

Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation

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Summary

1. Over 5000 trees were grown in plots of differing diversity levels (1, 3 and 6 species) in a plantation established in Panama. Four and five years after establishment, we analysed parameters related to the productivity of this tropical plantation (tree survival, height and biomass as well as plot basal area) to test for the presence of biodiversity effects. The relative importance of environmental heterogeneity (such as soil, topography, and drainage) and biodiversity on tree growth and mortality was determined using partial redundancy analysis.

2. Hierarchical clustering revealed nine different soil clusters based on soil quality and drainage. By chance, the six-species plots were apparently established on more variable soils than on the other diversity levels. We found little evidence for spatial autocorrelation between subplots, with the exception of four subplots located on a ridge that extends on the North–South axis of the plantation and corresponds to a zone of higher productivity.

3. The redundancy analysis indicated that environmental heterogeneity and biodiversity together explained around 50% of the variation in subplot productivity and tree mortality. Environment explained 35–57% of the variation in productivity and mortality, respectively, whereas diversity explained an additional 23–30%.

4. Our simulation model revealed a significant positive effect of biodiversity on growth but no effect of biodiversity on mortality. The standardized effect sizes that we used to detect over- or under-yielding or no effect in comparison with monoculture were highly variable and the variability was largely explained by traits related to site topography.

5. *Synthesis.* In our tropical tree plantation, we detected biodiversity effects at a scale relevant to conservation and quantified the relative importance of environmental heterogeneity and diversity on tree growth and mortality. Our results support the idea that environmental factors could act as hidden sources of variability in biodiversity experiments. Environmental and spatial heterogeneity induced variable responses to biodiversity and amplified the differences between three- and six-species plots. Species identity explained more variation in productivity than did the species diversity. One species, *Cedrela odorata*, was associated with increased productivity.

Key-words: biodiversity and ecosystem function, environmental and spatial heterogeneity, productivity, redundancy analysis, tree growth and mortality, tropical tree plantations

Introduction

Understanding the connection between biodiversity and the maintenance of ecosystem processes is a major research focus in ecology (Loreau *et al.* 2001; Hooper *et al.* 2005; Wright *et al.* 2006). Srivastava & Vellend (2005) found that 62% of the

studies supported a positive relationship between biodiversity and ecosystem function (BEF). This relationship, however, varies according to the ecosystems (grassland, trees), the specific site characteristics, the species and the number of trophic levels studied, the experimental methods used, and the type of traits measured (Srivastava & Vellend 2005; Balvanera *et al.* 2006 but see Cardinale *et al.* 2006). Recently, the relevance of BEF research to conservation has been questioned (Srivastava

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& Vellend 2005) because of its bias towards plants and grasslands, as well as the short time periods and small spatial scales that characterize much of the experimental work (Schlapfer & Schmid 1999; Naeem & Wright 2003; Carnus *et al.* 2006). In consequence, there is a need to study the BEF relationship in more complex systems and at larger spatial scales (Scherer-Lorenzen *et al.* 2005; Balvanera *et al.* 2006).

The Sardinilla field site, a native tropical tree biodiversity plantation in Central Panama, is one of four plantations worldwide, the others being in Finland, Germany and Borneo, designed to explore BEF relationships at a scale relevant to forest management (<http://www.biotree.bgc-jena.mpg.de/mission/index.html>). Established in a humid tropical climate over approximately 6 ha of land previously dedicated to cattle ranching, the plantation was designed to bridge the gap between the first phase of small-scale BEF experiments and questions relevant to landscape perspectives. In a previous paper, we developed a simulation model that allows partitioning of the effects of biodiversity on tree growth and mortality, two key components of yield in a plantation context (Potvin & Gotelli 2008). We reported an overall significant, positive, biodiversity effect on plot basal area caused mostly by enhanced individual growth in mixed-species plots. The analysis however also highlighted important variation between plots with regard to the magnitude of this biodiversity effect.

Here, we search for the cause of such variation with a special focus on environmental heterogeneity and spatial patterns. Although abundant research has demonstrated that abiotic factors have a significant influence on ecosystem processes (Schlapfer & Schmid 1999), very few BEF studies have attempted to incorporate extrinsic factors (Spehn *et al.* 2005), such as environmental variability, into the analysis. The possibility that the effect of species diversity may be masked by abiotic heterogeneity has been discussed (Huston & McBride 2002). Our main hypothesis is that environmental heterogeneity, potentially a large source of variation, could hide/confound BEF effects. To test this hypothesis we (i) characterized the environmental heterogeneity over the approximately 6 ha of our plantation, (ii) statistically partitioned the variation in tree productivity and mortality due to environmental heterogeneity, species identity and species diversity, and (iii) classified over- and under-yielding subplots using spatial and environmental explanatory variables.

Methods

TREE ESTABLISHMENT AND GROWTH

The study was conducted over 2 years (2005–06) in a tree plantation, located in Sardinilla in the Buena Vista region of central Panama (9°19'30" N, 79°38'00" W), approximately 20 km from Barro Colorado Island (BCI). The plantation lies at an elevation of 70 m a.s.l., and its overall slope is < 17%. The site was cleared of forest in 1953, cultivated for 2–3 years, and then used to graze cattle for 46 years. The soils are mostly clayish, with *Typic Tropudalfs* making up the upper slopes and *Aquic Tropudalfs* in the low lying areas (Potvin *et al.* 2005). The plantation layout prevented establishment of plots in the lowest part of the field (Fig. 1) to ensure, as much as possible,

Table 1. Average biophysical characteristics of plots assigned to different diversity levels in the Sardinilla plantation. Soil bulk density (g cm^{-3}), soil pH, %N in soil, Average height of the water table during the wet season (Ave wt, cm), Maximum height of the water table (cm), number of days with water table > 30 cm. Data are means across each diversity level with associated standard

	Monoculture	three-species	six-species
Bulk density	0.592 ± 0.118	0.575 ± 0.017	0.603 ± 0.072
pH	5.68 ± 0.16	5.90 ± 0.34	5.65 ± 0.28
Ave. wet	18.1 ± 8.5	19.4 ± 7.5	26.7 ± 8.0
Max height	41.9 ± 7.5	43.6 ± 3.7	41.6 ± 10.8
Days > 30	4.3 ± 2.6	5.0 ± 2.2	7.2 ± 3.1

that water logging would not impede tree development. Across the site soil bulk density was $0.591 \pm 0.039 \text{ g cm}^{-3}$ with a pH of 5.73 ± 0.21 (Table 1). Soil carbon content was high with an average across subplots of $56.6\% \pm 5.8$ while average soil nitrogen content was $47.8\% \pm 4.4$.

The plantation was established in 2001 with six native tree species: *Luehea seemanii* (LS), *Cordia alliodora* (CA), *Anacardium excelsum* (AE), *Hura crepitans* (HC), *Cedrela odorata* (CO) and *Tabebuia rosea* (TR). Species selection was guided by three criteria: (i) ability to grow in the harsh conditions prevailing in a pasture, (ii) important economic (CO, AE, CO, TR) or ecological role (HC and LS); and (iii) range of relative growth rate on BCI (9.1% for LS to 2.3% for CO). Twenty-four diversity plots of $2081 \pm 84 \text{ m}^2$ were planted: six 6-species and six 3-species plots as well as 12 monocultures (Scherer-Lorenzen *et al.* 2005). The levels of diversity were randomly assigned to all plots in the landscape with the exception of the TR and AE monocultures that were placed in the wetter east flank of the plantation due to their ability to tolerate water-logged soils (Fig. 1). To avoid excessive water logging in the lower lying plots, drainage ditches were dug in 2002. The ditches are between 30 and 60 cm deep and approximately 60 cm wide. They were dug to channel the flow of the runoff during heavy rainfall events.

As indicators of tree growth, the height and diameter of all individual saplings ($n > 5000$) were measured at the beginning of the dry season (December and January) in 2005 and 2006. For saplings with height < 2 m, we measured basal diameter (diameter at 10 cm from the ground), while for saplings with height > 2 m, we measured both basal diameter and d.b.h. (1.3 m). For individuals with multiple stems, all stems were measured.

ENVIRONMENTAL PARAMETERS

Prior to the establishment of the plantation, in June 2001, baseline soil bulk density, % carbon, % nitrogen, and pH were collected along a 15 m grid (offset by 0.5 m as to not disturb the soil where the trees would be planted; Abraham 2004). In 2005, 15 additional environmental variables with an emphasis on soil, topography and drainage were recorded (Appendix S1 in Supplementary Material). Because of variation in topography, environmental heterogeneity was characterized by dividing each plot into four approximately equal subplots (approximately $12 \times 12 \text{ m}$). In January 2005, Munsell soil charts were used to determine soil colour, for both wet and dry soils, at depths of both 10 and 50 cm, in the middle of each subplot. Munsell values were converted to numerical values, using the following formula for redness rating (RR):

$$\text{RR} = \frac{((10 \times H) \times C)}{V} \quad \text{eqn 1}$$

environment matrix and then with the two components of the diversity matrix: species identity and richness. Forward selection was used to rank the explanatory variables in their order of importance, reducing the size of the two explanatory matrices. The best explanatory variables were selected sequentially on the basis of maximum extra fit and the statistical significance of each selected variable was estimated with a Monte Carlo permutation test (999 permutations). When the effect of adding a variable was no longer significant ($P > 0.1$), no further variables were added.

The variation of the response matrices was partitioned using the *varpart* function of VEGAN 1.6–1.0 statistical package of R 2.2.1 (Oksanen *et al.* 2005). It is assumed that the sources of variation are linear combinations of factors: Environment = [a + d + f + g], Sp identity = [b + d + c + g], Sp richness = [c + e + f + g], Env. + Sp id = [a + b + d + e + f + g], Env. + Sp rich = [a + c + d + e + f + g], Sp rich + Sp id = [b + c + d + e + f + g] while total variation is All = [a + b + c + d + e + f + g] (after Borcard *et al.* 1992). Decomposition therefore proceeds by subtracting different factors to isolate each component (e.g. Environment controlled for Species identity and richness can be obtained by the following calculation: Environment alone [a] = All [a + b + c + d + e + f + g] – Sp rich + Sp id [b + c + d + e + f + g]). The outcome is a partitioning of the variance, similar to partial regression, allowing us to isolate the effect of a factor on the productivity and the mortality matrix. Partitioning yielded the following fractions: [a] variation explained by the environment alone (i.e. removing any variation due to species richness and identity), [b] variation explained by species identity alone (i.e. removing variation due to environment and species richness), [c] variation explained by species richness alone (i.e. removing variation due to environment and species identity). The significance of the [a], [b] and [c] fractions was tested using the partial redundancy analysis function of CANOCO; in which explanatory variables (environmental and diversity) can be turned into co-variables in order to adjust for their effect on the productivity data (ter Braak & Smilauer 1988).

Biodiversity modelling

We further examined the relative effect of environmental heterogeneity, biodiversity and spatial pattern on tree growth data in 2006. To do so, basal area ($\text{m}^2 \text{ha}^{-1}$) was estimated for all individual trees and scaled up at the subplot level by summing the data. The existence of a biodiversity effect was tested using two bootstrap models that separated the effects of individual tree growth and mortality on the subplots' basal area of mixtures compared to monocultures (details in Potvin & Gotelli 2008). For each model, 1000 null mixture assemblages were created by randomly sampling trees, with replacement, from monoculture plots. To enhance the generality of our modelling, trees were sampled without considering species identity. Any difference between observed and simulated data therefore indicates that mixtures differ significantly from monocultures. A standardized effect size (SES), measuring the differences in standard deviations between observed and simulated basal area, was calculated as:

$$\frac{(\text{Observed Basal Area} - \text{Mean Simulated Basal Area})}{(\text{Standard Deviation of Simulated Basal Area})}$$

SES values were generated for a growth model and a mortality model. In the growth model, differences between the observed and simulated data would reflect differences in the growth of individual trees in mixtures vs. monocultures. Similarly, in the mortality model, differences between observed and simulated data would reflect differences in the mortality rates of trees in monoculture vs. mixture. The SESs generated by these two models were analysed by Student *t*-test

against a null value of 0 in the absence of biodiversity effect. Variation in SES was further analysed by an analysis of variance model (ANOVA) with Mixture (three or six-species), Plots nested within Mixture, and Subplots nested within Plots as the factors of interest, Mixture being treated as fixed effects. Unless specified otherwise, the statistical analyses were carried out using SYSTAT version 10.2 and the bootstrap models were written in S-Plus version 6.2.

Using the software application SAM (Spatial Analysis for Macroecology) version 1.1 (Rangel *et al.* 2006) we calculated Moran's I for tree growth and mortality SES values between all possible pairs of subplots, which were placed into 10 distance classes. Moran's I is a measure of the degree of pair-wise spatial autocorrelation in the response variable as a function of the distance between subplots. The distance classes are measured in units of the number of grid cells separating each pair of subplots (i.e. approximately 22 m). Significant levels of observed values of Moran's I were determined with 1000 bootstrap randomizations. We also used SAM to conduct a local analysis of Moran's I, which reveals the particular subplots that are contributing to non-randomness.

Finally, discriminant analyses, using the results of our bootstrap models, served to classify mixed-species subplots as over-yielding (SES > 2), under-yielding (SES < -2), or showing no differences (-2 < SES < 2) when compared with monocultures. Because of the differences in species composition, subplots with three- or six-species were analysed separately. The discriminant classification considered subplot elevation, soil cluster (defined by the hierarchical clustering) and position along the East–West (*X*) and North–South (*Y*) axes of the plantation as classification variables. Variables were centred and standardized prior to the analysis.

Results

ENVIRONMENTAL CHARACTERISTICS

The approximately 6 ha field in which the plantation was established encompassed a total elevation range (lowest to highest point) of 7–8 m (Fig. 1). The elevations of the subplots were variable (CV = 0.56) and most were coded, on a relative scale, as moderate to steep slope (Appendix S1). The direction of the slope was variable, with 48 subplots sloping in the western direction, and 33 in the eastern direction. These orientations correspond to the presence of a small ridge which runs North–South through the middle of the plantation, and drains towards the West and East (Fig. 1). The PCA biplot (Fig. 2) suggests that subplots can be grouped in three clusters based on environmental parameters. One group of subplots is characterized by high redness rating of surface soils, both wet and dry, and high soil bulk density. A second group of subplots is characterized by high redness ranking for deeper soils (50 cm), both wet and dry, while a third group of subplots are characterized by traits related to drainage. Soil pH was the most variable of the soil related traits. ANOVA revealed significant differences in pH within Subplots nested within Plots ($F_{41,41} = 1.78$, $P < 0.001$) and between Plots nested within Diversity ($F_{11,41} = 4.5$, $P < 0.01$) but not between Diversity levels. The pH recorded in the three-species plots was more basic than that of six-species and monoculture plots (Table 1). There were no significant differences among subplots in soil bulk density, soil %N, and %C. Three traits related to drainage

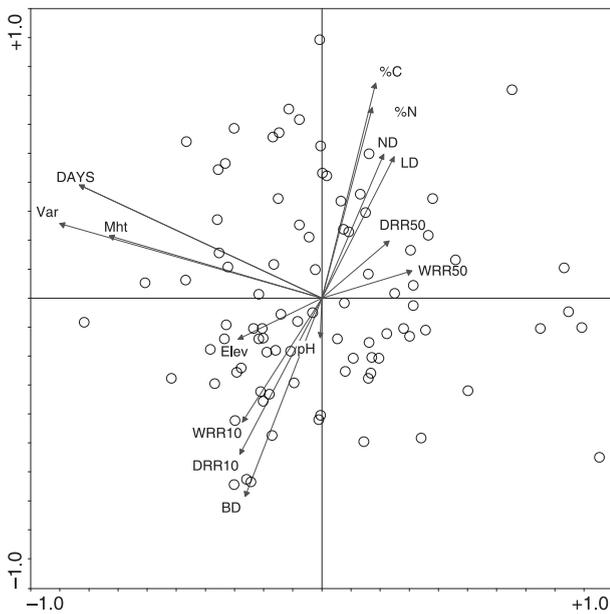


Fig. 2. Biplot diagram of the PCA of the environmental matrix. The biplot displays inter-sample relationship (distances between subplots). Due to multidimensionality, the environmental variables were standardized. Arrows refer to environmental variables and circles refer to the 88 subplots. Circles which are closer to each other are environmentally similar. Abbreviations are as follows: var: variance in height of the water table; Mht: Maximum height of the water table; days: number of days with the water table > 30 cm; Elev: subplot relative elevation; WRR10–WRR50: wet soil redness rating at 10 and 50 cm depth; DRR10–DRR50: dry soil redness rating at 10 and 50 cm depth; BD: soil bulk density; LD: total length of ditches; ND: number of ditches.

also show significant differences associated with diversity treatment ($F_{2,11} = 8.26$, $P = 0.01$, $F_{2,11} = 7.6$, $P < 0.01$ respectively for average height of the water table and number of days with water > 30 cm) or subplots ($F_{41,41} = 1.93$, $P < 0.05$ for maximum height of the water table). Finally, the majority of subplots have few or no ditches: 59 of the 88 subplots had no ditches but eight subplots had more than five ditches. Table 1 suggests

that in spite of their random positioning, the six-species plots were established, by chance, in parts of the field with the poorest drainage.

Hierarchical clustering of soil and drainage variables revealed the presence of nine different soil clusters in the plantation. Two of these soil clusters (code 2–3) contain 77% of the subplots (Fig. 3). These two clusters are characterized by intermediate soil bulk density and drainage. Some other soil clusters were clearly separated: two subplots with a more basic soil with pH 6.66 and 6.75 (code 9, subplots T54 and T53); four subplots with elevated soil bulk density ranging 0.803–0.708 g cm⁻³ (code 8, subplots A61, A62, A63, and TR12), two subplots with high soil N and C (code 6, subplots LS13, HC11), two other ones with high C (code 7, subplots A14, T21), two plots with the poorest drainage (code 4, subplots CO11, LS24) and a last cluster of five subplots with low water table in the wet season (code 1, HC23, CA14, LS23, A13, TR14). According to our clustering, the three-species subplots were established, by chance, over four different soil clusters, whereas six-species subplots were established over eight soil clusters representing the extremes of the site (Fig. 3).

PARTITIONING THE ENVIRONMENTAL AND DIVERSITY EFFECTS

The ordination of the 2005 productivity matrix by the environment matrix resulted in the forward selection of 11 environmental variables (Fig. 4a). The overall test of significance illustrates a significant canonical relationship between the environmental variable and plot/tree productivity ($P < 0.01$ after 999 permutations; Table 2). Percent slope had the highest loading on the first canonical axis ($r = 0.57$) and was most closely related to high productivity as estimated by average tree height and tree biomass per subplot (Fig. 4a). Subplots with steeper slopes apparently sustained bigger trees, possibly due to better drainage: the centroid for absence of ditches had the second largest correlation with canonical axis 1 ($r = 0.47$) and subplot relative elevation was positively correlated to average tree height (Fig. 4a).

Table 2. A. Sources of variation and B. Variance partitioning results from the redundancy analyses of the 2005 productivity matrix (Supplementary Material Appendix S2). Due to the bias associated with R squared values, adjusted R squared values were computed as, Adj. R^2 adjusted = $1 - ((1 - R^2) \times (\text{total degrees of freedom}/\text{residual degrees of freedom}))$

Sources of variation	DF	R^2	Adj. R^2	% of the explained variation	F -ratio	P -value
A. Sources of variation						
Environment	11	0.536	0.469		7.987	0.001
Species identity	3	0.153	0.123		8.019	0.001
Species richness	3	0.226	0.198		8.168	0.001
Env. + Sp identity	14	0.615	0.542			
Env. + Sp richness	14	0.57	0.488			
Sp rich + Sp identity	6	0.42	0.377			
All	17	0.663	0.581			
B. Decomposed variation						
Environment controlled for Sp identity and richness	11		0.204	35.11	4.304	0.001
Species identity controlled for Env. and Sp richness	3		0.093	16.01	5.943	0.001
Species richness controlled for Env. and Sp identity	3		0.039	6.71	2.931	0.005
Unexplained			0.419			

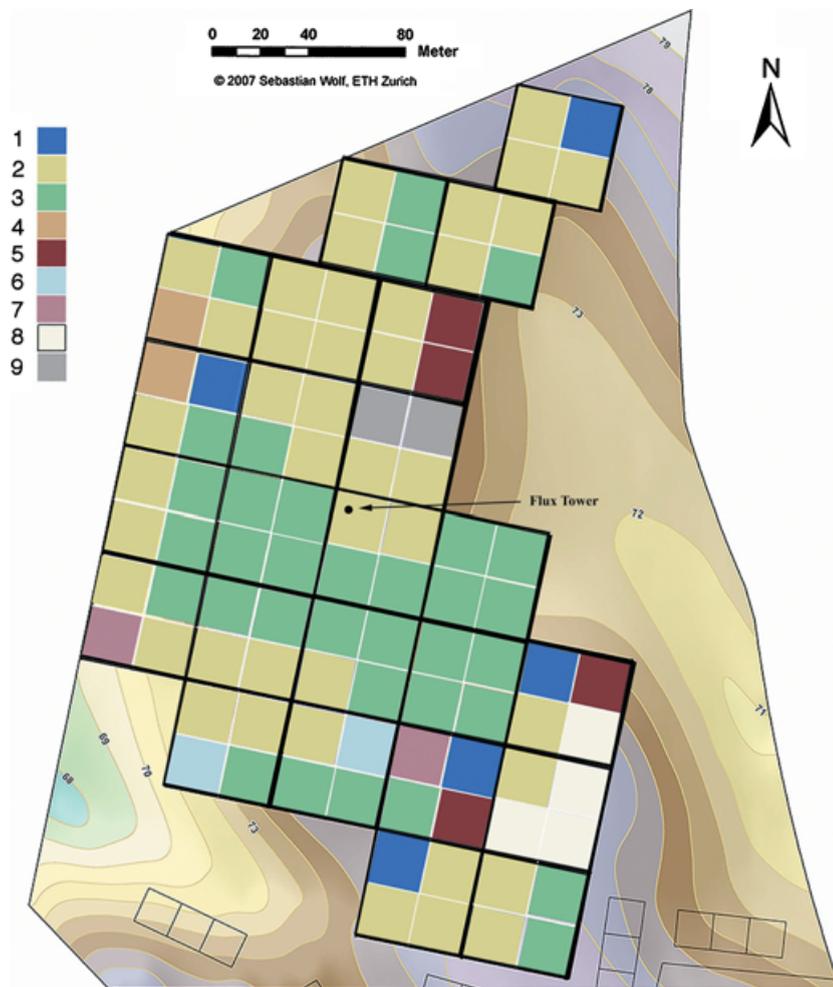


Fig. 3. Mapping of the different soil clusters for the 96 different subplots of the Sardinilla plantation. Each soil cluster identified by a principal components analysis is represented by a different colour (coded 1–9: 1 – low water table; 2 and 3 – average for all soil characteristics; 4 – high water table; 5 – different isolated soil types; 6 – high %C and %N; 7 – high %C; 8 – high soil bulk density and 9 – high soil pH. The base map is a courtesy of Sebastian Wolf, ETH Zurich.

The ordination of the 2005 productivity matrix by the diversity matrix also revealed a significant canonical relationship ($P < 0.01$ after 999 permutations; Table 2). Of the seven explanatory variables retained in the analysis, the presence of *C. odorata* most highly correlated with the ordination of sites along the first axis ($r = 0.383$), while the presence of *T. rosea* was most highly correlated with the second axis ($r = -0.363$; Fig. 4b). This ordination biplot suggests that the most productive plots were those containing *C. odorata*, and the least productive are those with *A. excelsum*. Furthermore, the three-species plots were the most productive, as shown by their association with height and biomass (Fig. 4b).

We decomposed the variation of the productivity matrix. The adjusted R^2 showed that the different sources of variation collectively explained 58.1% of the productivity data (Table 2a). The effect of environment alone accounted for one-third of this explained variation (Table 2b). Taken together, the effect of species identity and richness explained another 23% with species identity explaining more variation than species richness (Table 2a). The variation explained by these three fractions was statistically significant.

The variation in the total and annual mortality was found to have a significant canonical relationship with both the

environment and diversity matrices ($P > 0.001$) (Table 2a). The ordinations of the mortality matrix resulted in the forward selection of five environmental and seven diversity variables (Fig. 4c,d). The length of ditches (LD) and moderate herbaceous density (HI2) were correlated with the first axis ($r = 0.503$, $r = -0.382$, respectively). Longer ditches and greater water logging were associated with increased mortality (Fig. 4c). Furthermore, subplots with little or no herbaceous growth have higher percent biomass and experienced the lowest rates of mortality. It is important here to note the direction of cause and effect: greater tree growth results in less light reaching the understorey, and thus less herbaceous growth.

In the ordination of the mortality matrix, the presence of monocultures was positively correlated with the first axis ($r = 0.444$), and it can be seen from the ordination diagram that monocultures experienced lower rates of mortality (Fig. 4d). *Cordia alliodora* and *A. excelsum* mortality were negatively correlated to the first axis ($r = -0.313$, $r = -0.427$, respectively). Mortality for *C. alliodora* was the highest of all species but *A. excelsum* also suffered significant mortality. We were not able to identify specific cause of mortality in *Anacardium*. The seedlings established well, but showed relatively high mortality rates through time.

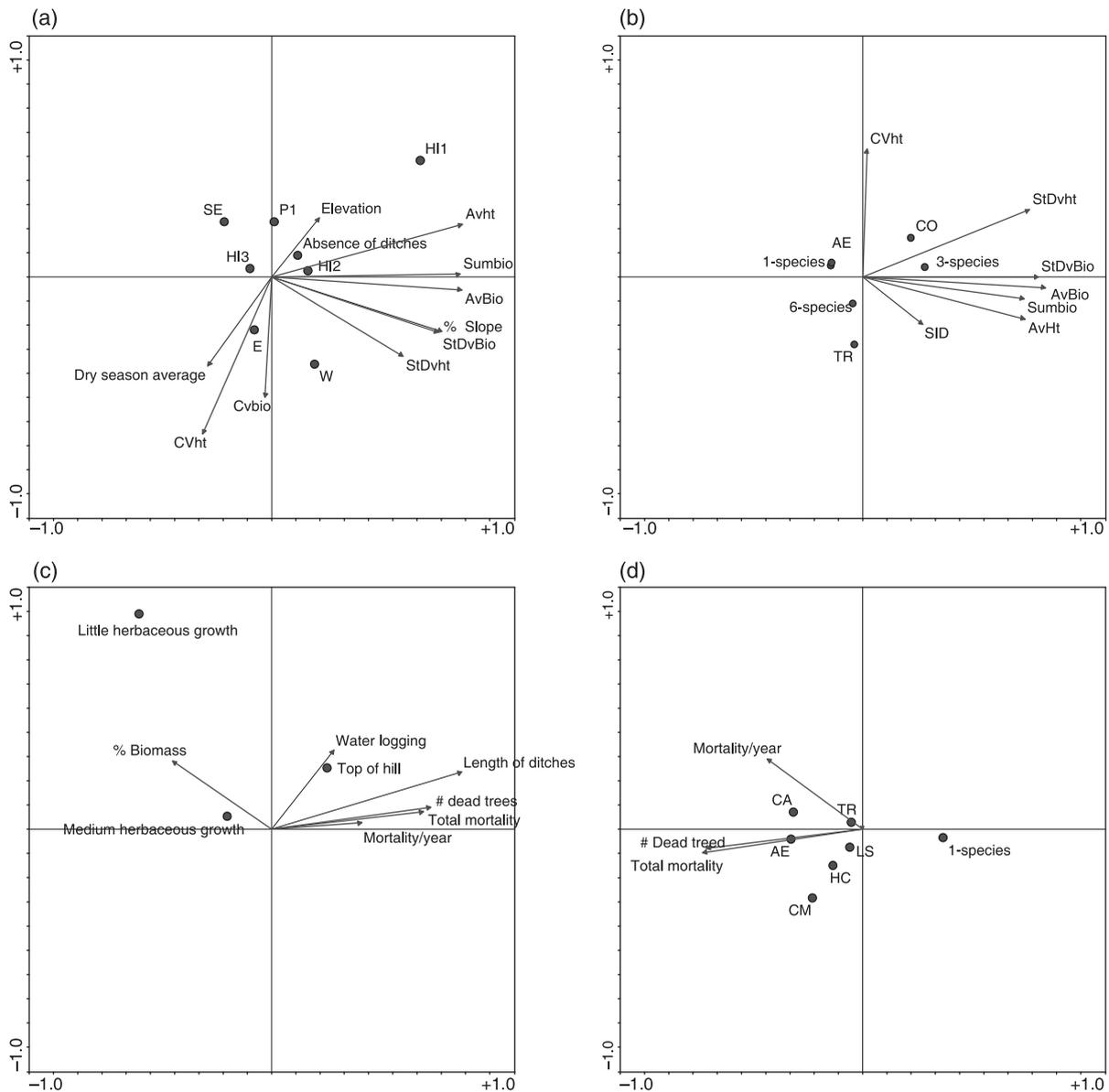


Fig. 4. Correlation biplots from RDAs of 2005 (a) productivity matrix constrained by environmental and (b) diversity variables and for the (c) mortality constrained by environmental and (d) diversity variables. The environmental variables pertained to the density of the herbaceous layer (HI2-open, HI2-moderate, HI3-dense), water logging (e.g. dry season average, absence of ditches), soil characteristics (e.g. %C) and topography (e.g. facing: West, E-East, SE-South East, position in the landscape: P1 – top of the ridge) (See Appendix S1 for further variable definitions). The diversity variables are monocultures, three- and six-species plots as well as Simpson's diversity index (SDI) and species presence as abbreviated in Fig. 1. The productivity variables pertain to either tree or plot biomass or height (See Supplementary Material Appendix S2). Response and explanatory variables are represented as arrows and nominal explanatory variables are represented by circles (lying at the centroids of the sites where they occur). Angles between arrows indicate their correlation, and the projection at right angle of a centroid on either species vectors or canonical axes approximates the value of the variable on that axis. The longer the arrow, the more important the variable is.

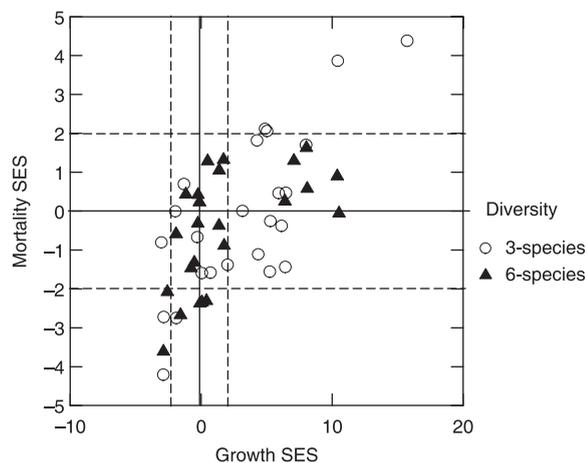
In this experiment, the environment and diversity matrices collectively explained 50% of the variation in tree mortality (Table 3a), but environment alone explained nearly twice as much variation (57%) as species identity and richness together (30%). While species identity had greater explanatory power than species richness, species richness is a more important source of variation for the mortality matrix than for the productivity matrix (Table 3a). Partial RDAs of these three fractions were statistically significant.

BIODIVERSITY MODELLING

We developed simulation models explicitly accounting for growth and mortality of individual trees (Potvin & Gotelli 2008) to test for the presence of biodiversity effects and applied these simulations to the 2006 tree data. The models rely on SES to determine whether a subplot is over-, under-yielding or not responding to biodiversity. The SES of the two simulation models also showed large variation among subplots

Table 3. A. Sources of variation and B. Variance partitioning results from the redundancy analyses of the 2005 mortality matrix (Supplementary Material Appendix S2). Adj. R^2 as in Table 2

	d.f.	R^2	Adj. R^2	% of the explained variation	F -ratio	P -value
A. Sources of Variation						
Environment	5	0.323	0.282		7.823	0.001
Species identity	6	0.217	0.159		3.737	0.001
Species richness	1	0.124	0.114		12.187	0.001
Env. + Sp identity	11	0.503	0.431			
Env. + Sp richness	6	0.453	0.412			
Sp rich + Sp identity	7	0.276	0.213			
All	12	0.566	0.496			
B. Decomposed variation						
Environment controlled for Sp identity and richness	5		0.284	57.25	10.015	0.001
Species identity controlled for Env. and Sp richness	6		0.084	16.93	3.259	0.001
Species richness controlled for Env. and Sp identity	1		0.065	13.10	10.88	0.001
Unexplained			0.503			

**Fig. 5.** Scatterplot of the growth and mortality standardized effect size (SES), measuring the differences in standard deviations between observed and simulated basal area, from the individual 48 mixed-species subplots. Subplots are over-yielding (SES > 2), under-yielding (SES < -2), or showing no differences (-2 < SES < 2) when compared with monocultures. The zero line indicates null effect of biodiversity.

(Fig. 5). In the plantation, 63% of the three-species subplots and 25% of the six-species subplots show significant over-yielding for growth vis-à-vis monocultures (i.e. SES > 2), while 13% of the three-species subplots and 4% of the six-species subplots showed significant under-yielding (i.e. SES < -2) (Fig. 5). Although we observed no significant over-yielding for mortality in the six-species subplots, 17% of the three-species subplots showed an effect. For three-species subplots, mean SES was 3.33, while it was 1.89 for the six-species subplots and t -test revealed significant biodiversity effect for both the three-species ($t_{23} = 3.49$, $P < 0.01$) and six-species ($t_{23} = 2.27$, $P < 0.05$) subplots when compared with a null value of 0. The mortality simulations were never significantly different from zero.

Despite the identical initial composition of six-species subplots, their SESs for the growth simulation ranged from 10.52 to -2.87 (Fig. 5). We hypothesized that such variation in SES across the plantation was caused by environmental hetero-

geneity. The nested ANOVA showed that, although the Mixture effect was never significant, the Plot effect was statistically significant for both simulation models ($F_{10,36} = 2.72$, $P < 0.05$ and $F_{10,36} = 3.98$, $P < 0.001$ respectively for the growth and the mortality models).

We used Moran's I to measure spatial autocorrelation of growth and mortality responses across the entire plantation. In a previous analysis (Potvin & Gotelli 2008), we found that Moran's I calculated at the plot level did not deviate from randomness for any distance class ($P > 0.05$). However, in this current analysis, we did detect spatial autocorrelation at the subplot level. For the growth data, there was a small amount of spatial autocorrelation. Moran's I was significantly positive for the smallest distance (i.e. adjacent subplots 22 m apart from another; $I = 0.289$, $P < 0.01$), but significantly negative for distance-class eight (distance of approximately 176 m; $I = -0.283$, $P < 0.001$). The remaining eight distance-classes did not deviate from randomness. The analysis of local Moran's I revealed a string of four adjacent subplots (and a 5th nearby subplot) that were contributing to non-randomness. The spatial location of these subplots corresponds to the location of the ridge of high productivity that runs through the centre of the plot (Fig. 1). For the mortality data, only the second distance-class showed a marginally significant pattern of negative spatial autocorrelation ($I = -0.161$, $P < 0.05$); the remaining nine distance-classes were non-significant. Three subplots contributed to this non-randomness, but these subplots were scattered throughout the plantation and did not exhibit any obvious spatial pattern or association with environmental variables.

Discriminant analyses were used to classify subplots based on the output of our bootstrap models and shed light on the interaction between diversity and environment. Growth and mortality SESs were assigned to three groups: over-yielding, under-yielding or non-significant. The predictive power of the analyses ranged between 75% and 58%. For the three-species subplots, position along the North–South axis of the plantation (Y) was the variable with the highest loading on the first canonical axis for growth, and on the second axis for mortality (Table 4). The group score for the over-yielding

Table 4. Standardized classification for the discrimination of growth and mortality SES between no effect, over-yielding or under-yielding compared with monocultures. Soil cluster were determined by hierarchical clustering analysis and *X* and *Y* represent the coordinates of the plots as shown in Fig. 1

	Traits	Axis 1	Axis 2
Diversity: 6 Growth SES	Elevation	0.426	0.994
	Soil cluster	-0.348	-0.388
	X	1.361	0.636
	Y	-0.146	-0.926
Diversity: 3 Growth SES	Elevation	0.774	1.058
	Y	-1.441	0.073
	Soil cluster	-0.739	0.570
Diversity: 6 Mortality SES	Elevation	1.129	-0.236
	Soil cluster	0.389	0.708
Diversity: 3 Mortality SES	Elevation	1.153	0.373
	Y	-0.293	-1.342

subplots (-0.772, 0.018) indicated that these plots were found on the Southern part of the plantation (i.e. where the *Y* coordinate has a high value; Fig. 1). For the six-species subplot, position along the East–West axis in the plantation had the highest loading on the first canonical axis classifying growth SES (Table 4). In this case over-yielding subplots were positioned toward the west (Fig. 1). Whereas position is playing an important role to classify the growth SES of subplots of both diversity levels, elevation is the key loading factor in the case of mortality (Table 4).

Discussion

Traditionally, plant ecologists have recognized that environmental conditions are key to determine species distribution (e.g. Whittaker 1956). For example, edaphic factors were recognized, early on, as important in the maintenance of local diversity in tropical forests (Ashton 1969; Gentry 1981). While recent theoretical developments have de-emphasized the importance of such deterministic factors (Hubbell 2001), Harms *et al.* (2001) examined the role of habitat in explaining species distribution in the permanent 50-ha plot of BCI. They reported that several species showed clear association with habitats and that a small swamp was the most distinct habitat. John *et al.* (2007) analysed the variation in soil nutrients in three neotropical forest plots (La Planada, Colombia; Yasuni, Ecuador and BCI, Panama) and concluded that the distribution of 40% of the species showed affinities with soil nutrients.

In Sardinilla, both the spatial statistics and the discriminant analysis suggest that variation in topography and elevation led to non-random responses to biodiversity levels. Several soil characteristics measured prior to tree establishment (soil bulk density, soil pH, nitrogen and carbon content) showed little spatial variability while geostatistical analyses revealed evidence of soil compaction and of homogenization of soil properties (Abraham 2004). Yet, soil colour was a highly variable parameter, changing according to the topography and the soil moisture regime. Soils of a reddish colour were found in the highest lying subplots, while the low lying areas were

characterized more by yellowish and grey horizons. Yellowing can be a characteristic of poorly drained soils (Fritsch *et al.* 2005), so subplots in low lying areas may be expected to have these characteristic mottled soils. Spatial pattern underlying the SES used to quantify the effect of biodiversity on tree growth and mortality suggests that the small ridge provided the best microhabitat for tree growth, possibly by reducing water logging.

In spite of the fact that a controlled field experiment was established in an initially 'homogeneous' site, small-scale spatial heterogeneity clearly had an impact on productivity. Classical niche theory would suggest that variation in productivity is mediated by species-specific responses to small-scale spatial heterogeneity within the plantation. Abundant research has demonstrated that tree species differ in the ways in which they acquire, store, and recycle nutrients (Cuevas & Lugo 1998; Forrester *et al.* 2006). Species-specific traits, such as the ability to fix nitrogen, can have significant influences on ecological processes (Tilman 1999). In Sardinilla, across all of the diversity treatments, *C. odorata* was the species most associated with high productivity, thus reiterating the importance of species identity. *Cedrela* is a preferred native timber species because of its straight bole and reduced biomass allocation to branches (Dutilleul and Potvin, unpubl. data). Conversely, *A. excelsum*, the species associated with lowest productivity, allocates most biomass to branches, suggesting that intrinsic species characteristics such as architecture are important determinants of productivity.

An extensive literature review examining the link between ecosystem function and biodiversity (Hooper *et al.* 2005) revealed that ecosystem properties were apparently more influenced by abiotic conditions than by species richness, a conclusion corroborated by our study. Indeed, the multivariate analysis that we conducted to partition variation in traits related to tree height and biomass allows, for the first time, a hierarchical analysis of different sources of variation acting together in a biodiversity plantation (see Schmid *et al.* 2002). We found that the explanatory power of the environment matrix was higher than that of the diversity matrix for both productivity and mortality. Environmental heterogeneity explains approximately twice as much variation in productivity as the diversity matrix. Nevertheless, we were able to attribute 23% of the variation in growth and 30% of the variation in mortality to components of diversity (species identity and richness together).

The additive partitioning method developed by Loreau & Hector (2001) revealed a significant positive complementarity effect for plot basal area and a significant negative effect of selection. These opposing forces resulted in a net non-significant biodiversity effect (M. Sarlo, C. Healy & C. Potvin, unpubl. data). This result is consistent with the present finding that both species identity and richness affect productivity. In a recent attempt to reconcile historical and contemporary perspectives on the diversity-productivity debate, Gross & Cardinale (2007) suggested that selection would be the driving force in communities where resource supply did not allow coexistence. Conversely, they argued that complementarity would occur when resource

supply allows species coexistence. Chesson *et al.* (2001), on the other hand, proposed that heterogeneous systems function as the collection of environmental patches with independent optima. Under their model, each environmental patch would evolve and eventually would be dominated by a different, best adapted species (the 'selection effect'). Across the entire landscape, ecosystem function should therefore not be affected by environmental heterogeneity. In our experimental plantation, the identity and position of individual trees were assigned rather than being the result of natural processes. The Chesson *et al.* (2001) model is therefore not directly applicable. However, our partitioning of variation with RDAs suggest that the 'selection effect' may indeed be the mechanism through which biodiversity has the largest positive impact on ecosystem function since the species identity matrix had a greater explanatory power than the species richness one.

According to Fridley (2002) and Vilà *et al.* (2005), diversity effects in BEF experiments can be hidden by differences in resource availability. Environmental conditions can also influence complementarity between species, suggesting that the diversity effect is dependent upon its interaction with the environment (Hooper *et al.* 2005; Potvin *et al.* 2006). The interaction between species richness and the environment was illustrated experimentally by Fridley (2003), who manipulated plant species identity and richness at different levels of soil fertility and light availability. His results indicated that the over-yielding of mixtures was dependent on the environment, whereby an increase in soil fertility and sunlight translated to an increase in productivity. Another experiment conducted by Boyden *et al.* (2005) showed that in mixtures of *Eucalyptus saligna* and *Falcataria sp.* (a nitrogen-fixer), growth was dependent upon the soil nutrient supply: species were only found to be more productive in mixtures when soils had high nitrogen levels. In our study, environmental heterogeneity did not hide the biodiversity effect but apparently amplified it since half of the three-species plots are positioned on the ridge explaining why they were more productive than the six-species plots.

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Supplementary material

The following supplemental material is available for this article:

Appendix S1 Description of environmental variables belonging to the environmental matrix.

Appendix S2 Entries in the (a) productivity, (b) mortality and (c) diversity matrices.

This material is available as part of the online article from:

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