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Does tree diversity increase wood production in pine forests?

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Abstract Recent experimental advances on the positive effect of species richness on ecosystem productivity highlight the need to explore this relationship in communities other than grasslands and using non-synthetic experiments. We investigated whether wood production in forests dominated by Aleppo pine (*Pinus halepensis*) and Pyrenean Scots pine (*Pinus sylvestris*) differed between monospecific and mixed forests (2–5 species) using the Ecological and Forest Inventory of Catalonia (IEFC) database which contains biotic and environmental characteristics for 10,644 field plots distributed within a 31,944 km^2 area in Catalonia (NE Spain). We found that in Pyrenean Scots pine forests wood production was not significantly different between monospecific and mixed plots. In contrast, in Aleppo pine forests wood production was greater in mixed plots than in monospecific plots. However, when climate, bedrock types, radiation and successional stage per plot were included in the analysis, species richness was no longer a significant factor. Aleppo pine forests had the highest productivity in plots located in humid climates and on marls and sandstone bedrocks. Climate did not influence wood production in Pyrenean Scots pine forests, but it was highest on sandstone and consolidated alluvial materials. For both pine forests wood production was negatively correlated with successional stage. Radiation did not influence wood production. Our analysis emphasizes the influence of macroenvironmental factors and temporal variation on tree productivity at the regional scale. Well-conducted forest surveys are an excellent source of data to test for the association between diversity and productivity driven by large-scale environmental factors.

Keywords Mediterranean forests · Mixed forest · *Pinus halepensis* · *Pinus sylvestris* · Species richness

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Introduction

Whether species plant diversity increases ecosystem productivity has attracted much attention (Kaiser 2000; Schwarth et al. 2000; Loreau et al. 2001). Field experiments have found that productivity measured as plant biomass increases with species richness (Hector et al. 1999). However, other studies suggest that this relationship might not be due to species richness but to less conspicuous factors, such as differences in soil fertility or to species identity (Huston 1997). Indeed, it has been argued that high diversity stands have a higher probability of containing the most productive species by random draw from the species pool (sampling or selection effect). One more caveat to the study of the diversity-productivity relationship is that almost all studies have been conducted in herbaceous systems. It is time to ask whether this relationship holds in other terrestrial ecosystems.

Some ecosystems such as forests are too complex to test the relationship between diversity and productivity experimentally. In that case, the empirical approach should rely on the exploration of observational field surveys. Globally, monospecific stands and monocultures of the most productive species have been favoured for pulp and timber production. At the same time and in some regions, mixed forests have been maintained for landscape aesthetics, conservation of wildlife, and the belief that they are more resistant to disease and to disturbances such as wind or fire (Kerr et al. 1992). Nevertheless, the concept of a potential increase in productivity in mixed tree stands has not generally been incorporated into forestry and conservation practice (Kelty 1992).

At the local scale, foresters have compared planted monospecific stands with adjacent two-species mixed stands. In temperate forests, there are studies showing that the two-species mixed stands had greater yields than monocultures (Assmann 1970; Polero 1981; Kawahara and Yamamoto 1986) or than the less productive species, but not necessarily greater yields than the best monoculture (Kelty 1992). At the regional scale, diversity-productivity relationships might be confounded by environmental factors. For example, extensive surveys in the tropics have found that tree diversity is related to soil nutrients (Huston 1980) and annual rainfall (Gentry 1982) in a hump-backed-type relationship. It is thus necessary to account for environmental factors when relating tree diversity to tree productivity.

Pine-dominated forests are very common in the Mediterranean Basin (Barbéro et al. 1998). We studied *Pinus halepensis* and *Pinus sylvestris* forests, the two major pine species in Catalonia. The area of distribution of these species is large due to their biological traits (i.e. high seed productivity at early age and good germination after fire for *P. halepensis*) and changes in land use (Barbéro et al. 1998). Both species are colonizing the increasing extension of abandoned fields and grasslands in Catalonia. The expansion of these two species is also attributable to the reinforcement of reafforestation programs that were conducted during the second half of the last century. Most of these pine forests form mixed forests with other tree species, for instance *P. halepensis* with *Quercus ilex* and *P. sylvestris* with *Quercus humilis*. In this study we compare wood production between monospecific and mixed stands. Data were analysed from the Ecological and Forest Inventory of Catalonia (IEFC), which is an extensive database on the forests of Catalonia. The dataset allows us to relate wood production at the stand level to species richness and certain environmental parameters.

Materials and methods

Study area

Catalonia (ca. 31,900 km^2) is located in the northeast 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 longitude and 40°30'N and 42°40'N latitude. There is a climatic-topographic gradient from the Pyrenees to the south with a temperate-boreal climate to a Mediterranean climate with mild winters (January mean minimum temperature of 1.5°C) and warm dry summers (July mean maximum temperature of 28.8°C). Mean annual precipitation ranges from 530 to 1,500 mm. In the extensive Mediterranean area there is a continental, semi-arid tendency inland towards the west, with cold winters (January mean minimum temperature of −2°C) and very hot summers (July mean maximum temperature of 33.5°C), and low rainfall (350–650 mm).

The data set: the IEFC database

The IEFC database is extensive and includes the customary information of forest inventories and additional data related to functional aspects of forest ecosystems (Gracia et al. 2000–2002; http://www.creaf.uab.es/iefc). The database compiles information from 10,644 sampling plots (10 m radius) randomly distributed throughout the country. Sampling was conducted from 1988 to 1998 at a density of one plot per km^2 of natural or managed forest. The IEFC database includes observations on 95 tree species from 43 genera. The most dominant species are *Pinus halepensis* (present in 20% of sampling plots), *P. sylvestris* (19%) and *Quercus ilex* (16%). Recently, the IEFC dataset has incorporated complementary topographic, climatic and geological data for each plot.

For each tree with a diameter at breast height (DBH) above 5 cm, its species identity was annotated and the height and DBH measured. When more than five tree species occurred within the same sampling plot (this represents less than 5% of the plots), only the five most abundant species were recorded. In all plots, for each representative tree species (one or more) of a diameter class >5 cm a tree core was sampled to calculate age and annual tree growth over the last 5 years. Plot wood production per year was calculated as $P=(B_5–B_0)/5$, where B_0 is the plot wood biomass per area 5 years before sampling and B_5 is the plot wood biomass per area during the sampling. Wood biomass (B) was estimated using the allometric equation:

$B=\pi(\mathrm{DBH}/2)^2\ HKD_{\mathrm{w}}$ where DBH is the tree diameter without bark at breast height, H is the tree height, K is the tapering and D_{w} the wood density.

For this study we selected only plots in which the dominant (basal area >25% of the total per plot) species was *P. sylvestris* (408 plots) or *P. halepensis* (447 plots) and for which we had environmental data (see below). Dominance of *P. sylvestris* ranged from 38.6% to 100% of total basal area, and dominance of *P. halepensis* from 26.7% to 100%.

Study species

P. sylvestris L. (Pyrenean Scots pine) and *P. halepensis* Mill. (Aleppo pine) are fast-growing, non-resprouting trees widely distributed both in temperate-boreal Europe-Asia and the Mediterranean Basin (Richardson and Rundel 1998). These two species have complementary distributions in Catalonia determined by the environmental conditions they require and by the influence of humans over thousands of years. *P. halepensis* is a thermophilous species distributed over the whole area except in the north and in the west. *P. sylvestris* is distributed in the Pyrenees mountains (north of Catalonia) and in three mountainous areas further south. According to the IEFC, plots dominated by *P. halepensis* are located from sea level to 870 m. In contrast, *P. sylvestris* plots are located from 110 to 1,990 m above sea level.

Statistical analysis

Because the number of species per plot only ranged from one to five, its effect on plot wood production was first analyzed by a one-way ANOVA for each pine species with the number of species as the main effect. However, when comparing tree mixtures with pure stands across sites, we had to take into account the following key factors known to influence tree productivity: (1) the total tree density or size of the stand should be held constant, (2) the successional stage should not differ between stands, and finally (3) the patterns should not be confounded with environmental gradients.

To account for differences in tree density we used wood production/basal area ratio (P/BA hereafter) instead of wood production as the dependent variable. Information on the successional stage of the plot was not gathered, but we used the age of the oldest tree sampled as a substitute for it. To test for the effect of confounding environmental gradients, we selected three integrative parameters: climate type, bedrock type and total spring solar radiation. Climate type and bedrock type were used as the main variables of regional environmental conditions. Each plot was assigned to one of the nine climate categories of the Thornthwaite index (Thornthwaite 1948) and to one of the seven bedrock types according to a simplification of the hydrogeological map of Catalonia. The bedrock types are: (1) marls, (2) sandstones, (3) limestones, (4) unconsolidated alluvium materials, (5) consolidated alluvium materials, (6) clays and silts and (7) 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 and Tenhunen 1984; Chaves and Rodrigues 1987). Total spring solar radiation was calculated by a model on the basis of latitude, longitude, altitude, slope, aspect and the percentage of visible sky and the mean monthly cloud cover of the region (Gracia et al. 2000–2002). We deliberately chose not to include those single environmental parameters influencing radiation because our purpose was not to predict wood production but to assess if there was an association between species richness and wood production independent of confounding abiotic effects.

The effect of species richness, climate type, bedrock type, radiation and successional stage on plot P/BA for each pine species plot was analyzed by a general linear model approach, following the JMP package (Anonymous 1992) which gives the significance of each effect using F-tests calculated after removing each effect from the whole model. A model that included all five independent variables was built for each pine species plot.

If mixed forests had higher productivity than monospecific plots, we tested whether the dominant pine species, *P. halepensis* and *P. sylvestris*, would do better in the mixed forests than in monocultures by calculating the proportional deviation of pine wood production of each dominant pine species from its expected value as $D\text{i}=(O\text{i}-E\text{i})/E\text{i}$, where Oi= the observed wood production and Ei= proportion of the basal area of the pine in the plot × the average wood production in monospecific plots. A value of Di=0 means that the presence of other species does not modify wood production, Di>0 means that the other species have a positive effect on pine wood production, and Di<0 means that the other species have a detrimental effect on pine wood production (Loreau 1998).

Results

The most common tree species found in association with *Pinus halepensis* were *Quercus ilex* (38. 2%), deciduous oaks (21.2%), *P. nigra* (12.3%) and *P. pinea* (12.2%). Species richness when considered alone had a significant effect on wood production ($F_{4,\ 442}$ =9.85, P<0.0001) and on P/BA ($F_{4,\ 442}$=4.97, P<0.0006). Wood production was greater in forests with two or more species than on monospecific stands (Scheffé-test, 0.001>P<0.037) (Fig. 1). The proportional deviation of *P. halepensis* wood production from its expected value in mixed plots was significantly higher than zero ($F_{4,\ 442}$=10.43, P=0.0001) but the proportional deviation was not significantly different among plots with two or more species ($F_{4,\ 260}$=1.33, P=0.26).

Nevertheless, the general linear analysis revealed that species richness had a non-significant effect on P/BA when other variables were included in the model ($F_{4,\ 406}$=0.78, P=0.54) (Table 1). The same result was found when comparing wood production values that were not corrected for basal area ($F_{4,\ 406}$=1.01, P=0.4). In contrast, climate and bedrock type influenced P/BA (Table 1). P/BA decreased significantly from semiarid plots to humid plots (Fisher test, 0.0001>P<0.012). P/BA was significantly lower on consolidated alluvial materials, limestones, clays and silts than on marls and sandstones (Fisher test, 0.008<P<0.05). Radiation had a non-significant effect on P/BA (Table 1). There was a negative correlation between successional stage and P/BA (Spearman rank correlation, R_{ho}=−0.35, P<0.0001). The model explained only 29% of the total deviance.

For *P. sylvestris* mixed forests were dominated by deciduous oaks (27.6%), *Q. ilex* (14.1%), *P. nigra* (12.9%) and *P. uncinata* (10%). Species richness when considered alone did not have a significant effect on wood production ($F_{4,\ 403}$=0.79, P=0.53) (Fig. 2) and P/BA ($F_{4,\ 403}$=1.38, P=0.24) nor on the model. Bedrock type had a

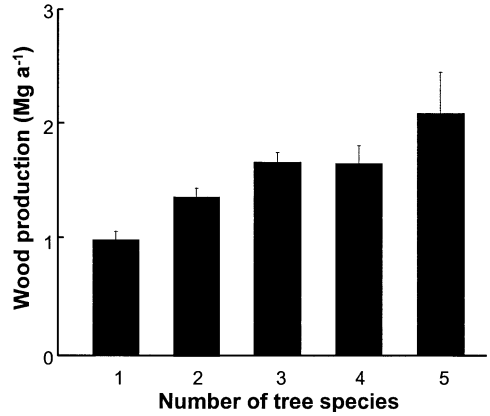

Fig. 1 Wood production (mean + SE) for monospecific and mixed *Pinus halepensis* stands in Catalonia

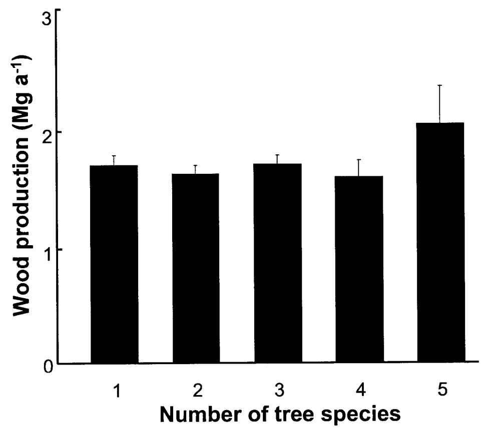

Fig. 2 Wood production (mean + SE) for monospecific and mixed *Pinus sylvestris* stands in Catalonia

Table 1 General linear model of environmental and biotic effects on wood production/ basal area ratio for *Pinus halepensis* and *P. sylvestris* forests in Catalonia

Source	*Pinus halepensis*			*Pinus sylvestris*		
	df	*F*	*P*	*df*	*F*	*P*
Whole model	18	8.94	<0.0001	19	4.41	<0.0001
Partial regressions						
Species richness	4	0.78	0.54	4	0.48	0.75
Climate type	6	12.55	<0.0001	7	1.36	0.22
Bedrock type	6	2.58	0.02	6	3.30	0.003
Radiation	1	0.10	0.75	1	0.60	0.44
Successional stage	1	36.38	<0.001	1	41.71	<0.001

significant effect on P/BA. P/BA was significantly lower in limestones, clays and silts than in sandstones and consolidated alluvium materials (Fisher test, $0.0001<P<0.05$). In contrast, climate type and radiation had no significant effect (Table 1). There was also a negative correlation between successional stage and P/BA (Spearman rank correlation, $R_{ho}=-0.36$, $P<0.0001$). The whole model explained less than 17% of the total deviance.

Discussion

At this regional scale we found that species richness does not affect the productivity of Aleppo pine and Pyrenean Scots forests. In contrast, pine forest productivity is related to environmental parameters and successional stage. Our study area covers a wide climatic, geological and topographic variation and we are certain that our survey was broad enough to include the whole existing range of tree species richness found in Catalan forests. Our results contradict recent analyses of the Forest Inventory and Analysis (FIA) database in the United States that have found a positive relationship between number of species in the canopy and growth and biomass both in early and late successional stands (Caspensen and Pacala 2001). However, that study did not control for other co-varying factors that could underline and confound the diversity-productivity relationship as we have demonstrated.

In an exhaustive review on the observed relationship between vascular plant species richness and productivity, Mittelbach et al. (2001) found that a hump-shaped relationship occurred most frequently. However, the null relationship was found in 36% of the studies at the regional scale and also within community types. Schläpfer and Smith (1999) reviewed studies conducted in forestry systems and concluded that relationships between productivity and richness were small or absent. This is not surprising if we consider that humans have favored monospecific plantations in the best sites in order to increase timber yield and reduce management costs (Kelty 1992). Monospecific plantations, even if unmanaged, can have higher aboveground biomass production than paired secondary forests dominated by the same species but in association with other tree species (Lugo 1992).

Inference recursive modeling between pine distribution and dominance and environmental variables has found that the distribution of pines in Catalonia is largely determined by altitude, and winter and spring rainfall. In contrast, their dominance is more closely related to biotic factors such as the basal area of coexisting *Pinus* and *Quercus* species (Rouget et al. 2001). For example, while the distribution of *P. halepensis* can be predicted by spring rainfall <165 mm and total annual rainfall <670 mm, it is predicted to be dominant when the basal area of other pines is less than 1.25 m^2/ha. Furthermore, according to the analysis, the association between *P. halepensis* and some co-occurring tree species can also be predicted by climatic variables. *P. halepensis* co-exists with *Q. ilex* in plots where annual rainfall is between 668 and 800 mm. In contrast, lower rainfall values determine the dominance of *P. halepensis*. An intensive survey conducted by Zavala et al. (2000) in the Montseny mountains also found that *P. halepensis* dominated in areas with more than 8 months of drought and on south-facing slopes, while mixed *P. halepensis-Q. ilex* forests were present in areas with a drought length between 4 and 8 months and on western and eastern facing slopes.

We found that climate type influenced the productivity of *P. halepensis* but not that of *P. sylvestris* plots. These differences between both species are probably related to a more restricted distribution of *P. sylvestris* in Catalonia compared to *P. halepensis*. More than 60% of the *P. sylvestris* plots are located in humid climate types, while for *P. halepensis* plots are spread between semiarid and humid climate types. At the local scale, radiation, an integrative measure which includes altitude and aspect did not influence tree productivity suggesting that macroclimatic characteristics are more important than local microclimatic variability in explaining patterns of rate of energy flow in these pine forests.

The bedrock type also had a significant effect on wood production in pine forests. This is an expected result as bedrock type can partially determine soil nutrient and water availability. We have found that the highest productivity is found on sandstones, suggesting that soil texture is playing a role in nutrient availability. Most of these sandstones are probably calcareous. More than 80% of *P. sylvestris* forests, which occupy 60% of the Pyrenean woodlands, are distributed on calcareous bedrocks (Pausas and Carreras 1999). Calcareous bedrock soils have a higher cation exchange capacity than soils on silicate bedrocks and this can positively influence the diversity of understorey species (Pausas and Carreras 1995).

Finally, successional stage had a negative effect on wood production. However, successional stage explained less than 16% of wood production variability. Our complete model also had a weak predictive power to explain differences in productivity. Mediterranean pine forests have a long history of human intervention (e.g. tree planting, clearing, fire, grazing) that can mask natural spatial and temporal patterns of pine dominance (Barbéro et al. 1998). For example, monospecific *P. halepensis* plots on poor soils can result from planting. Similarly, large areas of secondary forests dominated by *P. sylvestris* result probably from the harvesting of deciduous trees (mainly *Q. humilis*). These human activities, which might affect stand productivity, could not be reflected in the parameters available in the IEFC database.

In the Mediterranean Basin despite the quite large number of observational studies relating species richness to environmental factors in ecosystems other than grasslands (García et al. 1993; Rey-Benayas and Scheiner 1993; Pausas 1994; Ojeda et al. 1996) few studies have attempted to extrapolate the association between species diversity and ecosystem functioning. Recently, Troumbis and Mentsas (2000) found that Greek shrublands dominated by *Cistus salviifolius* were more productive in stands with a high diversity of other shrub species. Although our study does not confirm this trend we consider that forest inventories can be an excellent tool to test for species diversity-ecosystem functioning relationships at the regional scale (Bengtsson et al. 2002). Regardless of the observational analyses conducted, these forests are not consistent with the general claim that diversity increases ecosystem productivity (Loreau et al. 2001). However, if our goal is to manage forests to preserve biodiversity, species-rich forests have a value of their own, and are not merely a means to serve other functions (Simberloff 1999).

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