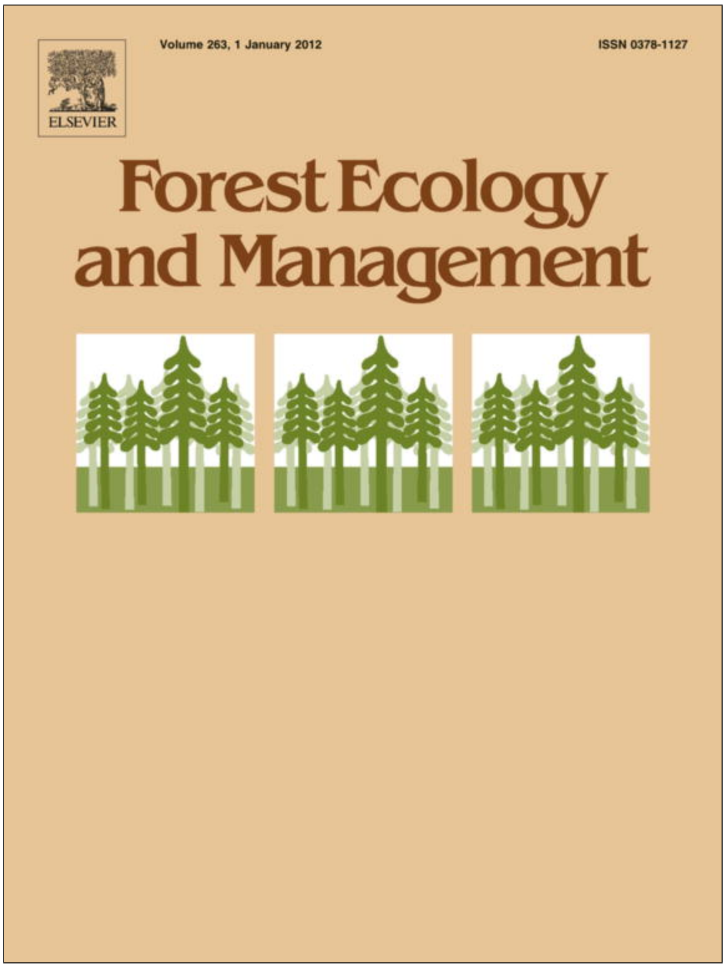
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Biodiversity–productivity relationships in small-scale mixed-species plantations using native species in Leyte province, Philippines

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ABSTRACT

In this study, we investigate the relationship between tree species diversity and production in 18 mixed-species plantations established under the Rainforestation Farming system in Leyte province, the Philippines. The aim was to quantify productivity in the mixed-species plantations in comparison to the monocultures, and identify key drivers of productivity including environmental conditions, stand structural characteristics and surrogate measures of biodiversity, i.e. species richness, Shannon's diversity index and functional groups. We found that monocultures had a much higher productivity than mixtures of the same and other species. In the mixtures, biodiversity and productivity did not have a simple relationship. Instead the proportion of exotic and native species, and the proportion of fast-growing species had a marginally significant positive effect on stand productivity, but no significant relationship was found with species richness or Shannon's diversity. Instead stand structural characteristics such as density and age were the strongest drivers of increased productivity. Production levels within the mixed-species plantations varied significantly between sites. Overall, we found that the productivity of mixed species plantations was driven more by the characteristics of species present and stand structural characteristics then by simply the number and abundance of species, which suggests management practices are key for balancing multiple objectives to meet sustainable development needs.

1. Introduction

Reforestation strategies to meet multiple objectives for sustainable development are urgently needed in much of the world's subtropical and tropical zones, with deforestation rates estimated at 13 million ha per year (FAO, 2006). Forest plantations constitute an estimated 4% of forest area, classified either as productive or protective plantations. Productive forest plantations (for wood and fibre) account for 78% of these, and protective plantations (for conservation of soil and water) account for 22% (FAO, 2006). Monoculture plantations have been used extensively in the tropics to reforest large areas of cleared and degraded land, and to meet demands for timber and income generation for local communities. Mixed species plantations have the potential of satisfying multiple goals (Díaz et al., 2009), but are perceived to be more difficult to implement, with unsubstantiated concerns that multi-species plantations may not be viable economically because of a loss of productivity (Wormald, 1992).

In recent years, numerous experiments have explored the relationship between primary plant productivity and increasing plant species or functional richness (Balvanera and Aguirre, 2006; Erskine et al., 2006; Forrester et al., 2005, 2006, 2004; Lugo, 1992; Naeem et al., 1994, 1995; Symstad et al., 2003; Tilman and Downing, 1994; Tilman et al., 1997a,b, 2001). Despite this extensive research, a generalised relationship between biodiversity and productivity has not been found. In a review of more than 200 studies investigating the relationship between species richness and productivity, Waide et al. (1999) found 30% showed a unimodal relationship, 26% positive linear, 12% negative linear, and 32% showed no significant relationship. Similarly, a recent analysis of 48 herbaceous dominated communities from five continents, found no consistent relationship between productivity and species richness at the local, regional or global-scale (Adler et al., 2011).

Two hypotheses have been proposed to explain this result – niche complementarity and sampling effect (Thompson et al., 2009). The complementarity hypothesis proposes that species-rich communities are able to more efficiently access and utilise limiting resources because they contain species with a diverse array of ecological attributes. Species are thought to complement each other allowing optimal resource use and a consequence is increased productivity (Cardinale et al., 2007; Hector, 1998; Loreau, 1998; Tilman, 1997; Tilman et al., 1997a). The sampling effect hypothesis posits that species rich communities are more productive because they have a higher probability of containing at least one species that is particularly efficient in using resources and converting these

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resources into biomass (Aarssen, 1997; Huston, 1980, 1997; Tilman et al., 1997a).

Reforesting degraded sites with mixed species plantations has been postulated as beneficial for increasing productivity and thus also providing carbon sequestration benefits (Díaz et al., 2009). Both the complementarity and sampling effect hypotheses suggests that mixed-species plantations have the potential to be more productive; although results have again been mixed. Several studies found a positive relationship between biodiversity and productivity in forests (Caspersen and Pacala, 2001; Erskine et al., 2006; Troumbis and Memtsas, 2000; Vilà et al., 2007); while other studies have found evidence of the sampling effect because the traits of certain species, generally dominants, were found to drive the relationship between biodiversity and productivity (Firn et al., 2007; Huston, 1980; Potvin et al., 2011; Redondo-brenes, 2007; Valverde-Barrantes, 2007; Wardle et al., 1997).

Given that a simple generalizable relationship between biodiversity and productivity has not been found, recent studies have taken a more complicated approach by incorporating abiotic factors into the relationship, e.g. 'Multivariate Productivity–Diversity' hypothesis by Cardinale et al. (2009). Abiotic factors (aspect, slope, and elevation) are known to influence species diversity, productivity and nutrient cycling at a site (Abrams, 1995; Liang et al., 2007; Mittelbach et al., 2001; Roise and Betters, 1981; Stage, 1976; Stage and Salas, 2007; Tilman and Downing, 1994; Waide et al., 1999). Hooper et al. (2005) found ecosystem properties were more influenced by abiotic conditions than by species richness. A recent study of more than 12,000 forests found a positive relationship between biodiversity and productivity in the boreal forests of Eastern Canada when climate (i.e. mean temperature) and environmental conditions (i.e. soil organic layer) were analysed with structural equation models (Paquette and Messier, 2011).

Despite these conflicting results many smallholders in the tropics grow trees in mixtures on their farms. They do so to diversify the variety of goods and services produced and to reduce risk (Lamb, 2011) and as such, there are many measures by which success of reforestation in the tropics can be measured (Le et al., 2011; Vanclay, 1989). Here, we investigate the relationship between tree species diversity, productivity (as measured by basal area growth) and abiotic factors of small-scale mixed-species plantations in Leyte province, the Philippines. In 1992, the Rainforestation Farming system established 28 small-scale mixed species plantations in local communities and on private properties in Leyte province (Milan, 1997a,b; Milan et al., 2004). The main objectives of the Rainforestation Farming were to grow mixed-species plantations to meet social, economic and environmental needs (Schulte, 1998, 2002). Approximately 100 endemic pioneer and Dipterocarp species, fruit trees and a limited number of exotic timber species were used to create small-scale plantations with the average area of about 1 ha (Margraf and Milan, 1997). We aimed to identify which environmental and biodiversity factors best explains variation in productivity at the Rainforestation sites. To achieve this, we examined correlations between productivity and species richness, species evenness, exotic/native tree species richness, and fast/slow growing tree species richness. We then use this information to make general recommendations for the design and establishment of future mixed-plantations.

2. Methods

2.1. Study area

Leyte is the eighth largest island in the Philippines and is situated in the middle of the Philippines archipelago and covers about 800,000 ha. It lies between 124°17′ and 125°18′ east longitude and between 9°55′ and 10°48′ north latitude (Milan, 1997a,b). Leyte island is characterised by the Leyte cordillera, which is a part of the Philippines fault line that runs from north to south (Kolb, 2003; Langenberger, 2000) that includes two provinces Leyte and Sounthern Leyte. The present climate of Leyte Province is characterised as a humid monsoon climate. Due to the presence of the high central mountain range, the climate in the eastern part of the island differs to that of the western part. The rainfall distribution generally shows a more pronounced maximum rain period of up to about 500 mm per month on the eastern side of Leyte compared to the western side with only about 300 mm per month. The annual precipitation level is up to 4000 mm in the mountainous areas of the island of Leyte. Although there is no pronounced dry season, the region experiences its lowest rainfall during the months of March, April and May (Jahn and Asio, 2001). The highest average rainfall occurs in December and the lowest in May. Dry periods of several months duration with rainfall of less than 100 mm, e.g. during the 'El Nino' of 1993, can occur. The average rainfall for the years 1980–2000 was 2686 mm with an annual variation of between 1775 in 1987 and 3697 mm in 1999 (Kolb, 2003). The average annual temperature at sea level is 27.5 °C and ranges from 26.3 to 28.7 °C. The difference between day and night temperatures is only about 5 °C around the mean, and the coldest and warmest months differ by only 2 °C. The relative humidity is always high and the average monthly level for the years 1980–2000 ranged from 75.1% in March to 80.1% in October (Kolb, 2003).

2.2. Data collection

Data were collected from 18 mixed-species plantations established under the Rainforestation Farming system. It was not possible to sample from all 28 plantations because several plantations had been detrimentally affected by fire, harvesting, clearing for other agricultural activities; because access was not granted by the land owners; or did not meet minimum requirements for measurements (e.g. trees greater than 5 cm dbh). The measurement was undertaken from February to March 2006 when the trees were aged between 6 and 11 years. Measurements of trees and site properties were collected from 82 randomly located circular plots with a radius of 5 m (78 m^2 area) in the centre or along the edges of the plantations. Each plot chosen contained at least seven trees greater than 5 cm in diameter. The number of plots designed in each site ranged from 1 to 12 plots per farm depending on the size of farm. All plots were established and trees in plots were permanently marked in the field. In each plot, all trees were counted and identified to the species level. With the assistance of local forestry researchers and drawing upon descriptions in the literature, including those from the Rainforestation Farming project, each species was classified into functional groups of species provenance (native or exotic species) and categorised generally according to expected rates of growth (fast, medium or slow growing species). Biodiversity factors including species richness, Shannon's index, exotic tree ratio and fast growing tree ratio were calculated here (Table 1). Basal area is highly correlated with tree volume and biomass and has been used as the index of plantation productivity in many studies (Erskine et al., 2006; Healy et al., 2008; Satoo and Madgwick, 1982). Therefore, measurements of stand basal area were derived from diameter over bark at breast height (1.3 m dbh) for all individual trees and scaled-up at the plot level by summing the data, as a surrogate measure for stand productivity (Avery and Burkhart, 1983).

Monocultures of exotic species also included in the mixed species plantations (i.e. *Swietenia macrophylla*, *Gmelina arborea* and *Samanea saman*) that were planted in Leyte province, aged 6–10 years were compared with the mixtures in terms of stand basal area (BA) and mean annual increment of stand basal area

Table 1
Stand summary for modelling (means derived from mixed species plots used in analysis).

Variables	Description	Unit	Range	Mean ± SE
Dependent variables (Productivity variable)				
BA	Stand basal area	$m^2\ ha^{-1}$	3.90–75.48	23.00 ± 1.58
MAIBA	Mean annual increment of stand basal area	$m^2\ ha^{-1}\ year^{-1}$	0.39–7.88	2.56 ± 0.18
Fixed variables				
– Stand biodiversity variables				
S	Species richness – number of species		2–12	4.7 ± 0.2
H	Shannon's diversity index		0.35–2.27	1.30 ± 0.05
E	Exotic tree ratio in total trees		0.00–1.00	0.33 ± 0.04
F	Fast growing tree ratio in total trees		0.00–1.00	0.45 ± 0.03
– Site characteristic variables				
A	Stand age	Year	6–11	9.2 ± 0.1
D	Stand density	Trees ha^{-1}	764–2674	1393 ± 5
TP	Plot topographic position (measured on a eight-point scale, 1 = crest/plateau and 8 = closed depth (valley bottom))		2–6	4.34 ± 0.17
SL	Plot slope (measured by looking down-slope on a six-point scale, 1 = level 0–3° and 6 = precipitous >45°)		1–6	2.33 ± 0.16
GR	Plot ground cover (measured by frequency of bare soil, leaf litter total, grass, herb, and ferns)		3613–53,111	21,687 ± 1598

Table 2
Variables to describe site characteristics.

Variable	Description
Slope	Degree slope measured looking down-slope on a six-point scale: 1 = level 0–3°; 2 = gentle 4–8°; 3 = moderate 9–16°; 4 = steep 17–26°; 5 = very steep 27–45°; and 6 = precipitous >45°
Topographical position	Slope position on a eight-point scale: 1 = crest/plateau; 2 = upper slope; 3 = midslope; 4 = lower slope; 5 = simple slope; 6 = low flat; 7 = open depth and 8 = closed depth (valley bottom)
Ground cover	Frequency of bare soil, leaf litter total, grass, herb, and ferns described on a six-point scale: 1: <1%; 2: 1–5%; 3: 5–25%; 4: 25–50%; 5: 50–75%; and 6: >75%

(MAIBA). Site characteristics such as slope, topographical position and aspect were described at each plot to examine the relationship with the tree performance across sites (Table 2).

2.3. Statistical analyses

To examine the relationship between biodiversity and site characteristics on stand productivity, we first used linear regressions to test a simple correlative relationship and then developed linear mixed effect models (West et al., 2007) with SPSS 18.0 statistical software©. We modelled productivity as a function of either species richness, Shannon's diversity index, or functional groups (i.e. exotic tree ratio and fast growing tree ratio), and stand age, stand density, and several environmental factors (slope, topography position and aspect) with a nested random effect structure of site/plot. Maximum likelihood was used when comparing nested models to simplify fixed effects. We used diagnostic plots to check model assumptions; there was no evidence of correlation of observations within groups and we assumed that within group errors were normally distributed.

We tested two main hypotheses:

(a) *Simple linear relationship between biodiversity-productivity:* We hypothesised that biodiversity (measured as species richness or Shannon's diversity index or exotic tree ratio or fast-growing tree ratio) had a positive effect on plot productivity (measured as stand basal area or mean annual increment in basal area). The general model used was: $P_i = \beta_0 + \beta_1 B_i + \varepsilon_i$, where P_i is productivity and B_i is biodiversity surrogate measure within a plot i; β_0 and β_1 represent the fixed intercept and the fixed effect of the covariate B_i; and ε_i represents the residual associated with the observation on an individual plot i.

(b) *The biodiversity–productivity relationship varies depending on site characteristics:* We hypothesised that biodiversity only had a positive effect on productivity when other site characteristics were also considered (i.e. stand age, stand density and environmental factors). The general model used was:

$$P_{ij} = \beta_0 + \beta_1 B_{ij} + \beta_2 A_{ij} + \beta_3 D_{ij} + \beta_4 TP_{ij} + \beta_5 SL_{ij} + \beta_6 GR_{ij}(\text{fixed}) + u_j + \varepsilon_{ij}(\text{random})$$

where P = productivity and B = biodiversity. P_{ij} represents the value of the dependent variables for plot i nested within site j; β_0 to β_6 represent the fixed intercept and the fixed effects of variables (where B_{ij} = biodiversity, A_{ij} = age, D_{ij} = density, TP_{ij} = plot topographical position, SL_{ij} = plot slope, and GR_{ij} = plot ground cover); u_j is the random effect associated with the intercept for site j and ε_{ij} represents the residual associated with the observation on an individual plot i.

The best-fit and simplest models were found by removing explanatory variables one at a time from the complete model. The simpler models were then compared to the more complex

Table 3
Productivity of stands with different functional tree groups.

	Origin classification		Growing rate classification	
	Native tree stands (exotic ratio ⩽0.5)	Exotic tree stands (exotic ratio >0.5)	Slower-growing tree stands (fast growing ratio ⩽0.5)	Fast-growing tree stands (fast growing ratio 0.5)
Mean BA (m^2/ha)	19.5 ± 2.3	32.5 ± 17.6	20.3 ± 11.5	27.9 ± 17.4
Mean MAIBA (m^2/ha/year)	2.3 ± 1.5	3.3 ± 1.8	2.4 ± 1.5	2.9 ± 1.7
ANOVA test between groups of stands	For BA: F = 15.676, sig. = 0.000 For MAIBA: F = 6.900, sig. = 0.010		For BA: F = 5.578, sig. = 0.021 For MAIBA: F = 1.656, sig. = 0.202	

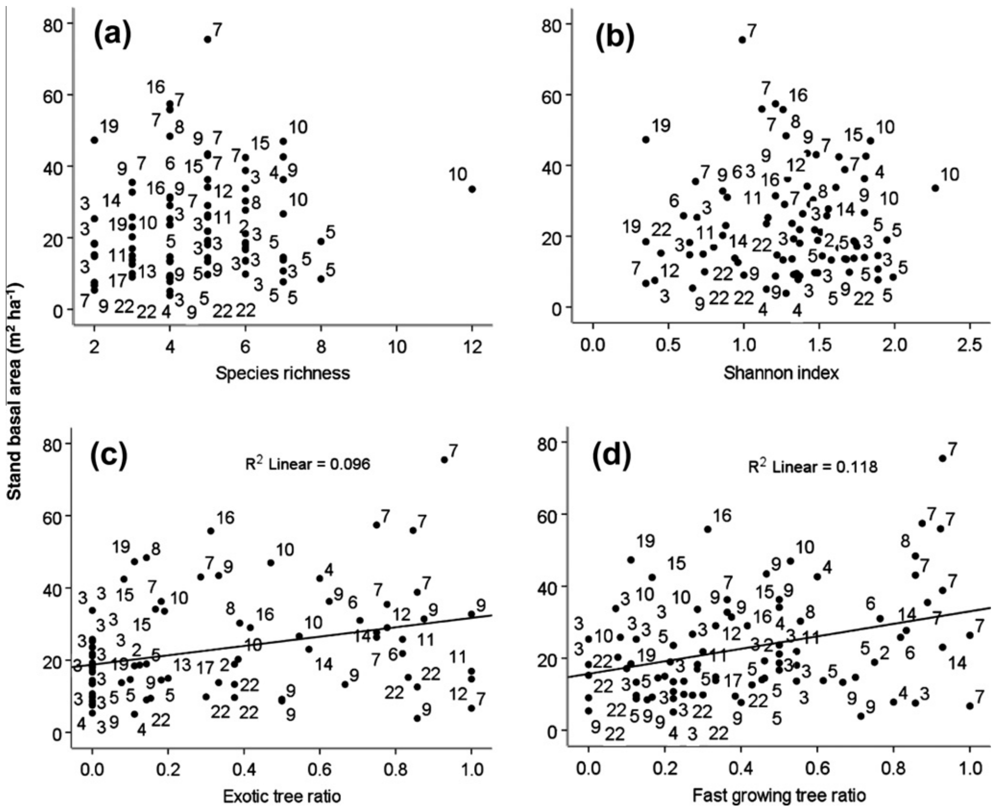

Fig. 1. The relationship between biodiversity indices of 5 m radius plots and productivity (stand basal area) in mixed species plantations in Leyte: (a) species richness ($p = 0.296$); (b) Shannon's index ($p = 0.814$); (c) exotic tree ratio ($p = 0.005$); and (d) fast growing tree ratio ($p = 0.002$). The numbers refer to the sites where the plots were located.

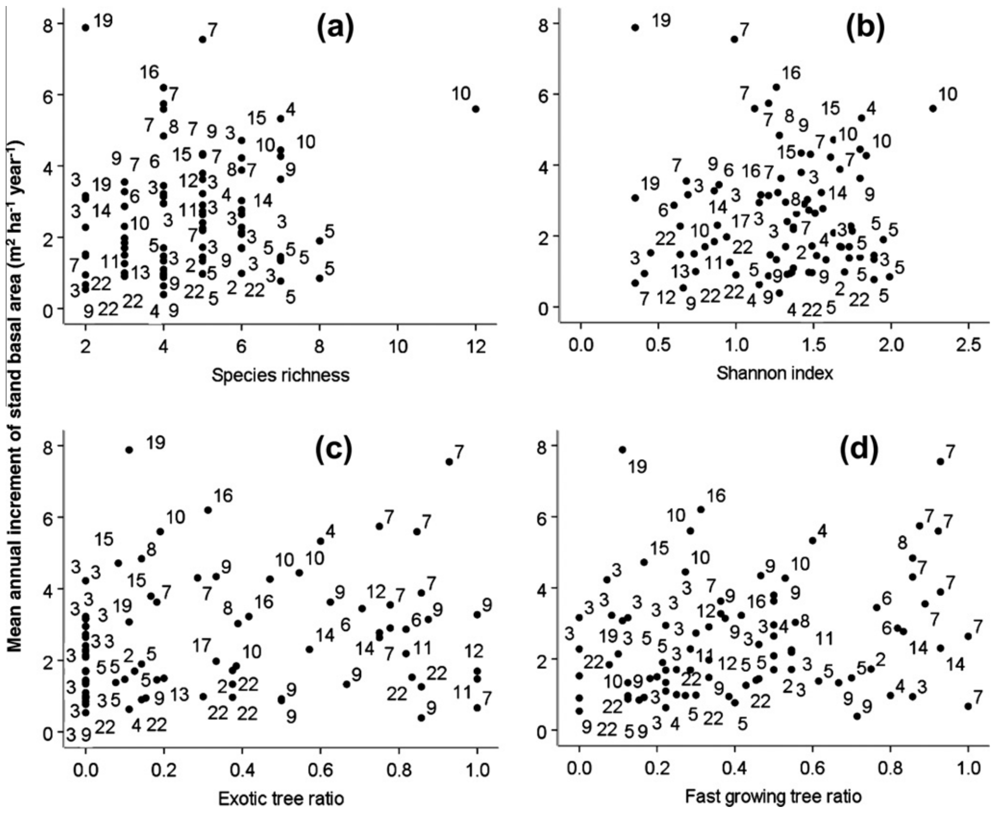

Fig. 2. The relationship between biodiversity indices and productivity (MAIBA – mean annual increment of stand basal area) in mixed species plantations in Leyte: (a) species richness ($p = 0.205$); (b) Shannon's index ($p = 0.901$); (c) exotic tree ratio ($p = 0.083$); and (d) fast-growing tree ratio ($p = 0.050$). The numbers refer to the sites where the plots were located.

Table 4
Linear regression models of the relationship between different biodiversity surrogate measures and plot productivity (S = species richness; H = Shannon's index; E = Exotic tree ratio; and F = Fast growing tree ratio).

Model	Variable	S	H	E	F	Estimate of biodiversity parameter	Sig. for biodiversity index
1	BA	√				0.943	0.296
2			√			0.867	0.814
3				√		12.942	**0.005**
4					√	14.372	**0.002**
5	MAIBA	√				0.129	0.205
6			√			0.052	0.901
7				√		0.909	0.083
8					√	0.928	0.116

Bold value indicates a significant relationship between a biodiversity surrogate measure and plot productivity.

models using likelihood ratio tests. We found similar results when we conducted model analyses using forward iterations, where we added one fixed effect variable at a time to a simpler model.

3. Results

3.1. Description of floristics

A total of 77 canopy species belonging to 32 families and 57 genera were recorded in the surveys of mixed species plantations, including 53 pioneer species, 13 fruit tree species, and 11 Dipterocarp species. Among the plots, the numbers of species ranged from 2 to 12, and the number of individual trees ranged from 7 to 21 for each plot. The number of trees per plot ranged between 7 and 14 trees per plot. A total of 20 exotic and 57 native tree species were found across plots. The exotic species comprised 26% of the total species and 33% of the total number of trees in plots. There were 33 fast-growing species found at plots accounting for 43% the total species and 45% of the total trees.

Both BA and MAIBA varied significantly depending on the ratio of exotic trees (Table 3). Similarly, there was a significant difference between stands with a higher abundance of slow growing than fast growing species when productivity was measured BA, but not in MAIBA. This result suggests stands with more fast-growing trees had a higher productivity than slower-growing tree stands, although growth rate did not differ significantly.

Comparisons of the productivity between mixtures and monocultures, showed monocultures were significantly higher than mixtures in terms of both BA and MAIBA $p < 0.001$. The monocultures achieved BA of 92.0 ± 12.1 m^2/ha and MAIBA of 10.9 ± 1.4 m^2/ha/year; whereas mixtures had BA of 23.0 ± 1.6 m^2/ha and MAIBA of 2.6 ± 0.2 m^2/ha/year.

3.2. Biodiversity–productivity relationship

We found no significant correlation between BA (plots) and species richness or Shannon's index (Fig. 1a and b); or between MAIBA and any biodiversity indices (Fig. 2). However, a significant positive relationship was found between stand basal area of plots and exotic tree ratios ($R^2 = 0.096$, $p = 0.005$) and fast growing tree ratios ($R^2 = 0.118$, $p = 0.002$) (Table 4; Fig. 1c and d). These correlations were weak, however, with the low R^2 values indicating that only 10% of variation between the exotic tree ratio and stand basal area and 12% of the variation of between fast-growing tree ratio and stand basal area was explained.

3.3. Biodiversity-productivity controlled by environmental factors

For the relationship with BA, only models which included each of the different surrogate measures of biodiversity (species richness, Shannon's diversity index, exotic tree ratio or fast growing tree ratio) and stand density variables were significant at $\alpha = 0.05$ (Table 5). Other factors such as stand age and environmental factors (topographical position, slope and ground cover) did not have a significant effect on productivity.

For MAIBA, only models of the relationship between MAIBA and biodiversity surrogates, stand density and stand age were accepted (Table 5), suggesting that biodiversity, stand density and stand age had a combined effect with stand age on the productivity, while environmental factors such as topographical position, slope, or ground cover had no impact on stand productivity.

Overall, stand density had the strongest significant positive effect on both BA and MAIBA (Fig. 3a and b), suggesting productivity increased when stand density increased (Table 5). Stand age had only a significant negative effect on MAIBA (Fig. 3c), suggesting productivity decreased as stands developed overtime, and may further suggest that thinning could be beneficial for maintaining productivity after 10 years.

Approximately 40% of variation in the growth or growth rate of stand basal area was found between sites (see site effect in Table 5). The relationship between productivity and species richness, Shannon's index, stand age or stand density varied between sites, with individual sites showing a positive, negative or no relationship. This

Table 5
Estimates and significance of fixed effects and covariance parameters (S = species richness; H = Shannon's index; E = exotic tree ratio; F = fast-growing tree ratio; A = stand age; and D = stand density).

	Model	Residual	Site variance	Site effect (%)
(a) Stand basal area (m^2/ha)				
I	Null model (random effects only)	128.465^{***}	68.719^{*}	34.9^{*}
I.1.2	$5.29 + 0.17S + 0.013D^{***}$	102.040^{***}	67.796^{*}	39.9^{*}
I.2.2	$4.98 + 0.83H + 0.013D^{***}$	101.873^{***}	62.313^{*}	38.0^{*}
I.3.2	$1.47 + 9.48E + 0.014D^{***}$	98.858^{***}	54.209	35.4
I.4.2	$3.41 + 5.21F + 0.013D^{***}$	103.227^{***}	53.210	34.0
Final model	$5.60 + 0.013D^{***}$	102.311^{***}	61.016^{*}	37.4
(b) Mean annual increment of stand basal area (m^2/ha/year)				
II	Null model	1.635^{***}	1.043^{*}	38.9^{*}
II.1.3	$4.33^{**} + 0.03SR - 0.4A^{*} + 0.001D^{***}$	1.230^{***}	0.756^{*}	38.1^{*}
II.2.3	$4.38^{**} + 0.07H - 0.41A^{*} + 0.001D^{***}$	1.231^{***}	0.756^{*}	38.0^{*}
II.3.3	$4.56^{**} + 1.08E - 0.47A^{**} + 0.001D^{***}$	1.200^{***}	0.633	34.5
II.4.4	$4.43^{**} + 0.38F - 0.42A^{**} + 0.001D^{***}$	1.244^{***}	0.685	35.5
Final model	$4.43^{**} - 0.41A^{*} + 0.001D^{***}$	1.235^{***}	0.743^{*}	37.6^{*}

Maximum likelihood estimation method was applied for models. *t*-Test was used for estimates of fixed effects and the Wald *Z* test for estimates of covariance parameters in selected models.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

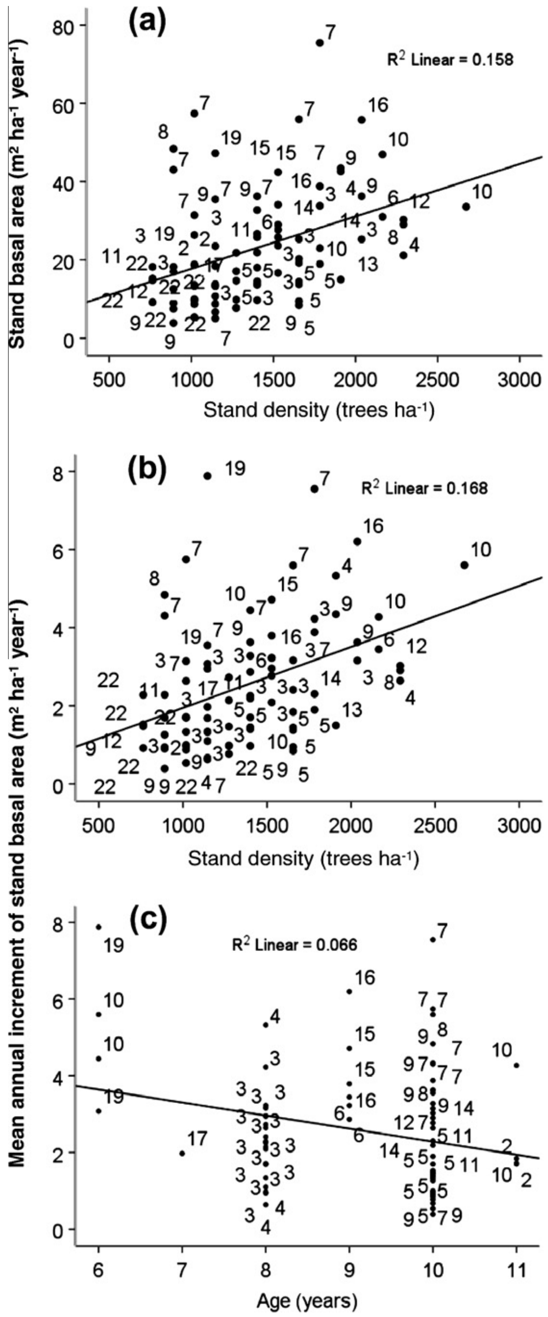

Fig. 3. The significant relationship between productivity of plots and stand factors: (a) stand basal area (BA) and stand age ($p = 0.000$); (b) mean annual increment of stand basal area (MAIBA) and stand age ($p = 0.000$); and (c) mean annual increment of stand basal area (MAIBA) and stand density ($p = 0.020$). The numbers refer to the sites where the plots were located.

result may suggest that environmental conditions at specific sites may influence additional species recruitment in the plantations overtime; however, overall stand density and age strongly influenced the relationship between biodiversity and productivity.

4. Discussion

4.1. Effects of biodiversity on stand productivity

We did not find a significant relationship between species richness or Shannon's diversity, and productivity, but functional groups, such as exotic and fast-growing trees, were positively correlated with stand productivity. However, none of the biodiversity surrogate measures were significantly related to productivity in our more complicated mixed effect models, which included stand structural and environmental characteristics, and also considered our nested sampling design. Other studies have also failed to find a relationship between biodiversity and productivity (Chen and Klinka, 2003; Vilà et al., 2003). For example, a study using the Ecological and Forest Inventory of Catalonia (NE Spain) also found no significant relationship in the Pyrenean Scots pine forests, but a positive relationship between species richness and wood production was found in the Aleppo pine forests. Species richness did not affect the productivity of the Aleppo pine and Pyrenean Scots forests, but the productivity was related to environmental parameters and successional stage (Vilà et al., 2003; Waide et al., 1999). Another study conducted in western hemlock and western red cedar stands of around 60 years old in southern coastal British Columbia found no positive mixed-species effect in aboveground productivity. Multiple regression indicated a positive relationship between annual net primary productivity and hemlock percentage within a given stand age and density (Chen and Klinka, 2003). In contrast to our results, other studies have found either a positive relationship between productivity and species richness in forest stands (Balvanera and Aguirre, 2006; Erskine et al., 2006; Fridley, 2001; Huston, 1980; Lugo, 1992), or a negative relationship (Firn et al., 2007; Huston, 1980; Jacob et al., 2010; Lugo, 1992).

Approximately 10% of the variation in stand basal area was explained by the ratio of exotic trees to total number of trees and 12% by the ratio of fast growing trees to total number of trees. This result provides some evidence of the sampling effect hypothesis as it suggests species characteristics impact significantly on stand productivity. A significant Pearson correlation of 0.44 was found between the exotic tree ratio and the fast growing tree ratio ($p < 0.01$). This indicates that a significant number of exotic species are the faster growing species in the mixed plantations, but there are still a number of native species that are fast growing. Overtime this relationship between biodiversity and productivity may change because of species loss and recruitment, environmental drivers such as light availability and natural and anthropogenic disturbances. At different growth stages, other relationships between biodiversity and productivity might be found. A positive relationship between functional diversity and productivity has also been found. For example, research by Paquette and Messier (2011) in temperate and boreal forests in north-eastern North America, revealed that functional diversity (or phylogenetic diversity) had a positive effect on productivity and explained 37% of the variation in tree productivity.

Using mixed effect models we found a significant relationship between productivity and species richness when stand age and density were also considered. This is in agreement with a study of the Douglas fir/western hemlock forest type in Oregon and Washington and the mixed-conifer forest type in California where a strong positive relationship was found between net basal area growth and tree-species diversity but only when stand characteristics were considered (Liang et al., 2005).

4.2. Effects of site characteristics and environment on the stand production

Contrary to our original expectations and other studies, we found no significant relationship between productivity and environmental variables such as topographical position, slope degree or ground cover. These findings are similar to those from a study in a Mexican tropical dry forest (Balvanera and Aguirre, 2006), which also found that environmental heterogeneity and productivity were not correlated. Similarly, a study in the conifer stands of western America, which examined the effect of site characteristics such as elevation, aspect and slope on the relationship between species diversity and forest basal area net growth, indicated that slope was the only factor that significantly affected this relationship in California mixed conifer forests, while there was no effect in the Douglas-fir/western hemlock forests in Oregon and Washington (Liang et al., 2007). These findings differ to other studies in a temperate climate which found that the relationship between diversity and productivity was driven by large-scale environmental factors (Healy et al., 2008; Paquette and Messier, 2011; Vilà et al., 2003; Waide et al., 1999). Paquette and Messier (2011) found that biodiversity had a positive and significant effect on tree productivity in climate and environmental conditions such as in the temperate, mixed and boreal forests of eastern Canada. Soil quality, drainage, and topography can strongly influence the relationship between species richness and biomass production (Healy et al., 2008).

Results of this study indicate that a greater stand growth was found at denser stands in the Rainforestation Farming at ages of around 10 years. However, this greater growth may be due to higher densities of these stands that were still not very high at that time. Conversely, growth may slow down in stands with a very high density because of competition between individuals. Several studies found that tree density can influence the growth of trees (Bullock and Burkhart, 2005; Grant et al., 2006), especially diameter growth, because the degree of competition in stands can be delayed when tree densities are low. The Big Scrub Rainforest Group suggested a density of 3000 trees ha^{-1} for reforestation plantings (Grant et al., 2006); while Kooyman (1996) found that at a density exceeding 1600 trees ha^{-1}, restoration rainforest plantings could show a poor performance of survival, growth and site capture.

This research found that stand production decreased as stand age increased. Some studies found the production of stands decreased with age because species interactions (both inter- and intraspecific influences) in mixed-species stands became more negative as stands aged (Forrester et al., 2011; Ryan et al., 1997). This differs from results found in a study in southern coastal British Columbia, which found overstory biomass increased linearly with stand age and annual net primary productivity increased with stand density in western hemlock and western red cedar mixed-species stands of around 60 years old (Chen and Klinka, 2003). However, productivity was related to environmental parameters and successional stages in Aleppo pine and Pyrenean Scots forests (Vilà et al., 2003; Waide et al., 1999). In summary, we found that the monoculture plantations had a higher productivity than the mixed plantations of the Rainforestation Farming. The mixed species that make up the Rainforestation plantations, however, could provide additional benefits to the community than just timber products. These include non-wood products (e.g. fruits or nuts, crops) or other ecological services such as improved watershed protection or biodiversity conservation which may not be the case in monoculture plantations of exotic species (Fahey and Jackson, 1997; Huynh, 2001; Lugo, 1997; Parrotta and Knowles, 1999). Also these plantations after 6–10 years have started to develop features characteristic of the local natural rainforest, e.g. a three-storey structure and a J-shaped size distribution with a numerous native species (Nguyen, 2011).

5. Conclusion

Overall we found that the characteristics of the species included in mixed species plantations, and how the stand is managed following planting in terms of thinning to manipulate stand density drive the biodiversity–productivity relations rather than simply species number in plantations, evidence of the sampling effect (Huston, 1997). This is key information for smallholder farmers and small restoration projects where multiple outputs are desirable including timber and biodiversity benefits. This study found that stand density was a key driver of productivity, which is encouraging as density can be controlled to ensure continued stand development. Productivity also decreased as stands aged, but reducing stand density over time may ameliorate this issue. These results contribute new information to the existing literature on biodiversity–productivity relationships in tropical forests, especially in the Philippines for which no reference related to the biodiversity–productivity relationship in mixed-species plantations could be found. It is also suggested that further studies should examine the role of key functional species on ecological or production functions as well as the relationship between diversity of native species and production.

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Appendix

See Appendix A–C.

Appendix A
Mixed effect models of stand basal area with a fixed effect structure of biodiversity surrogates and stand characteristics and a random effects structure of site/plot.

Model	Biodiversity surrogates					Stand characteristics				Models compared	−2 LL	Δ −2 LL	Sig. (χ^2)	Model chosen
	S	H	E	F	D	A	TP	SL	GR					
I	Random effects only										649.901			
I.1.1	√									I vs. I1.1	645.699	$\chi^2(1) = 4.202$	*	I.1.1
I.1.2	√				√					I.1.1 vs. I.1.2	632.402	$\chi^2(1) = 13.297$	***	I.1.2
I.1.3	√				√	√				I.1.2 vs. I.1.3	632.386	$\chi^2(1) = 0.016$	NS	I.1.2
I.1.4	√				√	√	√			I.1.2 vs. I.1.4	632.164	$\chi^2(2) = 0.238$	NS	I.1.2
I.1.5	√				√	√	√	√		I.1.2 vs. I.1.5	632.155	$\chi^2(3) = 0.247$	NS	I.1.2
I.1.6	√				√	√	√	√	√	I.1.2 vs. I.1.6	632.089	$\chi^2(4) = 0.313$	NS	**I.1.2**

(continued on next page)

Appendix A (*continued*)

Model	Biodiversity surrogates					Stand characteristics				Models compared	−2 LL	Δ −2 LL	Sig. (χ^2)	Model chosen
	S	H	E	F	D	A	TP	SL	GR					
I.2.1		√								I vs. I.2.1	647.403	$\chi^2(1) = 2.498$	NS	I
I.2.2		√			√					I vs. I.2.2	632.379	$\chi^2(2) = 17.522$	***	I.2.2
I.2.3		√			√	√				I.2.2 vs. I.2.3	632.369	$\chi^2(1) = 0.010$	NS	I.2.2
I.2.4		√			√	√	√			I.2.2 vs. I.2.4	632.153	$\chi^2(2) = 0.226$	NS	I.2.2
I.2.5		√			√	√	√	√		I.2.2 vs. I.2.5	632.147	$\chi^2(3) = 0.232$	NS	I.2.2
I.2.6		√			√	√	√	√	√	I.2.2 vs. I.2.6	632.077	$\chi^2(4) = 0.302$	NS	**I.2.2**
I.3.1			√							I vs. I.3.1	647.500	$\chi^2(1) = 2.401$	NS	I
I.3.2			√		√					I vs. I.3.2	628.691	$\chi^2(2) = 18.809$	***	I.3.2
I.3.3			√		√	√				I.3.2 vs. I.3.3	628.584	$\chi^2(1) = 0.107$	NS	I.3.2
I.3.4			√		√	√	√			I.3.2 vs. I.3.4	627.979	$\chi^2(2) = 0.712$	NS	I.3.2
I.3.5			√		√	√	√	√		I.3.2 vs. I.3.5	627.975	$\chi^2(3) = 0.716$	NS	I.3.2
I.3.6			√		√	√	√	√	√	I.3.2 vs. I.3.6	627.968	$\chi^2(4) = 0.723$	NS	**I.3.2**
I.4.1				√						I vs. I.4.1	648.756	$\chi^2(1) = 1.136$	NS	I
I.4.2				√	√					I vs. I.4.2	631.563	$\chi^2(2) = 18.338$	***	I.4.2
I.4.3				√	√	√				I.4.2 vs. I.4.3	631.555	$\chi^2(1) = 0.008$	NS	I.4.2
I.4.4				√	√	√	√			I.4.2 vs. I.4.4	631.255	$\chi^2(2) = 0.308$	NS	I.4.2
I.4.5				√	√	√	√	√		I.4.2 vs. I.4.5	631.200	$\chi^2(3) = 0.363$	NS	I.4.2
I.4.6				√	√	√	√	√	√	I.4.2 vs. I.4.6	631.115	$\chi^2(4) = 0.448$	NS	**I.4.2**

S = species richness; H = Shannon's index; E = exotic tree ratio; F = fast growing tree ratio; A = stand age; D = stand density; TP = stand topographical position; SL = stand slope; and GR = stand ground cover. Null model I was built with only random effect by site. The likelihood test for reference models with fixed effects used ML estimation. NS = not significant.

* $p < 0.05$.

*** $p < 0.001$.

Appendix B

Mixed effect models of mean annual increment of stand basal area with a fixed effect structure of biodiversity surrogates and stand characteristics and a random effects structure of site/plot.

Model	Biodiversity surrogates					Stand characteristics				Models compared	−2 LL	Δ −2 LL	Sig. (χ^2)	Model chosen
	S	H	E	F	D	A	TP	SL	GR					
II	Random effects only		294.017											
II.1.1	√									II vs. II.1.1	287.818	$\chi^2(1) = 6.199$	*	II.1.1
II.1.2	√				√					II.1.1 vs. II.1.2	276.285	$\chi^2(1) = 11.533$	***	II.1.2
II.1.3	√				√	√				II.1.2 vs. II.1.3	270.278	$\chi^2(1) = 6.007$	*	II.1.3
II.1.4	√				√	√	√			II.1.3 vs. II.1.4	270.073	$\chi^2(1) = 0.205$	NS	II.1.3
II.1.5	√				√	√	√	√		II.1.3 vs. II.1.5	270.060	$\chi^2(2) = 0.218$	NS	II.1.3
II.1.6	√				√	√	√	√	√	II.1.3 vs. II.1.6	270.043	$\chi^2(3) = 0.235$	NS	**II.1.3**
II.2.1		√								II vs. II.2.1	291.316	$\chi^2(1) = 2.701$	NS	II
II.2.2		√			√					II vs. II.2.2	276.731	$\chi^2(2)=17.286$	***	II.2.2
II.2.3		√			√	√				II.2.2 vs. II.2.3	270.315	$\chi^2(1) = 6.416$	*	II.2.3
II.2.4		√			√	√	√			II.2.3 vs. II.2.4	270.105	$\chi^2(1) = 0.210$	NS	II.2.3
II.2.5		√			√	√	√	√		II.2.3 vs. II.2.5	270.093	$\chi^2(2) = 0.222$	NS	II.2.3
II.2.6		√			√	√	√	√	√	II.2.3 vs. II.2.6	270.071	$\chi^2(3) = 0.236$	NS	**II.2.3**
II.3.1			√							II vs. II.3.1	293.034	$\chi^2(1) = 0.973$	NS	II
II.3.2			√		√					II vs. II.3.2	275.026	$\chi^2(2) = 18.991$	***	II.3.2
II.3.3			√		√	√				II.3.2 vs. II.3.3	266.523	$\chi^2(1) = 8.503$	**	II.3.3
II.3.4			√		√	√	√			II.3.3 vs. II.3.4	265.932	$\chi^2(1) = 0.591$	NS	II.3.3
II.3.5			√		√	√	√	√		II.3.3 vs. II.3.5	265.926	$\chi^2(2) = 0.597$	NS	II.3.3
II.3.6			√		√	√	√	√	√	II.3.3 vs. II.3.6	265.691	$\chi^2(3) = 0.832$	NS	**II.3.3**
II.4.1				√						II vs. II.4.1	293.943	$\chi^2(1) = 0.074$	NS	II
II.4.2				√	√					II vs. II.4.2	276.827	$\chi^2(2) = 17.190$	***	II.4.2
II.4.3				√	√	√				II.4.2 vs. II.4.3	269.976	$\chi^2(1) = 6.851$	**	II.4.3
II.4.4				√	√	√	√			II.4.3 vs. II.4.4	269.706	$\chi^2(1) = 0.270$	NS	II.4.3
II.4.5				√	√	√	√	√		II.4.3 vs. II.4.5	269.657	$\chi^2(2) = 0.219$	NS	II.4.3
II.4.6				√	√	√	√	√	√	II.4.3 vs. II.4.6	269.643	$\chi^2(3) = 0.333$	NS	**II.4.3**

S = species richness; H = Shannon's index; E = exotic tree ratio; F = fast growing tree ratio; A = stand age; D = stand density; TP = stand topographical position; SL = stand slope; and GR = stand ground cover. Null model II was built with only random effect by site. The likelihood test for reference models with fixed effects used ML estimation. NS = not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

Appendix C
Site characteristics and planting history of 18 of the mixed-species sites in Leyte Province, the Philippines (Milan et al., 2004).

Site	Site location	Year planted	Area (ha)	Density planted (trees/ha)	Soil type	Topography
02	Marcos	1995	0.61	5000	Clay loam	Slightly to moderately rolling
03	Catmon	1998	1.4	5000	Clay loam	Flat
04	Patag	1998	1.0	5000	Clay loam	Slightly rolling
05	Cienda	1996	0.9707	5000	Clay to clay loam	Flat
06	Pomponan	1997	0.38	5000	Clay loam	Slightly rolling
07	Punta	1996	5.442	5000	Limestone	Moderately rolling
08	Maitum	1996	0.478	5000	Clay loam	Slightly to moderately rolling
09	Mailhi	1996	3.22	5000	Clay to clay loam	Slightly to moderately rolling
10	Vila Solidasidad	1995	0.4377	5000	Clay	Flat
11	Maitum	1996	0.4686	5000	Limestone	Moderately rolling
12	Maitum	1996	0.9862	5000	Limestone	Slightly rolling
13	Maitum	1996	0.2518	5000	Clay loam	Moderately rolling
14	Pomponan	1996	0.9518	5000	Clay loam	Slightly to moderately rolling
15	Pomponan	1997	0.438	5000	Clay	Moderately rolling
16	Pomponan	1997	0.41	5000	Clay loam	Moderately rolling
17	Pomponan	1999	0.8475	5000	Sandy loam	Flat
19	Licuma	2000	0.25	5000	Clay loam	Moderately rolling
22	Milagro	1996	1.5	5000	Clay loam	Flat

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