

## LETTER

## Species richness and wood production: a positive association in Mediterranean forests

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### Abstract

A major debate in the study of biodiversity concerns its influence on ecosystem functioning. We compared whether wood production in forests was associated with tree functional group identity (i.e. deciduous, conifer or sclerophyllous), tree species richness (1–≥ 5) and tree functional group richness (1–3) by comparing more than 5000 permanent plots distributed across Catalonia (NE Spain). Deciduous forests were more productive than coniferous and sclerophyllous forests. Wood production increased with tree species richness. However, functional group richness increased wood production only in sclerophyllous forests. When other forest structure, environmental variables and management practices were included in the analysis, tree functional group identity and species richness still remained significant, while functional species richness did not. Our survey indicates that across a regional scale, and across a broad range of environmental conditions, a significant positive association exists between local tree species richness and wood production at least in typical early successional Mediterranean-type forests.

### Keywords

AET, ecosystem functioning, functional group, Mediterranean forests, mixed forests, permanent plot, plant yield, regional analysis, species diversity, tree wood production.

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### INTRODUCTION

There is increasing concern about the consequences of biodiversity loss for ecosystem functioning, especially regarding aspects such as productivity, stability or nutrient cycling (Loreau *et al.* 2001; Hooper *et al.* 2005). The study of the relationship between plant diversity and productivity has been approached by direct analysis of plant communities in natural systems or by conducting experiments with plant assemblages. Observed diversity–productivity relationships compare diversity across sites of differing productivity driven by environmental conditions. The available observational evidence shows that the relationship between diversity and productivity depends on the geographical scale and ecological organization (Waide *et al.* 1999; Mittelbach *et al.* 2001). Observational studies do not necessarily show causality and results are also very dependent on whether primary productivity is estimated directly or by surrogates (Groner & Novoplansky 2003). Furthermore, when productivity is estimated by surrogate variables of available energy such as rainfall or evapotranspiration, there is a danger of circular reasoning in debating diversity–

productivity–climate relationships (Whittaker & Heegaard 2003). Therefore, productivity estimations should be based on real measurements of C sequestration rates.

On the other hand, specifically designed experiments establishing different levels of local diversity have demonstrated a positive effect of plant diversity on productivity over a range of environmental conditions (Hector *et al.* 1999; Tilman *et al.* 2001). Although experiments provide causal information on the effect of plant diversity on ecosystem productivity, there is concern regarding the way in which the design of the experiments resembles the changes in species abundance and species losses that take place in real environmental and management conditions (Huston 1997; Grime 2002). Furthermore, in terrestrial ecosystems, most experiments have been conducted in grasslands by assembling herbaceous plant species. Synthesized grasslands allow for experimental results at a convenient spatial scale and time framework. However, most ecosystems require large areas and a long time to be imitated experimentally. This is the case for forests, in which the slow growth of tree species necessitates long-term studies in order to examine the diversity–productivity relationship.

Tree plantations that are designed to examine the diversity–productivity relationships meet this hypothesis (Scherer-Lorenzen *et al.* 2005).

Monospecific forest stands and monocultures of highly productive tree species have been extremely favoured for pulp and timber production (Kelty *et al.* 1992). At the same time, in some regions, mixed forests have been maintained for landscape aesthetics, conservation of wildlife, recreational purposes, higher diversity of forest products, and the belief that they are more resistant to disease and to disturbances such as wind or fire (Assmann 1970; Cannell *et al.* 1992; Kerr *et al.* 1992). However, the maintenance of tree diversity is not a routine part of forestry management.

There is observational evidence of a positive relationship between woody species richness and productivity at the regional and continental scale (reviewed by Whittaker & Heegaard 2003). For example, according to the Forest Inventory and Analysis database in the United States (more than 20 000 plots) there is a positive correlation between species richness and stand productivity (Caspersen & Pacala 2001). However, the lack of environmental description of stands hinders the interpretation of this correlation. Whether mixed stands are more productive than pure stands depends greatly on site conditions (Pretzsch 2005) and species composition (Assmann 1970; Kelty *et al.* 1992; Jones *et al.* 2005). Observational and experimental approaches (i.e. tree plantations) in forests should examine the relationship between species diversity and productivity while controlling for the effect of other co-varying factors such as environmental gradients and management practices that could underlie and confound the diversity–productivity relationships.

We tested if there is a positive association between local (i.e. alpha) tree species and functional group richness and stemwood production in stands across a region. For this purpose, we analysed a large data set from forest inventories surveying permanent plots across Catalonia. Permanent plots allow the measurement of tree stem growth directly in the field. Stemwood production in forests appears to be more relevant than total plant production for evaluating tree growth rates and competition interactions as it is through the investment in the physical structure of wood (and also roots) that plants compete with one another (Huston 1994). We also included other forest structure and environmental parameters in the analysis to account for possible confounding factors. Data were gathered from the Forest National Inventory of Spain (IFN). We compared more than 5000 permanent plots in Catalonia (NE Spain). To overcome some of the main caveats of observational analysis, we used a direct estimation of productivity and accounted for potential factors (i.e. forest structure, environmental and management parameters) influencing the

diversity–productivity relationship. We addressed the following questions: (1) Does mixed stands have more wood production than monospecific stands? (2) Does tree species and functional group richness affect wood production? (3) Does the effect depend upon tree functional group identity? and, finally (4) Is the effect of biodiversity confounded with the effect of other environmental, forest structure and management variables?

## MATERIAL AND METHODS

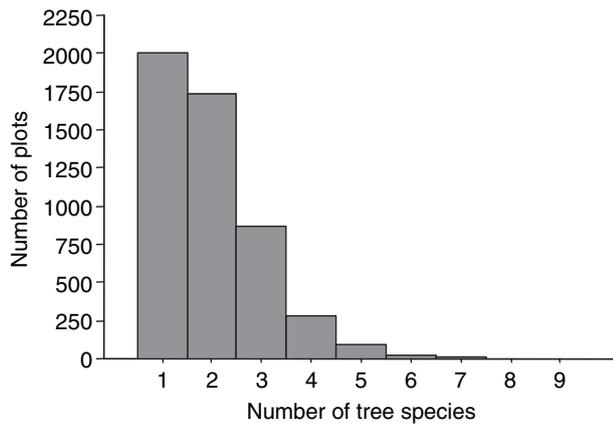
### Study area

Catalonia (ca. 31 900 km<sup>2</sup>) is located in the NE of the Iberian Peninsula, bounded in the north by the Pyrenees and in the east by the Mediterranean Sea. It is situated between 0°15'E and 3°15'E and 40°30'N and 42°40'N. Catalonia is the second most forested region of Spain (36% of its area being covered by forests) and the one with the most acute climatic gradient. There is a climatic-topographic gradient from the Pyrenees to the north with a temperate-alpine climate to a Mediterranean climate to the south. A continental semi-arid gradient can also be observed from the coast to inland. Overall, Catalonia encompass a large climatic gradient: mean annual precipitation ranges from 350 to 1500 mm, average winter (January) temperatures range from –2.4 to 9.5 °C and mean summer (July) temperatures from 6.6 to 27 °C. Therefore, forests account for a large phyto-geographic region, including Mediterranean, sub-Mediterranean, Eurosiberian and even Boreoalpine chorology (Ninyerola *et al.* 2000).

### The data set: the National Forest Inventory of Spain (IFN)

The IFN are national-scale extensive forestry databases of periodical forest surveys distributed throughout Spain (Villaescusa & Díaz 1998, Villanueva 2005). For this analysis we used data from fine-grained permanent plots surveyed from 1989 to 1990 (IFN2) and from 2000 to 2001 (IFN3) systematically distributed across the forest area in Catalonia, comprising a total of 8016 plots. According to forestry protocols plot size was not the same in all plots, and was chosen according to tree size in order to guarantee a representative tree size distribution. For the present study we selected only plots with a 15-m planar area radius as they were the most common. This made a total of 5069 plots for analysis.

The IFN2 survey was conducted at the same period and for the same region as the Ecological and Forest Inventory of Catalonia (IEFC) (Vilà *et al.* 2003, Ibáñez *et al.* 2005; Vilà *et al.* 2005). However, the two surveys did not visit the same plots and the methodology did not



**Figure 1** Number of plots with different tree species richness according to the IFN in Catalonia (NE Spain).

follow the same protocol. For example, the IFN2 did not estimate tree age or leaf area index (LAI) as in IEF3 (Gracia *et al.* 2003).

Overall, our analysis includes 51 tree species distributed into 28 genera. The most common species are *Pinus halepensis* L. (dominant in 25% of sampling plots), *P. sylvestris* L. (20%) and *Quercus ilex* L. (14%). Dominance refers to the most common species within a plot in terms of percentage basal area. The number of tree species per plot ranged from one to nine species. Plot frequency decreased monotonically with species richness. Most plots (40%) were monospecific followed by two (35%), three (17%), four (5.5%) and five (1.8%) species mixtures, plots with more than five species were less than 1% (Fig. 1). All species forming monospecific stands, except six only found in a few plots, were also present as dominant species in mixed stands. On average, in mixed plots, dominant species accounted for a basal area > 72% of the total per plot.

For each live stem tree with a diameter at breast height (DBH) of at least 7.5 cm, the species identity was annotated and the height and DBH measured. From each tree species we calculated the volume over bark (VOB):

$VOB = a + b (DBH)^2 H$ , where  $a$  and  $b$  are constants and  $H$  is tree height.

Wood volume (WV) as the volume under bark by the second order equation relating WV with VOB for each species (Ibáñez *et al.* 2005):

$WV = c + d VOB + e VOB^2$  where  $c$ ,  $d$  and  $e$  are constants

Wood biomass ( $B$ ) estimated as:

$B = WV \times Dw$ , where  $Dw$  is tree wood species density.

Stemwood production per stem was estimated as:

$WP = (Bs_3 - Bs_2)/t$ , where  $(Bs_3 - Bs_2)$  is the increase in biomass of surviving trees measured in IFN2 and still alive in IFN3, and  $t$ , the time elapsed between the two surveys.

Finally, total stemwood production per plot (wood production, hereafter) was estimated as:

$WP_t = \sum WP + Bn_3/t$  where  $Bn_3$  is the biomass of established new trees in IFN3. Detailed information on survey data analysis can be found in Ibáñez *et al.* (2005).

### Selection of independent variables and statistical analysis

As only 1.8% of the plots had five species and 1% had more than five species, for analysis we pooled all plots with five and more than five tree species (Fig. 1). Species richness was considered a categorical variable ranging from 1 to  $\geq 5$  species/plot. Tree species were classified as deciduous, coniferous or sclerophyllous (Table 1). Therefore, functional group richness ranged from 1 to 3.

To test if tree species and functional group richness on wood production differ between tree functional group identities, we conducted two two-way ANOVA: one on the effect of species richness and the functional group identity of the dominant tree species as fixed factors, and another on the effect of functional group richness and the functional group identity on wood production. The Fisher test was used to compare pair-wise significant differences in wood production.

To test if the effect of biodiversity was confounded with the effect of other explanatory variables, we selected the following environmental, forest structure and management variables. As potential environmental explanatory variables we selected the current annual evapotranspiration (AET) as the Thornthwaite index (Thornthwaite 1948), bedrock type, spring solar radiation and slope. We did not use specific climatic parameters (e.g. mean annual temperature, annual precipitation) because they are correlated with AET ( $r > 0.7$ ); altitude was also highly correlated ( $r = -0.98$ ) with AET. In Catalonia AET is represented by seven categories: (1) dry subhumid, (2) subhumid, (3) humid I, (4) humid II, (5) humid III, (6) humid IV and (7) hyperhumid. Nine bedrock types were classified according to a simplification of the hydrogeological map of Catalonia: (1) marls, (2) sandstones, (3) limestones, (4) unconsolidated alluvium materials, (5) consolidated alluvium materials, (6) clays and silts, (7) silicic, (8) volcanic and (9) others. Total spring solar radiation was chosen as a measure of local environmental variation because in Mediterranean regions water stress is very much dependent on radiation (Sala & Tenhunen 1984). Total spring solar radiation was calculated by a model on the basis of latitude, longitude, altitude, slope, aspect, the percentage of visible sky and the mean monthly cloud cover of the region. These environmental parameters were obtained at the Climatic Map of Catalonia website (<http://magno.uab.es/atles-climatic>).

As forest structure explanatory variables we tested the effect of current shrub cover, tree stem density and initial

**Table 1** Total wood production (mean  $\pm$  SE) in t ha<sup>-1</sup> year<sup>-1</sup> for monospecific and mixed forests dominated by particular tree species in Catalonia (NE Spain) according to the IFN. Significant differences within species with more than 10 replicates were tested with a *t*-test

Species	Type	Monospecific	Mixed	<i>t</i>
<i>Abies alba</i>	Conifer	2.36 (1)	2.03 $\pm$ 2.21 (2)	
<i>Acer campestre</i>	Deciduous		1.76 $\pm$ 0.57 (5)	
<i>Acer monspessulanum</i>	Deciduous	-0.002 (1)		
<i>Acer opalus</i>	Deciduous		0.58 $\pm$ 0.70 (5)	
<i>Alnus glutinosa</i>	Deciduous	1.10 (1)	3.22 $\pm$ 0.44 (3)	
<i>Arbutus unedo</i>	Sclerophyllous	0.81 $\pm$ 0.52 (2)	1.02 $\pm$ 0.85 (7)	
<i>Betula</i>	Deciduous	0.66 $\pm$ 0.20 (4)	0.94 $\pm$ 0.35 (8)	
<i>Betula pendula</i>	Deciduous	0.74 (1)	1.83 $\pm$ 0.51 (7)	
<i>Castanea sativa</i>	Deciduous	4.22 $\pm$ 0.75 (9)	1.99 $\pm$ 0.28 (25)	
<i>Cedrus atlantica</i>	Conifer		8.60 (1)	
<i>Celtis australis</i>	Deciduous		0.31 (1)	
<i>Corylus avellana</i>	Deciduous		1.47 $\pm$ 0.41 (7)	
<i>Crataegus monogyna</i>	Deciduous		1.96 $\pm$ 0.22 (2)	
<i>Eucalyptus camaldulensis</i>	Sclerophyllous	2.03 (1)	1.00 $\pm$ 0.14 (3)	
<i>Fagus sylvatica</i>	Deciduous	2.12 $\pm$ 0.37 (17)	2.51 $\pm$ 0.15 (76)	0.11 n.s.
<i>Fraxinus angustifolia</i>	Deciduous		1.52 $\pm$ 0.44 (4)	
<i>Fraxinus excelsior</i>	Deciduous	1.96 $\pm$ 1.45 (3)	0.76 $\pm$ 0.26 (11)	
<i>Larix decidua</i>	Conifer	3.53 (1)		
<i>Olea europaea</i>	Sclerophyllous	0.32 $\pm$ 0.21 (2)	-0.45 $\pm$ 0.50 (4)	
<i>Pinus halepensis</i>	Conifer	0.77 $\pm$ 0.03 (821)	1.32 $\pm$ 0.05 (439)	11.89***
<i>Pinus nigra</i>	Conifer	1.12 $\pm$ 0.06 (227)	1.30 $\pm$ 0.04 (494)	3.22**
<i>Pinus pinaster</i>	Conifer	2.40 $\pm$ 0.42 (17)	1.89 $\pm$ 0.155 (59)	1.15 n.s.
<i>Pinus pinea</i>	Conifer	0.81 $\pm$ 0.11 (37)	1.16 $\pm$ 0.06 (128)	3.18**
<i>Pinus radiata</i>	Conifer	4.37 $\pm$ 1.85 (2)	2.46 $\pm$ 0.135 (2)	
<i>Pinus sylvestris</i>	Conifer	1.59 $\pm$ 0.05 (418)	1.65 $\pm$ 0.04 (591)	1.73*
<i>Pinus uncinata</i>	Conifer	1.42 $\pm$ 0.11 (113)	1.97 $\pm$ 0.20 (54)	2.61**
<i>Pistacia terebinthus</i>	Sclerophyllous		0.29 (1)	
<i>Platanus hispanica</i>	Deciduous	4.01 $\pm$ 0.64 (3)	4.43 (1)	
<i>Populus alba</i>	Deciduous	0.14 (1)		
<i>Populus nigra</i>	Deciduous	1.60 (1)	1.98 $\pm$ 0.33 (2)	
<i>Populus tremula</i>	Deciduous	0.47 (1)	2.27 $\pm$ 0.40 (9)	
<i>Populus × canadensis</i>	Deciduous	4.69 $\pm$ 3.29 (2)	0.12 $\pm$ 0.15 (2)	
<i>Prunus</i>	Deciduous	0.25 (1)		
<i>Pseudotsuga menziesii</i>	Conifer		5.68 $\pm$ 1.72 (4)	
<i>Pyrus</i>	Deciduous	0.85 (1)		
<i>Quercus canariensis</i>	Deciduous		3.31 (1)	
<i>Quercus faginea</i>	Deciduous	0.55 $\pm$ 0.15 (18)	1.19 $\pm$ 0.15 (50)	3.16**
<i>Quercus pubescens</i>	Deciduous	0.73 $\pm$ 0.11 (40)	1.18 $\pm$ 0.09 (134)	3.24**
<i>Quercus ilex</i>	Sclerophyllous	1.01 $\pm$ 0.07 (131)	1.35 $\pm$ 0.04 (562)	4.72***
<i>Quercus petraea</i>	Deciduous	0.74 $\pm$ 0.20 (20)	1.54 $\pm$ 0.10 (84)	4.03***
<i>Quercus pyrenaica</i>	Deciduous		0.83 (1)	
<i>Quercus robur</i>	Deciduous		1.13 $\pm$ 0.37 (10)	
<i>Quercus suber</i>	Sclerophyllous	0.88 $\pm$ 0.09 (104)	0.91 $\pm$ 0.06 (209)	0.94 n.s.
<i>Robinia pseudacacia</i>	Deciduous		0.95 $\pm$ 0.87 (2)	
<i>Salix</i>	Deciduous	0.26 (1)	1.89 (1)	
<i>Salix atrocinerea</i>	Deciduous		6.08 $\pm$ 2.44 (3)	
<i>Sorbus aria</i>	Deciduous		0.33 (1)	
<i>Tilia</i>	Deciduous	0.45 (1)		
<i>Tilia cordata</i>	Deciduous		0.71 (1)	
<i>Ulmus minor</i>	Deciduous		1.28 (1)	

n.s., not significant; \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001.

tree basal area. As a management parameter we included whether there had been any sign (yes or no) of stem removal during the two dates of survey. Wood removal was assessed by the presence of stumps.

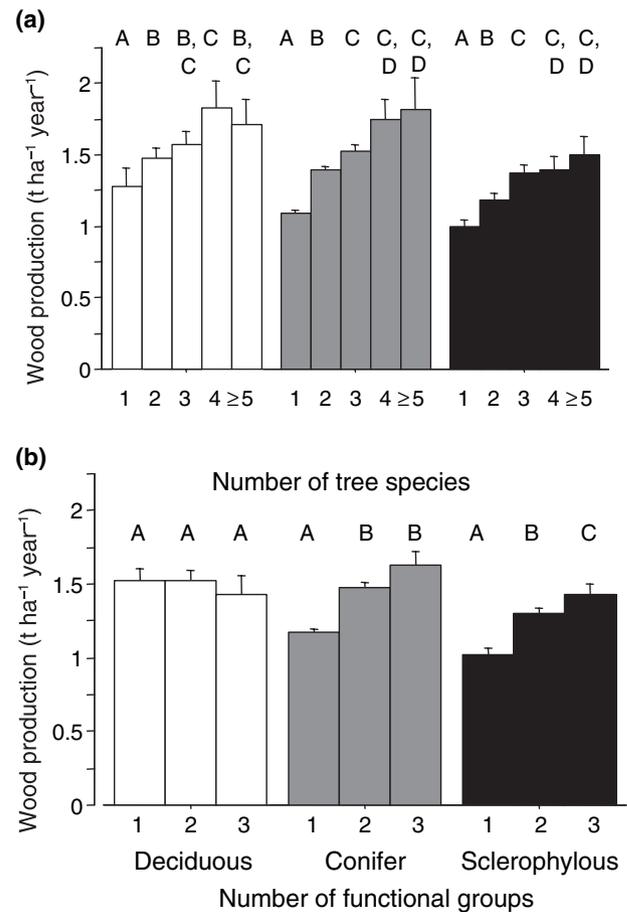
The effect of tree species and functional group richness, functional group identity and the above-mentioned environmental and forest structure factors on wood production was analysed by a general linear model approach (StatSoft, Inc. 2001) with sequential type I sums of squares (Schmid *et al.* 2002). Due to highly unbalanced data it was not possible to test for all the interactions between the dependent variables. However, we analysed if there was an interaction between basal area and species richness on productivity with an ANCOVA; between species richness and wood removal, and between species richness and AET with two-way ANOVA.

## RESULTS

On average, mixed forests had 30% more wood production than monospecific stands ( $t$ -test = 14.28,  $P < 0.0001$ ). For eight particular dominant species out of 13 we found mixed forests to have higher wood production than monospecific stands, lower wood production in only one species (*Castanea sativa*) and nonsignificant differences in four species (Table 1). The increase in wood production from monospecific to mixed forests ranged from 23.42% (two species per plot) to 48.86% (five species per plot).

Tree species richness had a positive effect on wood production when considering the three types of forests dominated by either sclerophilous, deciduous or conifer species (two-way ANOVA,  $F_{4,4843} = 30.81$ ,  $P < 0.0001$ ). Wood production was also significantly different between dominant tree functional group identities (two-way ANOVA,  $F_{2,4843} = 10.81$ ,  $P < 0.0001$ ). Forests dominated by deciduous tree species had the highest wood production (Fisher test,  $P < 0.0001$ ) and there were no significant differences between coniferous and sclerophilous forests (Fisher test,  $P = 0.15$ ). The interaction between tree species richness and functional group identity was nonsignificant ( $F_{8,4843} = 0.93$ ,  $P = 0.49$ ) indicating a positive relationship between tree species richness and productivity independently of tree functional group identity (Fig. 2a).

Similarly, plots with two and three functional groups had 19.09 and 24.39% more production than plots with only one functional group. Tree functional group richness also had a positive effect on wood production (two-way ANOVA,  $F_{2,4845} = 20.01$ ,  $P < 0.0001$ ). However, the interaction between functional group richness and the identity of the dominant functional group was significant ( $F_{4,4845} = 3.69$ ,  $P < 0.0001$ ): wood production increased steadily with functional group richness in sclerophilous forests; it did not differ between two and three functional groups in



**Figure 2** Wood production (mean + SE) for forests of increasing tree species richness (a) and functional group richness (b) dominated by deciduous (white), conifers (grey) and sclerophilous (black) trees in Catalonia (NE Spain) according to the IFN. Different letters above columns indicate significant differences among species or functional richness according to pair-wise Fisher tests.

conifer forests and was not significant in deciduous forests (Fig. 2b).

When environmental and forest structure variables were included in the model, tree species richness and functional group identity still remained significant but not functional group richness. Stem density, total basal area, wood removal, AET and slope had a significant positive effect on wood productivity, while radiation had a negative effect. Shrub cover had a nonsignificant effect (Table 2). While environmental and forest structure variables explained 13.2 and 40.6% of the variation of the model respectively; species richness explained 4.7% only.

On average, mixed forests had higher stem densities than monospecific forests ( $F_{4,5010} = 76.29$ ,  $P < 0.0001$ ). However, there was not a significant difference in stem density between plots with three, four, five or more than five tree

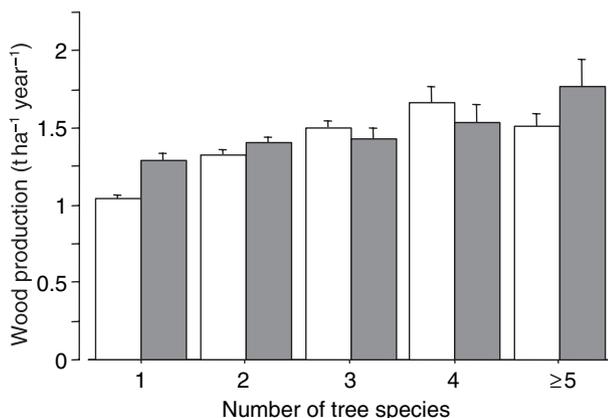
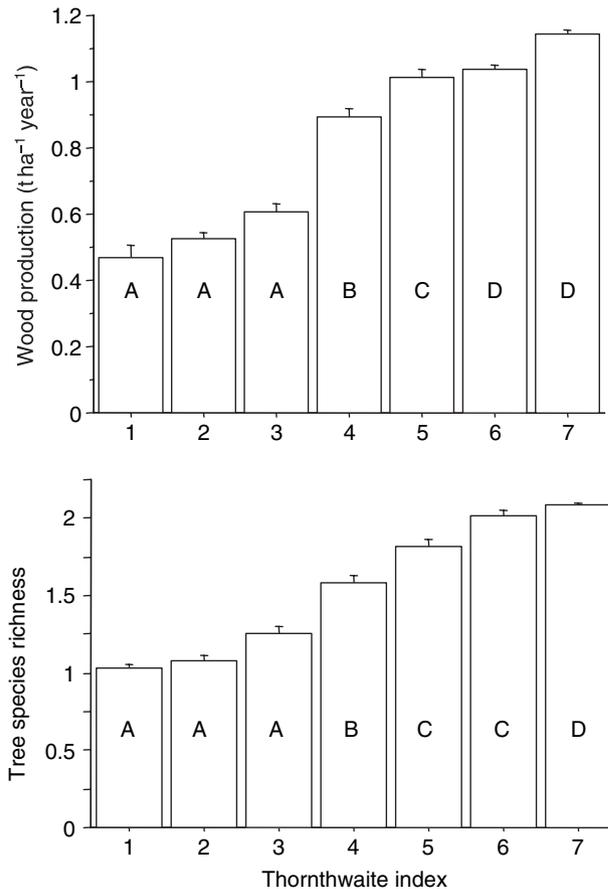
**Table 2** General linear model of environmental and biotic effects on tree wood production in Catalonia (NE Spain) forests according to the IFN

Source	d.f.	<i>F</i> -ratio	<i>P</i> -value
Tree richness	4	5.05	0.0005
Tree functional identity	2	195.21	< 0.0000001
Functional group richness	2	0.38	0.683
Stem density	1	839.03	< 0.0000001
Total basal area	1	7.08	0.008
Shrub cover	1	3.14	0.076
Wood removal	1	19.87	0.0000008
AET Thornthwaite	6	33.08	< 0.0000001
Bedrock type	8	4.57	< 0.000014
Slope	1	60.65	< 0.0000001
Radiation	1	60.06	< 0.0000001

AET, annual evapotranspiration.

species (Fisher test,  $0.288 \leq P \leq 0.933$ ). There was an interaction between total basal area and tree richness ( $F_{4,7715} = 15.53$ ,  $P < 0.0001$ ) indicating an increase in the intercept and a decrease in the slope in the regression lines between total basal area and productivity with increasing tree species richness.

One-third of plots had signs of harvested wood. Surprisingly, the frequency to which a forest had wood harvested increased steadily with tree species richness (i.e. 20% in monospecific plots to 45% in plots with  $\geq 5$  species). There was also an interaction between wood removal and tree richness ( $F_{4,4848} = 5.74$ ,  $P < 0.0001$ ) indicating that the effect of wood removal on wood production was dependent on tree richness: it was positive in both monospecific and highly species-rich plots (Fig. 3).

**Figure 3** Wood production (mean + SE) depending on wood removal for forests of increasing tree species richness in Catalonia (NE Spain) according to the IFN. White bars: no wood removal; grey bars: wood was removed.**Figure 4** Wood production (mean + SE) and tree species richness in relation to climate for forests in Catalonia (NE Spain) according to the IFN. Different letters inside columns indicate significant differences among Thornthwaite index categories according to pair-wise Fisher tests. Thornthwaite index categories: (1) dry subhumid, (2) subhumid, (3) humid I, (4) humid II, (5) humid III, (6) humid IV and (7) hyperhumid.

Similar to wood production, tree species richness also increased with AET (Fig. 4). However, there was no interaction between AET and species richness on wood production ( $F_{4,4848} = 0.81$ ,  $P = 0.679$ ), indicating that the positive association of wood production on species richness followed the same pattern independent of climate type.

## DISCUSSION

Several authors have stressed that studies of diversity-productivity relationships should be carried out across communities, taking into account environmental variability and using direct measurements (Bengtsson *et al.* 2002; Whittaker & Heegaard 2003). We found that in most forests, mixed forests had higher wood productivity than monospecific forests, and wood production was positively

associated with tree species richness. These results agree with the dominance of positive, monotonic productivity–plant species richness relationships found in data sets of regional extent (Gillman & Wright 2006).

Species richness has been the most common measure of biodiversity in biodiversity–ecosystem function studies. However, although ecosystem processes are closely related to plant functional traits, few field studies have disentangled the effect of species richness from the effect of functional richness (Hooper *et al.* 2002). We found that the association between tree species richness was more prevalent than that of functional group richness. The functional identity of the dominant tree species was more important than functional richness. In fact, the high productivity of deciduous forests is not affected by the addition of new functional groups into the community; on the contrary, the low productivity of sclerophyllous forests increases with the presence of the other functional groups. These differences in dominance and productivity would result from a better success of high light-use efficiency in short leaf longevity species (i.e. deciduous) in temperate climate conditions vs. a high success of drought-resistant, long leaf longevity species (i.e. sclerophyllous) in xeric Mediterranean conditions.

Furthermore, our analysis points to the role of composition of the dominant trees in determining productivity, and that the effect is not universal for all forest types (Wardle *et al.* 2000). A significant increase in wood production with mixing occurred in 62% of the forests belonging to *Pinus* and *Quercus* genera, it was nonsignificant in 31% (i.e. two *Pinus*, *Fagus sylvatica* and *Q. suber*) and negative in *Castanea sativa* forests. Therefore, with the observed patterns we cannot establish common life-history traits underlying an increase in wood production with diversity.

The influence of functional identity on wood production indicates a potential selection or sampling effect in the observed productivity–diversity relationship (Huston 1997). That is, the observed increase in wood production with tree richness is caused by increased probability to contain highly productive species when richness is high. In our study case, the presence of deciduous species might be the ones having a disproportionate effect on forest productivity.

The positive tree species richness–wood production relationship was still significant when environmental factors acting at the regional (AET, bedrock type) and local scale (slope, radiation), and forest structure parameters (tree basal area and shrub cover) were taken into account. The variation explained by the full model (46%) as well as by particular predictor variables was low, especially species richness (< 5%). This is, however, typical for analysis of large-scale surveillance data, appropriate goal of which is signal detection rather than explaining as much variation in the data as possible (Moller & Jennions 2002; Petit *et al.* 2004).

As expected, climate and AET influenced productivity (Richerson & Lum 1980; Currie & Paquin 1987). In fact, in many studies, AET has been used as a surrogate for productivity. AET is a measure of biologically available energy and is closely related to potential net primary productivity (Rosenzweig 1995). Wood production increased linearly from semiarid to hyper-humid climate types. Lithology type also had a significant effect on wood production. This was an expected result as it can determine soil nutrient and water availability. We have found the highest availability in alluvial, marls and volcanic soils, suggesting that soil age and structure also play an important role in nutrient availability.

At the local scale, productivity was positively related to slope and negatively to radiation. In fact, tree richness is the greatest in highly sloped areas and the lowest in flat areas ( $F_{4,5010} = 12.76$ ,  $P < 0.0001$ ), suggesting that stepped, shady and secluded sites such as cliffs and river fronts are refuges of tree species richness because they have difficult access for human management, and might also escape from disturbances such as wildfires compared with flat areas which are more prone to human intervention.

With regard to biotic factors, forests with high stem density and total basal area were more productive. However, the effect of basal area on productivity was dependent upon tree species richness: a decrease in the slope in the relationship between total basal area and wood production with increasing tree richness indicates that changes in wood production in forests with many tree species rely less on changes in basal area than in monospecific forests.

Unexpectedly, shrub cover did not influence wood production, suggesting that shrubs did not interfere with mature trees, and that environmental factors leading to higher tree performance might also be responsible for better shrub development (Vilà *et al.* 2005).

Overall, our results match species diversity–productivity patterns found in other parts of the world. For example, in Australia, Specht & Specht (1993) found a positive relationship between overstorey species (trees and tall shrubs) richness and canopy annual shoot growth. In Australia, the number of species increased with improving moisture balance (i.e. increase in the amount of annual radiation, reduction in aridity and duration of the growing season) indicating that productivity is also influenced by climate.

It is important to note that our study, while supporting a positive influence of diversity on productivity, does not demonstrate causality. We are concerned that the positive tree richness–productivity relationship that we observed within and across forest types could be confounded with other untested factors such as successional stage and canopy closure (Elliott & Swank 1994; Ryan *et al.* 1997; Murty &

McMurtrie 2000), or possibly both factors are limited by the same resources as in the case of other unproductive Mediterranean woody communities (Troumbis & Memtsas 2000). It has been shown that succession plays an important role in determining not only the diversity–productivity relationships but also the mechanisms underlying them. For example, in North American montane conifer forests, although canopy closure is positively related to tree diversity, there is evidence of the niche-differentiation species hypothesis acting only during the initial stages of stand development (DeClerck *et al.* 2005).

In a previous data set analysis conducted in Catalonia in which wood production was estimated by measuring tree rings of the last 5 years, we found that the positive diversity–productivity relationship was only evident before canopy closure, that is, for early successional or in physiologically stressed forests (Vilà *et al.* 2005). At advanced successional stages the relationship was not significant probably due to a decline in tree productivity with age (Ryan *et al.* 1997). Unfortunately, our stands comprise a broad environmental heterogeneity and stands cannot be classified along a successional gradient. Furthermore, for this survey we do not have information on stand age or LAI that could be used as surrogates of canopy closure and seral stage. However, the weak but positive correlation between standing biomass and wood production could be considered an indication that the analysed forests are at an early seral stage. In fact, Catalan forests are young: on average they are less than 60 years old (Vilà *et al.* 2005), and probably only in young forests a positive tree richness–productivity relationship is found.

Moreover, historical and management factors might also explain much of the variation in tree species richness and forest productivity. In fact we found that wood removal during the sampling interval increased wood production. However, this effect was idiosyncratically dependent on tree species richness. The Mediterranean Basin has a long history of human intervention (e.g. tree planting, fire, clearing, grazing) that can mask natural spatial and temporal patterns of species dominance, richness and productivity (Casals *et al.* 2005). For example, monospecific *P. halepensis* stands in dry areas have been promoted by seeding for restoration purposes after fire (Casals *et al.* 2005). However, despite these efforts, the extent of mixed forest (60%) surpasses that of monospecific stands as a result of woody colonization of abandoned agricultural lands and a decrease in domestic livestock (Casals *et al.* 2005). Nowadays, most Mediterranean Basin forests are not implicated in wood production and have a low monetary value; however, they have a multifunctional use based on leisure, aesthetics, animal refuge and non-wood products (e.g. cork, pine cones, acorns) (Cesaro *et al.* 1995; Raddi 1998).

Until now most experiments designed to study tree mixture effects on ecosystem functioning have been limited to comparisons between plantations of two-species mixtures, often 50 : 50 ratios, and pure stands (Assmann 1970; Kelty *et al.* 1992; Jones *et al.* 2005; Pretzsch 2005). Therefore, they do not represent the complexities of natural forests. Our analysis should be regarded as complementary to these experiments, supporting that in natural systems, where species assemblages are embedded in an intricate matrix of management scenarios and environmental and disturbance gradients, an increase in tree diversity is most commonly associated with an increase in stand wood production, and this has important implications for carbon offset forestry.

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