RESEARCH PAPER

Diversity increases carbon storage and tree productivity in Spanish forests

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ABSTRACT

Aim Biodiversity loss could reduce primary productivity and the carbon storage provided by forests; however, the mechanisms underpinning the effects of biodiversity on multiple ecosystem functions are not completely understood. Spanish forests are of particular interest because of the broad variation in environmental conditions and management history. We tested for the existence of a relationship between diversity effects and both carbon storage and tree productivity, and examined the relative importance of complementarity and selection mechanisms in a wide variety of forests, from cold deciduous Atlantic to xeric Mediterranean evergreen forests.

Location Continental Spain.

Methods We used *c.* 54,000 plots of the Spanish Forest Inventory and maximum likelihood techniques to quantify how climate, stand structure and diversity shape carbon storage and tree productivity. Diversity effects included both complementarity and selection mechanisms, measured respectively through functional diversity and functional identity measures.

Results Diversity had a significant effect on both carbon storage and tree productivity, even when controlling for confounding factors of climate and stand structure. A consistent positive effect of functional diversity on carbon storage and tree productivity was observed in all seven forest types studied. This relationship was not linear, and the largest changes in carbon storage and tree productivity were observed at low levels of functional diversity. However, the importance of complementarity effects was not consistent with the productivity of different forest types. Selection effects were particularly important in deciduous and Mediterranean pine forests, but had very little effect on mountain pines.

Main conclusions We found a generally positive effect of diversity on carbon storage and tree productivity, supported by both complementarity and selection mechanisms. Thus, both functionally diverse forests and functionally important species should be maintained to adequately preserve and promote key ecosystem functions such as carbon storage and tree productivity.

Keywords

Climate, community-weighted means of trait value, competition, continental Spain, diversity, ecosystem functions and services, forest management, maximum likelihood techniques, national forest inventory.

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INTRODUCTION

Under global change the increase in human-mediated modifications of ecosystems could lead to important losses of biodiversity (Cardinale *et al.*, 2012). Reductions in biodiversity may

alter the quality and number of ecosystem functions and services provided by terrestrial ecosystems (e.g. Isbell *et al.*, 2011). Thus, biodiversity–ecosystem functioning (BEF) relationships are an important topic in ecology and have been the subject of considerable debate during the last decades (e.g. Loreau *et al.*,

2001; Hooper *et al.*, 2012). Most studies of BEF relationships have used species richness as a measure of diversity (e.g. Maestre *et al.*, 2012). However, it has recently been shown that functional diversity better connects the underlying mechanisms of the effects of biodiversity on ecosystem functioning (e.g. Hooper *et al.*, 2005). Trait-based approaches are a promising avenue for disentangling the underlying mechanisms of the effects of diversity on productivity (see Mokany *et al.*, 2008; Paquette & Messier, 2011; Roscher *et al.*, 2012).

Two main, not mutually exclusive, mechanisms of the positive effects of diversity on ecosystem functioning have been proposed: the complementarity and the selection effects (Grime, 1998; Loreau & Hector, 2001). The *complementarity effect* increases ecosystem function through facilitation and niche partitioning, because functionally diverse species assemblages would enhance resource use efficiency and nutrient retention (Loreau, 2000; Morin *et al.*, 2011). Some authors have suggested that complementarity effects could be particularly important in low-productivity or harsh environments, where species interactions are less affected by competitive exclusion (Warren *et al.*, 2009; Paquette & Messier, 2011), but other authors have observed that complementarity effects are similar across different forest biomes (Zhang *et al.*, 2012). The *selection effect* (i.e. selection of particular species or functional traits) proposes that high species richness increases the probability of including the most productive species which will become dominant in the community (e.g. Cardinale *et al.*, 2007). Thus, selection effects are partially explained by the 'mass-ratio hypothesis' stating that levels of ecosystem function are mainly determined by the functional traits of dominant species (Grime, 1998; Mokany *et al.*, 2008; Roscher *et al.*, 2012). Both complementarity and selection effects simultaneously underlie the net effect of biodiversity on ecosystem function (Tilman, 1996; Mokany *et al.*, 2008).

Most BEF studies have been conducted in experimental grasslands testing the effects of species richness on ecosystem functions such as biomass production and nutrient cycling (e.g. Cardinale *et al.*, 2007). Studies conducted in forest systems, either planted or natural, are much more recent and scarce (e.g. Caspersen & Pacala, 2001; Vilà *et al.*, 2007). These studies have mainly been based on observational forest inventory data and measures of species diversity, and although they have highlighted the importance of functional trait approaches, most of them did not explicitly consider functional diversity and the underlying mechanisms of BEF relationships (Vilà *et al.*, 2007; Zhang *et al.*, 2012). The only study that, to our knowledge, has quantified the relative importance of complementarity and selection mechanisms in forest ecosystems suggests that both mechanisms could underlie BEF relationships, at least in simulated mesic temperate forests (Morin *et al.*, 2011). More research is needed to understand the role of BEF mechanisms in real forest communities differing in species composition, stand origin and environmental conditions along large bioclimatic gradients.

In this study, we conducted a large-scale assessment of two ecosystem functions (carbon storage and tree productivity) along wide climatic, forest structure and diversity gradients

using *c.* 54,000 plots distributed over forests in continental Spain. Continental Spain harbours a large variety of forest types, ranging from Atlantic deciduous broadleaved forests to sclerophyllous and Mediterranean pine forests (Costa *et al.*, 1997). Changes in tree carbon storage in Spanish forests depend on climatic and structural conditions (Vayreda *et al.*, 2012), and positive effects of species richness on tree productivity have already been reported (Vilà *et al.*, 2007, 2013). However, the underlying mechanisms and the role of functional diversity on both carbon storage and tree productivity are still poorly explored. Our main objectives are: (1) to analyse the sign and magnitude of BEF relationships in Spanish forests, expecting an effect of diversity on both carbon storage and tree productivity, even when controlling for climatic and structural effects in different forest types; and (2) to understand how complementarity and selection mechanisms affect carbon storage and tree productivity in different Spanish forest types, including natural and planted pine forests. Increasing our understanding of the underlying mechanisms of the effects of diversity on carbon storage and tree productivity is critical for guiding conservation actions and counteracting the effects of species loss on the functioning of forest ecosystems.

METHODS

Forest inventory dataset and estimation of carbon storage and tree productivity

We used data from continental Spain from the second and the third Spanish Forest Inventory (2SFI, 1986–96, and 3SFI, 1997–2007, respectively), that distributed plots over forest ecosystems on a 1-km^2 cell grid (Villanueva, 2004; see Appendix S1 in Supporting Information). We classified each plot of the SFI based on species abundance into one of the main vegetation types present in the Iberian Peninsula: deciduous, sclerophyllous, Mediterranean natural pines, mountain natural pines, Mediterranean planted pines, mountain planted pines and exotic forests (Fig. 1, Appendix S1).

We calculated *carbon storage* (Mg C ha^{-1}) of living trees, both aboveground and belowground, applying allometric equations according to Montero *et al.* (2005) at species, genus or family level for different species present in the Iberian Peninsula (Table S1). We calculated total tree biomass, considering both adult and regeneration information for the 53,817 plots of the 3SFI (Appendix S1), using the following equation:

$$\ln(b) = \alpha + \beta \ln(\text{d.b.h.}) \tag{1}$$

where *b* is the dry biomass of the above- or belowground fraction of the tree, d.b.h. is the diameter at breast height (1.30 m) of each tree and α and β are species-specific parameters for aboveground and belowground fractions. To obtain total carbon storage (Mg C ha^{-1}), we multiplied biomass by the species-specific carbon content of the biomass (Montero *et al.*, 2005), scaled-up to a hectare, and aggregated total carbon storage at species and plot levels.
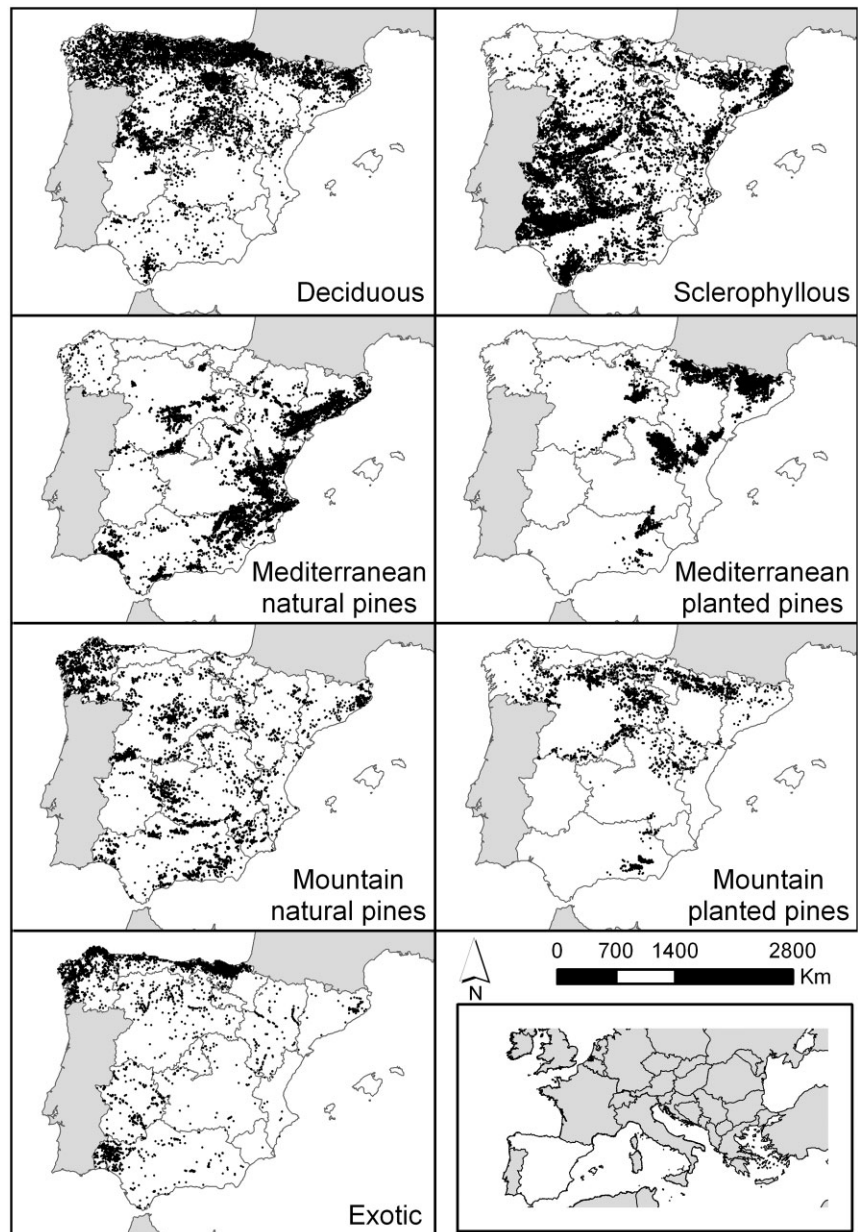
Figure 1 Maps of plots used in this study from the third Spanish Forest Inventory for the seven forest types included in the study. Map projection Universal Transverse Mercator 30N, European datum 1950.

Total tree productivity for each plot (TP$_p$), considering both aboveground and belowground biomass (Mg C ha^{-1} year^{-1}), was measured through the sum of the temporal variation in carbon storage of adult trees alive between the 2SFI and 3SFI (i.e. without including dead trees). From the initial 53,817 plots of 3SFI, we selected 32,110 plots for which data at the tree level were available in both inventories. We calculated tree productivity using the following equation:

$$TP_p = \sum \frac{C_{i,3SFI} - C_{i,2SFI}}{t} \tag{2}$$

where $C_{i,3FI}$ and $C_{i,2SFI}$ are the carbon accumulated in each live tree i (Mg C ha^{-1}) in the 3SFI and the 2SFI, respectively, and t is the time span between both inventories.

Abiotic and biotic determinants of carbon storage and tree productivity

Each of the SFI plots of the seven forest types defined was characterized by 33 abiotic variables, four stand structure variables and 30 diversity indices (Table S2). The abiotic variables included four topographic variables (altitude, slope, aspect and insolation), 25 climatic variables (calculated from temperature and precipitation information) and four edaphic variables (rockiness, texture, organic matter content and soil pH). The four stand structure variables included total cover fraction, tree cover fraction, stand tree density and coefficient of variation of tree height. The diversity variables included indices based on both species- and trait-based diversity indices. The species diversity indices included the monospecific or mixed character of the

stand, species richness and Shannon indices. The trait-based diversity indices were computed as (Appendix S1): (1) functional diversity (FD), measured through functional dispersion (Laliberté & Legendre, 2010) and used as a proxy of complementarity effects, and (2) functional identity (FI), measured through community-level weighted mean (CWM) and used as a proxy of selection effects (Lavorel *et al.*, 2008).

To calculate FD and FI indices we compiled species mean values for five key functional traits for the 120 tree species present in continental Spain: maximum height, wood density, seed mass, leaf mass per area and leaf nitrogen content per mass via the TRY initiative (http://www.try-db.org; Table S3) (Kattge *et al.*, 2011). These traits have been widely recognized as key traits of plant function: maximum height, wood density and seed mass are closely related to life-history strategy, while leaf mass per area (LMA) and leaf nitrogen content per mass are related to resource acquisition and plant growth strategy (Paquette & Messier, 2011; Swenson *et al.*, 2012). We computed the FD index for the five traits together, a subset of traits (seed mass, wood density and maximum height) often used in the BEF literature (e.g. Paquette & Messier, 2011) and for each trait separately based on both abundance and presence–absence matrixes. FI indices were computed for each trait separately, based on both abundance and presence–absence matrices (Appendix S1).

Prior to parameterizing our maximum likelihood models of carbon storage and tree productivity, we performed a variable selection over the large dataset of abiotic, structural and diversity variables. Using the techniques of principal components analysis (PCA) on all 29 highly correlated topographic and climatic predictors available, we selected, as representative of the climatic conditions of each plot, mean annual temperature (°C) and water deficit according to Emberger (mm; Emberger, 1930) (Appendix S1, Table S2). Edaphic variables were strongly related to forest type and showed little dispersion within each forest type (Appendix S1), therefore they were excluded from further analysis. In order to select representative variables of structural and diversity effects, we compared the strength of evidence for each independent factor separately using the Akaike information criterion (AIC) (Appendix S1). Models based on functional diversity, i.e. species functional traits, were a better fit to the data than models based on species diversity (Appendix S1). The FD index based on three traits (maximum height, wood density and seed mass) and calculated using presence/absence data was chosen as the best estimator of complementarity effects based on differences in the AIC (Appendix S1). The FI index based on LMA and calculated using abundance data was chosen as the best estimator of selection effects. As a result of the variable selection process, a final group of six variables was selected to be used as predictors of carbon storage and tree productivity (Table S4): two climatic variables (mean annual temperature and water deficit), two structural variables representative of density and heterogeneity effects (stand tree density and coefficient of variation of tree height, respectively) and two trait-based diversity variables representative of complementarity and selection effects (FD and FI, respectively).

Maximum likelihood analysis of carbon storage and tree productivity

We used maximum likelihood techniques and model selection for the analysis of carbon storage and tree productivity along climatic, structural and diversity gradients. Carbon storage (Mg C ha^{-1}) and tree productivity (Mg C ha^{-1} year^{-1}) were predicted as a function of maximum potential carbon storage (PCS) and maximum potential tree productivity (PTP), respectively, and three scalar modifiers ranging from 0 to 1 that quantified the effect on the average maximum PCS/PTP of local climatic conditions, stand structure and diversity effects. We defined different models of carbon storage and tree productivity that were analysed separately for each forest type based on the following functional form:

$$\text{Predicted} = \text{Potential} \times \text{Climatic effect} \\ \times \text{Structural effect} \times \text{Diversity effect.} \tag{3}$$

The PCS or PTP in this model is the parameter that represents the maximum value when the other factors are at optimal values (i.e. the maximum carbon storage or tree productivity that can be obtained for a certain forest type). The climatic effect was modelled using a bivariate Gaussian function:

$$\text{Climatic effect} = \exp\left[-\frac{1}{2}\left(\frac{\text{Temperature} - XT_a}{XT_b}\right)^2\right] \\ \times \exp\left[-\frac{1}{2}\left(\frac{\text{Water deficit} - XP_a}{XP_b}\right)^2\right] \tag{4}$$

where the parameters XT_a and XP_a represent the mean annual temperature and water deficit at which maximum carbon storage or productivity occurs, and XT_b and XP_b are the parameters that control the variance of the normal distribution (i.e. the breadth of the function).

The structural effect was modelled using a bivariate Gaussian function including density and structural heterogeneity effects:

$$\text{Structural effect} = \exp\left[-\frac{1}{2}\left(\frac{\text{Density} - XD_a}{XD_b}\right)^2\right] \\ \times \exp\left[-\frac{1}{2}\left(\frac{\text{Heterogeneity} - XH_a}{XH_b}\right)^2\right] \tag{5}$$

where the density effect is measured in terms of stand density (number of trees per hectare) and the structural heterogeneity effect is measured through the coefficient of variation of tree height. XD_a and XH_a are the tree density and coefficient of variation of tree height, respectively, at which maximum carbon storage or productivity occurs, and XD_b and XH_b are estimated parameters that control the breadth of the function.

The diversity effect was modelled using a variation of the exponential form for functional diversity (FD as a proxy of the complementarity effect) and a log-normal function for functional identity (FI as a proxy of the selection effect):

Table 1 Comparisons of alternative models of carbon storage (Mg C ha^{-1}) for the seven forest types studied using the Akaike information criterion (AIC).

Forest type	ΔAIC							R^2	Slope	n
	Full	No climate	No structure	No diversity	No FD	No FI	Null			
Deciduous	**0**	664	1,402	1,259	118	1,201	5263	0.38	0.99	11,125
Sclerophyllous	**0**	905	7,421	162	58	131	12,928	0.61	1.00	13,857
Mediterranean natural pines	**0**	590	2,696	623	553	185	5272	0.43	1.00	9382
Mountain natural pines	**0**	1,427	2,284	132	98	−5	3643	0.41	1.00	6895
Mediterranean planted pines	**0**	26	1,360	321	159	71	2057	0.34	1.00	3147
Mountain planted pines	**0**	150	810	39	64	4	1139	0.29	0.99	3349
Exotic	**0**	27	71	73	72	−4	356	0.18	0.99	1966

The full models include the effects of climate, structure and diversity (see equation 3) for each forest type. The models 'No climate', 'No structure' and 'No diversity' ignore the effect of climate, stand structure and functional diversity (FD), respectively. The null models ignore the climatic, structural and diversity effects. The best fitting model is given in a ΔAIC value of zero (bold), comparing the full model with models dropping the effect of climate, stand structure or diversity. We also tested the relative importance of FD (measured through functional dispersion of maximum height, wood density and seed mass) and functional identity (FI) (measured through community-weighted means of LMA) by ignoring its effects ('No FD' and 'No FI', respectively). n is the sample size (number of plots). For the best model (i.e. ΔAIC = 0) we show the slope and R^2 (1 − SEE/SST) for the relationship of the predicted and observed carbon storage.

$$\text{Diversity effect} = [1 - \exp(X\text{FD}_a \times \text{FD} - X\text{FD}_b)]$$
$$\times \exp\left[-\frac{1}{2}\left(\frac{\log(\text{FI}/X\text{FI}_a)}{X\text{FI}_b}\right)^2\right]. \quad (6)$$

The exponential form selected to model the effect of FD on carbon storage and tree productivity varied between 0 and 1. The parameter $X\text{FD}_a$ determines the shape of the effect of FD on the predicted variable and $X\text{FD}_b$ defines the intercept of the function. The parameter $X\text{FI}_a$ represents the community-weighted mean value at which maximum potential carbon storage or tree productivity occurs, and $X\text{FI}_b$ determines the breadth of the function.

We compared alternative models using differences in the AIC as an indicator of both parsimony and likelihood (Burnham & Anderson, 2002). We used a two-unit difference in AIC as a support interval to assess the strength of evidence of individual maximum likelihood parameter estimates, being roughly equivalent to the 95% support limit defined using a likelihood ratio test (Burnham & Anderson, 2002). The full model was compared with models that ignored the effect of climate, stand structure or diversity, and with the null or intercept-only model (i.e. ignoring the effect of climate, stand structure and diversity) for each response variable (i.e. carbon storage and tree productivity) and each forest type. Then, we tested the relative importance of FD and FI mechanisms based on differences in the AIC between the full model and models that ignored the effect of FD or FI (respectively) for each forest type.

The parameter estimates provide the basis for determining the magnitude of the effect of a given process, with maximum likelihood estimates of parameter values close to zero indicating no effect. We used simulated annealing optimization procedures to determine the parameters that maximize the log-likelihood of observing carbon storage and tree productivity with a normal error distribution given our data (Goffe et al., 1994). The R^2 of

the regression was used as a measure of goodness of fit (1 − SSE/SST; with SSE the sum of squares error and SST the sum of squares total) and the slope of the regression (with a zero intercept) of observed and predicted data was used as a measure of bias (an unbiased model having a slope of 1). The analyses were performed using the likelihood package 1.4 (Murphy, 2008) for the R statistical language (R Development Core Team, 2011).

RESULTS

Abiotic and biotic determinants of carbon storage

The effects of climate, stand structure and diversity on total carbon storage were included in the best model for all forest types (Table 1). All of the models produced unbiased estimates of carbon storage (i.e. slopes of predicted versus observed values were all close to 1 and R^2 ranged from 0.18 to 0.61 for carbon storage models; Table 1, Fig. S1). Stand structure was the most important factor for determining carbon storage (as indicated by the largest increase in AIC when the structural effect term was dropped from the full models) followed by the climatic and the diversity effects (Table 1, Fig. S2). The relative importance of the diversity effect on carbon storage was greater than that of the climate effect for deciduous, exotic and Mediterranean pine forests (both natural and planted), but lower for mountain pines (both natural and planted) and sclerophyllous forests (Table 1).

The effects of complementarity (measured as FD, through functional dispersion based on maximum height, wood density and seed mass) and selection (measured as FI, through CWM based on leaf mass area) differed among forest types. FD had a net positive effect on carbon storage in all forest types studied. We found nonlinear increases in carbon storage along functional diversity gradients for all forest types. Carbon storage increased at an average of 32% from monospecific (FD = 0) to
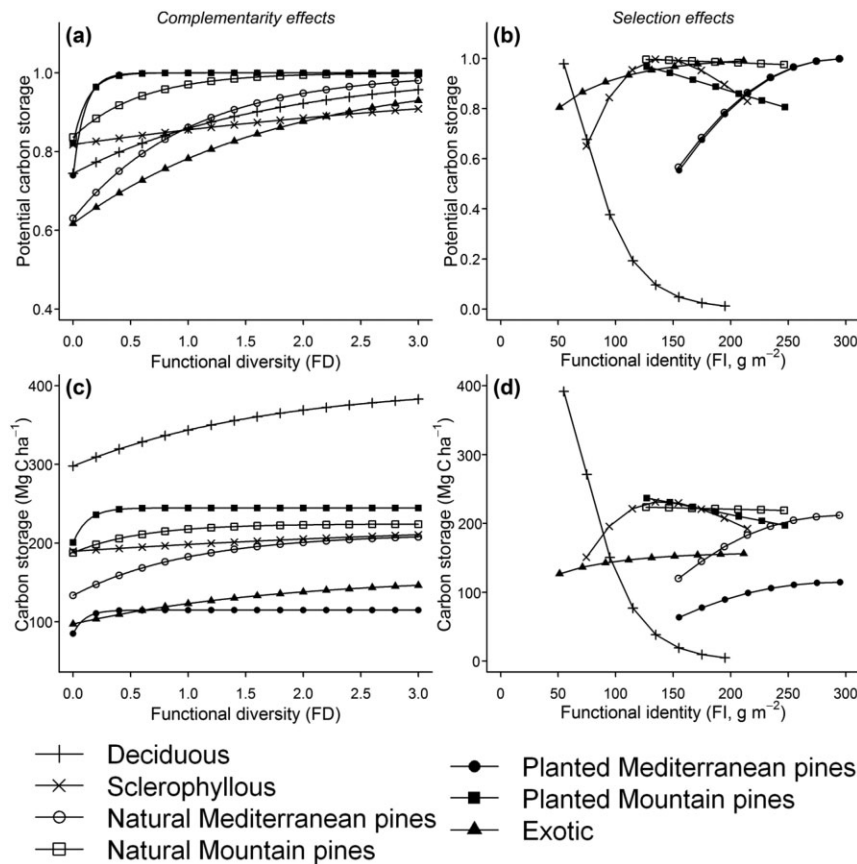
Figure 2 Predicted potential fraction (proportion) and total carbon storage (Mg C ha⁻¹) for each forest type along gradients of: functional diversity (FD) of maximum height, wood density and seed mass (a and c, respectively); and functional identity (FI) [measured through community-level weighted mean of leaf mass per area (g m⁻²)] (b and d, respectively). See Table S5 for the estimated parameters of the corresponding functions.

functionally diverse forests (FD ≈ 2) (Fig. 2a). It is interesting to note that all forest types experienced the strongest increases of carbon storage in the lower parts of the FD gradient (Fig. 2a,c). The magnitude of the effect of FD on carbon storage was larger for exotic, planted pine (both Mediterranean and mountain), natural Mediterranean pine and deciduous forests than for sclerophyllous and natural mountain pine forests (Fig. 2a).

FI had an effect on carbon storage models in five of the seven forest types (all but mountain and exotic forests; see ΔAIC in FD and FI, respectively, in Table 1). Carbon storage was maximized close to the most frequent values of LMA in each forest type (Fig. 2b,d): low values for deciduous forests (*c.* 81 g m⁻²), intermediate values of LMA in sclerophyllous forests (*c.* 145 g m⁻²) and high values of LMA in Mediterranean pine forests (*c.* 230 g m⁻²; Table S4). These results indicate the importance of selection effects, because carbon storage increases towards the mean LMA value observed in each forest type, which is mainly determined by the identity of the dominant species in each forest.

Abiotic and biotic determinants of tree productivity

The best models of tree productivity included the effects of climate, stand structure and diversity (Table 2), similar to those obtained for carbon storage. All models produced unbiased estimates of total tree productivity (i.e. slopes of predicted versus observed values were all close to 1 and R^2 ranged from 0.20 to 0.47; Table 2, Fig S3). The relative importance of the structural

effects on tree productivity was much greater than that of climate and diversity effects for all forest types (see ΔAIC in Table 2 and Fig. S4). Diversity had a larger effect on tree productivity than climate in deciduous and Mediterranean pine forests (natural and planted), whereas we observed the opposite pattern for the remaining forest types (Table 2).

Complementarity (measured as FD) generally had a positive but nonlinear effect on total tree productivity in all forest types (except exotic forests; Table 2, Fig. 3a). These effects were again particularly relevant in the lower parts of the FD gradient, where slight changes in FD generally correlate with large increases in potential tree productivity (Fig. 3a). Tree productivity increased at an average of 21% from monospecific (FD = 0) to functionally diverse forests (FD ≈ 2) (Fig. 3a). The absolute effect of FD on potential tree productivity was larger for deciduous, sclerophyllous and natural Mediterranean pine forests than for mountain pines, planted Mediterranean pines and exotic forests (see relative changes in potential tree productivity, Fig. 3a).

FI had an effect on total tree productivity in four of the seven forest types studied (deciduous, sclerophyllous, Mediterranean natural pines and exotic forests; Table 2), with the relative importance of FI being greater than FD (Table 2). We observed maximum potential tree productivity towards the most frequent values of LMA in each forest type: low values for deciduous forests, intermediate values in sclerophyllous forests and high values in Mediterranean pine forests (Table S4). The absolute effect of FI on tree productivity was particularly strong for

Table 2 Comparisons of alternative models of total tree productivity (Mg C ha^{-1} year^{-1}) for the seven forest types studied using the Akaike information criterion (AIC).

	ΔAIC							R^2	Slope	n
Forest type	Full	No Climate	No Structure	No Diversity	No FD	No FI	Null			
Deciduous	**0**	286	713	542	282	312	2267	0.36	0.99	5109
Sclerophyllous	**0**	571	2753	145	128	−2	5735	0.43	1.00	9071
Mediterranean natural pines	**0**	459	1920	547	173	434	3357	0.41	1.00	6455
Mountain natural pines	**0**	990	2489	13	7	−14	3187	0.47	1.00	5078
Mediterranean planted pines	**0**	247	949	300	8	209	1617	0.40	1.00	3147
Mountain planted pines	**0**	346	671	10	7	−8	937	0.38	0.99	2021
Exotic	**0**	11	46	10	−3	11	88	0.20	0.99	517

The full models include the effects of climate, structure and diversity (see equation 3) for each forest type. The models 'No climate', 'No structure' and 'No diversity' ignore the effect of climate, stand structure and functional diversity (FD), respectively. The null models ignore the climatic, structural and diversity effects. The best fitting model is given in ΔAIC value of zero (bold), comparing the full model with models dropping the effect of climate, stand structure or diversity. We also tested the relative importance of FD (measured through functional dispersion of maximum height, wood density and seed mass) and functional identity (FI) (measured through community-weighted means of LMA) by ignoring its effects ('No FD' and 'No FI', respectively). n is the sample size (number of plots). For the best model (i.e. ΔAIC = 0) we show the slope and R^2 (1 − SEE/SST) for the relationship of the predicted and observed tree productivity.

deciduous and Mediterranean pine forests, but it had almost no effect on mountain pine and exotic forests (Fig. 3b).

DISCUSSION

Diversity effects on carbon storage and tree productivity

Our results show a generally positive effect of FD on carbon storage and tree productivity in a wide variety of forests, from cold deciduous Atlantic to xeric Mediterranean evergreen forests. The net effect of diversity on both carbon storage and tree productivity was detected even when controlling for potentially confounding structural and climatic factors. The effect of diversity was lower than the effect of stand structure, but diversity effects were greater than or equal to the climatic effects (Tables 1 & 2). Our results agree with previous studies suggesting that stand structure is the main variable affecting carbon stock change in Iberian forests (e.g. Vayreda et al., 2012). As expected, climate also influenced carbon storage and tree productivity (e.g. Vilà et al., 2007). However, climate had a smaller effect than diversity indices which could indicate that climatic conditions constrain the maximum limit of carbon storage and tree productivity, thus explaining it relatively little contribution (Stegen et al., 2011). Other potential drivers of carbon storage and tree productivity, such as soil fertility (Wardle et al., 2008) or historical management (Vilà et al., 2005), could not be explored because of their unavailability at the large scale used in this study (e.g. Gómez-Aparicio et al., 2011).

In our models, functional diversity indices were better predictors of carbon storage and tree productivity than tree species richness (Appendix S1, Fig. S5). Other authors have previously reported positive or neutral effects of species diversity on wood production in Spanish forests (Vilà et al., 2003, 2007). Although

Vilà et al. (2007) considered the effects of functional groups, the role of FD per se and the underlying mechanisms of diversity effects in Spanish forests have not been previously explored. Our results therefore support recent findings that suggest the need to go beyond species richness and consider FD and FI to better understand the underlying mechanisms of BEF relationships (e.g. Morin et al., 2011; Paquette & Messier, 2011). The trait-based approaches used here directly and indirectly assess those mechanisms, because ecosystem functions are governed by species dominance, distribution and functional traits (e.g. Mokany et al., 2008).

We used both FD and FI based on different functional traits to quantify complementarity and selection mechanisms on ecosystem functions in the main natural and planted forests of continental Spain. Model comparison allowed us to identify the traits related to FD (maximum height, wood density and seed mass; Appendix S1). These traits are related to reproduction, growth and successional status (Paquette & Messier, 2011; Swenson et al., 2012). Thus, these three traits indicate that different life-history strategies and their variability help to quantify the breadth of their niche (i.e. determining when species use resources differently) (Hooper et al., 2005). We found that FD indices based on presence–absence matrices, rather than abundances, better explained productivity and carbon storage (see also Paquette & Messier, 2011). This raises the question of the scale at which complementarity may occur, and the relative 'quantity' of a given species required for it to increase niche partitioning, questions already raised by Petchey & Gaston (2006) but which remain largely unanswered. In our case LMA was the best predictor among the CWM indices calculated for each trait. LMA is a functional trait that directly affects tree growth and thus determines plant performance and species dominance in forests (Díaz et al., 2004; Wright et al., 2004). In accordance with Morin et al. (2011), we conclude that for forests
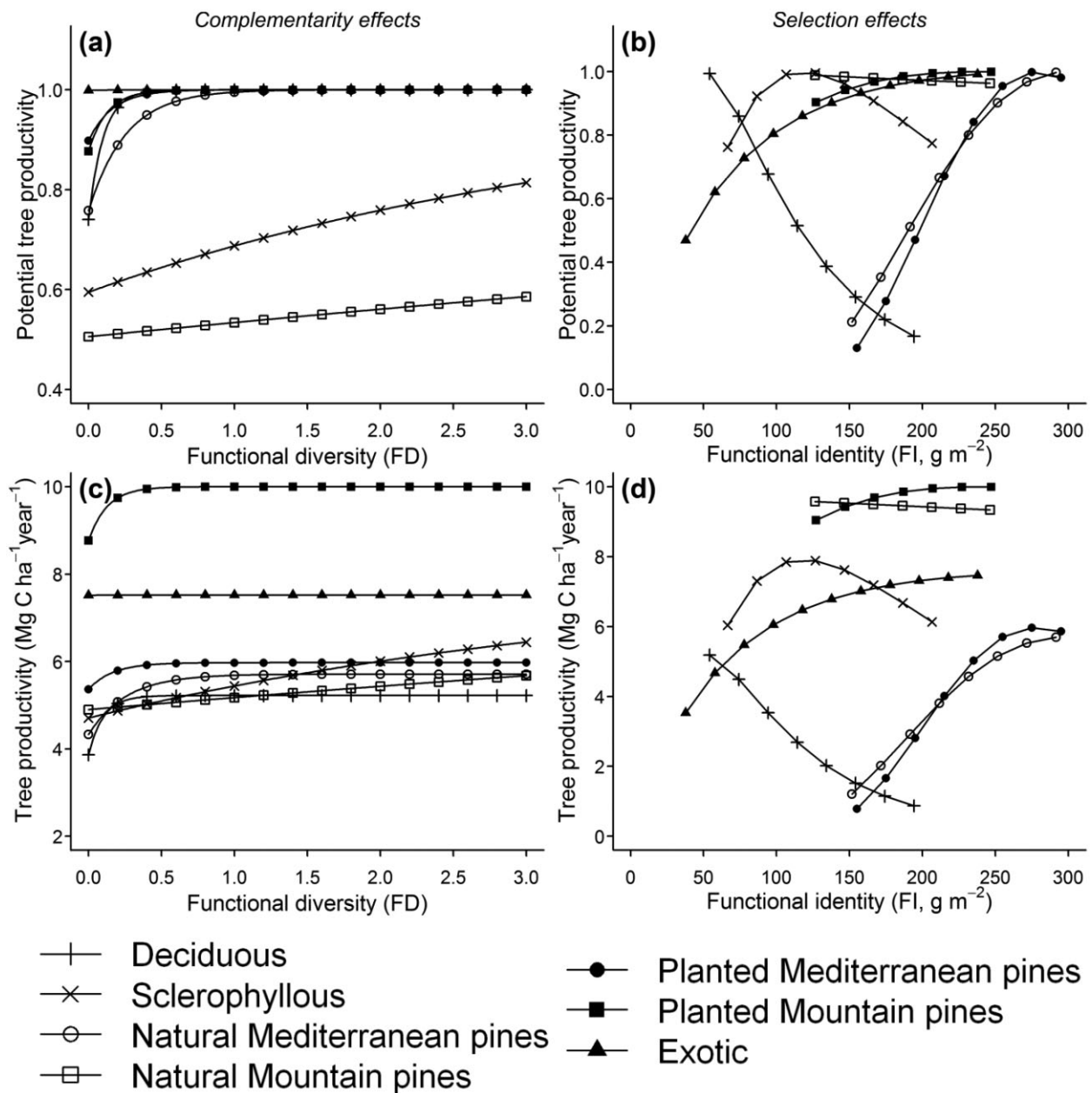
Figure 3 Predicted potential fraction (proportion) and tree productivity (Mg C ha^{-1} year^{-1}) for each forest type along gradients of: functional diversity (FD) of maximum height, wood density and seed mass (a and c, respectively); and functional identity (FI) [measured through community-level weighted mean of leaf mass per area (g m^{-2})] (b and d, respectively). See Table S6 for the estimated parameters of the corresponding functions.

of continental Spain complementarity effects are linked to the interspecific variation of functional traits that determine resource use and acquisition, while selection effects depend on the mean values of species traits that are directly linked to plant performance.

Underlying mechanisms of diversity effects on carbon storage and tree productivity

Our results support the idea that both complementarity and selection components of biodiversity effects are not mutually exclusive (Tables 1 & 2): more functionally diverse forests that include certain species possessing key traits promote both carbon storage and tree productivity. Selection effects could be related to species being selectively favoured given a certain climate, causing a more complete utilization of limited resources (Tilman, 1999; Loreau, 2000). Loreau & Hector (2001) suggested that both positive complementarity and selection effects on productivity reflects the 'sampling effect', increasing the probability of sampling a dominant, high-biomass species in mixed forest but also increasing the probability of sampling a suite of complementary species. Our results confirm that

contrasting traits promote tree productivity and carbon storage, together with species-specific selection effects based on LMA, as previously suggested in other forest types (Paquette & Messier, 2011; Zhang *et al.*, 2012).

The BEF relationship observed along FD (i.e. the complementarity effect) was positive but not linear, showing the largest changes of carbon storage and tree productivity at low FD values (Figs 2a & 3a). It has been suggested that the positive relation between species richness and ecosystem function increases until an asymptote is reached where functional redundancy and niche overlap occur (e.g. Loreau *et al.*, 2001; Hooper *et al.*, 2005). This form of BEF relationship has been reported in a recent meta-analysis of forest productivity that showed that an asymptote was reached at around six species (Zhang *et al.*, 2012). The largest changes in carbon storage and tree productivity occurred at low FD values, suggesting that most benefits are found when moving away from monospecific stands, and later the increase of ecosystem functions is expected to saturate (e.g. Loreau, 2000).

Our results suggest that complementarity effects are relevant for all types of Spanish forests, regardless of their productivity. For example, deciduous forests show the greatest effects of complementarity on potential tree productivity (a 25% productivity increase along the FD gradient; Fig. 3a) despite having an intermediate mean productivity within the seven forest types considered (1.36 ± 1.30 Mg C ha^{-1} year^{-1}; Table S4). Therefore, we did not find strong support for a larger role of complementarity in low-productive or more stressful environments (where facilitation may be more important) than in high-productive environments (where competitive exclusion is expected to dominate species interactions), as suggested by previous theoretical (Warren *et al.*, 2009) and observational studies (Paquette & Messier, 2011). This lack of a clear relationship between complementarity and productivity could be due to the complexities and ambiguities associated with the definition of 'stressful conditions' at the community level, since each forest type is composed of individuals and species both adapted to and limited by local conditions (e.g. Körner, 2004). Because the concept of stress is better applied at the species level, each individual species could either be favoured by facilitation or impaired by competition (Holmgren *et al.*, 1997), with stress and facilitation increasing as environmental conditions deviate from a species' ecophysiological optimum (Greiner La Peyre *et al.*, 2001).

We found that selection effects based on species identity and dominance (measured as FI using CWM based on LMA) had a positive effect on carbon storage and tree productivity. The selection effect was particularly large in Mediterranean pines and deciduous forests (Table S4). The leaf economic spectrum predicts that low LMA should promote productivity (e.g. Wright *et al.*, 2004; Morin *et al.*, 2011). However, Mediterranean pines had their maximum productivity at high LMA, which could be related to traits favoured by and adapted to arid and semi-arid conditions (Wright *et al.*, 2005). Moreover, these forest types usually form mixed forests of functionally contrasting species, because Mediterranean pine species and hardwoods could coexist or alternate depending on the environmental heterogeneity and disturbance regime (Zavala *et al.*, 2000;

Gómez-Aparicio *et al.*, 2011). Therefore, spatial differences in species dominance could lead to the greater importance of selection mechanisms in Mediterranean pine and Atlantic forests, causing the large variation in carbon storage and tree productivity observed along the FI gradient (Figs 2b & 3b). On the other hand, we observed that mountain forests had the lowest sensitivity to selection effects (Figs 2b & 3b). This could be due to the fact that mountain forests tend to mix with functionally similar species, including mostly conifers typical of high altitudes (Costa *et al.*, 1997), and therefore mountain forests have high monospecificity and low FD.

CONCLUSIONS

Our results demonstrate that FD is crucial in maintaining ecosystem functions in Spanish forests along large bioclimatic gradients. Thus, carbon storage and tree productivity increase at an average of 32% and 21%, respectively, from monospecific to functionally diverse forests, which agrees with previous studies that found an average increment of productivity of 24% from forest monocultures to polycultures (Zhang *et al.*, 2012; Vilà *et al.*, 2013). Moreover, our results indicate that BEF relationships and complementarity effects are not substantially affected by the origin of the stand, with diversity having a positive effect on carbon storage and tree productivity in both natural and planted Spanish forests. These findings suggest that results obtained in experimentally controlled environments (the large majority of the BEF research so far; Adler *et al.*, 2011) could also be applicable to natural systems.

Maintaining diverse forests in the Iberian Peninsula in particular, and in the Mediterranean region in general, should be considered both an important challenge and a necessity. The Mediterranean region is particularly vulnerable to climate change as well as habitat loss, fragmentation and increases in fire frequency (Schröter *et al.*, 2005; Pausas *et al.*, 2008). As a consequence, potential losses of biodiversity could be particularly large in this area, and therefore also their negative effects on ecosystem functions and related services (Lindner *et al.*, 2010). Our results indicate that BEF relationships are maintained through both complementarity and selection effects. Therefore, we conclude that management efforts should aim at promoting both functionally diverse forests and functionally important species, which could act as insurance for the maintenance of key ecosystem functions such as carbon storage and tree productivity.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Observed versus predicted carbon storage for the best model in each forest type.

Figure S2 Predicted potential carbon storage as function of mean annual temperature, water deficit, tree density and tree height coefficient of variation for each forest type.

Figure S3 Observed versus predicted tree productivity for the best model in each forest type.

Figure S4 Predicted potential tree productivity as function of mean annual temperature, water deficit, tree density and tree height coefficient of variation for each forest type.

Figure S5 Predicted potential carbon storage and tree productivity as function of tree species richness.

Table S1 List of species names and family, forest type and species used to calculate the carbon storage and tree productivity.

Table S2 Description of the potential predictor variables of carbon storage and tree productivity.

Table S3 Functional traits used to compute trait-based diversity indices.

BIOSKETCH

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