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1   **==Diversity== increases carbon storage and tree productivity in Spanish**

2   **forests**

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17   Running title: Diversity effects on forest carbon storage and productivity.

18   **ABSTRACT**

19   **Aim** Biodiversity loss could reduce primary productivity and carbon storage provided

20   by forests; however the underpinning mechanisms of biodiversity effects on multiple

21   ecosystem functions are not completely understood. Spanish forests are of particular

22   interest because of the broad variation in environmental conditions and management

23   history. We tested for the existence of a relationship among diversity effects and both

24   carbon storage and tree productivity, and examined the relative importance of

25   complementarity and selection mechanisms in a wide variety of forests, from cold

26   deciduous Atlantic to xeric Mediterranean evergreen forests.

27   **Location** Continental Spain.

28   **Methods** We used *c.* 54,000 plots of the Spanish Forest Inventory and maximum

29   likelihood techniques to quantify how climate, stand structure and diversity shape

30   carbon storage and tree productivity. Diversity effects included both complementarity

31   and selection mechanisms, measured respectively through functional diversity and

32   functional identity measures.

33   **Results** Diversity had a significant effect on both carbon storage and tree productivity,

34   even when controlling for climatic and stand structural confounding factors. A

35   consistent positive effect of functional diversity on carbon storage and tree productivity

36   was observed in all seven forest types studied. This relationship was not linear, and the

37   largest changes in carbon storage and tree productivity were observed at low functional

38   diversity levels. However, the importance of complementarity effects was not consistent

39   with the productivity of different forest types. Selection effects were particularly

40   important in deciduous and Mediterranean pine forests, but had very little effect on

41   mountain pines.

42   **Main conclusions** We found a generally positive effect of diversity on carbon storage

43   and tree productivity, supported by both complementarity and selection mechanisms.

44   Thus, both functionally diverse forests and functionally important species should be

45   maintained to adequately preserve and promote key ecosystem functions such as carbon

46   storage and tree productivity.

47   **Keywords:** climate, competition, ecosystem functions and services, forest management,

48   functional diversity, functional identity, maximum likelihood techniques, national forest

49   inventory.

INTRODUCTION

Under global change the increase of human-mediated modifications in ecosystems could lead to important biodiversity losses (Cardinale *et al.*, 2012). Reductions of biodiversity may alter the quality and quantity 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 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 biodiversity effects to ecosystem functioning (e.g. Hooper *et al.*, 2005). Trait based approaches are a promising avenue to disentangle the underlying mechanisms of the diversity effects on productivity (see Mokany *et al.*, 2008; Paquette & Messier, 2011; Roscher *et al.*, 2012).

Two main non-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 an 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 productive or harsh environments, where species interactions are less affected by competitive exclusion (Warren *et al.*, 2009; Paquette & Messier, 2011). Yet, 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

75   which will become dominant in the community (e.g. Cardinale *et al.*, 2007). Thus,

76   selection effects are partially explained by the "mass-ratio hypothesis" stating that

77   ecosystem function levels are mainly determined by the functional traits of dominant

78   species (Grime, 1998; Mokany *et al.*, 2008; Roscher *et al.*, 2012). Both

79   complementarity and selection effects simultaneously underlie the net biodiversity

80   effect on ecosystem function (Tilman, 1996; Mokany *et al.*, 2008).

81   Most BEF studies have been conducted in experimental grasslands testing the

82   effects of species richness on ecosystem functions such as biomass production and

83   nutrient cycling (e.g. Cardinale *et al.*, 2007). Studies conducted in forest systems, either

84   planted or natural, are much more recent and scarce (e.g. Caspersen & Pacala, 2001;

85   Vilà *et al.*, 2007). These studies have mainly been based on observational forest

86   inventory data and species diversity measures, and although they highlighted the

87   importance of functional trait approaches, most of them did not explicitly consider

88   functional diversity and the underlying mechanisms of BEF relationships (Vilà *et al.*,

89   2007; Zhang *et al.*, 2012). The only study that, to our knowledge, has quantified the

90   relative importance of complementarity and selection mechanisms in forest ecosystems

91   suggests that both mechanisms could underlie BEF relationships, at least in simulated

92   mesic temperate forests (Morin *et al.*, 2011). More research is needed to understand the

93   role of BEF mechanisms in real forest communities differing in species composition,

94   stand origin and environmental conditions along large bioclimatic gradients.

95   In this study, we conducted a large-scale assessment of two ecosystem functions

96   (carbon storage and tree productivity) along wide climatic, forest structure and diversity

97   gradients using *c.* 54,000 plots distributed over forests in continental Spain. Continental

98   Spain harbors a high variety of forest types, ranging from Atlantic deciduous

99   broadleaved forests to sclerophyllous and Mediterranean pine forests (Costa *et al.*,

100   1997). Changes in tree carbon storage in Spanish forests depend on climatic and

101   structural conditions (Vayreda *et al.*, 2012) and positive effects of species <mark>richness</mark> on

102   tree productivity have already been reported (Vilà *et al.*, 2007; Vilà *et al.*, 2013).

103   However, the underlying mechanisms and the role of functional diversity on both

104   carbon storage and tree productivity are still poorly explored. Our main objectives are:

105   (i) to analyze the sign and magnitude of BEF relationships in Spanish forests, expecting

106   an effect of diversity on both carbon storage and tree productivity, even when

107   controlling for climatic and structural effects in different forest types; and (ii) to

108   understand how complementarity and selection mechanisms affect carbon storage and

109   tree productivity in different Spanish forest types, including natural and planted pine

110   forests. Increasing our understanding about the underlying mechanisms of diversity

111   effects on carbon storage and tree productivity is critical for guiding conservation

112   actions and counteracting the effects of species loss on forest ecosystem functioning.

113   **METHODS**

114

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

116   **productivity**

117

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^2 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^{-1}) 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:

131

132    $Ln\,(b) = \alpha + \beta \cdot Ln\,(d.b.h.)$ (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 *α* and *β* are species-

136   specific parameters for aboveground and belowground fractions. To obtain total carbon

137   storage (Mg C ha^{-1}), we multiplied biomass by the species-specific carbon content of

138 the biomass (Montero *et al.*, 2005), scaled-up to hectare, and aggregated total carbon

139 storage at species and plot levels.

140   **Total tree productivity** for each plot (TP_p considering both aboveground and

141 belowground biomass, Mg C ha^{-1} yr^{-1}) was measured through the sum of the temporal

142 variation in carbon storage of adult trees alive between the 2SFI and 3SFI (i.e. without

143 including dead trees). From the initial 53,817 plots of the 3SFI, we selected 32,110 plots

144 for which data at the tree level were available in both inventories. We calculated tree

145 productivity using the following equation:

146

147 $$TP_p = \sum \frac{C_{i,SFI3} - C_{i,SFI2}}{t} \tag{2}$$

148

149   where $C_{i,SFI3}$ and $C_{i,SFI2}$ are the carbon accumulated in each live tree i (Mg C ha^{-}

150 ^{1}) in the 3SFI and the 2SFI respectively, and t is the time span between both inventories.

151

152 **Abiotic and biotic determinants of carbon storage and tree productivity**

153 Each of the SFI plots of the seven forest types defined were characterized by 33 abiotic

154 variables, four stand structure variables, and 30 diversity indices (Table S2). The abiotic

155 variables included four topographic variables (altitude, slope, aspect and insolation), 25

156 climatic variables (calculated from temperature and precipitation information), and four

157 edaphic variables (rockiness, texture, organic matter content and soil pH). The four

158 stand structure variables included total cover fraction, tree cover fraction, stand tree

159 density, and coefficient of variation of tree height. The diversity variables included

160 indices based on both species and trait-based diversity indices. The species diversity

161 indices included the monospecific or mixed character of the stand, species richness and

162 Shannon indices. The trait-based diversity indices were computed as (Appendix S1): (i)

163 functional diversity (FD), measured through functional dispersion (Laliberté &

164 Legendre, 2010) and used as a proxy of complementarity effects; and (ii) functional

165 identity (FI), measured through community-level weighted means (CWM) and used as a

166 proxy of selection effects (Lavorel *et al.*, 2008).

167   To calculate functional diversity (FD) and identity (FI) indices we compiled

168 species mean values for five key functional traits for the 120 tree species present in

169 continental Spain: maximum height, wood density, seed mass, leaf mass per area and

170 leaf nitrogen content per mass via the TRY initiative (http://www.try-db.org; Table S3;

171 Kattge *et al.*, 2011). These traits have been widely recognized as key traits of plant

172 function: maximum height, wood density and seed mass are closely related to life

173 history strategy, while leaf mass per area and leaf nitrogen content per mass are related

174 to resource acquisition and plant growth strategy (Paquette & Messier, 2011; Swenson

175 *et al.*, 2012). We computed the FD index for the five traits together, a subset of traits

176 (seed mass, wood density, and maximum height) often used in the BEF literature (e.g.

177 Paquette & Messier, 2011), and for each trait separately based on both abundance and

178 presence–absence matrixes. FI indices were computed for each trait separately, based on

179 both abundance and presence–absence matrices (Appendix S1).

180   Prior to parameterizing our maximum likelihood models of carbon storage and

181 tree productivity, we performed a variable selection over the large dataset of abiotic,

182 structural and diversity variables. Using PCA techniques on all twenty-nine highly

183 correlated topographic and climatic predictors available, we selected, as representative

184 of the climatic conditions of each plot, mean annual temperature (ºC) and water deficit

185 according to Emberger (mm) (Appendix S1 and Table S2). Edaphic variables were

186 strongly related to forest type and showed little dispersion within each forest type

187 (Appendix S1), therefore they were excluded from further analysis. In order to select

188   representative variables of structural and diversity effects, we compared the strength of

189   evidence for each independent factor separately using the Akaike Information Criterion

190   (AIC) (Appendix S1). Models based on functional diversity, i.e. species functional

191   traits, were a better fit to the data than models based on species diversity (Appendix S1).

192   The FD index based on three traits (maximum height, wood density and seed mass) and

193   calculated using presence/absence data was chosen as the best estimator of

194   complementarity effects based on AIC differences (Appendix S1). The FI index based

195   on leaf mass per area (LMA) and calculated using abundance data was chosen as the

196   best estimator of selection effects. As a result of the variable selection process, a final

197   group of six variables was selected to be used as predictors of carbon storage and tree

198   productivity (Table S4): two climatic variables (mean annual temperature and water

199   deficit), two structural variables representative of density and heterogeneity effects

200   (stand tree density and coefficient of variation of tree height, respectively) and two trait-

201   based diversity variables representative of complementarity and selection effects (FD

202   and FI, respectively).

203

204   **Maximum likelihood analysis of carbon storage and tree productivity**

205

206   We used maximum likelihood techniques and model selection for the analysis of carbon

207   storage and tree productivity along climatic, structural and diversity gradients. Carbon

208   storage (Mg C ha^{-1}) and tree productivity (Mg C ha^{-1} yr^{-1}) were predicted as a function

209   of maximum potential carbon storage (PCS) and maximum potential tree productivity

210   (PTP), respectively, and three scalar modifiers ranging from 0 to 1 that quantified the

211   effect on the average maximum PCS/PTP of local climatic conditions, stand structure

212   and diversity effects. We defined different models of carbon storage and tree

213 productivity that were analyzed separately for each forest type based on the following

214 functional form:

215

216 $Predicted = Potential \times Climatic\ effect \times Structural\ effect \times Diversity\ effect$ (3)

217

218   The potential carbon storage (PCS) or potential tree productivity (PTP) in this

219 model is a parameter that represents the maximum value when the other factors are at

220 optimal values (i.e. the maximum carbon storage or tree productivity that can be

221 obtained for a certain forest type). The *climatic effect* was modeled using a bivariate

222 Gaussian function:

223

224 $Climatic\ effect = \ exp\left[-\frac{1}{2}\left(\frac{Temperature-XT_a}{XT_b}\right)^2\right] \times exp\left[-\frac{1}{2}\left(\frac{Water\ deficit-XP_a}{XP_b}\right)^2\right]$ (4)

225

226   where the parameters XT_a and XP_a represent the mean annual temperature and

227 water deficit at which maximum carbon storage or productivity occurs, and XT_b and

228 XP_b are the parameters that control the variance of the normal distribution (i.e. the

229 breadth of the function).

230   The *structural effect* was modeled using a bivariate Gaussian function including

231 density and structural heterogeneity effects:

232

233 $Structural\ effect = \ exp\left[-\frac{1}{2}\left(\frac{Density-XD_a}{XD_b}\right)^2\right] \times exp\left[-\frac{1}{2}\left(\frac{Heterogeneity-XH_a}{XH_b}\right)^2\right]$ (5)

234

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

236 and the structural heterogeneity effect is measured through the coefficient of variation

237 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):

243

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

245

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

262 full model and models that ignored the effect of FD or FI (respectively) for each forest

263 type.

264   The parameter estimates provide the basis for determining the magnitude of the

265 effect of a given process, with maximum likelihood estimates of parameter values close

266 to zero indicating no effect. We used simulated annealing optimization procedures to

267 determine the parameters that maximize the log-likelihood of observing carbon storage

268 and tree productivity with a normal error distribution given our data (Goffe *et al.*, 1994).

269 The R^2 of the regression was used as a measure of goodness of fit (1 - SSE/SST, SSE:

270 sum of squares error, SST: sum of squares total) and the slope of the regression (with a

271 zero intercept) of observed and predicted data was used as a measure of bias (an

272 unbiased model having a slope of 1). The analyses were performed using the likelihood

273 package 1.4 (Murphy, 2008) for the R statistical language (R Development Core Team,

274 2011).

275   **RESULTS**

276

277   **Abiotic and biotic determinants of carbon storage**

278

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

300 mountain), natural Mediterranean pine and deciduous forests than for sclerophyllous

301 and natural mountain pine forests (Fig. 2(a)).

302   Functional identity had an effect on carbon storage models in five of the seven

303 forest types (all but mountain and exotic forests; see ΔAIC in FD and FI respectively,

304 Table 1). Carbon storage was maximised close to the most frequent values of leaf mass

305 per area (LMA) in each forest type (Fig. 2(b,d)): low values for deciduous forests (*c.* 81

306 g m^{-2}), intermediate values of LMA in sclerophyllous forests (*c.* 145 g m^{-2}), and high

307 values of LMA in Mediterranean pine forests (*c.* 230 g m^{-2}; Table S4). These results

308 indicate the importance of selection effects, because carbon storage increases towards

309 the mean LMA value observed in each forest type, which is mainly determined by the

310 identity of the dominant species in each forest.

311

312 **Abiotic and biotic determinants of tree productivity**

313

314 The best models of tree productivity included the effects of climate, stand structure and

315 diversity (Table 2), similar to those obtained for carbon storage. All models produced

316 unbiased estimates of total tree productivity (i.e. slopes of predicted versus observed

317 values were all close to 1 and R^2 ranged from 0.20 to 0.47; Table 2 and Fig S3). The

318 relative importance of the structural effects on tree productivity was much greater than

319 that of climate and diversity effects for all forest types (see ΔAIC, Table 2 and Fig. S4).

320 Diversity had a larger effect on tree productivity than climate in deciduous and

321 Mediterranean pine forests (natural and planted), whereas we observed the opposite

322 pattern for the rest of the forest types (Table 2).

323   Complementarity (measured as FD) generally had a positive but non-linear

324 effect on total tree productivity in all forest types (except exotic forests; Table 2, Fig.

325   3(a)). These effects were again particularly relevant in the lower parts of the FD

326   gradient, where slight changes in FD generally correlate to large increases in potential

327   tree productivity (Fig. 3(a)). Tree productivity increased at an average of 21% from

328   monospecific (FD = 0) to functionally diverse forests (FD *c.* 2) (Fig. 3(a)). The absolute

329   effect of FD on potential tree productivity was larger for deciduous, sclerophyllous and

330   natural Mediterranean pine forests than for mountain pines, planted Mediterranean pines

331   and exotic forests (see relative changes in potential tree productivity, Fig. 3(a)).

332   Functional identity had an effect on total tree productivity in four of the seven

333   forest types studied (deciduous, sclerophyllous, Mediterranean natural pines and exotic

334   forests, Table 2), with the relative importance of FI being greater than FD (Table 2). We

335   observed maximum potential tree productivity towards the most frequent values of

336   LMA in each forest type: low values for deciduous forests, intermediate values in

337   sclerophyllous forests, and high values in Mediterranean pine forests (Table S4). The

338   absolute effect of FI on tree productivity was particularly strong for deciduous and

339   Mediterranean pine forests, but it had almost no effect on mountain pine and exotic

340   forests (Fig. 3(b)).

341 **DISCUSSION**

342

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

344

345 Our results show a general positive effect of functional diversity on carbon storage and

346 tree productivity in a wide variety of forests, from cold deciduous Atlantic to xeric

347 Mediterranean evergreen forests. The net effect of diversity on both carbon storage and

348 tree productivity was detected even when controlling for potentially confounding

349 structural and climatic factors. The effect of diversity was lower than the effect of stand

350 structure, but diversity effects were greater or equal to the climatic effects (Table 2, 3).

351 Our results agree with previous studies suggesting that stand structure is the main

352 variable affecting carbon stock change in Iberian forests (e.g. Vayreda *et al.*, 2012). As

353 expected, climate also influenced carbon storage and tree productivity (e.g. Vila *et al.*,

354 2007). However, its lower effect than diversity indices could indicate that climatic

355 conditions constrain the maximum limit of carbon storage and tree productivity, thus

356 explaining it relatively little contribution (Stegen *et al.*, 2011). Other potential drivers of

357 carbon storage and tree productivity such as soil fertility (Wardle *et al.*, 2008) or

358 historical management (Vilà *et al.*, 2005) could not be explored because of their

359 unavailability at the large-scale used in this study (e.g. Gómez-Aparicio *et al.*, 2011).

360 In our models, functional diversity indices were better predictors of carbon

361 storage and tree productivity than tree species richness (Appendix S1 and Fig. S5).

362 Other authors have previously reported positive or neutral effects of species diversity on

363 wood production in Spanish forests (Vilà *et al.*, 2003; Vilà *et al.*, 2007). Although Vilà

364 *et al.* (2007) considered the effects of functional groups, the role of functional diversity

365 *per se* and the underlying mechanisms of diversity effects in Spanish forests have not

366 been previously explored. Our results therefore support recent findings that suggest the

367 need to go beyond species richness and consider functional diversity and identity to

368 better understand the underlying mechanisms of BEF relationships (e.g. Morin *et al.*,

369 2011; Paquette & Messier, 2011). The trait-based approaches used here directly and

370 indirectly assess those mechanisms, because ecosystem functions are governed by

371 species dominance, distribution and functional traits (e.g. Mokany *et al.*, 2008).

372   We used both functional diversity and identity based on different functional

373 traits to quantify complementarity and selection mechanisms on ecosystem functions in

374 the main natural and planted forests of continental Spain. Model comparison allowed us

375 to identify the traits related to FD (maximum height, wood density and seed mass;

376 Appendix S1). These traits are related to reproduction, growth and successional status

377 (Paquette & Messier, 2011; Swenson *et al.*, 2012). Thus, these three traits indicate

378 different life-history strategies and their variability helps to quantify the breadth of their

379 niche (i.e. determining when species use resources differently) (Hooper *et al.*, 2005).

380 We obtained that FD indices based on presence–absence matrices, rather than

381 abundances, better explained productivity and carbon storage (see also Paquette &

382 Messier, 2011). This raises the question of the scale at which complementarity may

383 occur, and the relative "quantity" of a given species required for it to increase niche

384 partitioning, questions already raised by Petchey & Gaston (2006), but which remain

385 largely unanswered. In our case leaf mass per area was the best predictor among the

386 CWM indices calculated for each trait. LMA is a functional trait that directly affects

387 tree growth and thus determines plant performance and species dominance in forests

388 (Díaz *et al.*, 2004; Wright *et al.*, 2004). In accordance with Morin *et al.* (2011), we

389 conclude that for forests of continental Spain complementarity effects are linked to the

390 interspecific variation of functional traits that determine resource use and acquisition,

391 while selection effects depend on the mean values of species traits that are directly

392 linked to plant performance.

393

Underlying mechanisms of diversity effects on carbon storage and tree productivity

396

397 Our results support the idea that both complementarity and selection components of

398 biodiversity effects are not mutually exclusive (Tables 1 and 2): more functionally

399 diverse forests that include certain species possessing key traits promote both carbon

400 storage and tree productivity. Selection effects could be related with species being

401 selectively favoured given a certain climate, causing a more complete utilization of

402 limited resources (Tilman, 1999; Loreau, 2000). Loreau & Hector (2001) suggested that

403 both positive complementarity and selection effects on productivity reflects the

404 "sampling effect", increasing the probability of sampling a dominant, high-biomass

405 species in mixed forest, but also increasing the probability of sampling a suite of

406 complementary species. Our results confirm that contrasting traits promote tree

407 productivity and carbon storage, together with species-specific selection effects based

408 on leaf mass per area, as previously suggested in other forest types (Paquette & Messier,

409 2011; Zhang *et al.*, 2012).

410   The BEF relationship observed along FD (i.e. complementarity effect) was

411 positive but not linear, showing the largest changes of carbon storage and tree

412 productivity at low FD values (Figs 2(a) and 3(a)). It has been suggested that the

413 positive relation between species richness and ecosystem function increases until an

414 asymptote is reached where functional redundancy and niche overlap occurs (e.g.

415 Loreau *et al.*, 2001; Hooper *et al.*, 2005). This form of BEF relationship has been

416 reported in a recent meta-analysis of forest productivity that showed that an asymptote

417 was reached at around six species (Zhang *et al.*, 2012). The largest changes on carbon

418 storage and tree productivity occurred at low FD values suggesting that most benefits

419 are found when moving away from monospecific stands, and later the increase of

420 ecosystem functions is expected to saturate (e.g. Loreau, 2000).

421   Our results suggest that complementarity effects are relevant for all types of

422 Spanish forests, regardless of their productivity. For example, deciduous forests show

423 the greatest effects of complementarity on potential tree productivity (a 25%

424 productivity increase along the FD gradient, Fig. 3(a)) despite having an intermediate

425 mean productivity within the seven forest types considered (1.36 ± 1.30 Mg C ha^{-1} yr^{-1},

426 Table S4). Therefore, we did not find strong support for a larger role of

427 complementarity in low-productive or more stressful environments (where facilitation

428 may be more important) than in high-productive environments (where competitive

429 exclusion is expected to dominate species interactions), as suggested by previous

430 theoretical (Warren *et al.*, 2009) and observational studies (Paquette & Messier, 2011).

431 This lack of a clear relationship between complementarity and productivity could be due

432 to the complexities and ambiguities associated with the definition of "stressful

433 conditions" at the community level, since each forest type is composed of individuals

434 and species both adapted to and limited by local conditions (e.g. Körner, 2004). Because

435 the concept of stress is better applied at the species level, each individual species could

436 either be favored by facilitation or impaired by competition (Holmgren *et al.*, 2007),

437 with stress and facilitation increasing as environmental conditions deviate from a

438 species´ ecophysiological optimum (Greiner La Peyre *et al.*, 2001).

439   We found that selection effects based on species identity and dominance

440 (measured as functional identity using CWM based on LMA) had a positive effect on

441   carbon storage and tree productivity. The selection effect was particularly large in

442   Mediterranean pines and deciduous forests (Table S4). The leaf economic spectrum

443   predicts that low LMA should promote productivity (e.g. Wright *et al.*, 2004; Morin *et*

444   *al.*, 2011). However, Mediterranean pines had their maximum productivity at high LMA

445   which could be related with traits favoured by and adapted to arid and semi-arid

446   conditions (Wright *et al.*, 2005). Moreover, these forest types usually form mixed

447   forests of functionally contrasting species, because Mediterranean pine species and

448   hardwoods could coexist or alternate depending on the environmental heterogeneity and

449   disturbance regime (Zavala *et al.*, 2000; Gómez-Aparicio *et al.*, 2011). Therefore,

450   spatial differences in species dominance could lead to the greater importance of

451   selection mechanisms in Mediterranean pine and Atlantic forests, causing the large

452   variation in carbon storage and tree productivity observed along FI gradient (Figs 2(b)

453   and 3(b)). On the other hand, we observed that mountain forests had the lowest

454   sensitivity to selection effects (Figs 2(b) and 3(b)). This could be due to the fact that

455   mountain forests tend to mix with functionally similar species including mostly conifers

456   typical of high altitudes (Costa *et al.*, 1997), and therefore mountain forests have high

457   monospecificity and low FD.

458

459 Conclusions

460   Our results demonstrate that functional diversity is crucial in maintaining ecosystem

461   functions in Spanish forests along large bioclimatic gradients. Thus, carbon storage and

462   tree productivity increase at an average of 32% and 21%, respectively, from

463   monospecific to functionally diverse forests, which agrees with previous studies finding

464   a 24% average increment of productivity from forest monocultures to polycultures

465   (Zhang *et al.*, 2012; Vilá *et al.*, 2013). Moreover, our results indicate that BEF

466   relationships and complementarity effects are not substantially affected by the origin of

467   the stand, with diversity having a positive effect on carbon storage and tree productivity

468   in both natural and planted Spanish forests. These findings suggest that results obtained

469   in experimentally controlled environments (the large majority of the BEF research so

470   far; Adler *et al.*, 2011) could also be applicable to natural systems.

471   Maintaining diverse forests in the Iberian Peninsula in particular, and in the

472   Mediterranean region in general, should be considered both an important challenge and

473   a necessity. The Mediterranean region is particularly vulnerable to climate change as

474   well as habitat loss, fragmentation, and fire frequency increases (Schröter *et al.*, 2005;

475   Pausas *et al.*, 2008). As a consequence, potential biodiversity losses could be

476   particularly large in this area, and therefore their negative effects on ecosystem

477   functions and related services as well (Lindner *et al.*, 2010). Our results indicate that

478   BEF relationships are maintained through both complementarity and selection effects.

479   Therefore, we conclude that management efforts should aim at promoting both

480   functionally diverse forests and functionally important species, which could act as

481   insurance for the maintenance of key ecosystem functions such as carbon storage and

482   tree productivity.

483 **ACKNOWLEDGEMENTS**

497

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674 --

675 **SUPPORTING INFORMATION**

676 Additional supporting information may be found in the online version of this article:

677 **Appendix S1** Further details regarding the methods used and variable selection.

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

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

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

683 **Table S4** Mean values of carbon storage, tree productivity and the rest of the predictor
684 variables included in the best model. Number of plots and species composition of each
685 forest type is also given.

686 **Table S5** Parameter estimates and two-unit support intervals for the most parsimonious
687 total carbon storage model for each of the seven forest types defined.

688 **Table S6** Parameter estimates and two-unit support intervals for the most parsimonious
689 tree productivity model for each of the seven forest types defined.

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

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

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

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

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

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705 --

706 **Biosketch**

707 **Paloma Ruiz-Benito** is a post-doctoral researcher at the Forest Ecology and Restoration

708 Group (Alcalá University) under FUNDIV project (http://www.fundiveurope.eu/). For

709 her PhD she studied key ecosystem processes and services along large abiotic and biotic

710 gradients to assess potential effects of global change on Iberian forest structure and

711 dynamics, and the implications for their restoration and conservation.

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

Forest type	Full	No climate	No structure	No diversity	No FD	No FI	Null	R^2	Slope	N
				ΔAIC						
Deciduous	**0**	664	1,402	1,259	118	1,201	5,263	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	5,272	0.43	1.00	9,382
Mountain natural pines	**0**	1,427	2,284	132	98	-5	3,643	0.41	1.00	6,895
Meditarranean planted pines	**0**	26	1,360	321	159	71	2,057	0.34	1.00	3,147
Mountain planted pines	**0**	150	810	39	64	4	1,139	0.29	0.99	3,349
Exotic	**0**	27	71	73	72	-4	356	0.18	0.99	1,966

The full models include the effects of climate, structure and diversity (see Eqn (2)) for each forest type. The models 'No climate', 'No structure', 'No diversity', ignore the effect of climate, stand structure, and functional diversity, 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 functional diversity (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.

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

Forest type	Full	ΔAIC						R^2	Slope	*N*
		No Climate	No Structure	No Diversity	No FD	No FI	Null			
Deciduous	**0**	286	713	542	282	312	2,267	0.36	0.99	5,109
Sclerophyllous	**0**	571	2,753	145	128	-2	5,735	0.43	1.00	9,071
Mediterranean natural pines	**0**	459	1,920	547	173	434	3,357	0.41	1.00	6,455
Mountain natural pines	**0**	990	2,489	13	7	-14	3,187	0.47	1.00	5,078
Mediterranean planted pines	**0**	247	949	300	8	209	1,617	0.40	1.00	3,147
Mountain planted pines	**0**	346	671	10	7	-8	937	0.38	0.99	2,021
Exotic	**0**	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 ΔAIC 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. ΔAIC = 0) we show the slope and R^2 (1 – SEE/SST) for the relationship of the
731 predicted and observed tree productivity.

732 **FIGURE LEGENDS**

733

734 **Figure 1** Map of plots used in this study from the third Spanish Forest Inventory for the

735 seven forest types included in the study.

736 Map projection UTM 30N, European Datum 1950

737

738 **Figure 2** Predicted potential fraction (proportion) and total carbon storage (Mg C ha^{-1})

739 for each forest type along gradients of: functional diversity (FD) of maximum height,

740 wood density and seed mass ((a) and (c), respectively); and functional identity (FI,

741 measured through CWM of leaf mass per area (g m^{-2})) ((b) and (d), respectively). See

742 Table S5 for the estimated parameters of the corresponding functions.

743

744 **Figure 3** Predicted potential fraction (proportion) and tree productivity (Mg C ha^{-1} yr^{-1})

745 for each forest type along gradients of: functional diversity (FD) of maximum height,

746 wood density and seed mass ((a) and (c), respectively); and functional identity (FI,

747 measured through CWM of leaf mass per area (g m^{-2})) ((b) and (d), respectively). See

748 Table S6 for the estimated parameters of the corresponding functions.

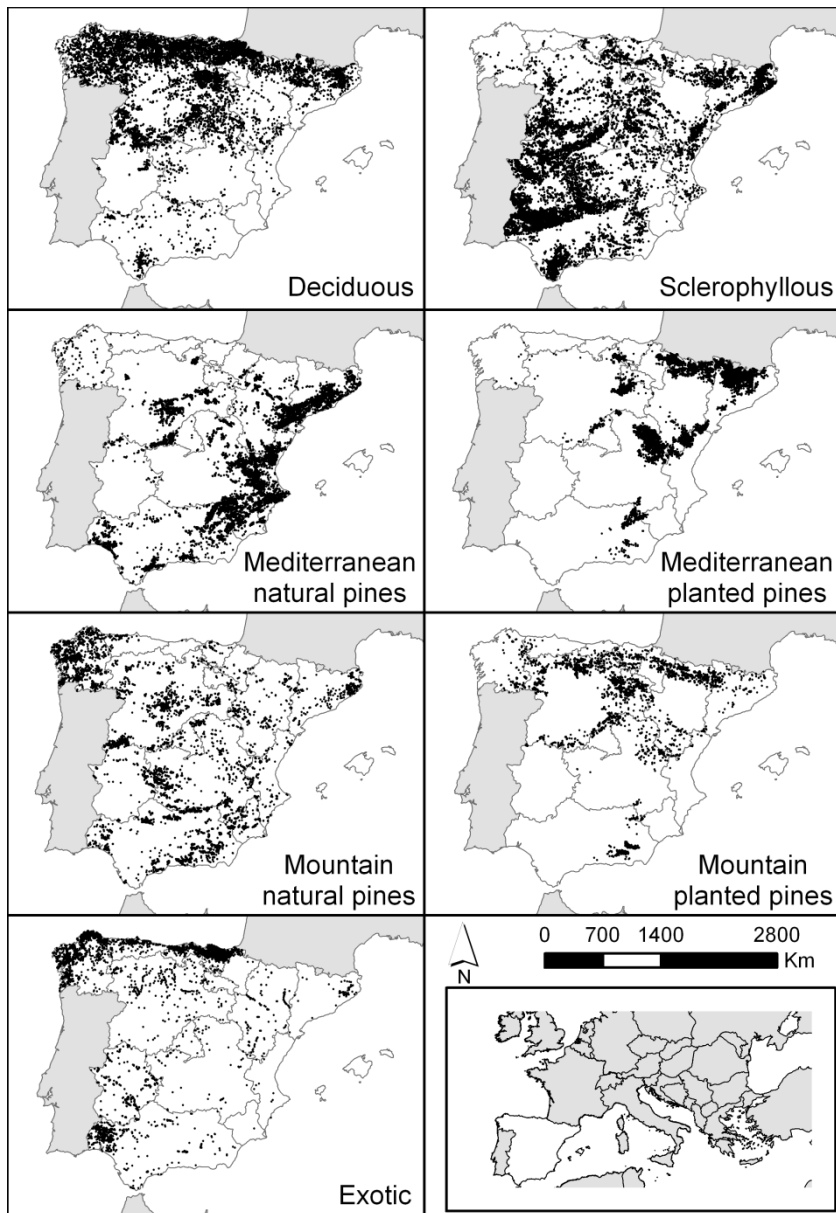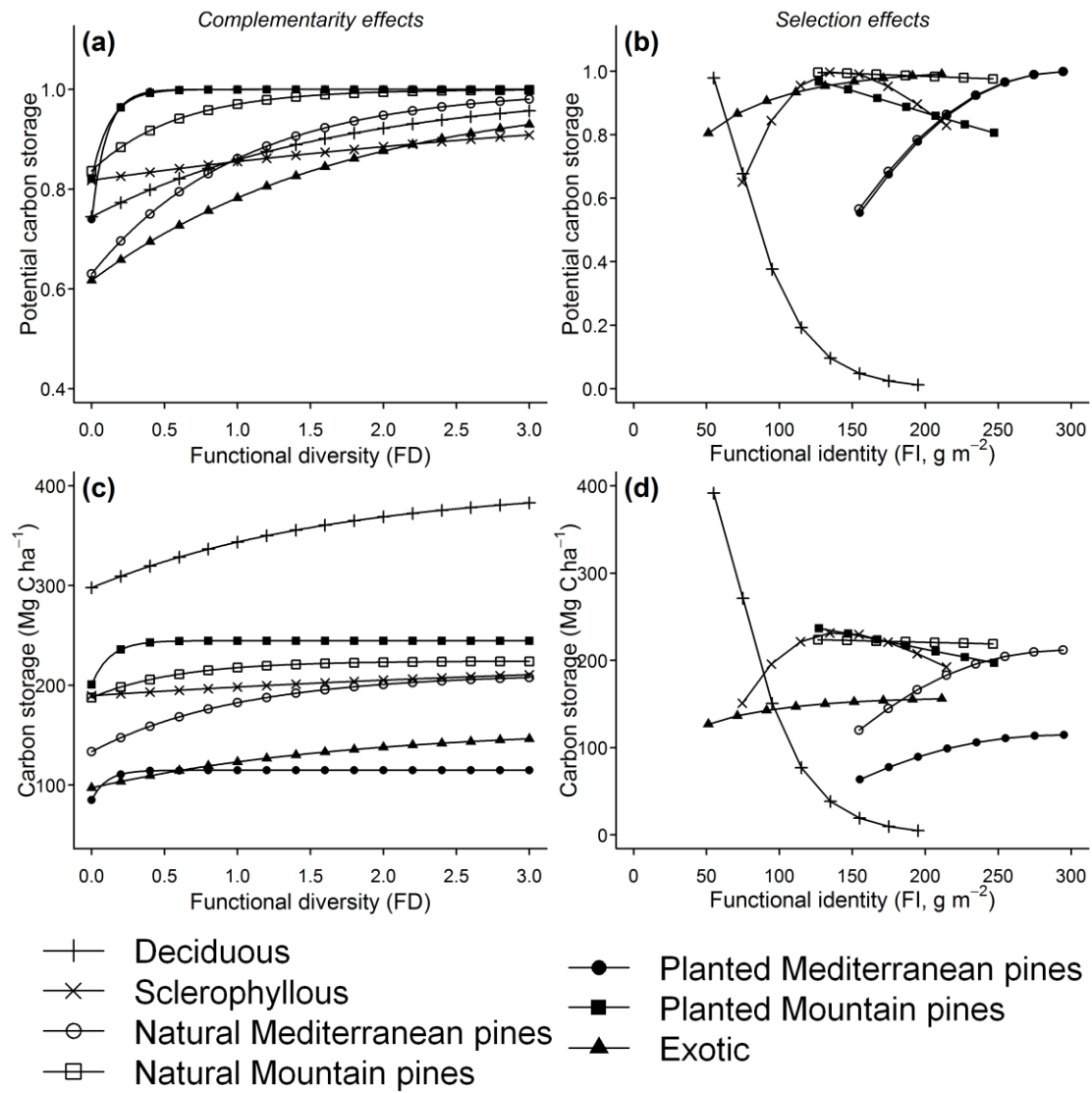**Figure 1**

Figure 2

Figure 3