

1    **“New forests” from the XX century are a relevant contribution for C storage in the**  
2    **Iberian Peninsula**

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16    **Shortened title:** New forests and C storage in the Iberian Peninsula

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18    **Author contributions:** AVC, JME, JV and JP conceived the study; AVC, JME and JP  
19    performed the research; AVC analyzed data; AVC, JME, JV and JP wrote the paper.

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26 **Abstract**

27 Land-use changes are one of the major drivers of global change. In many developed  
28 countries socioeconomic changes have induced forest expansion during the last  
29 centuries, with still seldom explored implications for ecosystem services. We assessed  
30 the growth rate and the contribution of these “new forests” on C storage under the  
31 imprint of land-use history from Mediterranean to temperate forests in two  
32 biogeographical regions in the Iberian Peninsula, using data from 6,422 plots of the  
33 Spanish National Forest Inventory (1986-2007) and the land-cover map of 1956 to  
34 distinguish among pre-existing and new forests (appeared after 1956). Almost a quarter  
35 of current forests were new forests and they represented the 22% of the total C pool.  
36 New forests maintained similar C stocks than pre-existing ones ( $\sim 45 \text{ Mg ha}^{-1}$ ), but they  
37 are growing at rates 25% higher. Considering the whole Spanish forested territory the  
38 new forest growth rate would offset around the 9% of the rate of total C emitted in  
39 Spain between 1986 and 2007. The effects of land-use history on forest growth and C  
40 stocks varied with environmental conditions (e.g. growth of new forests in areas with  
41 less water availability was higher than in pre-existing ones), supporting the idea that  
42 agricultural legacies may prevail in the long-term. In a time when European forests  
43 exhibit the first signs of carbon sink saturation, our study endows a relevant ecological  
44 role to new forests appeared in the second half of the XX century.

45

46 **Keywords:** agricultural abandonment, growth rates, C stocks, land-use history,  
47 environmental conditions, forest transitions, new forests, pre-existing forests.

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49

50 **Introduction**

51

52 Land-use changes are one of the major drivers of global environmental change (Turner  
53 II and others 2007) and socioeconomic development is altering forest ecosystems at  
54 accelerated rates. Indeed, while deforestation is the main cause of forest lost in the  
55 tropics (Laurance 1999), forest transitions have induced a widespread forest expansion  
56 in many developed countries over the last centuries (Meyfroidt and Lambin 2011).  
57 These shifts have profound ecological implications given the key functions and services  
58 forests globally provide, including regulation of nutrient and water cycling, and  
59 atmospheric composition and climate (Millennium Ecosystem Assessment 2005). Yet,  
60 while there is an extensive literature covering the dramatic negative ecological and  
61 socioeconomic consequences of deforestation for ecosystem services (Malhi and others  
62 2008), the effects of forest expansion have been less addressed (but see Kauppi and  
63 others 2006).

64

65 Forest ecosystems provide essential ecosystem services. For example, they represent  
66 around the 45% and 50% of terrestrial C stocks and net primary production,  
67 respectively, and also regulate the major terrestrial fluxes of C between the atmosphere  
68 and the biosphere (Bonan 2008). Land-use changes are an important driver of forest C  
69 dynamics worldwide, and the potential for C accumulation and storage of forests  
70 depend on ecosystem history together with ecosystem dynamics and environmental  
71 conditions at present (Pan and others 2011). In Europe, forests have been a net sink of C  
72 during the last decades as they are mostly recovering from extensive clearing in the past  
73 (Ciais and others 2008; Erb and others 2013). Moreover, it has been also estimated that  
74 forest cover has increased by ~ 25% across the continent during the second half of the

75 XX century as a consequence of transitions from croplands and grasslands to woodlands  
76 (Fuchs and others 2013). Therefore, contemporary C stocks and dynamics in forests are  
77 not merely the outcome of a shift in management practices in forests, but also owing to  
78 the recent establishment of new forests over abandoned croplands and pastures (e.g.  
79 Kuemmerle and others 2015). Although the relevance for C accumulation of new forests  
80 established after land abandonment has been suggested (e.g. Hooker and Compton  
81 2003), their contribution to C storage in comparison to pre-existing forests and the role  
82 that environmental conditions may have in this accumulation pattern remain  
83 unexplored.

84

85 Land-use history can leave important lasting signals in natural ecosystems (Foster and  
86 others 2003). Consequently, land-use legacies effects might be expected to occur on the  
87 patterns of productivity of new forests expanded in abandoned cropland areas *vs.* pre-  
88 existing forests as a result of the past allocation of croplands to the areas with better site  
89 quality (i.e. flat and with deeper soils) while forests remained in sites with poorer  
90 conditions (i.e. steep slopes). Moreover, enhancement of soil conditions (e.g.  
91 fertilization, amelioration of soil structure) has been a traditional practice carried out in  
92 croplands to sustain crop productivity (Cramer and others 2008). Although afforested  
93 ecosystems can recover conditions comparable to undisturbed ones in many aspects  
94 after crop abandonment (Flinn and Marks 2007), agricultural legacies may last in the  
95 long-term, such that can be seen in soil properties and nutrient content, biochemical  
96 processes, as well as in the vegetation structure and diversity patterns (Compton and  
97 Boone 2000; Dambrine and others 2007; Gerstner and others 2014; Leuschner and  
98 others 2014). Differences owing to land-use-legacies could be predicted to increase in

99 those sites with the less favorable conditions (e.g. lowest rainfall availability or poorest  
100 site quality).

101

102 The northern rim of the Mediterranean Basin is one of the most evident examples of  
103 forest transition in Europe after being managed for millennia (Blondel and Aronson  
104 1995). This forest transition includes two processes: i.e. the recovery of forests from a  
105 long-history of human exploitation (Grove and Rackham 2001) and the expansion of  
106 new forests to agricultural areas abandoned during the last century (e.g. Basnou and  
107 others 2013). Although the northern rim of the Mediterranean Basin has been the latest  
108 European region where forests transitions took place (Mather 1990), and global change  
109 is increasing their vulnerability (Schröter and others 2005), the contribution of new  
110 forests and the imprint of past land-uses on C accumulation and storage at a  
111 macroecological scale is largely unknown.

112

113 In this study, we aim at assessing the contribution of new forests appeared after 1956 in  
114 two biogeographical regions in the Iberian Peninsula on forest growth rate (in terms of  
115 C gain and C storage) and the imprint of land-use legacies on current C dynamics of  
116 Mediterranean and temperate forests. We hypothesize that: (1) as a result of an intense  
117 process of agricultural abandonment during the second half of the XX century, new  
118 forests will represent a substantial part of forest ecosystems and C stocks as a whole; (2)  
119 because new forests are growing in former agricultural areas and these were  
120 traditionally located in higher quality sites new forests will grow at higher rates than  
121 pre-existing ones; and (3) this land-use legacies effect will be more apparent under  
122 effects of environmental stress. To do so we analyzed 6,422 plots of the Spanish  
123 National Forest Inventory to identify the relative contribution of new forests (appeared

124 after 1956) on growth rates and C stocks, as well as the potential interaction among  
125 land-use history and environmental conditions.

126

## 127 **Material and methods**

### 128 *Study area*

129 The study area encompasses two large territories in the Iberian Peninsula (Fig. 1):  
130 Andalusia (87,268 km<sup>2</sup>) and Catalonia (32,114 km<sup>2</sup>), located in the southern and the  
131 northeastern Iberian Peninsula, respectively (Fig. 1B-C) where both detailed  
132 cartography of land use changes from the second half of the XX century and forest  
133 inventories were available. These regions include a substantial altitudinal gradient, from  
134 sea level to more than 3,000 m a.s.l., including both coastal and continental land areas.  
135 The geographic location of these territories, together with the range of influences and  
136 the mountainous orography, determines a very heterogeneous climate. The climatic  
137 gradient in both regions ranges from a temperate-alpine climate in Sierra Nevada  
138 (Andalusia) and in the Pyrenees (Catalonia) to a Mediterranean climate in most of the  
139 territory. There is also a continentality gradient from coastal to inland areas, with  
140 increasing thermal amplitudes inland. Mean annual temperature ranges from 18°C (on  
141 the southern coast) to 3°C (in mountain areas) in both regions, and annual rainfall varies  
142 from 140 mm to more than 2,000 mm in Andalusia and from 400 mm to more than  
143 1,500 mm in Catalonia (Climatic Digital Atlas of the Iberian Peninsula; Ninyerola and  
144 others 2005). This climate variability and the geographic location of these territories are  
145 the main factors explaining the existence of a rich and varied flora. Vegetation types  
146 include Mediterranean, sub-Mediterranean, Eurosiberian and Boreoalpine chorologies.  
147 Forest covers approximately 2.9 x 10<sup>6</sup> ha in Andalusia and 1.6 x 10<sup>6</sup> ha in Catalonia,  
148 representing around the 33% and the 50% of the whole territory respectively (Spanish

149 Ministry of Agriculture, Food and Environment). In both regions forests are mainly  
150 dominated by conifer and broadleaved (deciduous and evergreen) species. Forest types  
151 include: Atlantic, sub-Atlantic and sub-Mediterranean deciduous forests; montane, sub-  
152 Alpine, and Mediterranean coniferous forests; Mediterranean sclerophyllous, and  
153 evergreen scrublands and forests.

154

## 155 *Data sources*

### 156 *Forest inventory data*

157 We used data from the Spanish National Forest Inventory (IFN; Villaescusa and Díaz  
158 1998; Villanueva 2005). The IFN is an extensive database of periodical forest surveys  
159 distributed systematically across the forested areas (i.e. those with a tree cover of at  
160 least 5%) in Spain repeatedly sampled across time. The IFN is based on a network of  
161 permanent plots at a density of 1 plot km<sup>-2</sup>, which allows forest characterization and  
162 includes exhaustive information on the composition of canopy and understory woody  
163 species, as well as on forest structure. Within the plots, all adult trees ( $\geq 7.5$  cm in  
164 diameter at breast height [dbh]) were labeled, measured for dbh and height, identified to  
165 species, and censused for mortality. Sampling followed a nested circular-plot design,  
166 i.e. plot size depended on the dbh of the measured trees to guarantee a representative  
167 sampling of the tree size distribution. Therefore, all trees with dbh  $\geq 7.5$  cm were  
168 measured within 5 m of the centre of the plots, trees with dbh  $\geq 12.5$  cm were also  
169 measured between 5 and 10 m around the centre of the plots, whereas trees with dbh  $\geq$   
170 22.5 cm and dbh  $\geq 42.5$  cm were also considered within 10–15 m and 15–25 m around  
171 the centre of the plots, respectively. We used data from the permanent plots surveyed in  
172 the second inventory (IFN2; 1986-1996) and revisited again in the third one (IFN3;  
173 1997-2007). We excluded plots with evidence of recent disturbances (mainly fire, but

174 also storms, and other) detected during the IFN3, and with presence of exotic species  
175 (mostly actively planted) in any of the two inventories, in order to assess the patterns of  
176 growth and stocks over the same set of plots, and also to avoid potential biases in our  
177 analyses.

178

### 179 *Growth rates and C stocks*

180 Estimates of growth rates and C stocks included in this study were restricted to the  
181 aboveground compartment of adult trees ( $\text{dbh} \geq 7.5 \text{ cm}$ ) alive between the two  
182 inventories (i.e. without including dead trees). To compute carbon content per tree we  
183 applied allometric equations obtained in different studies to the data of each IFN2 and  
184 IFN3 plot. Aboveground biomass (AGB) of each living tree was computed using  
185 specific equations as a function of DBH and height (H) developed in the Ecological  
186 Forest Inventory of Catalonia (IEFC, Gracia and others 2004a):  $\text{AGB} = a \cdot \text{DBH}^b \cdot H^c$ ,  
187 where a, b and c are specific coefficients for the different species. For the least  
188 common species we applied the coefficients of generalized equations obtained for the  
189 different functional groups (coniferous, deciduous and sclerophyllous species). Total C  
190 amount of each living tree was determined by multiplying aboveground biomass by the  
191 specific C content of the species obtained in the IEFC from oven-dried samples (Gracia  
192 and others 2004b). Growth rate ( $\text{Mg C ha}^{-1} \text{ year}^{-1}$ ) for each plot was estimated in terms  
193 of C gain as the sum of C increment due to growth of surviving trees and C of ingrowth  
194 of new trees to the canopy (i.e. new trees with  $\text{dbh} \geq 7.5 \text{ cm}$ ) between the two surveys,  
195 divided by the number of years elapsed between measurements. We used total C  
196 amount of living trees per each plot at the IFN3 as an estimate of current C stocks ( $\text{Mg}$   
197  $\text{ha}^{-1}$ ).

198

199 *Land-use history*

200 Land-use history of each IFN plot was obtained by overlapping the geographic location  
201 of the IFN plots with land-cover maps of 1956-1957, available for the whole territory of  
202 Andalusia and for more than 50% of the territory of Catalonia (Figure 1). This land-  
203 cover map was digitized by on screen photo-interpretation of historical aerial  
204 photographs (Basnou and others 2013) available in the archives of the Spanish army.  
205 The definition of forest and scrubland in these maps was essentially the same as the  
206 used in the National Forestry Inventories, as stands with at least 5% of tree cover were  
207 classified as forests while the rest were considered as scrublands (Villanueva 2005).  
208 Combining them with the 1956-1957 land-cover maps, the IFN plots were then  
209 classified in three types of land-use history, according to their historical land-use in  
210 1956 and to the corresponding transition: (1) *Forest–Forest* (hereafter F–F),  
211 corresponding to preexisting forests in 1956; (2) *Crop–Forest* (hereafter C–F),  
212 corresponding to current forests growing on existing crops in 1956; and (3)  
213 *Scrubland/grassland–Forest* (hereafter SG–F), corresponding to current forests growing  
214 on existing scrublands or grasslands in 1956. The overlapping of these two data sources  
215 (i.e. IFN plots and land-cover map of 1956) allowed us to identify the land-use history  
216 of each IFN plot, and to distinguish between pre-existing forests (F–F) and new forests  
217 (C–F and SG–F). The final sample size resulted in a total of 6,422 plots, 3,753  
218 distributed in Andalusia and 2,669 in Catalonia.

219

220 *Environmental factors*

221 *Climatic gradient.* Climatic data for each IFN plot was obtained from the Climatic  
222 Digital Atlas of the Iberian Peninsula (Ninyerola and others 2005), a set of digital maps  
223 at 200 x 200 m resolution with mean annual and monthly data for precipitation and

224 maximum, mean and minimum temperatures (reference period 1959-1999). We used an  
225 index of water availability (WAI [%]) to characterize the climatic conditions for each  
226 plot. WAI was calculated as:  $[(P-PET)/PET] \times 100$ , where P is mean annual  
227 precipitation (in mm) and PET is annual potential evapotranspiration (in mm; calculated  
228 following the Hargreaves-Samani [1982] method). Negative values of WAI correspond  
229 to dry sites and positive to wet sites.

230 *Site conditions.* The following variables were used to characterize other environmental  
231 conditions for each IFN plot: (1) Terrain slope as a topographical measure, estimated as  
232 the maximum slope (°) in the center of the plot; (2) Distance to the coast (in m) as a  
233 measure of continentality; and (3) Management, i.e. commercial cutting or thinning  
234 between the IFN2 and IFN3, as a measure of recent human disturbance (managed /  
235 unmanaged).

236 *Biotic conditions.* Forest type, structure and development were used to characterize the  
237 biotic conditions of each plot. Forest type was established according to the tree  
238 dominant species within each plot, determined through the highest percentage in basal  
239 area using measured trees ( $dbh \geq 7.5$  cm). We distinguished four forest types:  
240 deciduous, mediterranean pines, mountain pines and sclerophyllous (see list of  
241 dominant species in Appendix A). To account for the effects of initial forest structure  
242 and forest development on patterns of growth rates we used C stocks ( $Mg\ ha^{-1}$ ) of living  
243 trees and stand density of living trees ( $trees\ ha^{-1}$ ) at the beginning of the study period  
244 (i.e. at the IFN2). In the case of current C stocks (i.e. at the IFN3) we only used stand  
245 density of living trees ( $trees\ ha^{-1}$ ) at the IFN3 as a measure of forest structure and degree  
246 of stand development.

247

248 ***Data analyses***

249 The effects of land-use history and environmental factors on growth rates and C stocks  
250 were explored by means of linear models (LMs). The relevance of each source of  
251 variation was assessed by comparisons using differences in the AIC (Akaike  
252 Information Criterion) among sets of alternative models. A significant effect (at level  $\alpha$   
253 = 0.05) of a variable included in a model was considered to be important as source of  
254 variation when the  $\Delta$ AIC was at least of 4 units (Burnham and Anderson 2002) under  
255 comparison with the same model excluding the targeted variable.

256

257 We started by fitting a null intercept-model for each response variable (i.e. growth rates  
258 and C stocks). To test overall differences in the averages of growth rates and C stocks  
259 among types of land-use history, we added land-use history as explanatory variable. We  
260 then assessed the importance of land-use history as source of variation by comparing  
261 this model with the null model.

262

263 Because the observed differences among types of land-use history may result from  
264 environmental heterogeneity and stand structure, we included all these effects as  
265 explanatory variables (i.e. forest type, stand density, C stocks at the IFN2, WAI, terrain  
266 slope, distance to the coast and management). We constructed a saturated model which  
267 included the effects of land-use history and the other factors, as well as the interaction  
268 between these factors with land-use history. Region was also included as explanatory  
269 variable to take into account overall differences between the two biogeographical areas.

270 Starting from the saturated model, we created the fully crossed set of models and ranked  
271 them from lowest to highest AIC. All best models (lowest AIC) within 4 AIC units were  
272 considered to be equivalent in terms of fit (Burnham and Anderson 2002). The relative  
273 importance as source of variation of land-use history, forest type, stand structure,

274 environmental factors, and interactions included in the best adequate model (i.e. lowest  
275 AIC) was evaluated by examining their inclusion in the other candidate models, and  
276 assessed based on relative  $\Delta$ AIC when comparing the best adequate model with an  
277 alternative model with an identical structure of explanatory variables but ignoring the  
278 targeted explanatory variable one at a time. Coefficients of determination were used to  
279 assess the contribution (in %) of explanatory variables in explaining variability of  
280 growth rates and C stocks.

281

282 To satisfy normality assumptions, Box-cox transformations were applied on the two  
283 response variables, i.e. growth rates and C stocks, while stand density and C stocks at  
284 the IFN2, and distance to the coast were  $\log_e$  and square root transformed, respectively.

285 Correlations between explanatory variables were always  $< 0.45$ . The residuals of the  
286 models did not show deviation from normality and were not spatially correlated.

287 Analyses were carried out with R software version 3.1.1 (R Development Core Team,  
288 2014).

289

## 290 **Results**

### 291 *Characterizing new forests*

292 Overall, 23% of the 6,422 plots were crops, scrublands or grasslands in 1956, i.e. close  
293 to a quarter of forests of these two large regions as a whole are new forests.

294 Specifically, 5% of forest plots were crops while 18% were scrublands or grasslands in  
295 1956 (Table 1). Similar patterns were observed within each region (Table 1). Across all  
296 forest plots, sclerophyllous and Mediterranean pine forests were dominant, although this  
297 trend slightly changed within new forests, being sclerophyllous forests comparatively  
298 less represented (Table 2A). Mean plot characteristics, i.e. forest structure and

299 development, climatic and site conditions, as well as management intensity, across all  
300 plots and per types of land-use history are shown in Table 2B.

301

### 302 *Overall effects of land-use history on growth rates and C stocks*

303 On average, new forests showed growth rates 25% higher than pre-existing forests.

304 Mean growth rates were  $1.21 \pm 0.01$  Mg C ha<sup>-1</sup> year<sup>-1</sup> for F–F,  $1.73 \pm 0.06$  Mg C ha<sup>-1</sup>

305 year<sup>-1</sup> for C–F, and  $1.45 \pm 0.03$  Mg C ha<sup>-1</sup> year<sup>-1</sup> for SG–F (Table 2B). These growth

306 rates were significantly higher for new forests in comparison to pre-existing forests

307 when tested in the LM with land-use history as single explanatory variable (Fig. 2A; see

308 Appendix B for parameter estimates). Land-use history explained a small proportion ( $R^2$

309 = 3%) of variability in growth rates. However, land-use history was relevant as direct

310 source of variation when the model was compared with the null model (Table 3A).

311

312 C stocks of new forests represented about the 22% of the total C pool. Current C stocks

313 differed significantly between pre-existing and new forests (Fig. 2B; see Appendix B

314 for parameter estimates), with average values of  $45 \pm 0.4$  Mg ha<sup>-1</sup> for F–F,  $49 \pm 1.6$  Mg

315 ha<sup>-1</sup> for C–F and  $42 \pm 0.7$  Mg ha<sup>-1</sup> for SG–F (Table 2B). Although land-use history was

316 relevant as direct source of variation of current C stocks (Table 3A), the model

317 containing land-use history as single explanatory variable explained less than 1% of

318 total variability (Table 3A).

319

### 320 *Interplay between land-use history and environmental conditions*

321 The best adequate model for growth rates included the effects of land-use history, stand

322 density, initial C stock, forest type, WAI, terrain slope, management, region as well as

323 the interaction land-use history  $\times$  WAI (see Appendix C for parameter estimates).

324 Explanatory variables explained a substantial proportion of total variability ( $R^2 = 65\%$ ).  
325 Land-use history and the interaction land-use history  $\times$  WAI emerged as relevant  
326 sources of variation in comparison with the models excluding their effects one at a time  
327 (Table 3B). There were other 11 candidate models ( $\Delta AIC \leq 4$  under comparison with  
328 the best adequate model) which always included the effects of land-use history and its  
329 interaction with WAI. Therefore, the effect of land-use history on growth rates varied  
330 along the gradient of water availability (Fig. 3). Interestingly, new forests showed  
331 higher growth rates in drier sites than pre-existing forests, while in wet sites the rates  
332 were similar (Fig. 3). For example, at WAI values of  $-50\%$  the predicted growth rates  
333 for new forests were in average 20% higher than those for pre-existing forests, while at  
334 WAI values of  $50\%$  the predicted rates were comparatively similar. In the two land-  
335 history trajectories deciduous and Mediterranean pine forests showed higher growth  
336 rates than forests of mountain pines and sclerophyllous species (Appendix D).  
337 Additionally, growth rates were higher with increasing stand density and initial C  
338 stocks, and also were higher in unmanaged forests and in flatter slopes (Appendix D).  
339 Finally, differences between regions were also observed (Appendix D). The relative  
340 importance of stand structure, forest type and region effects on growth rates was much  
341 greater than any other source of variation (see the high positive  $\Delta AIC$  when the effects  
342 of structural variables, forest type and region were excluded one at a time from the  
343 model; Table 3B). Interestingly, however, the relative importance of land-use history  
344 effects was comparatively similar to management effects, and higher than the effects of  
345 climate and site conditions (Table 3B).  
346  
347 The best adequate model for C stocks included the interactions of forest type, stand  
348 density, WAI and distance to the coast with land-use history, as well as the effects of

349 management, terrain slope and region (see Appendix C for parameter estimates).  
350 Explanatory variables explained a large proportion of total variability ( $R^2 = 49\%$ ). Land-  
351 use history emerged as relevant source of variation under comparison with the model  
352 excluding its effects (Table 3B). All interactions were significant and also relevant as  
353 sources of variation when compared with the same model excluding the targeted  
354 interaction one at a time (Table 3B). There were other 2 candidate models ( $\Delta AIC \leq 4$   
355 under comparison with the best adequate model) which always included the effects of  
356 land-use history and all interactions. Differences in C stocks among types of land-use  
357 history were dependent on forest type. C stocks for new forests were predicted to be in  
358 average similar to those of pre-existing forests in Mediterranean pines and  
359 sclerophyllous, but 41% and 18% lower than pre-existing forests for deciduous and  
360 mountain pines, respectively (Fig. 4A). On average, C stocks of new forests were  
361 predicted to be lower than pre-existing forests at low stand densities (e.g. 27% lower at  
362  $\sim 250$  trees  $ha^{-1}$ ), but higher at high stand densities (e.g. 9% higher at  $\sim 4000$  trees  $ha^{-1}$ )  
363 (Fig. 4B). C stocks among land-use history types varied along the gradient of water  
364 availability (Fig. 4C). Under dry conditions, on average C stocks were similar among  
365 land-use history types, but were higher for pre-existing forests under wet conditions  
366 (e.g. 36% higher in average at WAI = 50%). C stocks for pre-existing forests were  
367 higher than new forests at large distances to the coast (e.g. 23% higher in average at  
368  $\sim 150,000$  m), but were higher for C–F at short distances to the coast (e.g. 11% and 23%  
369 higher than F–F and SG–F, respectively, at  $\sim 10,000$  m) (Fig. 4D). Additionally, C  
370 stocks were higher in unmanaged forests and in flatter slopes, and differences between  
371 regions were also observed (Appendix D). Stand density was the most important factor  
372 determining C stocks followed by climate and forest type (Table 3B). The relative

373 importance of land-use history effect on C stocks was higher to that of site conditions,  
374 management and region (Table 3B).

375

## 376 **Discussion**

377 Even though the steady growth of forest area over recent decades in Europe is a well-  
378 known phenomenon (e.g. more than 0.8 million hectares since 1990 according to Forest  
379 Europe 2015) their relevance in terms of the provision of ecosystem services, like C  
380 sequestration, has been seldom explored. Thus, to the extent our study system may be  
381 considered representative of Mediterranean ecosystems and part of Temperate ones in  
382 Europe, three main elements are specially relevant: (1) almost a quarter of forests are  
383 less than 50 years old with a previous and recent history of non-forest use, now  
384 becoming a fundamental piece of current forest ecosystems as a whole, (2) new forests  
385 represent the 22% of the total C pool, and are growing at rates 25% higher than pre-  
386 existing forests while the amount of C stored is similar in the two forest types, and (3)  
387 the imprint of land-use history is apparent on current growth rates and C stocks of  
388 forests interacting with environmental variables, such as water availability, forest type  
389 and structure or distance to the coast.

390

### 391 ***The relevance new forests***

392 New forests have spread at accelerated rates on former non-forested land. Certainly,  
393 forest transitions have been a fundamental process in our study system. Almost a  
394 quarter of current forests were croplands, and scrublands or grasslands half a century  
395 ago, suggesting a high forest increase during this time. The most reliable data on forest  
396 increase across time in Spain is provided by the SISPARES database  
397 ([www.sispares.com](http://www.sispares.com)), made up by 215 landscape samples randomly distributed across

398 the Spanish territory accounting for land-cover maps of 1956, 1984 and 1999. These  
399 data show a net increase in forest cover by 14% in Spain between 1956 and 1999 (rate ~  
400 0.33% year<sup>-1</sup>). This observed rate of net increase of forest cover is nearly equal to the  
401 assessed in other regions of the northern rim of the Mediterranean Basin such as the  
402 Italian Peninsula (rate ~ 0.35% year<sup>-1</sup>, 1960 – 2000; Falcucci and others 2007), but it is  
403 somewhat lower than the estimated rate for the whole Europe (rate ~ 0.42% year<sup>-1</sup>, 1950  
404 – 2010; Fuchs and others 2013). The rapid expansion of forests during the last half of  
405 the XX century in our study area might be explained by a fast forest community  
406 assembly after land abandonment by a pool of species with a marked pioneer habit that,  
407 remaining constricted in scrublands and hedgerows in the past, were able to  
408 spontaneously colonize croplands as soon as management ceased (Basnou and others  
409 2016). Notwithstanding this, reforestation programs conducted from the 50s might also  
410 have played a key role in forest recovery in many areas of Mediterranean Europe  
411 (Barberó 1998; Iriarte-Goñi and others 2013).

412

413 This is the first time the relative contribution of new forests in forest growth rates and C  
414 storage is empirically assessed at a macroecological scale in Europe (but see e.g.  
415 Kuemmerle and others 2015 for a simulation approach). The emergence of these new  
416 forests may result into generalized changes in ecosystem function, including C cycling  
417 dynamics and storage in forest biomass (Rudel and others 2005). Although there is  
418 plenty evidence that Northern hemisphere woodlands have been sequestering C during  
419 the last century and decades (e.g. Houghton and others 1999; Ciais and others 2008;  
420 Bellassen and others 2011; Vayreda and others 2012), our approach allows identifying  
421 the magnitude of recent land-use changes on C dynamics, i.e. new forests represent the  
422 22% of the total C pool and are growing at a rate 25% higher than pre-existing ones.

423 These results provide signs on two fundamental aspects. Firstly, many forests (pre-  
424 existing forests here) may be reaching maturity and, as a consequence, have lower  
425 potential for C accumulation. Although empirical evidences indicate that old-growth  
426 forests may continue to accumulate C (Luyssaert and others 2008), the observed  
427 differences in growth between pre-existing and new forests (even after accounting for  
428 biotic and abiotic factors) could suggest a decline in productivity with age (Tang and  
429 others 2014) and early signs of C sink saturation (Nabuurs and others 2013). Moreover,  
430 it should be taken into account that many of these pre-existing forests are oak coppices  
431 repeatedly exploited for centuries for charcoal or firewood extraction by means of  
432 selective thinning (Terradas and others 1999). This particular forestry practice, based on  
433 the vigorous resprouting of these species, involves a reduced genetic replacement and  
434 may entail, in the long term, lower growth rates (see Espelta and others 1995).

435 Secondly, our results show that new forests are already playing an important role in C  
436 accumulation. For example, if we extrapolate our results to the whole Spanish forested  
437 territory of ca.  $18.6 \cdot 10^6$  ha (Spanish Ministry of Agriculture, Food and Environment)  
438 and we assume the % of new forests and the growth rates observed in our two regional  
439 areas, new forests in Spain as a whole might have gained C at  $\sim 6.5 \cdot 10^6$  Mg C year<sup>-1</sup>  
440 during the lag of time the forest inventories were carried out (i.e. 1986 – 2007).

441 Interestingly, this rate would have offset around the 9% of the average rate of total C  
442 emitted in Spain during the same period ( $\sim 7.4 \cdot 10^7$  Mg C year<sup>-1</sup>; Carbon Dioxide  
443 Information Analysis Center, US Department of Energy). Taken together, our results  
444 suggest that new forests are already relevant in the mitigation of C emissions and that  
445 they will become a substantial C sink in the longer.

446

447 Interestingly new forests exhibited higher growth rates and similar C stocks than pre-  
448 existing ones in spite they presented, according to the forest inventory surveys, more  
449 signs of management (e.g. 44% of C-F and 33% of SG-F plots had been managed in  
450 comparison of 31% in the F-F category). Even though we lack information about the  
451 intensity of management in the two forest types, we can suggest several hypotheses to  
452 explain why new forests are being more exploited and why they still maintain higher  
453 rates of C gain. Preferential exploitation of new forests may be due to: 1) they occupy  
454 former croplands located in flat and more accessible areas (Basnou and others 2016)  
455 where costs of forest exploitation are lower and 2) they are mostly composed by  
456 conifers (see Table 2, Basnou and others 2016) with higher commercial value than  
457 sclerophyllous pre-existing forests, highly exploited for charcoal production in the past  
458 but mostly abandoned during the second half of the XX century (Terradas 1999).  
459 Concerning the higher growth rates of new forests in spite of being more exploited, this  
460 could be mediated by the dominance of pines in this forest type (see Table 2) with  
461 higher growth rates and faster recruitment dynamics (Zavala and others 2000) than the  
462 sclerophyllous species (e.g. *Quercus spp*) predominant in pre-existing forests.

463

#### 464 ***The interaction among legacies of land-uses and environmental conditions***

465 Land-use history remained as relevant source of variation after accounting for  
466 environmental variability although, in agreement with other studies, stand structure was  
467 the most important factor explaining patterns of growth rates and C storage (e.g.  
468 Vayreda and others 2012). However, it is important to stress that the effects of land-use  
469 history were similar in magnitude, or even higher, than the effects of climate, site  
470 conditions and management. Interestingly, these effects of land-use history on growth  
471 rates and C stocks varied along some environmental gradients.

472

473 Our results bring support to the idea that the legacies of agriculture in the past might  
474 prevail in the long-term. It has been suggested and well documented that water  
475 availability is the key limiting factor of forest biomass and C dynamics in Iberian  
476 forests (Vilà and others 2007; Vayreda and others 2012; Ruiz-Benito and others 2014).  
477 However, our results suggest that the effects of water availability were mostly relevant  
478 in pre-existing forests. As a consequence, the observed patterns under drought  
479 conditions, i.e. higher growth rates in new forests as compared to pre-existing forests  
480 and similar amounts of C stored among land-use history types, are probably driven by a  
481 combination of ecological mechanisms that could partly prevent or buffer new forests  
482 from severe drought stress. Past decisions on allocation of land for agriculture in flat  
483 areas and deeper soils as well as the continuous amelioration of soil structure by the  
484 agricultural practices (e.g. ploughing and manuring) might help to explain why new  
485 forests are more able to overcome water shortage in the C dynamics. Moreover, past  
486 fertilization can last for more than a century and affect growth dynamics of trees  
487 established after crop abandonment (von Oheimb and others 2014). Accordingly,  
488 former fertilization might have left nutrient-enriched soils in new forests, enhancing  
489 biomass allocation to the aboveground compartment in new forests (Vicca and others  
490 2012) and helping nutrient regulation (Fernández-Martínez and others 2014) which  
491 could partly mitigate the detrimental effects of water stress on C acquisition. However,  
492 the empirical validation of these hypotheses is an important challenge for the future,  
493 given that soil data at the scale of this study is not currently available and because other  
494 confounding factors might also be relevant, e.g. growth saturation and the dominance of  
495 slow-growing species in pre-existing forests, differences in the time of abandonment  
496 among biogeographical regions or differences in structural and species diversity.

497

498 In addition to the effects of water availability, C storage varied among land-use history  
499 types in interaction with forest types, stand density and distance to the coast.  
500 Particularly, it has been argued that changes in species richness and functional  
501 composition might affect productivity and C storage in Mediterranean forests (e.g. Vilà  
502 and others 2007; Ruíz-Benito and others 2014). However, it is interesting to note that  
503 new forests stored similar amounts of C than pre-existing ones in Mediterranean pine  
504 and sclerophyllous forests. These results suggest that these two contrasted groups of  
505 Mediterranean tree species are able to establish well on abandoned lands through  
506 different processes of secondary succession (Sheffer 2012) and reach in few decades  
507 structural conditions similar to those of pre-existing forests (see examples in Rodrigo  
508 and others 2004). Recent works in part of the study area (Basnou and others 2016)  
509 showed that differences in species richness and composition between pre-existing and  
510 recent forests are not so dramatic as expected: i.e. community assembly in terms of  
511 species richness is fast enough to exhaust most colonization credit in these recent  
512 forests. On the other hand, the expected successional differences in species composition  
513 between forests types are less clear than expected due to (i) the strong pressure that pre-  
514 existing forests have undergone along their history, and (ii) the main role of niche  
515 factors in woody species assemblage. Thus, pine species also are common in managed  
516 pre-existing forests, especially when these are growing in dry, thin-soil stands. In the  
517 present work, there was also evidence that the effect of stand density on C stocks was  
518 stronger in new forests, evidencing again their early stage of development still far away  
519 from the limit of C storage (Nabuurs and others 2003). Additionally, forests growing on  
520 abandoned crops (i.e. C – F) at short distances to the coast showed higher C stocks.  
521 Agricultural intensification, socioeconomic development and urbanization in the

522 Mediterranean basin have been especially intense along the coast (Vallejo and others  
523 2005), so probably reflecting an earlier abandonment of agricultural activities in coastal  
524 areas (see also from the effects of distance from the cost on the assembly of new forest  
525 communities, Basnou and others 2016). Finally, we cannot discard that other important  
526 global change drivers in the Mediterranean basin such as fire regimes and CO<sub>2</sub>  
527 fertilization, interacting with the different land-use histories, might have also  
528 contributed to the observed differences between new and pre-existing forests.

529

### 530 *Implications for conservation and management*

531 In a time when the rapid increase in the emission of CO<sub>2</sub> has turned to be one of the  
532 main ecological and societal challenge to be addressed by scientists and policymakers,  
533 our study endows an important ecological role to new forests. First, new forests  
534 represent a noticeable part of forest ecosystems studied and their overall C sink, and are  
535 growing at higher rates than pre-existing forests. Moreover, our findings suggest that  
536 new forests have been playing a relevant role in counterbalancing the emission of CO<sub>2</sub>,  
537 in recent decades and they will continue accumulating C in the mid-term with a great  
538 potential to play a non-negligible role in the global terrestrial C sink in the long. To  
539 what extent the patterns observed may be similar in other areas in the world, and  
540 designing appropriate conservation and management practices in new forests are  
541 challenging topics deserving attention. Particularly because the ultimate drivers of  
542 returning forests (e.g. socioeconomic, fossil-fuel based energy system) will not last  
543 forever so new forests might be bound to play a noticeable role in providing ecosystem  
544 services to the human population (Navarro & Pereira 2012), especially in the advent of  
545 a new green economy in which increasing pressure on forest products (timber, wood)  
546 might substantially affect C stocks. It must be also considered that the widespread

547 expansion of new forests and the increase of standing biomass in a half of a century  
548 might also increase risk and vulnerability to natural disturbances such as fire, storms,  
549 droughts and pests. Therefore, at the same time new forests reach maturity and their  
550 rates of increase in C accumulation decline there is a high likelihood of C sink  
551 saturation, and release of huge amounts of C if management and conservation strategies  
552 are not revised and properly implemented (Nabuurs and others 2013). This strongly  
553 supports the integration of production together with conservation in new forests  
554 management, to sustain the potential for global change mitigation and the multiple  
555 ecosystem services they provide (Chazdon 2008).

556

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719 **Table legends**

720 **Table 1.** (A) Sample size (total and for each region) according to land-use history types;  
721 and (B) Proportion of plots (total and for each region) according to land-use history  
722 types. Land-use history types: F–F, *Forest–Forest*; C–F, *Crop–Forest*; SG–F,  
723 *Scrubland/grassland–Forest*.

724 **Table 2.** (A) Proportion of plots per each forest type across all plots and according to  
725 types of land-use history; (B) Mean  $\pm$  SE of growth rates, C stocks and environmental  
726 factors across all plots and according to types of land-use history. Land-use history  
727 types: F–F, *Forest–Forest*; C–F, *Crop–Forest*; SG–F, *Scrubland/grassland–Forest*.

728 **Table 3.** Outcome of the LMs comparisons testing (A) the direct effects of land-use  
729 history on growth rates and C stocks; and (B) the relative contribution of variables  
730 included in the best adequate models explaining growth rates and C stocks. In *a*, a  
731 significant effect (at level  $\alpha = 0.05$ ) of land-use history when included as explanatory  
732 variable in the model was considered to be relevant as source of variation when the AIC  
733 was at least 4 units lower under comparison with the null model. In *b*, the relative  
734 importance of land-use history, environmental factors and interactions as source of  
735 variation was assessed based on the positive  $\Delta$ AIC when comparing the best adequate  
736 model with an alternative model with the same structure of explanatory variables but  
737 ignoring the targeted source of variation one at a time. AIC: Akaike information  
738 criterion; n.i. not included in the best adequate model; n.t.: not tested

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744 **Table 1**

<b>(A) N plots</b>	<b>All plots</b>	<b>F-F</b>	<b>C-F</b>	<b>SG-F</b>
Total	6,422	4,954	331	1,137
Andalusia	3,753	2,916	111	726
Catalunya	2,669	2,038	220	411
<b>(B) % plots</b>	<b>All plots</b>	<b>F-F</b>	<b>C-F</b>	<b>SG-F</b>
Total	100	77	5	18
Andalusia	58	78	3	19
Catalunya	42	76	8	15

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759 **Table 2**

<b>(A) % plots per Forest type</b>	<b>All plots</b>	<b>Forest</b>	<b>Crop</b>	<b>Shrubland</b>
Deciduous	8	9	10	6
Mediterranean pines	35	30	48	52
Mountain pines	22	20	26	32
Sclerophyllous	35	42	16	10
<b>(B) Plot characteristics</b>	<b>All plots</b>	<b>Forest</b>	<b>Crop</b>	<b>Shrubland</b>
Growth rate (Mg ha <sup>-1</sup> year <sup>-1</sup> )	1.28 ± 0.01	1.21 ± 0.01	1.73 ± 0.06	1.45 ± 0.03
C stocks IFN3 (Mg ha <sup>-1</sup> )	44.7 ± 0.4	45.0 ± 0.4	49.0 ± 1.6	42.0 ± 0.7
C stocks IFN2 ( Mg ha <sup>-1</sup> )	34.1 ± 0.3	35.2 ± 0.4	36.0 ± 1.4	28.4 ± 0.6
Stand density IFN3 (trees ha <sup>-1</sup> )	654 ± 7.4	620 ± 8.4	816 ± 31	754 ± 17
Stand density IFN2 (trees ha <sup>-1</sup> )	614 ± 6.7	571 ± 7.5	795 ± 31	747 ± 16
WAI (%)	- 31.4 ± 0.3	- 30.1 ± 0.3	- 33.4 ± 1.1	- 36.0 ± 0.7
Terrain slope (°)	20.8 ± 0.1	20.6 ± 0.1	19.1 ± 0.5	21.4 ± 0.3
Distance to the coast (m)	66,806 ± 615	67,746 ± 704	43,877 ± 1901	69,385 ± 1492
Management (% plots)	32	31	44	33

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765 **Table 3**

(A)	Growth rate			C stocks		
	df <sub>model</sub>	AIC	ΔAIC	df <sub>model</sub>	AIC	ΔAIC
Model	2	16,212		2	21,238	
Null model	2	16,212		2	21,238	
Land-use history	4	16,022	- 190	4	21,223	- 15
(B)	Growth rate rate			C stocks		
	df <sub>model</sub>	AIC	ΔAIC	df <sub>model</sub>	AIC	ΔAIC
Best adequate model	15	9,559		25	16,965	
No Land-use-history	11	9,644	85	11	17,146	181
No Stand density	14	11,732	2,173	22	19,619	2,654
No C stocks at the IFN2	14	10,385	826	n.t		
No Forest Type	12	9,747	188	16	17,251	286
No WAI	12	9,598	39	22	17,645	680
No Terrain slope	14	9,617	58	24	17,038	73
No distance to the coast	n.i			22	17,003	38
No Management	14	9,649	91	24	16,980	15
No Region	14	9,788	229	24	16,983	18
No Land-use history × WAI	13	9,567	8	23	16,971	6
No Land-use history × Stand density	n.i			23	17,021	56
No Land-use history × Forest Type	n.i			19	16,998	33
No Land-use history × Distance to the coast	n.i			23	16,974	9
No Land-use history × C stocks at the IFN2	n.i			n.t		
No Land-use history × Terrain slope	n.i			n.i		
No Land-use history × Management	n.i			n.i		

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769 **Figure legends**

770 **Figure 1.** (A) Location of Andalusia and Catalonia in the Iberian Peninsula, and  
771 distribution of the sampling plots of the National Forest Inventory of Spain (IFN); (B)  
772 Distribution of the sampling plots of the IFN in Catalonia; and (C) Distribution of the  
773 sampling plots of the IFN in Andalusia. Land-use history types: F–F, *Forest–Forest*; C–  
774 F, *Crop–Forest*; SG–F, *Scrubland/grassland–Forest* (see *Material and methods* section  
775 for a detailed description).

776 **Figure 2.** Boxplots of (A) growth rates and (B) C stocks as a function of types of land-  
777 use history. The limits of boxes indicate the first and third quartiles, and the horizontal  
778 line within boxes corresponds to the median. The upper whisker extends from the third  
779 quartile to the highest value within 1.5 x IQR (inter-quartile range) of the third quartile.  
780 The lower whisker extends from the first quartile to the lowest value within 1.5 x IQR  
781 of the first quartile. Different letters between land-use history types represent significant  
782 differences according to the LMs testing the overall effect of land-use history on the  
783 response variables (see Table 3 and Appendix B). Grey crosses are outliers. Land-use  
784 history types: F–F, *Forest–Forest*; C–F, *Crop–Forest*; SG–F, *Scrubland/grassland–*  
785 *Forest*.

786 **Figure 3.** Predicted effects (mean and 95% confidence intervals) of land-use history on  
787 growth rates along the gradient of WAI. Predicted values were based on the WAI  
788 effects of the best adequate model (see Appendix C) and were averaged across the  
789 levels of categorical variables (forest type, management and region). The effects of the  
790 other covariates were fixed at the observed mean. Approximate confidence intervals of  
791 the prediction were calculated from the variance-covariance matrix of the explanatory  
792 variables ( $\pm 2 \times \text{SE of prediction}$ ). Land-use history types: F–F, *Forest–Forest*; C–F,  
793 *Crop–Forest*; SG–F, *Scrubland/grassland–Forest*.

794 **Figure 4.** Predicted effects (mean and 95% confidence intervals) of land-history on C  
795 stocks along the gradients of (A) forest type; (B) stand density; (C) WAI; and (D)  
796 distance to the coast. Predicted values were based on the effects of explanatory  
797 variables of the best adequate model (see Appendix C) and were averaged across the  
798 levels of categorical variables (forest type, management and/or region). The effects of  
799 the other covariates were fixed at the observed mean. Approximate confidence intervals  
800 of the prediction were calculated from the variance-covariance matrix of the explanatory  
801 variables ( $\pm 2 \times$  SE of prediction). In A different letters correspond to significant  
802 differences among forest types according to Tukey's post hoc tests. Land-use history  
803 types: F-F, *Forest-Forest*; C-F, *Crop-Forest*; SG-F, *Scrubland/grassland-Forest*.

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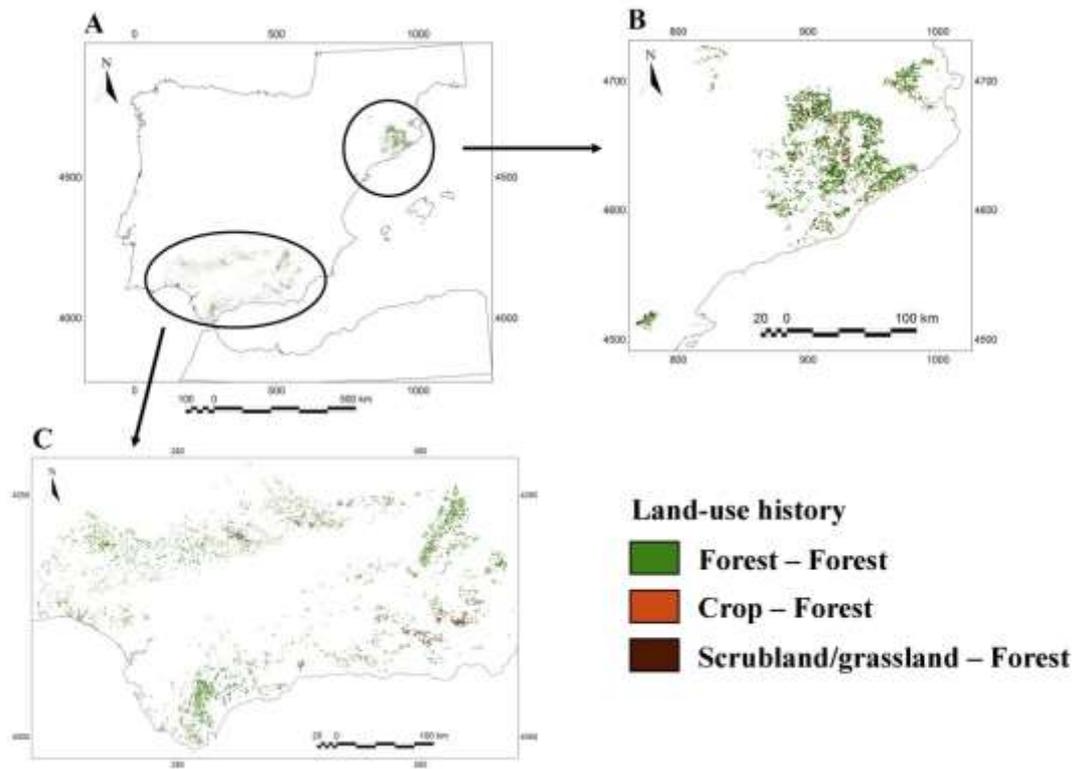
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819 **Figure 1**



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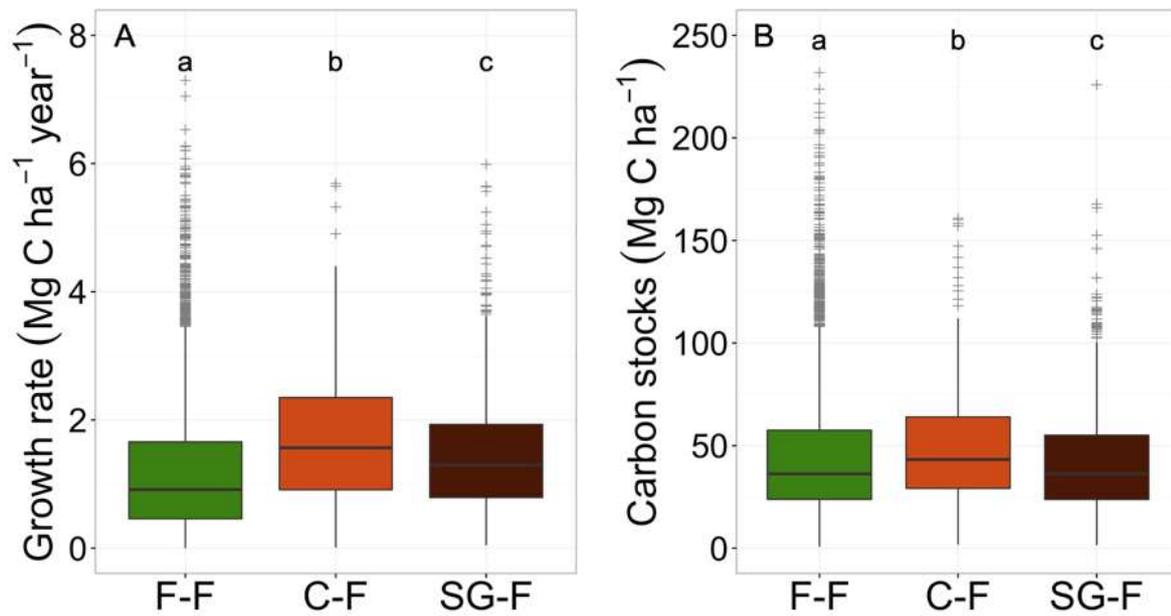
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834 **Figure 2**

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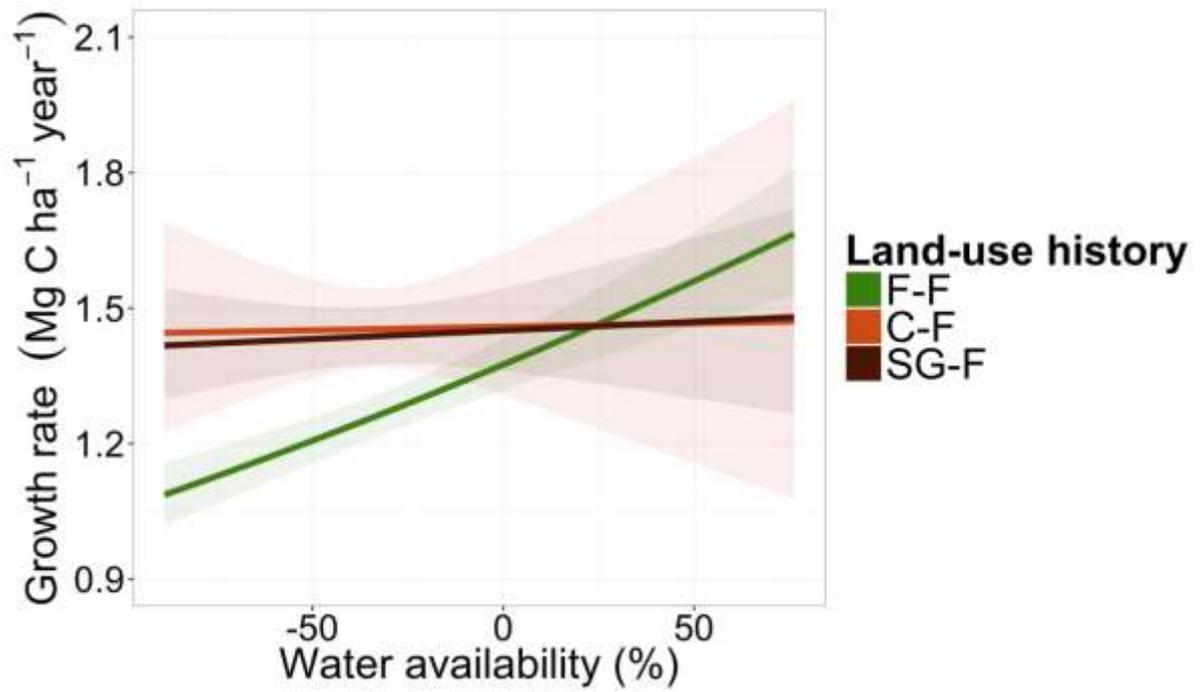
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850 **Figure 3**

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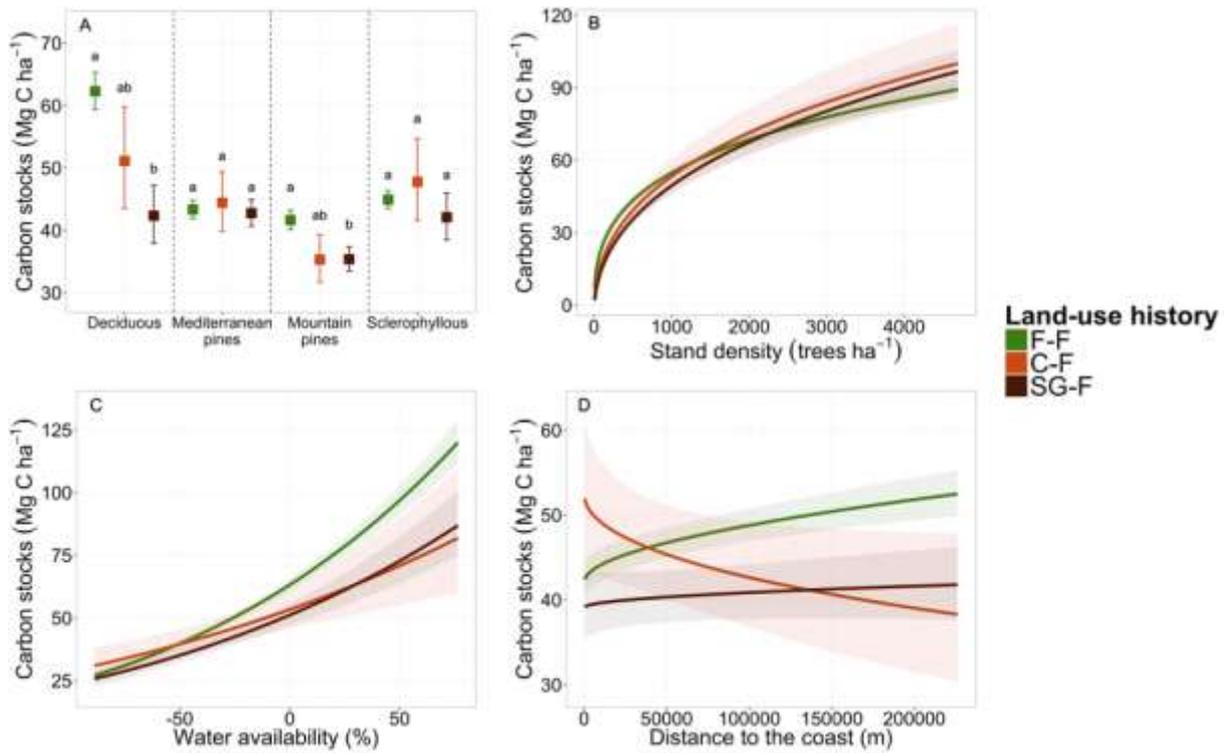
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866 **Figure 4**

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