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Biodiversity correlates with regional patterns of forest litter pools

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Abstract We compared litter pools of more than 1,000 forests differing in tree species' diversity over a large scale in Catalonia (NE Spain). Monospecific forests always had smaller litter pools than mixed (from 2 to 5 tree species) forests. Whether there was a positive effect beyond two species mixtures depended on the species and functional identity of the dominant tree species. In sclerophyllous forests the positive effect of diversity was a step-function from one to more species. However, in conifers, litter pools increased constantly with tree diversity. The identity of the dominant tree species and functional type had also a significant effect on litter pools. For instance, forests dominated by sclerophyllous tree species had larger litter pools than forests dominated by deciduous and conifer tree species. When other forest structure parameters (i.e. tree basal area, wood production, successional stage, shrub cover and leaf area index) and environmental factors (i.e. mean annual temperature, mean annual precipitation, annual evapotranspiration and hillside position) where included in the analysis only leaf area index, basal area, wood production and mean temperature influenced litter pools positively. Our analysis emphasizes that at the regional scale, the litter compartment can be as influenced by biodiversity components as by other forest structure and climate components. In mixed forests, species and functional identity of the trees determine whether litter pools increase with tree diversity.

Keywords Climate · Mediterranean forests · Mixed forests · Species diversity

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Introduction

Plant species diversity has been examined as a factor influencing decomposition. Most experiments testing the effect of standing plant diversity or litter diversity on decomposition have found that the effect is marginal or idiosyncratic, and there is no general trend (Wardle et al. 1997; Hector et al. 2000; Knops et al. 2001). It has been hypothesized that this absence of a general effect of plant diversity on decomposition results in species diversity causing higher standing litter pools since it implies an increased aboveground biomass production and litter production (Knops et al. 2001). However, this hypothesis remains to be tested.

In forests, litter mixture is likely to be the rule rather than the exception. In forests, most experiments on decomposition only focus on two or three species mixtures and have found that the effects of the species interaction seem to be species specific and mixture specific (Taylor et al. 1989; Blair et al. 1990; Kemmedson 1991; Fyles and Fyles 1993). Forests are too complex to test the relationship between species diversity and ecosystem functioning experimentally. Under these circumstances, the empirical approach mainly relies on observational field surveys. This is not an inconvenience because observational studies show patterns under real environmental and management conditions (Grime 2002). However, unfortunately, correlative evidence alone cannot distinguish cause from effect. In such studies, especially when conducting large-scale observations, it is important to place the effects of species diversity in the context of other factors which can influence ecosystem functioning. For instance, macroclimatic and topographic factors and temporal variation have an overriding effect on ecosystem processes due to their influence on resource supply (Bengtsson et al. 2002; Huston and McBride 2002). For example, an extensive Mediterranean forest survey has shown that the positive relationship between tree richness and wood production is driven by water availability and successional factors (Vilà et al. 2003). Similarly, it has been shown along a moisture gradient in Hawaii that temperature and precipitation have greater effects on litter decomposition than species identity and therefore litter quality (Vitousek et al. 1994).

We present a regional analysis of litter pools in a broad range of forests with the following objectives: (1) To test if forest litter pools are related to tree species richness, tree functional type and/or the identity of the dominant tree species, and (2) To determine which other ecological factors (i.e. forest structure, environmental factors) can influence litter pools. Data were gathered from the Ecological and Forest Inventory of Catalonia (IEFC), which is an extensive database on the forests of Catalonia (NE Spain). Because of its geographical situation, Catalonia contains tree species of the following chorological classes: Mediterranean, sub-Mediterranean, Eurosiberian and Boreoalpine. In an analysis using the IEFC dataset we found that the positive effect of tree species richness on wood production was confounded with differences in climate and successional stage (Vilà et al. 2003). Litterfall is a major component of primary productivity which it is positively correlated with primary productivity. Furthermore, litterfall together with decomposition determine litter pools. Therefore, we expect forest litter pools to be related to wood production but not necessarily to tree species richness.

Materials and methods

Study area

Catalonia (ca. 31,900 km^2) is located in the northeast of Spain, bounded in the north by the Pyrenees and on 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), very hot summers (July mean maximum temperature of 33.5°C) and low rainfall (350–650 mm).

The data set: the Forest and Ecological Inventory of Catalonia

The IEFC is an extensive database that includes the customary information in 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 region. Sampling was conducted from 1988 to 1998 at a density of one plot per km^2 of natural or managed forest. The IEFC includes observations on 95 tree species from 43 genera. Species were regarded as trees according to the Flora Europaea (Tutin et al. 1993) and the Official Journal of the European Communities number L161 (22 June 1987). The most dominant species are *Pinus halepensis* (present in 20% of sampling plots), *P. sylvestris* (19%) and *Quercus ilex* (16%).

Almost three-quarters (73.3%) of the plots are mixed, with tree species richness ranging from two to five species, with a mode of two species mixtures (29.9% of plots) and five species mixtures being the least common (6.2%). All the species forming monospecific stands are also present in mixed stands.

For each live tree with a diameter at breast height (DBH) greater than 5 cm, the species identity was annotated and the height and DBH measured. Plot wood production (*P*) per year was estimated 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 algometric equation:

$$B = \pi(DBH/2)\chi HKD_w \tag{1}$$

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 a subset of plots (n =1,616) in which standing litter pools were assessed once during the forest inventory. In each plot, four 25×25 cm^2 subplots of the L and F soil horizons were collected. Subplots were located on intact soils. We are certain that wood litter proceeding from management practices (i.e. understorey clearing, branch removal, etc) was not enclosed in the litter pool. Each subplot was located at 6 m from the center of the plot oriented at the N, S, E and W positions. Live plant parts (e.g. roots), small stones and humified soil organic matter were sorted out from the litter samples and the litter was then weighed after oven drying at 105°C to constant mass.

Selection of independent variables and statistical analysis

Several tests were conducted to explore the relationship between biodiversity components and litter pools and to answer the following questions:

- Does tree species richness affect litter pools? Because the number of tree species per plot only ranged from one to five species, species richness was considered a categorical variable. We conducted an ANOVA with species richness as the main effect and litter pools as the dependent variable on the whole dataset and also restricting to a subset of data of forests dominated by particular species namely *Quercus ilex*, *Pinus halepensis* and *P. sylvestris*. A dominant tree species was defined as the one with basal area >50% of the total per plot.
- Does tree species richness affect litter pools taking into account functional identity of the dominant tree species? The effect of species richness and the functional type of the dominant tree species (i.e. conifer, sclerophyllous and deciduous) on litter pools was analyzed with a two-way ANOVA.
- Does the identity of the dominant tree species and monospecificity affect litter pools? For this analysis we chose the ten most common and dominant tree species. In this analysis we could not test for the interaction between the identity of the dominant species and tree species richness because there were too many missing cells. Therefore, we used monospecificity as a surrogate for species richness. Monospecificity had two levels: monospecific or mixed (i.e. two or more tree species) plots. The effect of tree species identity and monospecificity was analyzed with a two-way ANOVA.
- Do other forest structure and environmental variables influence litter pools? Is the effect of biodiversity confounded with the effect of other explanatory variables? As forest structure variables, we chose leaf area index, tree basal area, timber productivity, total shrub cover and age of the oldest tree as a surrogate for successional stage. Besides total shrub cover, the IEFC dataset does not provide more precise information on the type and structure of the understorey that could be included in the analysis. Obviously the understorey contributes to the forest litter pool. Plots ranged from 2 to 100% of understorey cover. Plots with shrub cover >80% had significantly more litter pools than plots with less understorey (t -value=2.97, P =0.003). Nevertheless, because on average in Mediterranean forests the aboveground biomass of the understorey is less than 10% of the total aboveground biomass (Ibánez et al. 1999), we are confident that forest litter is mainly composed of tree litter. Furthermore,

there is a positive relationship between number of tree species and shrub cover ($F_{4,2077}$=14.20, P <0.0001). Therefore, we are certain that forest litter pools are not uncoupled from the tree canopy.

To test for the effect of confounding environmental gradients, we selected annual precipitation, mean annual temperature, evapotranspiration (EVT) and hillside position. Because litter pools at the same location are subjected to strong seasonality, we also included the season of sampling per plot as a dependent variable. The climatic and EVT parameters were obtained from the Climatic Map of Catalonia (http://magno.uab.es/atles-climatic). In this map, EVP values are classified into four categories: 427–572 mm, 572–712 mm, 712–855 mm and 855–997 mm. The following seven hillside positions were used: summit, upper hillside, middle hillside, lower hillside, flat, local depression and valley-bottom.

The effect of tree species richness, the functional type of the dominant tree and the above-mentioned forest structure and environmental factors on litter pools per plot was analyzed by a general linear model (GLM) approach, following the JMP software (Anonymous 1992). The GLM allows the inclusion of continuous and categorical variables in the model. The model gives the significance of each variable using F -tests calculated after removing each variable from the whole model. In this analysis species richness was included as a continuous variable. Due to highly unbalanced data it was not possible to test for interactions between the dependent variables.

Results

Does tree species richness affect litter pools?

Litter pools ranged from 0 Mg ha^{-1} to 56.08 Mg ha^{-1}. By including the whole dataset we found that species richness had a significant effect on litter pools ($F_{4,1610}$=12.44, P <0.0001). Mixed forests have larger litter pools than monospecific stands (Fisher's PLSD, P <0.0001). However, there were not significant differences between plots with two or more tree species (Fisher's PLSD, 0.06< P <0.91) (Fig. 1).

Tree species richness had also a significant effect on litter pools in forests dominated by *P. sylvestris* ($F_{4,232}$=3.87, P =0.005), *P. halepensis* ($F_{4,\ 379}$=3.08, P =0.02) and by *Q. ilex* ($F_{4,255}$=2.81, P =0.03). In *P. sylvestris* forests, monospecific stands had the smallest litter pools and stands with five tree species, the largest. In *P. halepensis* forests, monospecific and two species stands had smaller litter pools than stands with three or four tree species, and finally in *Q. ilex* forests, monospecific stands had smaller litter pools than two or three tree species forests (Fig. 2).

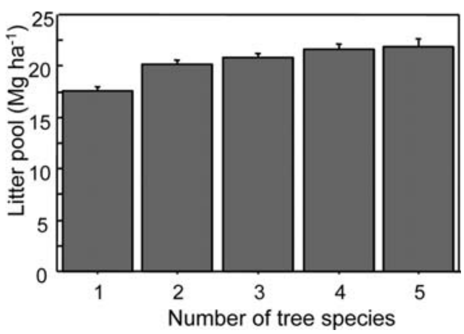

Fig. 1 Litter pools (mean + SE) for monospecific and mixed forests in Catalonia (NE Spain) according to the Forest and Ecological Inventory of Catalonia (IEFC)

Does tree species richness affect litter pools when taking into account functional identity of the dominant tree species?

Tree species richness continued to have a positive effect on litter pools when considering the functional identity of the dominant species ($F_{4,1601}$=7.22, P <0.0001). Mixed forests had larger litter pools than monospecific forests (Fisher's PLSD, P <0.0001). Forests dominated by sclerophyllous tree species, namely *Quercus ilex*, *Q. suber*, *Eucalyptus globulus*, *Ilex aquifolium* and *Arbutus unedo* had larger litter pools than forests dominated by deciduous and conifer trees ($F_{2,1601}$=8.52, P =0.0002) (Fig. 3). The interaction between tree species richness and functional type was not significant ($F_{8,1601}$=0.96, P =0.46)

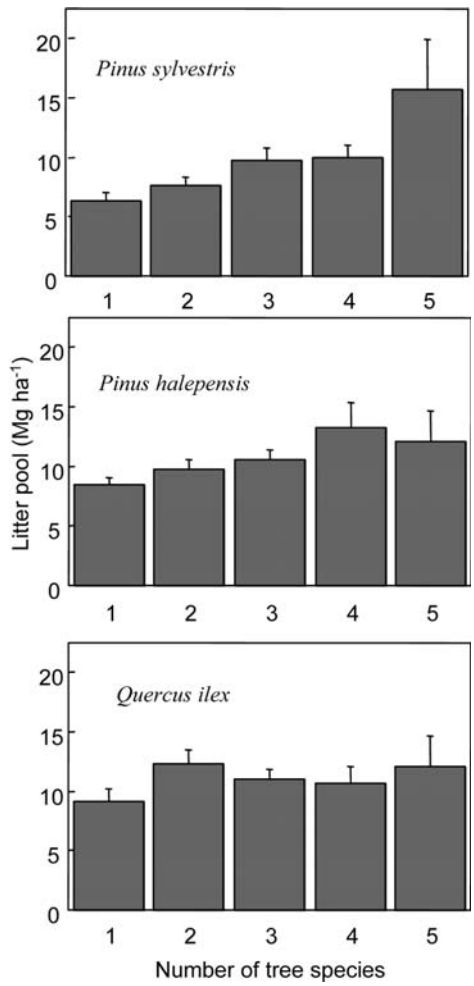

Fig. 2 Litter pools (mean + SE) for monospecific and mixed forests dominated (i.e. basal area >50% in 10 m radius plots) by the three most common tree species, *Pinus sylvestris*, *P. halepensis* and *Quercus ilex* in Catalonia (NE Spain) according to the IEFC

meaning that the effect of species richness was independent on functional identity. However, when each functional type was analyzed separately we found that in deciduous forests species richness had a non-significant effect on litter pools ($F_{4,238}$=0.67, P =0.61), in sclerophyllous forests the effect was merely a step-function from one to more than one species ($F_{4,377}$=5.28, P =0.0004) and in conifer forests monospecific forests had less litter pools than two species forests and the highest values were found in forests with four and five tree species ($F_{4,\ 985}$=8.91, P <0.0001) (Fig. 3).

Does the identity of the dominant tree species and monospecificity affect litter pools?

When grown in monoculture, forests differed widely in their litter pools ($F_{9,407}$=2.45, P=0.01). On average for the forests dominated by the ten most common tree species, mixed forest had larger litter pools than monospecific stands ($F_{1,1382}$=13.44, P =0.0003) (Fig. 4).

Do other forest structure and environmental variables influence litter pools?

When several forest structure and climatic variables were included in the model, only tree functional type (marginal effect), tree richness, leaf area index, total basal area, wood productivity and mean annual temperature had a significant effect in litter pools (Table 1). However, these parameters explained 13% of the variation in litter pools. Forests with a higher basal area, wood production and leaf area index had larger litter pools (Fig. 5). When mean annual temperature was substituted by mean temperature in spring and autumn, the period in which soil microfauna are more active, the results were not significantly different.

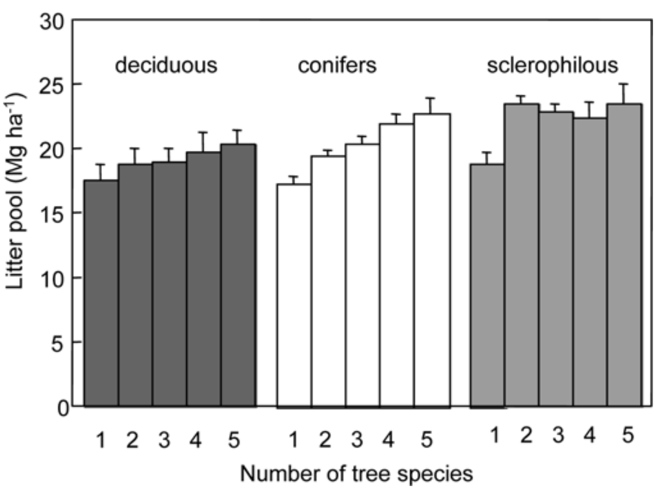

Fig. 3 Litter pools (mean + SE) for monospecific and mixed forests dominated by deciduous, conifers and sclerophyllous trees in Catalonia (NE Spain) according to the IEFC

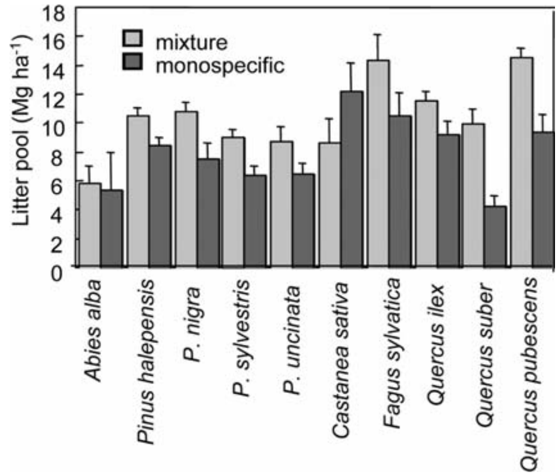

Fig. 4 Litter pools (mean + SE) for monospecific and mixed forests dominated (i.e. basal area >50% in 10 m radius plots) by particular tree species in Catalonia (NE Spain) according to the IEFC

Table 1 General linear model of environmental and biotic effects on litter pools in forests of Catalonia (NE Spain)

Source	*df*	*F* ratio	*P*
Tree richness	1	13.82	0.0002
Tree functional type	2	2.548	0.08
Leaf area index	1	10.73	0.001
Productivity	1	5.08	0.02
Total basal area	1	12.21	0.0005
Shrub cover	1	0.18	0.67
Age	1	0.02	0.89
EVT	3	1.25	0.61
Precipitation	1	0.96	0.33
Mean temperature	1	27.48	<0.0001
Hill site position	6	1.18	0.31
Seasonality	3	1.12	0.34

Discussion

We have found that two tree species mixtures have higher litter pools than monospecific tree stands. However, whether more than two tree species in the stand increase litter pools, depends on the species and functional identity of the dominant tree species. For example, in sclerophyllous forests, species richness effect was a step-function from one to more than one tree species; in conifers there was a positive effect of tree species richness with more than two tree species. We hypothesize that for forests, because not all tree species have overlapping canopies, an increase in forest tree species diversity does not necessarily increase litter pools at a random location within the stand. Probably, mixed forests develop a spatially heterogeneous mosaic of litter mixtures and litter pools depending on the spatial distribution of overstorey and understorey species which might differ among mixed forests types.

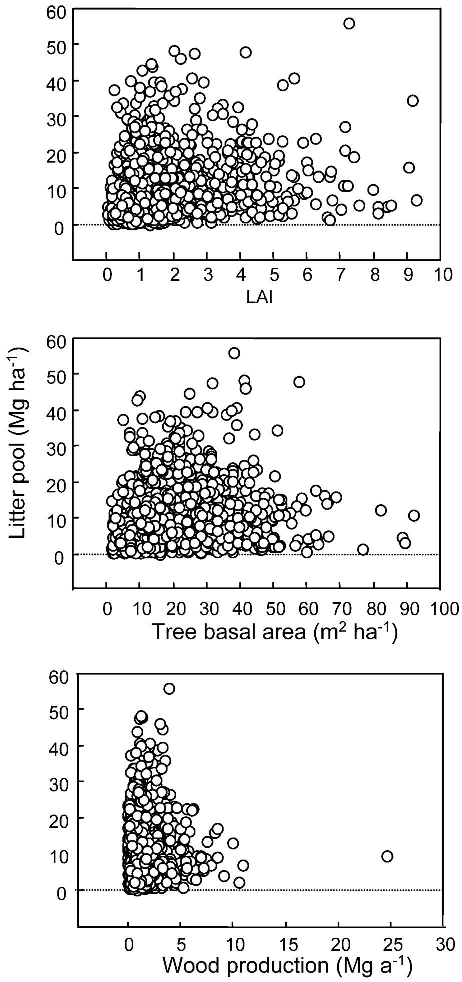

Fig. 5 Relationship between litter pools and leaf area index, plot tree basal area and wood production in Catalan forests according to the IEFC

Besides tree species richness, the identity of dominant trees and functional type also affect influence litter pools. We have found the largest litter pools in sclerophyllous forests. In general, slow growing species tend to incorporate more nutrients into secondary compounds, have poor litter quality and consequently have a slower leaf litter decomposition which promotes the accumulation of organic matter relative to faster growing plants that accumulate secondary compounds to a lesser extent. Most Catalan sclerophyllous forests are dominated by *Q. ilex*, a species that indeed has slow growth and low decomposition rates compared to conifers (Gillon et al. 1999). Sclerophyllous forests also have larger litter pools than deciduous forests. However, although on average sclerophyllous species do have poorer litter quality than deciduous species (Gallardo and Merino 1993) they do not necessarily decompose more slowly (Gillon et al. 1999) suggesting that the larger amount of litter in sclerophyllous forests is not only due to poor litter quality. In fact, patterns of decomposition and standing litter pools depend directly on litter production and litter quality and indirectly on microclimate and differences in the decomposer community (Swift et al. 1979).

Leaf area index, tree basal area and productivity also had a positive effect on litter pools. In a previous exploration of the IEFC dataset we did not find a significant association between tree species richness and wood production when other environmental factors were taken into account (Vilà et al. 2003). Instead in this study, litter pools depended on wood production and tree richness, suggesting that wood production and tree richness have an independent direct effect on litter pools and that the effect of species richness is not mediated by wood production. It was also striking to find that the existence of a shrub understorey did not increase litter pools, suggesting that although shrub cover was high (mean±SE, 63.10±0.59%) what controls litter pools is the existence of a closed tree canopy. The predictive power of forest structure variables on litter pools ranged within the values for the amount of variance accounted by ecological factors (Moller and Jennions 2002) and could be classified as “medium” according to Cohen (1988).

Our survey encompasses a broad range of climatic conditions ranging from temperate to semiarid. Mean annual temperature ranged from 3 to 16.2°C and mean annual precipitation from 354.1 to 1,311.7 mm. We found that although temperature had a significant effect on litter pools, it did not explain much of its variation, suggesting that changes in temperature alone might not modify litter pools. Our results mirror laboratory microcosm experimental studies that have shown that rates of litter decomposition can depend more on the identity of the species than on differences in temperature (Hobbie 1996).

In conclusion, although our survey is only a snapshot at the interface between the ecosystem aboveground and the soil compartment it shows that the amount of aboveground dead organic matter depends on several components of biodiversity. Monospecific forests have lower litter pools than mixed forests in which the species and functional identity of the dominant trees will determine differences in litter pools with species richness. Because litter pools are an essential component of C and nutrient cycling, the effects of tree species richness, the identity of tree species and functional types on litter pools have direct implications for forest conservation and management (e.g. forest plantations, selective thinning, invasion by alien trees, etc) that can drastically change ecosystem properties.

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