2b). The litter of Tr had a positive effect on Ls diameter growth. Taking both sides of the interactions into account, the most mutually beneficial pairwise species combinations were Ae–Co, Tr–Ls, Ls–Co, Tr–Hc, and Ae–Tr. We conclude that litter-mediated interactions contributed to positive diversity effects in the Sardinilla plantation. Moreover, these diversity effects resulted from the contributions of contrasting pairwise interactions, which ranged from competitive to facilitative.

Temporal changes in diversity effects

From year 5 after planting, mixtures yielded significantly more than expected from species-specific growth and mortality rates in monoculture (Fig. 3). Diversity effects significantly increased over time ($F_{1,8} = 11.54$, $P = 0.0094$; Appendix A: Table A1), but took more time to start developing in six-species mixtures than in three-species mixtures. Although three-species mixtures overyielded more than six-species mixtures ($F_{1,8} = 8.15$, $P = 0.021$), the rate of increase with time was not significantly different between the two diversity treatments ($F_{1,8} = 0.62$, $P = 0.45$).

DISCUSSION

The loss of biodiversity due to deforestation and the growing amount of land allocated to monoculture tree plantations raises concerns about the significance of tree diversity for ecosystem functioning (Bunker et al. 2005, Carnus et al. 2006). However, predicting the ecological consequences of species loss requires the identification of the mechanisms underlying the effects of diversity (Loreau and Hector 2001). Here, we disentangled the contributions of light and residual neighborhood interactions to overyielding in a tropical tree plantation. We found positive diversity effects of similar strength for canopy and shaded trees. We developed linear mixed models of individual tree growth that partition the effects of neighbors into the effect of shading and the residual effect of litter production. These models demonstrated that litter-mediated interactions (1) were at play, (2) contributed to overyielding by concentrating competition within species, and (3) produced contrasting pairwise interactions that ranged from competitive to facilitative. Consistent with litter-mediated biodiversity effects, we finally showed that the magnitude of overyielding increased over time.

Litter-mediated interactions

Our analysis contributes to unraveling the specific mechanisms underlying biodiversity effects in forest ecosystems. Less intense competition for light in mixture was proposed as the mechanism driving overyielding in the Sardinilla plantation (Potvin and Dutilleul 2009). However, because tree growth is generally an increasing but decelerating function of light (e.g., Pacala et al.

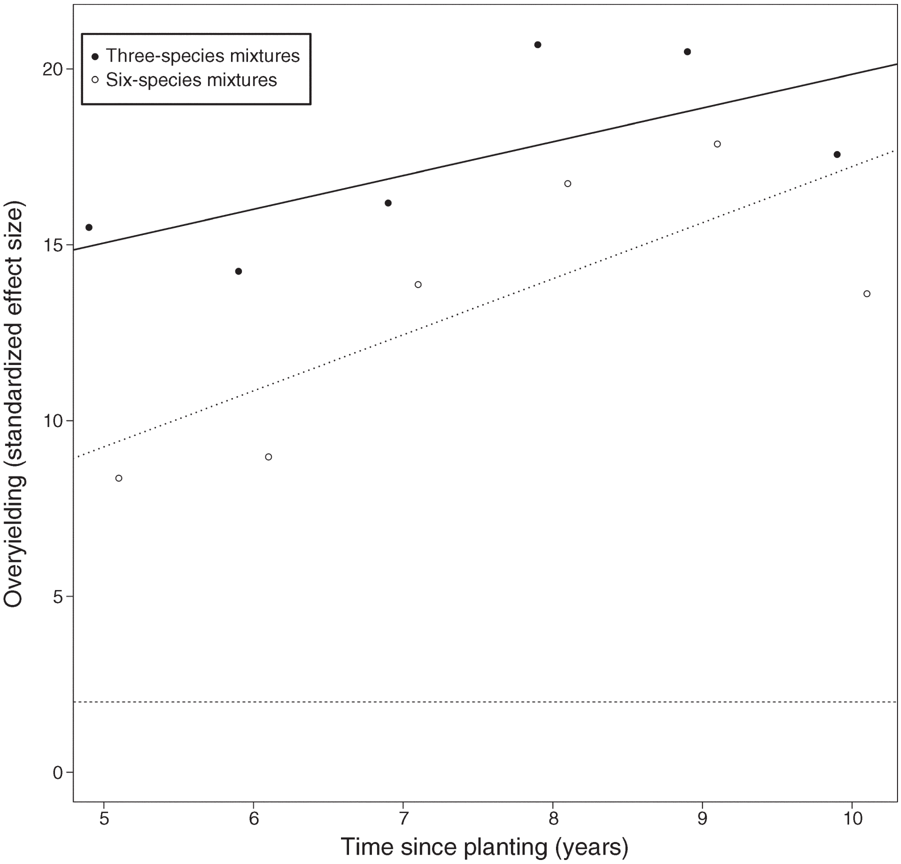

FIG. 3. Temporal changes in the magnitude of overyielding. Symbols show diversity effects on yields, as measured by the standardized deviation (SES) of summed basal area in mixtures from null expectations based on observed monoculture growth and mortality. Plots are grouped by diversity treatment: three-species mixtures (solid symbols) and six-species mixtures (open symbols). Trend lines are shown for the two diversity levels. The horizontal line corresponds to SES = 2; SES > 2 indicates significant overyielding at a 5% confidence level.

1994, Rueger et al. 2011), the effects of increased light availability are stronger on the growth of small, shaded trees than for canopy trees that are closer to light saturation. If overyielding were fully explained by less intense competition for light in mixtures, the effects of competition alleviation would thus be weaker for canopy trees, which would not overyield as strongly as smaller trees. The fact that diversity effects were similar for canopy and shaded trees is therefore a first indication that light was not the sole driver of overyielding. This conclusion was confirmed by our tree growth models, which revealed that, once the effects of shading were factored out, the residual effect of neighboring trees was more negative within than between species. Nevertheless, shaded trees displayed slightly stronger overyielding than canopy trees in the six-species mixtures, whereas the reverse was true in thee-species mixtures. This pattern might result from stronger light-mediated diversity effects at the highest diversity level (J. Sapijanskas, A. Paquette, C. Potvin, N. Kunert, and M. Loreau, *unpublished manuscript*). Although our results do not exclude light as a major explanatory factor (we even found that light partitioning contributed to overyielding in the Sardinilla experiment), our present study demonstrates that other processes can also play an important role. As suggested by Coomes and Grubb (2000), the strong emphasis on light competition in forest ecosystems may merely reflect our poor understanding of belowground processes.

When the effects of shading were factored out, litter production by neighbors was a far better predictor of neighbor effects on growth than traditional crowding indices based on basal area. We interpret this result as evidence for litter-mediated interactions. Although litter production may be correlated with transpiration and water might be limiting in the dry season, a detailed analysis of tree transpiration found no difference in mean daily sap flux density between monocultures and mixtures for a given species, and concluded that water was unlikely to constrain interspecific interactions (Kunert et al. 2012). Moreover, interactions mediated by water are unlikely to be facilitative, and hence cannot explain the significantly positive effect of neighbor litter production that we detected for one species pair. Our interpretation is further supported by a recent litter manipulation experiment that demonstrated the ability of tropical trees to respond to leaf litter nutrient inputs by increasing leaf and litter production within months of litter addition (Wood et al. 2009). Although Wood et al. (2009) found no effect on wood growth within a single year, responses to neighbor litter production may be integrated over time in our plantation. Litter production depends on a tree's requirements, but also on the amount of nutrients returned and shared with neighbors so that competitive and facilitative interactions are possible. Pretzsch and Schutze (2009) showed in temperate stands that Norway spruce benefited from a continuous "facilitation" by European beech, which, they argued, improved nutrient supply by deeper soil exploitation, higher turnover, and humus activation. Moreover, if the residual neighbor effects were still to capture some shading effects in our models, the interaction coefficients would be biased toward negative values. If anything, our analysis may thus underestimate positive litter-mediated interactions.

Our results corroborate the mounting evidence suggesting that belowground processes play a much greater role than usually assumed on growth and survival in forests (Coomes and Grubb 2000, Wright et al. 2011), even for understory seedlings in low light conditions (Holste et al. 2011). Our methods do not allow us to identify any particular resource that is being competed for belowground and we cannot rule out the involvement of soil microbial communities or pathogens. In addition, there is no reason to believe that a single resource is competed for, or that the same mechanism (e.g., competition for nutrients, pathogens, mycorrhizal associations) drives all the pairwise interactions (Coates et al. 2009). Nevertheless, modified litter decomposition, dilution, and altered allocation of nutrients within tree biomass or improved nutrient use efficiencies in mixtures are unlikely to contribute to our findings. There was no overall effect of litter diversity on litter decomposition in the Sardinilla experiment, i.e., mixing species resulted in pure additive effects (Scherer-Lorenzen et al. 2007). Except for calcium concentrations in branches and stems, Oelmann et al. (2010) found no mixture effects on nutrient concentrations in leaves, branches, or stems in any of the studied tree species, and the only diversity effect on nitrogen and phosphorus use efficiencies (NUE, PUE) was a lower PUE in three-species mixtures (Zeugin et al. 2010).

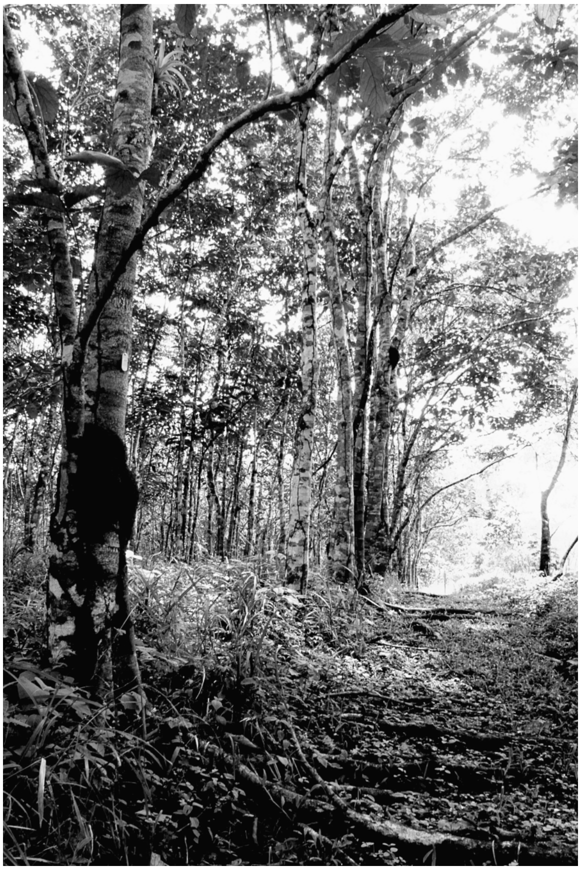

PLATE 1. View of a plot from the Sardinilla (Panama) experiment. Photo credit: Lisa Lutz.

In light of our results, we speculate that trees shared resources through their litter in a way that was beneficial at the community level thanks to complementary nutrient uptake and/or differences in limiting nutrients among species. Lower nutrient use efficiencies have often been related to higher nutrient availabilities (Vitousek 1982, Hidaka and Kitayama 2009); in Sardinilla, species causing the most negative litter effects had among the most nutrient-poor leaves, e.g., *Anacardium excelsium* (0.13 ± 0.024 %P, 1.57 ± 0.1 %N; all values mean ± SD) and *Luehea seemanii* (0.20 ± 0.024 %P, 2.18 ± 0.18 %N), whereas the relatively nutrient-rich *Cedrela odorata* (0.19 ± 0.028 %P, 2.36 ± 0.21 %N), *Hura crepitans* (0.33 ± 0.044 %P, 2.57 ± 0.29 %N), and *Tabebuia rosea* (0.22 ± 0.075 %P, 2.33 ± 0.32 %N) had no significantly negative interspecific effects (leaf nutrient data kindly provided by Zeugin et al. [2010]). In addition, Coll et al. (2008) found that *Tabebuia* produced few roots with long links, which increased soil exploitation efficiency, whereas *Luehea* presented more branched roots and allocated much less to taproot, which presumably improved resource capture through an increase in belowground surface. Although we did not perform any definite test, these observations of leaf and root traits are consistent with the nutrient-based hypothesis that we propose. Under this hypothesis, the increase in biodiversity effects over time may be interpreted as the manifestation of a positive feedback between litter nutrient recycling and less competitive inter- compared to intraspecific belowground interactions. Such a mechanism echoes the growing complementary effects found in temperate grasslands where N-fixers interact with C_4 grasses to increase N accumulation and biomass production through higher inputs coupled with improved nutrient retention (Fargione et al. 2007).

Temporal and spatial scales of interactions: implications for BEF research

Tree biodiversity experiments bring about new challenges pertaining to spatial scale. To unveil underlying mechanisms, investigations have to be undertaken at the scale of tree–tree interactions where competition and/or facilitation take place (Potvin and Dutilleul 2009). Accordingly, we found that the identity of neighbors is key to explain overyielding, indicating that for sessile organisms such as trees, the spatial distribution of diversity is of utmost importance. For any given level of diversity, the impact on ecosystem functioning may thus vary greatly depending on the frequency with which individuals with large trait differences interact across the landscape. For instance, although trait differences generally alleviated competitive interactions, neighborhoods of live trees displayed greater functional similarity relative to those of dead trees in the Luquillo Forest Dynamics Plots (Uriarte et al. 2010). There, environmental filtering hindered the potential for positive diversity effects by restricting functional diversity at the neighborhood scale. Great caution must therefore be taken in the analysis and interpretation of biodiversity effects when using nonspatial diversity metrics in natural forests (e.g., Paquette and Messier 2011), where the spatial distribution of trees is neither controlled nor well-mixed. Although trait-based approaches and the considerable research effort devoted to the development of appropriate functional diversity metrics hold great promise (Reiss et al. 2009), future progress in BEF research with trees will require accounting for the distribution of functional diversity in space. In particular, BEF spatial theory, which has been focused on patch dynamics and metacommunities, needs to be extended and needs to investigate whether the spatial structure built up through ecological dynamics (Turnbull et al. 2007) tends to exacerbate or dampen the effects of diversity generally detected at the neighborhood scale (e.g., Stoll and Newbery 2005, Coates et al. 2009, Uriarte et al. 2010).

BEF experiments with long-lived perennials also raise temporal scale issues. They involve extensive transients when both the magnitude and the mechanisms driving diversity effects may change over time (Cardinale et al. 2007). The strong neighborhood effects besides shading that we report might be temporary, because 77% of trees had more than half of their crown exposed to direct sun light at year 9. Overyielding was also mostly associated with diversity effects on growth; no effect on mortality had been detected at year 5 (Potvin and Gotelli 2008) and only 50 individual trees (24 in monoculture and 26 in mixtures) died between years 5 and 10. As more trees become light-limited and mortality consequently increases, light- and mortality-mediated diversity effects might gain in importance. On the other hand, litter-mediated effects are bound to develop as trees grow and leaf biomass increases before eventually reaching a peak (Ryan et al. 1997) or a plateau (Oliver and Larson 1996: Fig. 3.16). Accordingly, diversity effects built up over time in the Sardinilla plantation, with a small lag for six- compared to three-species mixtures. As Scherer-Lorenzen et al. (2007) hypothesized, nearly all of the most beneficial species combination are spatially diluted in the six-species mixtures: *Anacardium* trees have no *Cedrela* and only one *Tabebuia* individual among their direct neighbors, and *Luehea* is separated from *Cedrela* and *Tabebuia* (Appendix A: Fig. A1). Highlighting once more the importance of spatial structure, we conjecture that trees had to reach a threshold size allowing them to interact with more distant neighbors for the positive tree–tree interactions to start acting in six-species mixtures.

CONCLUSION

BEF research aims to understand and predict the potential consequences of species loss for the maintenance of functional ecosystems and the wide range of ecological "services" upon which human societies depend (Loreau 2010). Here, we have begun to unveil the mechanisms underlying strong biodiversity effects relevant to climate mitigation initiatives. Our results highlight the importance of litter-mediated interactions and question the current focus on light competition in forest ecosystems, which prevails to such an extent that it is the only mechanism included in most forest models. A predictive knowledge of BEF relationships in natural and managed forests will require a better understanding of the processes that structure functional diversity at the neighborhood scale, and of the resulting tree–tree interactions, especially belowground.

ACKNOWLEDGMENTS

We are grateful to Jose Monteza for invaluable help in maintaining the experimental plantation and data collection. Fabienne Zeugin kindly provided her data on leaf nutrient content. We thank Benoit Courbaud, Forest Isbell, Paul Leadley, Justin Marleau, Chadwick Oliver, Alain Paquette, and an anonymous reviewer for helpful comments that substantially strengthened the manuscript. Jurgis Sapijanskas was funded by the French Ministry of Agriculture. Catherine Potvin and Michel Loreau were funded by Discovery grants from the Natural Sciences and Engineering Research Council of Canada. Michel Loreau also acknowledges support by the Canada Research Chair Programme and the TULIP Laboratory of Excellence (ANR-10-LABX-41). The Sardinilla experiment is supported by the Smithsonian Tropical Research Institute.

LITERATURE CITED

Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9:1146–1156.

Bugmann, H. 2001. A review of forest gap models. Climatic Change 51:259–305.

Bunker, D. E., F. DeClerck, J. C. Bradford, R. K. Colwell, I. Perfecto, O. L. Phillips, M. Sankaran, and S. Naeem. 2005.

Species loss and aboveground carbon storage in a tropical forest. Science 310:1029–1031.

Burnham, K., and D. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Canadian Journal of Forest Research 34:778–787.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.

Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences USA 104:18123–18128.

Carnus, J. M., J. Parrotta, E. Brockerhoff, M. Arbez, H. Jactel, A. Kremer, D. Lamb, K. O'Hara, and B. Walters. 2006. Planted forests and biodiversity. Journal of Forestry 104:65–77.

Catovsky, S., M. A. Bradford, and A. Hector. 2002. Biodiversity and ecosystem productivity: implications for carbon storage. Oikos 97:443–448.

Coates, K. D., C. D. Canham, and P. T. LePage. 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. Journal of Ecology 97:118–130.

Coll, L., C. Potvin, C. Messier, and S. Delagrange. 2008. Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. Trees—Structure and Function 22:585–596.

Coomes, D. A., and R. B. Allen. 2007. Effects of size, competition and altitude on tree growth. Journal of Ecology 95:1084–1097.

Coomes, D. A., and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70:171–207.

Díaz, S., A. Hector, and D. A. Wardle. 2009. Biodiversity in forest carbon sequestration initiatives: not just a side benefit. Current Opinion in Environmental Sustainability 1:55–60.

Erskine, P. D., D. Lamb, and M. Bristow. 2006. Tree species diversity and ecosystem function: Can tropical multi-species plantations generate greater productivity? Forest Ecology and Management 233:205–210.

Ewel, J. J., and A. J. Hiremath. 2005. Plant–plant interactions in tropical forests. Pages 3–34 *in* D. Bursalem, M. Pinnard, and S. Hartley, editors. Biotic interactions in the tropics. Cambridge University Press, Cambridge, UK.

FAO. 2006. Global forest resources assessment 2005; progress towards sustainable forest management. Food and Agriculture Organization, Rome, Italy.

Fargione, J., D. Tilman, R. Dybzinski, J. HilleRisLambers, C. Clark, W. S. Harpole, J. M. H. Knops, P. B. Reich, and M. Loreau. 2007. From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. Proceedings of the Royal Society B 274:871–876.

Ferrari, J. B., and S. Sugita. 1996. A spatially explicit model of leaf litter fall in hemlock–hardwood forests. Canadian Journal of Forest Research 26:1905–1913.

Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. Ecology 83:2091–2096.

Hidaka, A., and K. Kitayama. 2009. Divergent patterns of photosynthetic phosphorus-use efficiency versus nitrogen-use efficiency of tree leaves along nutrient-availability gradients. Journal of Ecology 97:984–991.

Holste, E., R. Kobe, and C. Vriesendorp. 2011. Seedling growth responses to soil resources in the understory of a wet tropical forest. Ecology 92:1829–1838.

Kelty, M. J. 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. Forest Ecology and Management 28:237–257.

Kirwan, L., J. Connolly, J. A. Finn, C. Brophy, A. Luscher, D. Nyfeler, and M. T. Sebastià. 2009. Diversity-interaction modeling: estimating contributions of species identities and interactions to ecosystem function. Ecology 90:2032–2038.

Kunert, N., L. Schwendenmann, C. Potvin, and D. Holscher. 2012. Tree diversity enhances tree transpiration in a Panamanian forest plantation. Journal of Applied Ecology 49:135–144.

Lodge, D. J., W. H. McDowell, and C. P. McSwiney. 1994. The importance of nutrient pulses in tropical forests. Trends in Ecology and Evolution 9:384–387.

Loreau, M. 1998. Biodiversity and ecosystem functioning: A mechanistic model. Proceedings of the National Academy of Sciences USA 95:5632–5636.

Loreau, M. 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. Philosophical Transactions of the Royal Society B 365:49–60.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Millenium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, D.C., USA.

Oelmann, Y., C. Potvin, T. Mark, L. Werther, S. Tapernon, and W. Wilcke. 2010. Tree mixture effects on aboveground nutrient pools of trees in an experimental plantation in panama. Plant and Soil 326:199–212.

Oliver, C., and B. C. Larson. 1996. Forest stand dynamics. Updated edition. Wiley, New York, New York, USA.

Pacala, S., C. Canham, J. Silander, and R. Kobe. 1994. Sapling growth as a function of resources in a north temperate forest. Canadian Journal of Forest Research 24:2172–2183.

Paquette, A., and C. Messier. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Global Ecology and Biogeography 20:170–180.

Piotto, D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecology and Management 255:781–786.

Potvin, C., and P. Dutilleul. 2009. Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. Ecology 90:321–327.

Potvin, C., and N. J. Gotelli. 2008. Biodiversity enhances individual performance but does not affect survivorship in tropical trees. Ecology Letters 11:217–223.

Pretzsch, H., and G. Schutze. 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in central Europe: evidence on stand level and explanation on individual tree level. European Journal of Forest Research 128:183–204.

Purves, D., and S. Pacala. 2008. Predictive models of forest dynamics. Science 320:1452–1453.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends in Ecology and Evolution 24:505–514.

Rothe, A., and D. Binkley. 2001. Nutritional interactions in mixed species forests: a synthesis. Canadian Journal of Forest Research 31:1855–1870.

Rueger, N., U. Berger, S. P. Hubbell, G. Vieilledent, and R. Condit. 2011. Growth strategies of tropical tree species: Disentangling light and size effects. PLoS ONE 6(9):e25330.

Ryan, M., D. Binkley, and J. Fownes. 1997. Age-related decline in forest productivity: pattern and process. Advances in Ecological Research 27:213–262.

Scherer-Lorenzen, M., J. L. Bonilla, and C. Potvin. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116:2108–2124.

Stoll, P., and D. Newbery. 2005. Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. Ecology 86:3048–3062.

Turnbull, L. A., D. A. Coomes, D. W. Purves, and M. Rees. 2007. How spatial structure alters population and community dynamics in a natural plant community. Journal of Ecology 95:79–89.

Uriarte, M., N. G. Swenson, R. L. Chazdon, L. S. Comita, W. J. Kress, D. Erickson, J. Forero-Montana, J. K. Zimmerman, and J. Thompson. 2010. Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. Ecology Letters 13:1503–1514.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119:553–572.

Wood, T. E., D. Lawrence, D. A. Clark, and R. L. Chazdon. 2009. Rain forest nutrient cycling and productivity in response to large-scale litter manipulation. Ecology 90:109–121.

Wright, S. J., J. B. Yavitt, N. Wurzburger, B. L. Turner, E. V. J. Tanner, E. J. Sayer, L. S. Santiago, M. Kaspari, L. O. Hedin, K. E. Harms, M. N. Garcia, and M. D. Corre. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–1625.

Yachi, S., and M. Loreau. 2007. Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. Ecology Letters 10:54–62.

Zeugin, F., C. Potvin, J. Jansa, and M. Scherer-Lorenzen. 2010. Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation? Forest Ecology and Management 260:1424–1433.

Zinke, P. J. 1962. Pattern of influence of individual forest trees on soil properties. Ecology 43:130–133.

SUPPLEMENTAL MATERIAL

Appendix A

Figure showing the planting design and ANOVA table for the temporal change in the magnitude of overyielding (*Ecological Archives* E094-080-A1).

Appendix B

Allometric relationships of total leaf dry mass used as a proxy for litter production (*Ecological Archives* E094-080-A2).

Appendix C

Supplementary methods, relative strength of evidence, and goodness of fit for the growth models (*Ecological Archives* E094-080-A3).

Supplement

R code for the SES (standardized effect sizes) bootstrapping procedures and the hierarchy of linear mixed models of individual tree growth (*Ecological Archives* E094-080-S1).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.632p3.