



**Diversity increases carbon storage and tree productivity in Spanish forests**

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| Keywords:                     | climate, competition, ecosystem functions and services, forest management, functional diversity, functional identity, maximum likelihood techniques, national forest inventory  |
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View

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3 1 **Diversity** increases carbon storage and tree productivity in Spanish  
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3 18 **ABSTRACT**  
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6 19 **Aim** Biodiversity loss could reduce primary productivity and carbon storage provided  
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8 20 by forests; however the underpinning mechanisms of biodiversity effects on multiple  
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10 21 ecosystem functions are not completely understood. Spanish forests are of particular  
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12 22 interest because of the broad variation in environmental conditions and management  
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14 23 history. We tested for the existence of a relationship among diversity effects and both  
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16 24 carbon storage and tree productivity, and examined the relative importance of  
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18 25 complementarity and selection mechanisms in a wide variety of forests, from cold  
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20 26 deciduous Atlantic to xeric Mediterranean evergreen forests.

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24 27 **Location** Continental Spain.  
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26 28 **Methods** We used *c.* 54,000 plots of the Spanish Forest Inventory and maximum  
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28 29 likelihood techniques to quantify how climate, stand structure and diversity shape  
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30 30 carbon storage and tree productivity. Diversity effects included both complementarity  
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32 31 and selection mechanisms, measured respectively through functional diversity and  
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34 32 functional identity measures.  
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37 33 **Results** Diversity had a significant effect on both carbon storage and tree productivity,  
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39 34 even when controlling for climatic and stand structural confounding factors. A  
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41 35 consistent positive effect of functional diversity on carbon storage and tree productivity  
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43 36 was observed in all seven forest types studied. This relationship was not linear, and the  
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45 37 largest changes in carbon storage and tree productivity were observed at low functional  
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47 38 diversity levels. However, the importance of complementarity effects was not consistent  
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49 39 with the productivity of different forest types. Selection effects were particularly  
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51 40 important in deciduous and Mediterranean pine forests, but had very little effect on  
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53 41 mountain pines.  
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3 42 **Main conclusions** We found a generally positive effect of diversity on carbon storage  
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5 43 and tree productivity, supported by both complementarity and selection mechanisms.  
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7 44 Thus, both functionally diverse forests and functionally important species should be  
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9 45 maintained to adequately preserve and promote key ecosystem functions such as carbon  
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11 46 storage and tree productivity.

12  
13 47 **Keywords:** climate, competition, community-weighted means of trait value, continental  
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15 48 Spain, diversity, ecosystem functions and services, forest management, maximum  
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17 49 likelihood techniques, national forest inventory.  
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For Peer Review

## 50 INTRODUCTION

51 Under global change the increase of human-mediated modifications in ecosystems could  
52 lead to important biodiversity losses (Cardinale *et al.*, 2012). Reductions of biodiversity  
53 may alter the quality and quantity of ecosystem functions and services provided by  
54 terrestrial ecosystems (e.g. Isbell *et al.*, 2011). Thus, biodiversity-ecosystem functioning  
55 (BEF) relationships are an important topic in ecology and have been subject of  
56 considerable debate during the last decades (e.g. Loreau *et al.*, 2001; Hooper *et al.*,  
57 2012). Most studies of BEF relationships have used species richness as a measure of  
58 diversity (e.g. Maestre *et al.*, 2012). However, it has recently been shown that functional  
59 diversity better connects the underlying mechanisms of biodiversity effects to  
60 ecosystem functioning (e.g. Hooper *et al.*, 2005). Trait based approaches are a  
61 promising avenue to disentangle the underlying mechanisms of the diversity effects on  
62 productivity (see Mokany *et al.*, 2008; Paquette & Messier, 2011; Roscher *et al.*, 2012).

63 Two main non-exclusive mechanisms of the positive effects of **diversity** on  
64 ecosystem functioning have been proposed: the complementarity and the selection  
65 effects (Grime, 1998; Loreau & Hector, 2001). The *complementarity effect* increases an  
66 ecosystem function through facilitation and niche partitioning, because functionally  
67 diverse species assemblages would enhance resource use efficiency and nutrient  
68 retention (Loreau, 2000; Morin *et al.*, 2011). Some authors have suggested that  
69 complementarity effects could be particularly important in low productive or harsh  
70 environments, where species interactions are less affected by competitive exclusion  
71 (Warren *et al.*, 2009; Paquette & Messier, 2011). Yet, other authors have observed that  
72 complementarity effects are similar across different forest biomes (Zhang *et al.*, 2012).  
73 The *selection effect* (i.e. selection of particular species or functional traits) proposes that  
74 high species richness increases the probability of including the most productive species

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3 75 which will become dominant in the community (e.g. Cardinale *et al.*, 2007). Thus,  
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5 76 selection effects are partially explained by the “mass-ratio hypothesis” stating that  
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7 77 ecosystem function levels are mainly determined by the functional traits of dominant  
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9 78 species (Grime, 1998; Mokany *et al.*, 2008; Roscher *et al.*, 2012). Both  
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11 79 complementarity and selection effects simultaneously underlie the net biodiversity  
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13 80 effect on ecosystem function (Tilman, 1996; Mokany *et al.*, 2008).

16 81 Most BEF studies have been conducted in experimental grasslands testing the  
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18 82 effects of species richness on ecosystem functions such as biomass production and  
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20 83 nutrient cycling (e.g. Cardinale *et al.*, 2007). Studies conducted in forest systems, either  
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22 84 planted or natural, are much more recent and scarce (e.g. Caspersen & Pacala, 2001;  
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24 85 Vilà *et al.*, 2007). These studies have mainly been based on observational forest  
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26 86 inventory data and species diversity measures, and although they highlighted the  
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28 87 importance of functional trait approaches, most of them did not explicitly consider  
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30 88 functional diversity and the underlying mechanisms of BEF relationships (Vilà *et al.*,  
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32 89 2007; Zhang *et al.*, 2012). The only study that, to our knowledge, has quantified the  
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34 90 relative importance of complementarity and selection mechanisms in forest ecosystems  
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36 91 suggests that both mechanisms could underlie BEF relationships, at least in simulated  
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38 92 mesic temperate forests (Morin *et al.*, 2011). More research is needed to understand the  
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40 93 role of BEF mechanisms in real forest communities differing in species composition,  
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42 94 stand origin and environmental conditions along large bioclimatic gradients.

47 95 In this study, we conducted a large-scale assessment of two ecosystem functions  
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49 96 (carbon storage and tree productivity) along wide climatic, forest structure and diversity  
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51 97 gradients using *c.* 54,000 plots distributed over forests in continental Spain. Continental  
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53 98 Spain harbors a high variety of forest types, ranging from Atlantic deciduous  
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55 99 broadleaved forests to sclerophyllous and Mediterranean pine forests (Costa *et al.*,  
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3 100 1997). Changes in tree carbon storage in Spanish forests depend on climatic and  
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5 101 structural conditions (Vayreda *et al.*, 2012) and positive effects of species richness on  
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7 102 tree productivity have already been reported (Vilà *et al.*, 2007; Vilà *et al.*, 2013).  
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9 103 However, the underlying mechanisms and the role of functional diversity on both  
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11 104 carbon storage and tree productivity are still poorly explored. Our main objectives are:  
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13 105 (i) to analyze the sign and magnitude of BEF relationships in Spanish forests, expecting  
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15 106 an effect of diversity on both carbon storage and tree productivity, even when  
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17 107 controlling for climatic and structural effects in different forest types; and (ii) to  
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19 108 understand how complementarity and selection mechanisms affect carbon storage and  
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21 109 tree productivity in different Spanish forest types, including natural and planted pine  
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23 110 forests. Increasing our understanding about the underlying mechanisms of diversity  
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25 111 effects on carbon storage and tree productivity is critical for guiding conservation  
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27 112 actions and counteracting the effects of species loss on forest ecosystem functioning.  
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113 **METHODS**

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115 **Forest Inventory dataset and estimation of carbon storage and tree**  
116 **productivity**

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118 We used data over continental Spain from the second and the third Spanish Forest  
119 Inventory (2SFI: 1986-1996 and 3SFI: 1997-2007, respectively), that distributed plots  
120 over forest ecosystems on a 1-km<sup>2</sup> cell grid (Villanueva, 2004; see Appendix S1 in  
121 Supporting Information). We classified each plot of the SFI based on species abundance  
122 into one of the main vegetation types present in the Iberian Peninsula: deciduous,  
123 sclerophyllous, Mediterranean natural pines, mountain natural pines, Mediterranean  
124 planted pines, mountain planted pines, and exotic forests (Fig. 1 and Appendix S1).

125 We calculated **carbon storage** of living trees (considering both aboveground  
126 and belowground, Mg C ha<sup>-1</sup>) applying allometric equations according to Montero *et al.*  
127 (2005) at species, genus or family level for different species present in the Iberian  
128 Peninsula (Table S1). We calculated total tree biomass, considering both adult and  
129 regeneration information for the 53,817 plots of the 3SFI (Appendix S1), using the  
130 following equation:

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$$132 \quad \ln(b) = \alpha + \beta \cdot \ln(d.b.h.) \quad (1)$$

133

134 where, *b* is the dry biomass of the above- or belowground fraction of the tree,  
135 *d.b.h.* is the diameter at breast height (1.30 m) of each tree, and  $\alpha$  and  $\beta$  are species-  
136 specific parameters for aboveground and belowground fractions. To obtain total carbon  
137 storage (Mg C ha<sup>-1</sup>), we multiplied biomass by the species-specific carbon content of

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3 138 the biomass (Montero *et al.*, 2005), scaled-up to hectare, and aggregated total carbon  
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5 139 storage at species and plot levels.  
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7 **Total tree productivity** for each plot ( $TP_p$  considering both aboveground and  
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9 belowground biomass,  $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ) was measured through the sum of the temporal  
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11 142 variation in carbon storage of adult trees alive between the 2SFI and 3SFI (i.e. without  
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13 143 including dead trees). From the initial 53,817 plots of the 3SFI, we selected 32,110 plots  
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16 144 for which data at the tree level were available in both inventories. We calculated tree  
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18 145 productivity using the following equation:  
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$$TP_p = \sum \frac{C_{i,SFI3} - C_{i,SFI2}}{t} \quad (2)$$
  
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26 148  
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28 149 where  $C_{i,SFI3}$  and  $C_{i,SFI2}$  are the carbon accumulated in each live tree  $i$  ( $\text{Mg C ha}^{-1}$ )  
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30 150 <sup>1</sup>) in the 3SFI and the 2SFI respectively, and  $t$  is the time span between both inventories.  
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### 32 151 33 34 152 **Abiotic and biotic determinants of carbon storage and tree productivity**

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37 153 Each of the SFI plots of the seven forest types defined were characterized by 33 abiotic  
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39 154 variables, four stand structure variables, and 30 diversity indices (Table S2). The abiotic  
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41 155 variables included four topographic variables (altitude, slope, aspect and insolation), 25  
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43 156 climatic variables (calculated from temperature and precipitation information), and four  
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45 157 edaphic variables (rockiness, texture, organic matter content and soil pH). The four  
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48 158 stand structure variables included total cover fraction, tree cover fraction, stand tree  
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50 159 density, and coefficient of variation of tree height. The diversity variables included  
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52 160 indices based on both species and trait-based diversity indices. The species diversity  
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54 161 indices included the monospecific or mixed character of the stand, species richness and  
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57 162 Shannon indices. The trait-based diversity indices were computed as (Appendix S1): (i)  
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3 163 functional diversity (FD), measured through functional dispersion (Laliberté &  
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5 164 Legendre, 2010) and used as a proxy of complementarity effects; and (ii) functional  
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7 165 identity (FI), measured through community-level weighted means (CWM) and used as a  
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10 166 proxy of selection effects (Lavorel *et al.*, 2008).

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12 To calculate functional diversity (FD) and identity (FI) indices we compiled  
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14 168 species mean values for five key functional traits for the 120 tree species present in  
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16 169 continental Spain: maximum height, wood density, seed mass, leaf mass per area and  
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18 170 leaf nitrogen content per mass via the TRY initiative (<http://www.try-db.org>; Table S3;  
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20 171 Kattge *et al.*, 2011). These traits have been widely recognized as key traits of plant  
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23 172 function: maximum height, wood density and seed mass are closely related to life  
24  
25 173 history strategy, while leaf mass per area and leaf nitrogen content per mass are related  
26  
27 174 to resource acquisition and plant growth strategy (Paquette & Messier, 2011; Swenson  
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29 175 *et al.*, 2012). We computed the FD index for the five traits together, a subset of traits  
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31 176 (seed mass, wood density, and maximum height) often used in the BEF literature (e.g.  
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33 177 Paquette & Messier, 2011), and for each trait separately based on both abundance and  
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35 178 presence–absence matrixes. FI indices were computed for each trait separately, based on  
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37 179 both abundance and presence–absence matrices (Appendix S1).

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41 180 Prior to parameterizing our maximum likelihood models of carbon storage and  
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43 181 tree productivity, we performed a variable selection over the large dataset of abiotic,  
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45 182 structural and diversity variables. Using PCA techniques on all twenty-nine highly  
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47 183 correlated topographic and climatic predictors available, we selected, as representative  
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49 184 of the climatic conditions of each plot, mean annual temperature (°C) and water deficit  
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51 185 according to Emberger (mm) (Appendix S1 and Table S2). Edaphic variables were  
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53 186 strongly related to forest type and showed little dispersion within each forest type  
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55 187 (Appendix S1), therefore they were excluded from further analysis. In order to select  
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3 188 representative variables of structural and diversity effects, we compared the strength of  
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5 189 evidence for each independent factor separately using the Akaike Information Criterion  
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7 190 (AIC) (Appendix S1). Models based on functional diversity, i.e. species functional  
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9 191 traits, were a better fit to the data than models based on species diversity (Appendix S1).  
10  
11 192 The FD index based on three traits (maximum height, wood density and seed mass) and  
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13 193 calculated using presence/absence data was chosen as the best estimator of  
14  
15 194 complementarity effects based on AIC differences (Appendix S1). The FI index based  
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17 195 on leaf mass per area (LMA) and calculated using abundance data was chosen as the  
18  
19 196 best estimator of selection effects. As a result of the variable selection process, a final  
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21 197 group of six variables was selected to be used as predictors of carbon storage and tree  
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23 198 productivity (Table S4): two climatic variables (mean annual temperature and water  
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25 199 deficit), two structural variables representative of density and heterogeneity effects  
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27 200 (stand tree density and coefficient of variation of tree height, respectively) and two trait-  
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29 201 based diversity variables representative of complementarity and selection effects (FD  
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31 202 and FI, respectively).  
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#### 37 38 204 **Maximum likelihood analysis of carbon storage and tree productivity**

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41 206 We used maximum likelihood techniques and model selection for the analysis of carbon  
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43 207 storage and tree productivity along climatic, structural and diversity gradients. Carbon  
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45 208 storage ( $\text{Mg C ha}^{-1}$ ) and tree productivity ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ) were predicted as a function  
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47 209 of maximum potential carbon storage (PCS) and maximum potential tree productivity  
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49 210 (PTP), respectively, and three scalar modifiers ranging from 0 to 1 that quantified the  
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51 211 effect on the average maximum PCS/PTP of local climatic conditions, stand structure  
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53 212 and diversity effects. We defined different models of carbon storage and tree  
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productivity that were analyzed separately for each forest type based on the following functional form:

$$Predicted = Potential \times Climatic\ effect \times Structural\ effect \times Diversity\ effect \quad (3)$$

The potential carbon storage (PCS) or potential tree productivity (PTP) in this model is a 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 modeled using a bivariate Gaussian function:

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

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 modeled using a bivariate Gaussian function including density and structural heterogeneity effects:

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

where the density effect is measured in terms of stand density (No. trees  $ha^{-1}$ ) 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

238 height, respectively, at which maximum carbon storage or productivity occurs, and  $XD_b$   
 239 and  $XH_b$  are estimated parameters that control the breadth of the function.

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

$$244 \text{ Diversity effect} = [1 - \exp(XFD_a \cdot FD - XFD_b)] \times \exp \left[ -\frac{1}{2} \left( \frac{\log(\frac{FI}{XFI_a})}{XFI_b} \right)^2 \right] \quad (6)$$

246 The exponential form selected to model the effect of FD on carbon storage and  
 247 tree productivity varied between 0 and 1. The parameter  $XFD_a$  determines the shape of  
 248 the effect of FD on the predicted variable and  $XFD_b$  defines the intercept of the  
 249 function. The parameter  $XFI_a$  represents the community-weighted mean value at which  
 250 maximum potential carbon storage or tree productivity occurs, and  $XFI_b$  determines the  
 251 breadth of the function.

252 We compared alternate models using differences in AIC (Akaike Information  
 253 Criterion) as an indicator of both parsimony and likelihood (Burnham & Anderson,  
 254 2002). We used two-units difference in AIC as a support interval to assess the strength  
 255 of evidence of individual maximum likelihood parameter estimates, being roughly  
 256 equivalent to the 95% support limit defined using a likelihood ratio test (Burnham &  
 257 Anderson, 2002). The full model was compared with models that ignored the effect of  
 258 climate, stand structure or diversity, and with the null or intercept-only model (i.e.  
 259 ignoring the effect of climate, stand structure and diversity) for each response variable  
 260 (i.e. carbon storage and tree productivity) and each forest type. Then, we tested the  
 261 relative importance of FD and FI mechanisms based on AIC differences between the

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3 262 full model and models that ignored the effect of FD or FI (respectively) for each forest  
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7 264 The parameter estimates provide the basis for determining the magnitude of the  
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9 265 effect of a given process, with maximum likelihood estimates of parameter values close  
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11 266 to zero indicating no effect. We used simulated annealing optimization procedures to  
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13 267 determine the parameters that maximize the log-likelihood of observing carbon storage  
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15 268 and tree productivity with a normal error distribution given our data (Goffe *et al.*, 1994).  
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17 269 The  $R^2$  of the regression was used as a measure of goodness of fit ( $1 - SSE/SST$ , SSE:  
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19 270 sum of squares error, SST: sum of squares total) and the slope of the regression (with a  
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21 271 zero intercept) of observed and predicted data was used as a measure of bias (an  
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23 272 unbiased model having a slope of 1). The analyses were performed using the likelihood  
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25 273 package 1.4 (Murphy, 2008) for the R statistical language (R Development Core Team,  
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27 274 2011).  
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## 275 RESULTS

276

### 277 Abiotic and biotic determinants of carbon storage

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279 The effects of climate, stand structure and diversity on total carbon storage were  
280 included in the best model for all forest types (Table 1). All of the models produced  
281 unbiased estimates of carbon storage (i.e. slopes of predicted versus observed values  
282 were all close to 1 and  $R^2$  ranged from 0.18 to 0.61 for carbon storage models; Table 1  
283 and Fig. S1). Stand structure was the most important factor for determining carbon  
284 storage (as indicated by the largest increase in AIC when the structural effect term was  
285 dropped from the full models) followed by the climatic and the diversity effects (Table  
286 1 and Fig. S2). The relative importance of the diversity effect on carbon storage was  
287 greater than that of the climate effect for deciduous, exotic and Mediterranean pine  
288 forests (both natural and planted), but lower for mountain pines (both natural and  
289 planted) and sclerophyllous forests (Table 1).

290 The effects of complementarity (measured as functional diversity, i.e. FD,  
291 through functional dispersion based on maximum height, wood density and seed mass)  
292 and selection (measured as functional identity, i.e. FI, through CWM based on leaf mass  
293 area) differed among forest types. FD had a net positive effect on carbon storage in all  
294 forest types studied. We found non-linear increases in carbon storage along functional  
295 diversity gradients for all forest types. Carbon storage increased at an average of 32%  
296 from monospecific (FD = 0) to functionally diverse forests (FD *c.* 2) (Fig. 2(a)). It is  
297 interesting to note that all forest types experienced the strongest increases of carbon  
298 storage in the lower parts of the FD gradient (Fig. 2(a,c)). The magnitude of the effect  
299 of FD on carbon storage was larger for exotic, planted pine (both Mediterranean and

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3 300 mountain), natural Mediterranean pine and deciduous forests than for sclerophyllous  
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5 301 and natural mountain pine forests (Fig. 2(a)).  
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7 302 Functional identity had an effect on carbon storage models in five of the seven  
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9 303 forest types (all but mountain and exotic forests; see  $\Delta AIC$  in FD and FI respectively,  
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11 304 Table 1). Carbon storage was maximised close to the most frequent values of leaf mass  
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13 305 per area (LMA) in each forest type (Fig. 2(b,d)): low values for deciduous forests (*c.* 81  
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15 306  $\text{g m}^{-2}$ ), intermediate values of LMA in sclerophyllous forests (*c.* 145  $\text{g m}^{-2}$ ), and high  
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17 307 values of LMA in Mediterranean pine forests (*c.* 230  $\text{g m}^{-2}$ ; Table S4). These results  
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19 308 indicate the importance of selection effects, because carbon storage increases towards  
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21 309 the mean LMA value observed in each forest type, which is mainly determined by the  
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23 310 identity of the dominant species in each forest.  
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### 30 312 **Abiotic and biotic determinants of tree productivity**

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34 314 The best models of tree productivity included the effects of climate, stand structure and  
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36 315 diversity (Table 2), similar to those obtained for carbon storage. All models produced  
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38 316 unbiased estimates of total tree productivity (i.e. slopes of predicted versus observed  
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40 317 values were all close to 1 and  $R^2$  ranged from 0.20 to 0.47; Table 2 and Fig S3). The  
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42 318 relative importance of the structural effects on tree productivity was much greater than  
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44 319 that of climate and diversity effects for all forest types (see  $\Delta AIC$ , Table 2 and Fig. S4).  
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46 320 Diversity had a larger effect on tree productivity than climate in deciduous and  
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48 321 Mediterranean pine forests (natural and planted), whereas we observed the opposite  
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50 322 pattern for the rest of the forest types (Table 2).  
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54 323 Complementarity (measured as FD) generally had a positive but non-linear  
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56 324 effect on total tree productivity in all forest types (except exotic forests; Table 2, Fig.  
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3 325 3(a)). These effects were again particularly relevant in the lower parts of the FD  
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5 326 gradient, where slight changes in FD generally correlate to large increases in potential  
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7 327 tree productivity (Fig. 3(a)). Tree productivity increased at an average of 21% from  
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9 328 monospecific (FD = 0) to functionally diverse forests (FD *c.* 2) (Fig. 3(a)). The absolute  
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11 329 effect of FD on potential tree productivity was larger for deciduous, sclerophyllous and  
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13 330 natural Mediterranean pine forests than for mountain pines, planted Mediterranean pines  
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15 331 and exotic forests (see relative changes in potential tree productivity, Fig. 3(a)).

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18 332 Functional identity had an effect on total tree productivity in four of the seven  
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20 333 forest types studied (deciduous, sclerophyllous, Mediterranean natural pines and exotic  
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22 334 forests, Table 2), with the relative importance of FI being greater than FD (Table 2). We  
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24 335 observed maximum potential tree productivity towards the most frequent values of  
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26 336 LMA in each forest type: low values for deciduous forests, intermediate values in  
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28 337 sclerophyllous forests, and high values in Mediterranean pine forests (Table S4). The  
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30 338 absolute effect of FI on tree productivity was particularly strong for deciduous and  
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32 339 Mediterranean pine forests, but it had almost no effect on mountain pine and exotic  
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34 340 forests (Fig. 3(b)).  
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3 341 **DISCUSSION**

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7 343 **Diversity effects on carbon storage and tree productivity**

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11 345 Our results show a general positive effect of functional diversity on carbon storage and  
12 346 tree productivity in a wide variety of forests, from cold deciduous Atlantic to xeric  
13 347 Mediterranean evergreen forests. The net effect of diversity on both carbon storage and  
14 348 tree productivity was detected even when controlling for potentially confounding  
15 349 structural and climatic factors. The effect of diversity was lower than the effect of stand  
16 350 structure, but diversity effects were greater or equal to the climatic effects (Table 2, 3).

17 351 Our results agree with previous studies suggesting that stand structure is the main  
18 352 variable affecting carbon stock change in Iberian forests (e.g. Vayreda *et al.*, 2012). As  
19 353 expected, climate also influenced carbon storage and tree productivity (e.g. Vila *et al.*,  
20 354 2007). However, its lower effect than diversity indices could indicate that climatic  
21 355 conditions constrain the maximum limit of carbon storage and tree productivity, thus  
22 356 explaining its relatively little contribution (Stegen *et al.*, 2011). Other potential drivers of  
23 357 carbon storage and tree productivity such as soil fertility (Wardle *et al.*, 2008) or  
24 358 historical management (Vilà *et al.*, 2005) could not be explored because of their  
25 359 unavailability at the large-scale used in this study (e.g. Gómez-Aparicio *et al.*, 2011).

26 360 In our models, functional diversity indices were better predictors of carbon  
27 361 storage and tree productivity than tree species richness (Appendix S1 and Fig. S5).

28 362 Other authors have previously reported positive or neutral effects of species diversity on  
29 363 wood production in Spanish forests (Vilà *et al.*, 2003; Vilà *et al.*, 2007). Although Vilà  
30 364 *et al.* (2007) considered the effects of functional groups, the role of functional diversity  
31 365 *per se* and the underlying mechanisms of diversity effects in Spanish forests have not

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3 366 been previously explored. Our results therefore support recent findings that suggest the  
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5 367 need to go beyond species richness and consider functional diversity and identity to  
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7 368 better understand the underlying mechanisms of BEF relationships (e.g. Morin *et al.*,  
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9 369 2011; Paquette & Messier, 2011). The trait-based approaches used here directly and  
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11 370 indirectly assess those mechanisms, because ecosystem functions are governed by  
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13 371 species dominance, distribution and functional traits (e.g. Mokany *et al.*, 2008).

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16 372 We used both functional diversity and identity based on different functional  
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18 373 traits to quantify complementarity and selection mechanisms on ecosystem functions in  
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20 374 the main natural and planted forests of continental Spain. Model comparison allowed us  
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22 375 to identify the traits related to FD (maximum height, wood density and seed mass;  
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24 376 Appendix S1). These traits are related to reproduction, growth and successional status  
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26 377 (Paquette & Messier, 2011; Swenson *et al.*, 2012). Thus, these three traits indicate  
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28 378 different life-history strategies and their variability helps to quantify the breadth of their  
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30 379 niche (i.e. determining when species use resources differently) (Hooper *et al.*, 2005).  
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32 380 We obtained that FD indices based on presence–absence matrices, rather than  
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34 381 abundances, better explained productivity and carbon storage (see also Paquette &  
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36 382 Messier, 2011). This raises the question of the scale at which complementarity may  
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38 383 occur, and the relative "quantity" of a given species required for it to increase niche  
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40 384 partitioning, questions already raised by Petchey & Gaston (2006), but which remain  
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42 385 largely unanswered. In our case leaf mass per area was the best predictor among the  
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44 386 CWM indices calculated for each trait. LMA is a functional trait that directly affects  
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46 387 tree growth and thus determines plant performance and species dominance in forests  
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48 388 (Díaz *et al.*, 2004; Wright *et al.*, 2004). In accordance with Morin *et al.* (2011), we  
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50 389 conclude that for forests of continental Spain complementarity effects are linked to the  
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52 390 interspecific variation of functional traits that determine resource use and acquisition,  
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3 391 while selection effects depend on the mean values of species traits that are directly  
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5 392 linked to plant performance.  
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10 394 **Underlying mechanisms of diversity effects on carbon storage and tree**  
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12 395 **productivity**

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16 397 Our results support the idea that both complementarity and selection components of  
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18 398 biodiversity effects are not mutually exclusive (Tables 1 and 2): more functionally  
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20 399 diverse forests that include certain species possessing key traits promote both carbon  
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22 400 storage and tree productivity. Selection effects could be related with species being  
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24 401 selectively favoured given a certain climate, causing a more complete utilization of  
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26 402 limited resources (Tilman, 1999; Loreau, 2000). Loreau & Hector (2001) suggested that  
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28 403 both positive complementarity and selection effects on productivity reflects the  
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30 404 “sampling effect”, increasing the probability of sampling a dominant, high-biomass  
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32 405 species in mixed forest, but also increasing the probability of sampling a suite of  
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34 406 complementary species. Our results confirm that contrasting traits promote tree  
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36 407 productivity and carbon storage, together with species-specific selection effects based  
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38 408 on leaf mass per area, as previously suggested in other forest types (Paquette & Messier,  
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40 409 2011; Zhang *et al.*, 2012).

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45 410 The BEF relationship observed along FD (i.e. complementarity effect) was  
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47 411 positive but not linear, showing the largest changes of carbon storage and tree  
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49 412 productivity at low FD values (Figs 2(a) and 3(a)). It has been suggested that the  
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51 413 positive relation between species richness and ecosystem function increases until an  
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53 414 asymptote is reached where functional redundancy and niche overlap occurs (e.g.  
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55 415 Loreau *et al.*, 2001; Hooper *et al.*, 2005). This form of BEF relationship has been  
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3 416 reported in a recent meta-analysis of forest productivity that showed that an asymptote  
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5 417 was reached at around six species (Zhang *et al.*, 2012). The largest changes on carbon  
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7 418 storage and tree productivity occurred at low FD values suggesting that most benefits  
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9 419 are found when moving away from monospecific stands, and later the increase of  
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11 420 ecosystem functions is expected to saturate (e.g. Loreau, 2000).

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14 421 Our results suggest that complementarity effects are relevant for all types of  
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16 422 Spanish forests, regardless of their productivity. For example, deciduous forests show  
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18 423 the greatest effects of complementarity on potential tree productivity (a 25%  
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20 424 productivity increase along the FD gradient, Fig. 3(a)) despite having an intermediate  
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22 425 mean productivity within the seven forest types considered ( $1.36 \pm 1.30 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ,  
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24 426 Table S4). Therefore, we did not find strong support for a larger role of  
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26 427 complementarity in low-productive or more stressful environments (where facilitation  
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28 428 may be more important) than in high-productive environments (where competitive  
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30 429 exclusion is expected to dominate species interactions), as suggested by previous  
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32 430 theoretical (Warren *et al.*, 2009) and observational studies (Paquette & Messier, 2011).  
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34 431 This lack of a clear relationship between complementarity and productivity could be due  
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36 432 to the complexities and ambiguities associated with the definition of "stressful  
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38 433 conditions" at the community level, since each forest type is composed of individuals  
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40 434 and species both adapted to and limited by local conditions (e.g. Körner, 2004). Because  
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42 435 the concept of stress is better applied at the species level, each individual species could  
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44 436 either be favored by facilitation or impaired by competition (Holmgren *et al.*, 2007),  
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46 437 with stress and facilitation increasing as environmental conditions deviate from a  
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48 438 species' ecophysiological optimum (Greiner La Peyre *et al.*, 2001).

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54 439 We found that selection effects based on species identity and dominance  
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56 440 (measured as functional identity using CWM based on LMA) had a positive effect on  
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3 441 carbon storage and tree productivity. The selection effect was particularly large in  
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5 442 Mediterranean pines and deciduous forests (Table S4). The leaf economic spectrum  
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7 443 predicts that low LMA should promote productivity (e.g. Wright *et al.*, 2004; Morin *et*  
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9 444 *al.*, 2011). However, Mediterranean pines had their maximum productivity at high LMA  
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11 445 which could be related with traits favoured by and adapted to arid and semi-arid  
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13 446 conditions (Wright *et al.*, 2005). Moreover, these forest types usually form mixed  
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15 447 forests of functionally contrasting species, because Mediterranean pine species and  
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17 448 hardwoods could coexist or alternate depending on the environmental heterogeneity and  
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19 449 disturbance regime (Zavala *et al.*, 2000; Gómez-Aparicio *et al.*, 2011). Therefore,  
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21 450 spatial differences in species dominance could lead to the greater importance of  
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23 451 selection mechanisms in Mediterranean pine and Atlantic forests, causing the large  
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25 452 variation in carbon storage and tree productivity observed along FI gradient (Figs 2(b)  
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27 453 and 3(b)). On the other hand, we observed that mountain forests had the lowest  
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29 454 sensitivity to selection effects (Figs 2(b) and 3(b)). This could be due to the fact that  
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31 455 mountain forests tend to mix with functionally similar species including mostly conifers  
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33 456 typical of high altitudes (Costa *et al.*, 1997), and therefore mountain forests have high  
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35 457 monospecificity and low FD.  
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## 43 **Conclusions**

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45 460 Our results demonstrate that functional diversity is crucial in maintaining ecosystem  
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47 461 functions in Spanish forests along large bioclimatic gradients. Thus, carbon storage and  
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49 462 tree productivity increase at an average of 32% and 21%, respectively, from  
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51 463 monospecific to functionally diverse forests, which agrees with previous studies finding  
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53 464 a 24% average increment of productivity from forest monocultures to polycultures  
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55 465 (Zhang *et al.*, 2012; Vilá *et al.*, 2013). Moreover, our results indicate that BEF  
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3 466 relationships and complementarity effects are not substantially affected by the origin of  
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5 467 the stand, with **diversity** having a positive effect on carbon storage and tree productivity  
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7 468 in both natural and planted Spanish forests. These findings suggest that results obtained  
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9 469 in experimentally controlled environments (the large majority of the BEF research so  
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11 470 far; Adler *et al.*, 2011) could also be applicable to natural systems.

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14 471 Maintaining diverse forests in the Iberian Peninsula in particular, and in the  
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16 472 Mediterranean region in general, should be considered both an important challenge and  
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18 473 a necessity. The Mediterranean region is particularly vulnerable to climate change as  
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20 474 well as habitat loss, fragmentation, and fire frequency increases (Schröter *et al.*, 2005;  
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22 475 Pausas *et al.*, 2008). As a consequence, potential biodiversity losses could be  
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24 476 particularly large in this area, and therefore their negative effects on ecosystem  
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26 477 functions and related services as well (Lindner *et al.*, 2010). Our results indicate that  
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28 478 BEF relationships are maintained through both complementarity and selection effects.  
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30 479 Therefore, we conclude that management efforts should aim at promoting both  
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32 480 functionally diverse forests and functionally important species, which could act as  
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34 481 insurance for the maintenance of key ecosystem functions such as carbon storage and  
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36 482 tree productivity.  
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5 675 **SUPPORTING INFORMATION**  
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7 676 Additional supporting information may be found in the online version of this article:  
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9 677 **Appendix S1** Further details regarding the methods used and variable selection.  
10 678 **Table S1** List of species names and family, forest type, and species used to calculate the  
11 679 carbon storage and tree productivity.  
12 680 **Table S2** Description of the potential predictor variables of carbon storage and tree  
13 681 productivity.  
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15 682 **Table S3** Functional traits used to compute trait-based diversity indices.  
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17 683 **Table S4** Mean values of carbon storage, tree productivity and the rest of the predictor  
18 684 variables included in the best model. Number of plots and species composition of each  
19 685 forest type is also given.  
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21 686 **Table S5** Parameter estimates and two-unit support intervals for the most parsimonious  
22 687 total carbon storage model for each of the seven forest types defined.  
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24 688 **Table S6** Parameter estimates and two-unit support intervals for the most parsimonious  
25 689 tree productivity model for each of the seven forest types defined.  
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27 690 **Figure S1** Observed versus predicted carbon storage for the best model in each forest  
28 691 type.  
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30 692 **Figure S2** Predicted potential carbon storage as function of mean annual temperature,  
31 693 water deficit, tree density and tree height coefficient of variation for each forest type.  
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33 694 **Figure S3** Observed versus predicted tree productivity for the best model in each forest  
34 695 type.  
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36 696 **Figure S4** Predicted potential tree productivity as function of mean annual temperature,  
37 697 water deficit, tree density and tree height coefficient of variation for each forest type.  
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39 698 **Figure S5** Predicted potential carbon storage and tree productivity as function of tree  
40 699 species richness.  
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3 706 **Biosketch**  
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5 707 **Paloma Ruiz-Benito** is a post-doctoral researcher at the Forest Ecology and Restoration  
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7 708 Group (Alcalá University) under FUNDIV project (<http://www.fundiveurope.eu/>). For  
8  
9 709 her PhD she studied key ecosystem processes and services along large abiotic and biotic  
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11 710 gradients to assess potential effects of global change on Iberian forest structure and  
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14 711 dynamics, and the implications for their restoration and conservation.  
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712 **Table 1** Comparisons of alternate models of carbon storage (Mg C ha<sup>-1</sup>) for the seven forest types studied using Akaike Information  
 713 Criterion (AIC).

| Forest type                 | ΔAIC     |            |              |              |       |       | R <sup>2</sup> | Slope | N    |        |
|-----------------------------|----------|------------|--------------|--------------|-------|-------|----------------|-------|------|--------|
|                             | Full     | No climate | No structure | No diversity | No FD | No FI |                |       |      |        |
| Deciduous                   | <b>0</b> | 664        | 1,402        | 1,259        | 118   | 1,201 | 5,263          | 0.38  | 0.99 | 11,125 |
| Sclerophyllous              | <b>0</b> | 905        | 7,421        | 162          | 58    | 131   | 12,928         | 0.61  | 1.00 | 13,857 |
| Mediterranean natural pines | <b>0</b> | 590        | 2,696        | 623          | 553   | 185   | 5,272          | 0.43  | 1.00 | 9,382  |
| Mountain natural pines      | <b>0</b> | 1,427      | 2,284        | 132          | 98    | -5    | 3,643          | 0.41  | 1.00 | 6,895  |
| Mediterranean planted pines | <b>0</b> | 26         | 1,360        | 321          | 159   | 71    | 2,057          | 0.34  | 1.00 | 3,147  |
| Mountain planted pines      | <b>0</b> | 150        | 810          | 39           | 64    | 4     | 1,139          | 0.29  | 0.99 | 3,349  |
| Exotic                      | <b>0</b> | 27         | 71           | 73           | 72    | -4    | 356            | 0.18  | 0.99 | 1,966  |

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



722 **Table 2** Comparisons of alternate models of total tree productivity ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ) for the seven forest types studied using Akaike Information  
 723 Criterion (AIC).

| Forest type                 | $\Delta\text{AIC}$ |            |              |              |       |       | Null  | $R^2$ | Slope | $N$   |
|-----------------------------|--------------------|------------|--------------|--------------|-------|-------|-------|-------|-------|-------|
|                             | Full               | No Climate | No Structure | No Diversity | No FD | No FI |       |       |       |       |
| Deciduous                   | <b>0</b>           | 286        | 713          | 542          | 282   | 312   | 2,267 | 0.36  | 0.99  | 5,109 |
| Sclerophyllous              | <b>0</b>           | 571        | 2,753        | 145          | 128   | -2    | 5,735 | 0.43  | 1.00  | 9,071 |
| Mediterranean natural pines | <b>0</b>           | 459        | 1,920        | 547          | 173   | 434   | 3,357 | 0.41  | 1.00  | 6,455 |
| Mountain natural pines      | <b>0</b>           | 990        | 2,489        | 13           | 7     | -14   | 3,187 | 0.47  | 1.00  | 5,078 |
| Mediterranean planted pines | <b>0</b>           | 247        | 949          | 300          | 8     | 209   | 1,617 | 0.40  | 1.00  | 3,147 |
| Mountain planted pines      | <b>0</b>           | 346        | 671          | 10           | 7     | -8    | 937   | 0.38  | 0.99  | 2,021 |
| Exotic                      | <b>0</b>           | 11         | 46           | 10           | -3    | 11    | 88    | 0.20  | 0.99  | 517   |

724 The full models include the effects of climate, structure and diversity (see Eqn (3)) for each forest type. The models ‘No climate’, ‘No structure’,  
 725 ‘No diversity’, ignore the effect of climate, stand structure, and functional diversity, respectively. The null models ignore the climatic, structural  
 726 and diversity effects. The best fitting model is given in  $\Delta\text{AIC}$  value of zero (bold), comparing the full model with models dropping the effect of  
 727 climate, stand structure or diversity. We also tested the relative importance of functional diversity (FD, measured through functional dispersion  
 728 of maximum height, wood density and seed mass) and functional identity (FI; measured through community-weighted means of LMA) by  
 729 ignoring its effects (‘No FD’ and ‘No FI’, respectively).  
 730  $N$  is the sample size (number of plots). For the best model (i.e.  $\Delta\text{AIC} = 0$ ) we show the slope and  $R^2$  ( $1 - \text{SEE}/\text{SST}$ ) for the relationship of the  
 731 predicted and observed tree productivity.

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3 732 **FIGURE LEGENDS**

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8 734 **Figure 1** Map of plots used in this study from the third Spanish Forest Inventory for the  
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10 735 seven forest types included in the study.

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12 736 Map projection UTM 30N, European Datum 1950

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17 738 **Figure 2** Predicted potential fraction (proportion) and total carbon storage ( $\text{Mg C ha}^{-1}$ )  
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19 739 for each forest type along gradients of: functional diversity (FD) of maximum height,  
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21 740 wood density and seed mass ((a) and (c), respectively); and functional identity (FI,  
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23 741 measured through CWM of leaf mass per area ( $\text{g m}^{-2}$ )) ((b) and (d), respectively). See  
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25 742 Table S5 for the estimated parameters of the corresponding functions.  
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31 744 **Figure 3** Predicted potential fraction (proportion) and tree productivity ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ )  
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33 745 for each forest type along gradients of: functional diversity (FD) of maximum height,  
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35 746 wood density and seed mass ((a) and (c), respectively); and functional identity (FI,  
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37 747 measured through CWM of leaf mass per area ( $\text{g m}^{-2}$ )) ((b) and (d), respectively). See  
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39 748 Table S6 for the estimated parameters of the corresponding functions.  
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Figure 1

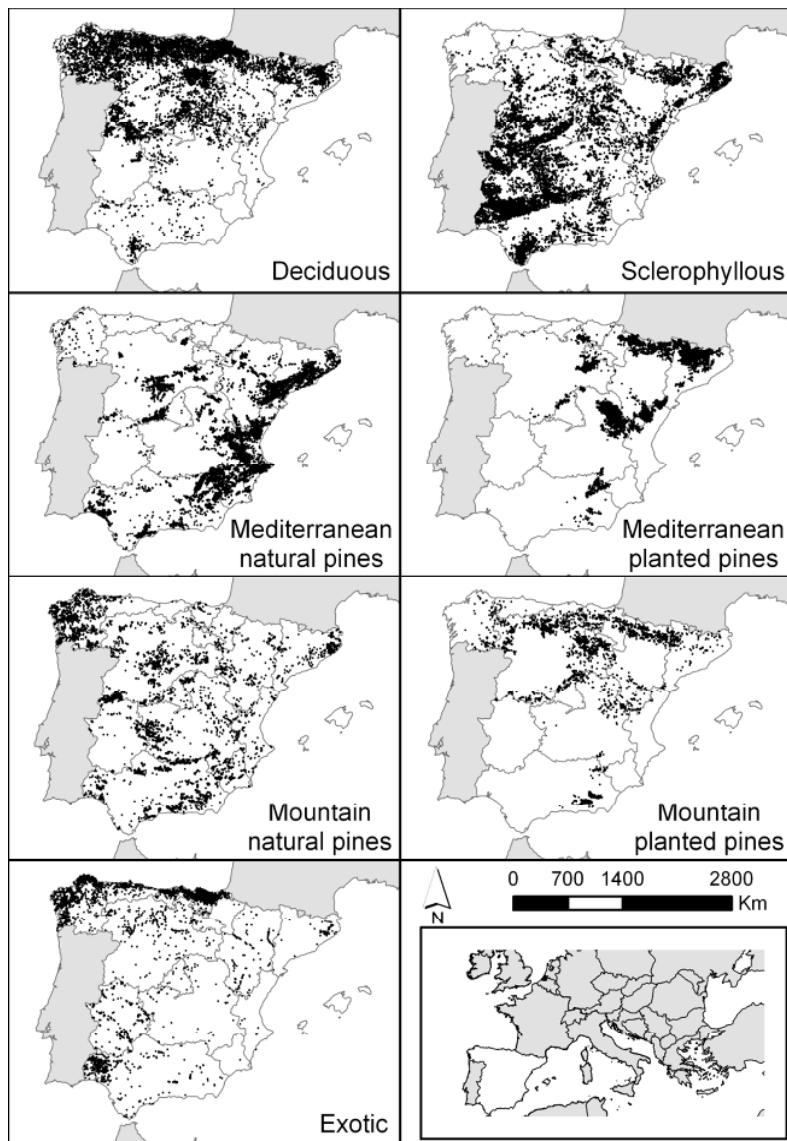
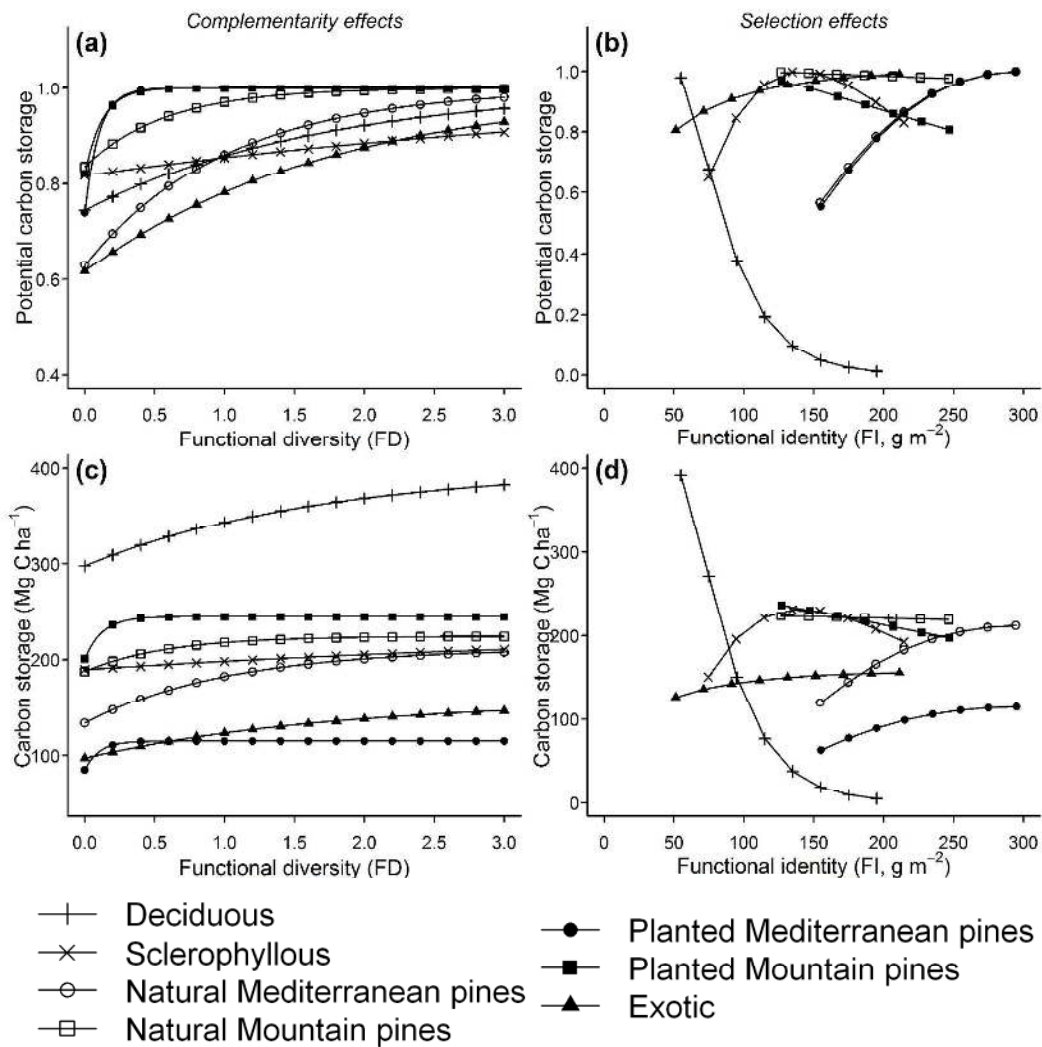


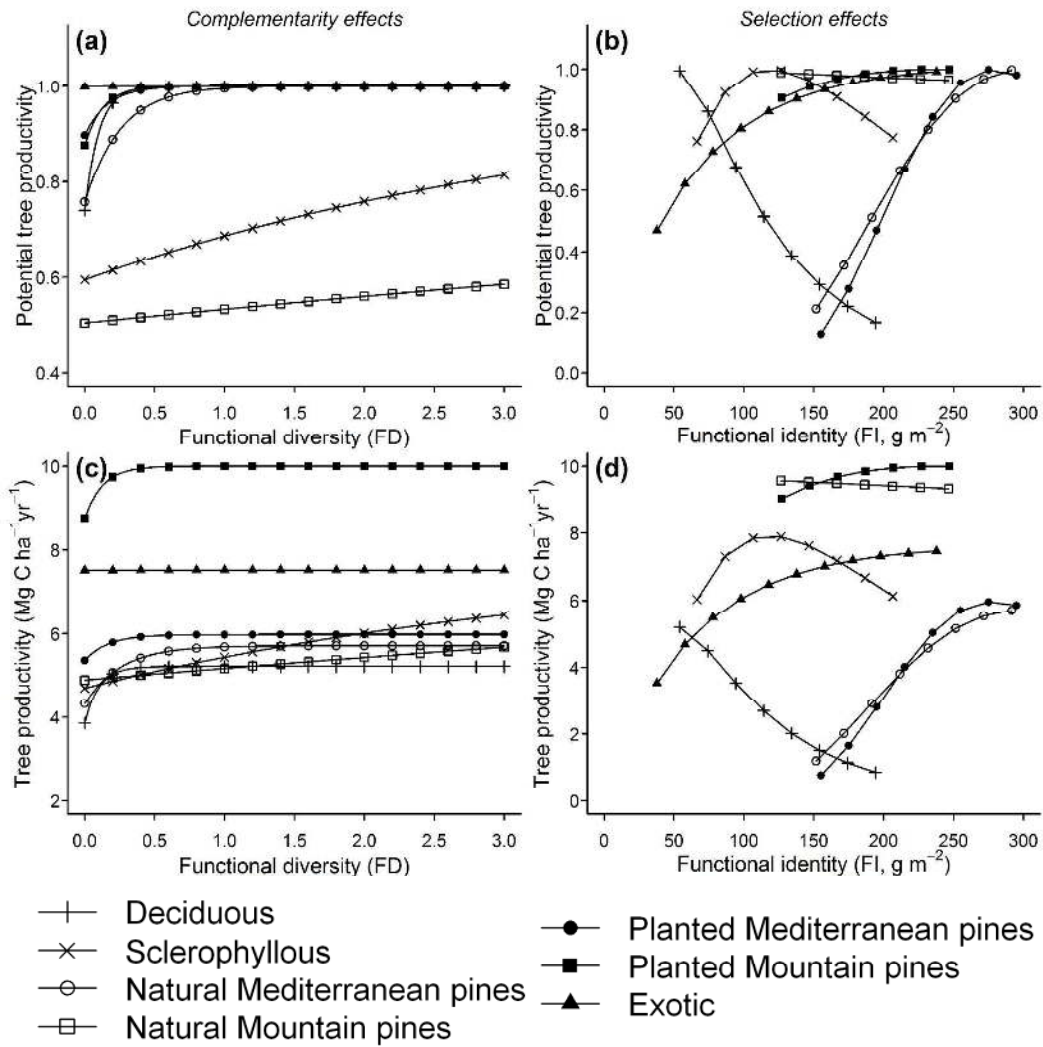
Figure 2



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Figure 3



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