LETTER

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

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Abstract

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

Keywords

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

Ecology Letters (2008) 11: 217–223

INTRODUCTION

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

According to the Food and Agriculture Organization, tree plantations cover 272 million hectares worldwide, and their extent is continuously increasing (FRA 2005). Nevertheless, over 99% of tree plantations consist of monocultures of a small number of exotic species (Nichols *et al.* 2006). Understanding the potential role of biodiversity in tree plantations is therefore of great importance for the efficient management of ecosystem services (Erskine *et al.* 2006; Vila *et al.* 2007). We analysed data from the first experiment applying the BEF methodology to a tree plantation (Scherer-Lorenzen *et al.* 2005).

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

MATERIALS AND METHODS

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

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

Six plots each received all six species, six plots each received a unique three species combination, and 12 plots received the six monoculture plantings, with two replicate plots per monoculture. All species planted in mixed-species plots were represented in monoculture, allowing to properly control for sampling effects in the analyses. The three-species plots were established using random combinations of either: Ca or Ls, Ae or Hc and Co or Tr to ensure representation of fastest and slowest growing species in each block. Seedlings were fertilized three times during the first growing season (2001) and the grass around them was cut to the ground to avoid competition with herbaceous vegetation. Thereafter, the plantation was cleaned of undergrowth three times per year. All cleaning was-3398o6(plant5t6mon)nofirstingin the simulation model follow a normal distribution, and we have confirmed by a goodness-of-fit test that the simulated distributions do not differ significantly from a normal distribution ($P > 0.05$). Although the simulations generated P-values for individual plots, we tested hypotheses across sets of plots by comparing replicate SES values with one-sample t-tests. All simulation models were written in S-PLUS, version 6.2.

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

Growth model

For the growth model, we used the observed mortality probabilities for each species in the mixed-species plots,

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

of an highly performing species. In Sardinilla, enhanced yield can be attributed almost entirely to increases in growth of individual trees in mixed-species plots. We speculate that the mechanism underlying enhanced growth relates to competition for light which is apparently stronger in monocultures