Tree species diversity and ecosystem function: Can tropical multi-species plantations generate greater productivity?

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Abstract

Results from the humid tropics of Australia demonstrate that diverse plantations can achieve greater productivity than monocultures. We found that increases in both the observed species number and the effective species richness were significantly related to increased levels of productivity as measured by stand basal area or mean individual tree basal area. Four of five plantation species were more productive in mixtures with other species than in monocultures, offering on average, a 55% increase in mean tree basal area. A general linear model suggests that species richness had a significant effect on mean individual tree basal area when environmental variables were included in the model. As monoculture plantations are currently the preferred reforestation method throughout the tropics these results suggest that significant productivity and ecological gains could be made if multi-species plantations are more broadly pursued.

Keywords: *Agathis robusta*; *Araucaria cunninghamii*; *Eucalyptus cloeziana*; *E. pellita*; *E. tereticornis*; Mixed-species; Polyculture; Monoculture

1. Introduction

Over the last decade a number of studies in experimental temperate grasslands have asserted that species richness or species diversity increases productivity (Hector et al., 1999; Loreau and Hector, 2001; Tilman et al., 1997, 1996). The nature of this relationship remains unclear and there is also uncertainty as to how those results can be transferred to other systems or used to improve productivity on degraded lands at a landscape or regional level (Loreau et al., 2001). Nevertheless, the positive relationship between species richness and productivity and other ecosystem functions has been used as a persuasive argument for the conservation of biodiversity (Schwartz et al., 2000). Nowhere is this argument more important than in the highly diverse tropical humid forests, which have been, and continue to be, significantly degraded by human activities (Achard et al., 2002; Vanclay, 2005).

It is difficult to ecologically restore degraded tropical forests, but practitioners presently have a variety of methods at their disposal (Lamb and Gilmour, 2003) and some promising results are being obtained (Parrotta and Knowles, 1999; Parrotta et al., 1997a; Tucker and Murphy, 1997). However, these methods require considerable ecological knowledge and are very costly (Erskine, 2002). In most situations there is neither the knowledge, the funds, nor the incentives to encourage landholders to replant these complex forests (Lamb et al., 2005). Nevertheless reforestation does occur in some deforested tropical areas, generally as monoculture plantations of exotic species selected for either their high productivity or their tolerance of degraded soils. Industry and governments have driven the establishment of fast growing monoculture plantations to satisfy a growing demand for industrial wood products (Cossalter and Pye-Smith, 2003). These single species forests further contribute to land simplification in areas that were once highly diverse forests, although when they are established on degraded lands they can be catalysts for native forest regeneration, depending upon their proximity to seed sources and the silvicultural treatments applied (Lamb, 1998; Parrotta et al., 1997b).

The recent rapid expansion of fast growing monoculture plantations has resulted in a groundswell of community opposition in a number of tropical countries, as this type of reforestation does not provide many of the traditional forest goods used by communities and few of the ecological services (Scherr et al., 2004). Monocultures are also perceived to have largely negative impacts on the local environment (Cossalter

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and Pye-Smith, 2003). This does not mean that communities necessarily want to restore the original forests, but plantation systems with multiple species, using high value local species appear to be attracting increased interest in many parts of the tropical world (Erskine et al., 2005; Haggar et al., 1998; Pasicolan et al., 1997). These mixed species plantations may also be more productive than monocultures for three theoretical reasons. The complementarity hypothesis proposes that species-rich plantations are able to more efficiently access and utilise limiting resources because they contain species with a diverse array of ecological attributes (Kelty, 1992). As a consequence, more diverse plantations should have higher net primary production, and in a well-managed plantation, this should translate into larger timber volumes. The facilitation hypothesis suggests that plantations which use combinations of species that improve the growing conditions (i.e. nitrogen-fixing trees) for other species may facilitate increases in overall production of a mixed stand (Binkley et al., 2003; Forrester et al., 2006). Alternatively, the sampling effect hypothesis proposes that more diverse plantations demonstrate increased production because they have a higher chance of containing species that are ‘‘over-yielding’’ and highly efficient in their use of limiting resources. That is, one or two species within the community are largely responsible for any increase in production (Loreau et al., 2001). Determining which of these mechanisms achieve productivity increases in mixed species stands may encourage more diverse plantations to be established.

All levels of government encouraged reforestation with mixed species plantations during the 1990’s in the humid tropics of north-eastern Australia, after the Federal Government nominated all state owned rainforest in the region for registration on the Wet Tropics World Heritage Area (Vize et al., 2005). The Community Rainforest Reforestation Program (CRRP) was created when logging ceased in the natural forests as part of a compensation package to foster a plantation-based timber industry while also promoting regional conservation values. This program planted 1782 ha of mostly native rainforest and eucalypt species on privately owned agricultural lands in the region (Vize et al., 2005). A series of permanent sample plots were established in well-managed plantations larger than 2 ha to monitor the growth of trees across a range of sites (Keenan and Annandale, 1999). Using growth data from these plots we pose two research questions:

1. Are plantation diversity measures related to stand productivity?
2. What are the mechanisms underlying differences in plantation productivity?

2. Methods

The CRRP plantings were established between 1992 and 1996 on privately owned land that was cleared at least 60 years previously. Plantations were established across a latitudinal range from 15°26′ to 18°51′S on the lowlands and highlands (up to 900 m altitude). The tree species used were mostly those that could produce high-value, appearance-grade sawn timber from humid forests in the region. The plantings were generally established in plantation format with 600–800 trees per hectare and ranged from monocultures to intimate mixtures of eucalypts and rainforest species planted either at random or in alternate rows. The mixtures created were random assemblages though influenced by seedling availability at the time. Prior to planting the sites generally were ripped with an tractor or bulldozer and knockdown herbicide (e.g. glyphosate) sprayed along the planting rows. Post planting weed control consisted of both glyphosate and simazine herbicides. Tree seedlings were commonly fertilised with diammonium phosphate in a single application at planting, or a split application with half at planting and half at 6 months.

The selection of sample plots in CRRP plantations was limited to sites that had received adequate weed maintenance during the establishment phase. Plots were randomly located within plantations aged between 6 and 9.5 years, which were larger than 2 ha and aimed to include 60 trees, with 6 rows of 10 trees while avoiding the plantation boundary. The location, altitude and previous land use history were recorded for each plot (Bristow et al., 2005). Soil types were also recorded and assigned a potential nutrient supply index (Mackey, 1993). A linear regression analysis of site nutrient supply index and species richness suggested that there was no relationship ($r = -0.008$, $p = 0.956$) between the number of species in the plots and site quality. Mean annual rainfall and temperature for each plot was generated by ANUCLIM (Houlder et al., 2000), a software package which uses mathematical descriptions to estimate climate variables across Australia. Standard forestry growth measurements were made on the individual trees in the plots with the following information recorded: species identity, diameter over bark at 1.3 m (breast height-DBH) and total height. No volume equations or wood density measurements are available for the young tree species in the CRRP plantations. Therefore, accurate biomass estimates would have been problematic so plantation productivity was measured by mean tree basal area and stand basal area, which were derived from DBH and plot measurements. Basal area is nevertheless highly correlated with tree volume and biomass (Satoo and Madgwick, 1982) and is used as the measure of plantation productivity. Measures were standardised to 8 years using a linear regression growth model, to either interpolate or extrapolate the data to take account of the variation in planting years across the dataset.

The 53 plots used for analysis (see Table 1) contained between 1 and 8 tree species and had stocking rates between 350 and 700 stems per hectare after 8 years of growth. Five species from forests in the region (*Agathis robusta*, *Araucaria cunninghamii*, *Eucalyptus cloeziana*, *E. pellita* and *E. tereticornis*) were represented in monocultures and representatives of at least one of these species were in each of the other plots. Across all plots there was a total of 27 native and 3 exotic tree species. These exotic species comprised less than three percent of the total number of trees in the plots.

Two indices of plant diversity are used for analysis. The first index, ‘‘observed species number,’’ is the number of planted species observed within each plot. The second, ‘‘effective

Table 1
Characteristics of the sites used to assess the relationship between productivity and species diversity in the CRRP plantations

Site number[a]	Planting density (stems/ha)	Species number	Effective species richness[b]	Elevation (m)	Mean rainfall (mm/yr)	Soil type
2	709	2	1.6	750	1716	Basalt
3	667	4	2.4	750	1715	Basalt
4	766	3	1.6	703	3200	Basalt
5	667	7	4.4	703	3193	Basalt
6	833	7	3.8	799	1803	Basalt
8	667	1	1.0	799	1761	Basalt
11	667	3	2.1	720	1281	Basalt
13	667	8	6.6	750	1645	Basalt
14	667	5	2.8	674	1674	Basalt
15	667	1	1.0	685	1689	Basalt
16	556	3	1.7	680	1686	Basalt
18	571	2	1.2	799	1468	Metamorphic
19	800	2	1.3	780	1417	Metamorphic
24	714	5	4.7	729	2446	Basalt
26	1000	6	5.4	735	2444	Basalt
28	667	3	2.1	910	1469	Basalt
30	1143	1	1.0	1100	2175	Basalt
35	667	1	1.0	1100	2173	Basalt
36	800	4	2.5	1100	2179	Basalt
40	667	8	6.2	520	1363	Metamorphic
42	667	4	3.0	435	1478	Metamorphic
43	969	5	3.0	430	1476	Metamorphic
44	667	3	2.9	20	2286	Metamorphic
45	667	3	2.7	20	1855	Metamorphic
46	500	8	4.7	80	3412	Basalt
47	667	5	3.3	80	3412	Basalt
48	667	5	2.9	80	3412	Basalt
49	800	4	2.7	52	3483	Basalt
50	500	4	2.8	57	3484	Basalt
51	667	7	5.7	20	2470	Alluvium
52	667	7	5.6	20	2472	Alluvium
53	556	5	4.1	20	3273	Alluvium
56	667	1	1.0	40	3489	Basalt
58	667	6	5.0	40	3490	Basalt
59	667	4	3.2	50	2047	Alluvium
60	667	5	3.5	450	1377	Metamorphic
61	667	3	1.8	400	1378	Alluvium
62	667	2	1.9	400	1381	Alluvium
63	625	7	6.0	20	1936	Alluvium
67	833	8	6.8	10	1914	Alluvium
68	667	6	4.1	20	1795	Alluvium
70	625	8	6.1	20	1816	Alluvium
74	833	6	5.5	20	1837	Alluvium
75	833	6	4.7	20	1838	Alluvium
77	833	1	1.0	700	1180	Alluvium
79	833	4	3.0	660	1134	Alluvium
90	1000	8	6.7	20	1934	Metamorphic
91	1000	6	4.5	20	1934	Metamorphic
96	667	4	3.0	35	1611	Alluvium
97	667	7	5.2	35	1611	Alluvium
98	667	7	5.8	420	1631	Alluvium
99	667	1	1.0	409	1569	Metamorphic
111	667	5	3.6	50	1656	Alluvium

[a] Site numbers correspond to those in Queensland Department of Primary Industries and Fisheries, Experiment 799Ath.
[b] Effective species richness ($e^{H'}$) takes into account species diversity and evenness within the plantation stand.

species richness,'' is $e^{H'}$, where H' is the calculated Shannon Weiner diversity index based on the number of individuals of each species (Tilman et al., 1997). We use regression analysis to examine the effect of species diversity on productivity.

We recognised that patterns of productivity could be confounded by variable tree density and environmental gradients, as the measured plots contained a range of stocking rates and were spread across the wet tropics region of north eastern Australia. To account for differences in tree density we consequently used mean individual tree basal area (m^2/tree) rather than stand basal area (m^2/ha) as a dependant variable (although these two measures are highly correlated $r = 0.9004$

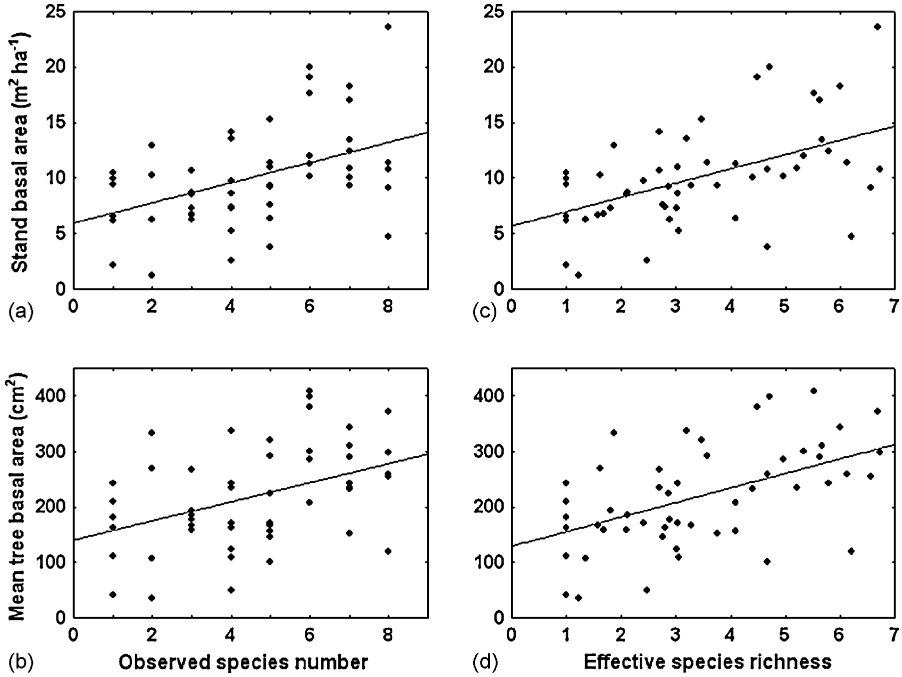

Fig. 1. The relationship between different measures of diversity and productivity in Community Rainforest Reforestation Program plantations. (a) Observed species richness and stand basal area ($N = 53$, $r^2 = 0.21$, $p = 0.001$). (b) Observed species richness and mean tree basal area ($N = 53$, $r^2 = 0.18$, $p = 0.001$). (c) Effective species richness and stand basal area ($N = 53$, $r^2 = 0.26$ $p < 0.001$). (d) Effective species richness and mean tree basal area ($N = 53$, $r^2 = 0.27$, $p < 0.001$).

$p < 0.001$; see Fig. 1). To test for the effect of most confounding environmental factors we selected the soil nutrient supply index, mean annual rainfall and temperature. Additionally, the presence of nitrogen fixing species is recognised as having the potential to increase the productivity of a stand and their presence or absence in a stand was also selected. The effect of species richness, soil nutrient supply, rainfall, temperature and the presence/absence of nitrogen fixing species on our productivity measure, mean tree basal area, was analysed using a general linear model. These measures were transformed for normality prior to analysis.

3. Results

We found that increases in both the observed species number and the effective species richness were significantly related to increased levels of productivity as measured by basal area (Fig. 1). Observed species number was significantly related to stand basal area (Fig. 1a) and also to the mean individual tree basal area (Fig. 1b) and explained around 20% of their variance. Effective species richness explained more than 25% of the variance and was also significant ($p < 0.001$) for both productivity measures (Figs. 1c and d). Although only five species were grown in monoculture, most of them were more productive in mixtures with other species. When grown in mixtures rather than monocultures the average tree basal area of *A. robusta*, *Eucalyptus cloeziana*, *E. pellita* and *E. tereticornis* were 115, 24, 18 and 63% larger, respectively. Stand basal area showed similar trends with 299, 6, 16 and 91% greater production in mixed plantations. Only *Araucaria cunninghamii* performed more poorly in mixtures with average basal area and stand basal area 16 and 10% lower, respectively, than in pure stands.

The general linear model (Table 2) also suggests that species richness had a significant effect on mean individual tree basal area when other variables were included in the model ($F_{1,47} = 5.03$, $p = 0.0297$). Mean annual temperature appeared to have a highly significant positive effect ($F_{1,47} = 16.34$, $p < 0.001$) indicating that the plots in the warmer lowlands were generally more productive than those in the cooler highlands. In contrast, rainfall, soil nutrient supply and the presence of potential nitrogen fixing species had no significant effect on the mean tree basal area. Overall the model explained 40% of the total deviance.

Table 2
Analysis of biotic and abiotic factors on regional plantation productivity

	d.f.	F	p
Whole model[a]	5	7.986	<0.0001
Partial regressions			
Effective species richness	1	5.028	0.0297
Mean annual temperature	1	16.336	0.0002
Mean annual rainfall	1	1.574	0.2158
Nutrient supply	1	3.650	0.0622
Presence of nitrogen fixing species	1	0.513	0.4772

Productivity, as measured by mean tree basal area, was tested using a general linear model. d.f. = degrees of freedom.
[a] Whole model adjusted $r^2 = 0.402$.

4. Discussion

Our finding that, at a regional scale, productivity increased with increasing species richness has not been observed before in forest plantation systems (Schlapfer and Schmid, 1999) but complements the relationship previously demonstrated in experimental grasslands. These productivity increases could be the result of a number of different mechanisms including complementarity, facilitation and/or the sampling effect. Although the plantations were not designed to rigorously test these mechanisms, some trends can be explored.

The combination of different crown architectures in mixtures, particularly the more open crowns of the faster growing eucalypt species compared with the denser canopies of rainforest species, may have been important. Alternate rows of eucalypts and mixed rainforest species was a design commonly used in the CRRP and this plantation format might have led to less intense interspecific competition between species for light in mixtures compared with the intraspecific competition a species would have experienced in a monoculture. Although little is known about the different root architecture or nutrient utilisation by species planted in the CRRP it is likely that there are differences between eucalypts and rainforest species (Schmidt et al., 1998) and reduced root competition for soil resources may have also contributed to productivity increases.

Facilitation did not appear to be an important mechanism. The low stocking rates of the plantations would have probably precluded faster growing species providing shade for light sensitive species for several years after planting. However, the plantations included three Meliaceae species which are prone to shoot tip borers in high light conditions. Growth of these trees may have been improved over time in mixtures as shade from faster growing neighbours would lead to reduced insect attack and, consequently, greater productivity (Keenan et al., 1995). Facilitation of growth by the fertilising effect of nitrogen fixing species (Binkley et al., 2003) was tested in the general linear model and was found not to be a significant factor.

On the other hand, the sampling effect could go some way to explaining the results. Although one of the 'over-yielding' species, *Eucalyptus pellita*, was planted as a monoculture, many of these 'over-yielding' species were only found in the mixture plots. Thus, the chance of having 'over-yielding' species in the plots increased with the diversity of the plots. There is no evidence that many of these over-yielding rainforest species do not establish well in monoculture but through the life of the CRRP there was greater importance placed on getting trees planted rather than experimenting with species and site matching.

The trends attributed to diversity were confounded by the effects of increasing temperature on the productivity of the stands. Trees planted in our plots were tropical species and their growth response is known to be related to temperature (Kitajima, 1996). On the other hand, rainfall and soil nutrient supply did not affect the overall productivity of the stands. Our results contrast with one of the few comparable studies of the diversity–productivity relationship involving trees carried out in temperate Catalonian pine forests (Vila et al., 2003). This found that climatic and soil factors rather than forest diversity were the main drivers of regional productivity.

Tree species planted in the CRRP were selected for their recognised desirable, appearance-grade timber valued in furniture, veneer and cabinet-making industries when extracted from native forests; and hence the program targeted species able to be manufactured into higher value products. Early-age sampling indicates that clearwood from plantation trees with favourable stem form is comparable with that extracted from native forests (Glencross and Nichols, 2005). Differences in effective stand density due to differing growth rates in mixed species plantations has lead to increased individual tree basal area, and hence quality and quantity of clearwood produced per stem, for *A. robusta*, *Eucalyptus cloeziana*, *E. pellita* and *E. tereticornis*. These species have probably increased their growth due to being in mixtures and if well managed these larger individual stems could produce more higher value clearwood, which would increase stand value.

This study suggests that having more species generally raises plantation productivity. These results should encourage the planting of a wider variety of species across the tropics and foster more research into the ecological and financial advantages and disadvantages of multi-species (including non-tree species) plantations. The consequences of increases in tree diversity and variations in compositional evenness on other ecological functions and processes across degraded tropical landscapes remains to be explored.

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