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 ($\sim 45$ 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.

48

49

**Introduction**

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

Forest ecosystems provide essential ecosystem services. For example, they represent around the 45% and 50% of terrestrial C stocks and net primary production, respectively, and also regulate the major terrestrial fluxes of C between the atmosphere and the biosphere (Bonan 2008). Land-use changes are an important driver of forest C dynamics worldwide, and the potential for C accumulation and storage of forests depend on ecosystem history together with ecosystem dynamics and environmental conditions at present (Pan and others 2011). In Europe, forests have been a net sink of C during the last decades as they are mostly recovering from extensive clearing in the past (Ciais and others 2008; Erb and others 2013). Moreover, it has been also estimated that 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$^2$) and Catalonia (32,114 km$^2$), 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$^6$ ha in Andalusia and 1.6 x 10$^6$ 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$^{-2}$, 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 (dbh $\geq$ 7.5 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): AGB = a $\cdot$ DBH b $\cdot$ H

187    c, 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 (Mg C ha$^{-1}$ 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 dbh $\geq$ 7.5 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 (Mg

197    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 (º) 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 α

253    = 0.05) of a variable included in a model was considered to be important as source of

254    variation when the ΔAIC 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 ΔAIC 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$^{-1}$ year$^{-1}$ for F–F, $1.73 \pm 0.06$ Mg C ha$^{-1}$

305    year$^{-1}$ for C–F, and $1.45 \pm 0.03$ Mg C ha$^{-1}$ year$^{-1}$ 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$^{-1}$ for F–F, $49 \pm 1.6$ Mg

315    ha$^{-1}$ for C–F and $42 \pm 0.7$ Mg ha$^{-1}$ 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    ~ 250 trees ha$^{-1}$), but higher at high stand densities (e.g. 9% higher at ~ 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    ~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 ~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), 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$^{-1}$). 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$^{-1}$, 1960 – 2000; Falcucci and others 2007), but it is

403    somewhat lower than the estimated rate for the whole Europe (rate ~ 0.42% year$^{-1}$, 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 $\sim 6.5 \cdot 10^6 \, \text{Mg C year}^{-1}$

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 ($\sim 7.4 \cdot 10^7 \, \text{Mg C year}^{-1}$; 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-exiting 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-exiting 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 $CO_2$

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 $CO_2$ 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 growingat 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 $CO_2$,

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).

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**Table legends**

**Table 1.** (A) Sample size (total and for each region) according to land-use history types;

and (B) Proportion of plots (total and for each region) according to land-use history

types. Land-use history types: F–F, *Forest–Forest*; C–F, *Crop–Forest*; SG–F,

*Scrubland/grassland–Forest*.

**Table 2.** (A) Proportion of plots per each forest type across all plots and according to

types of land-use history; (B) Mean ± SE of growth rates, C stocks and environmental

factors across all plots and according to types of land-use history. Land-use history

types: F–F, *Forest–Forest*; C–F, *Crop–Forest*; SG–F, *Scrubland/grassland–Forest*.

**Table 3.** Outcome of the LMs comparisons testing (A) the direct effects of land-use

history on growth rates and C stocks; and (B) the relative contribution of variables

included in the best adequate models explaining growth rates and C stocks. In *a*, a

significant effect (at level α = 0.05) of land-use history when included as explanatory

variable in the model was considered to be relevant as source of variation when the AIC

was at least 4 units lower under comparison with the null model. In *b*, the relative

importance of land-use history, environmental factors and interactions as source of

variation was assessed based on the positive ΔAIC when comparing the best adequate

model with an alternative model with the same structure of explanatory variables but

ignoring the targeted source of variation one at a time. AIC: Akaike information

criterion; n.i. not included in the best adequate model; n.t.: not tested

744    **Table 1**

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

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759 **Table 2**

| (A) % plots per Forest type | All plots | Forest | Crop | Shrubland |
|---|---|---|---|---|
| Deciduous | 8 | 9 | 10 | 6 |
| Mediterranean pines | 35 | 30 | 48 | 52 |
| Mountain pines | 22 | 20 | 26 | 32 |
| Sclerophyllous | 35 | 42 | 16 | 10 |
| **(B) Plot characteristics** | **All plots** | **Forest** | **Crop** | **Shrubland** |
| Growth rate (Mg ha$^{-1}$ year$^{-1}$) | 1.28 ± 0.01 | 1.21 ± 0.01 | 1.73 ± 0.06 | 1.45 ± 0.03 |
| C stocks IFN3 (Mg ha$^{-1}$) | 44.7 ± 0.4 | 45.0 ± 0.4 | 49.0 ± 1.6 | 42.0 ± 0.7 |
| C stocks IFN2 ( Mg ha$^{-1}$) | 34.1 ± 0.3 | 35.2 ± 0.4 | 36.0 ± 1.4 | 28.4 ± 0.6 |
| Stand density IFN3 (trees ha$^{-1}$) | 654 ± 7.4 | 620 ± 8.4 | 816 ± 31 | 754 ± 17 |
| Stand density IFN2 (trees ha$^{-1}$) | 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 (º) | 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 | | |
|---|---|---|---|---|---|---|
| Model | $df_{model}$ | AIC | ΔAIC | $df_{model}$ | AIC | ΔAIC |
| 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 | | |
| Model | $df_{model}$ | AIC | ΔAIC | $df_{model}$ | 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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**Figure legends**

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

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

**Figure 3.** Predicted effects (mean and 95% confidence intervals) of land-use history on growth rates along the gradient of WAI. Predicted values were based on the WAI effects of the best adequate model (see Appendix C) and were averaged across the levels of categorical variables (forest type, management and region). The effects of the other covariates were fixed at the observed mean. Approximate confidence intervals of the prediction were calculated from de variance-covariance matrix of the explanatory variables (± 2 × SE of prediction). Land-use history types: F–F, *Forest–Forest*; C–F, *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 de 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*.
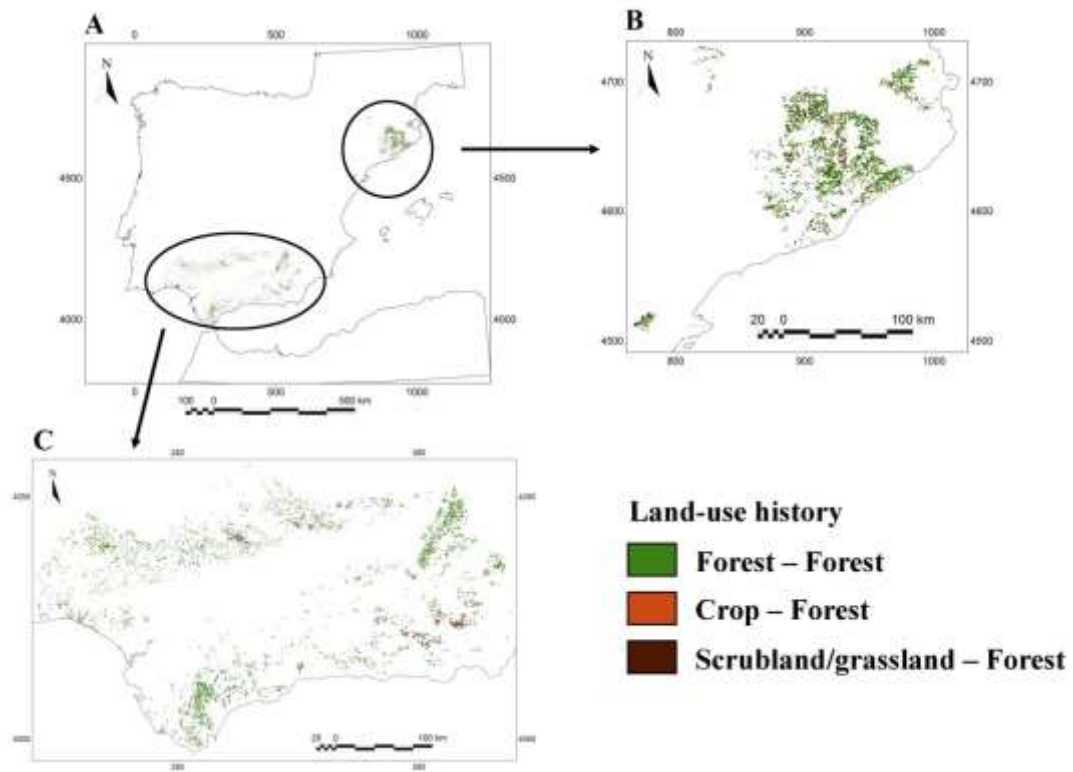
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819    **Figure 1**



Land-use history
- Forest – Forest
- Crop – Forest
- Scrubland/grassland – Forest

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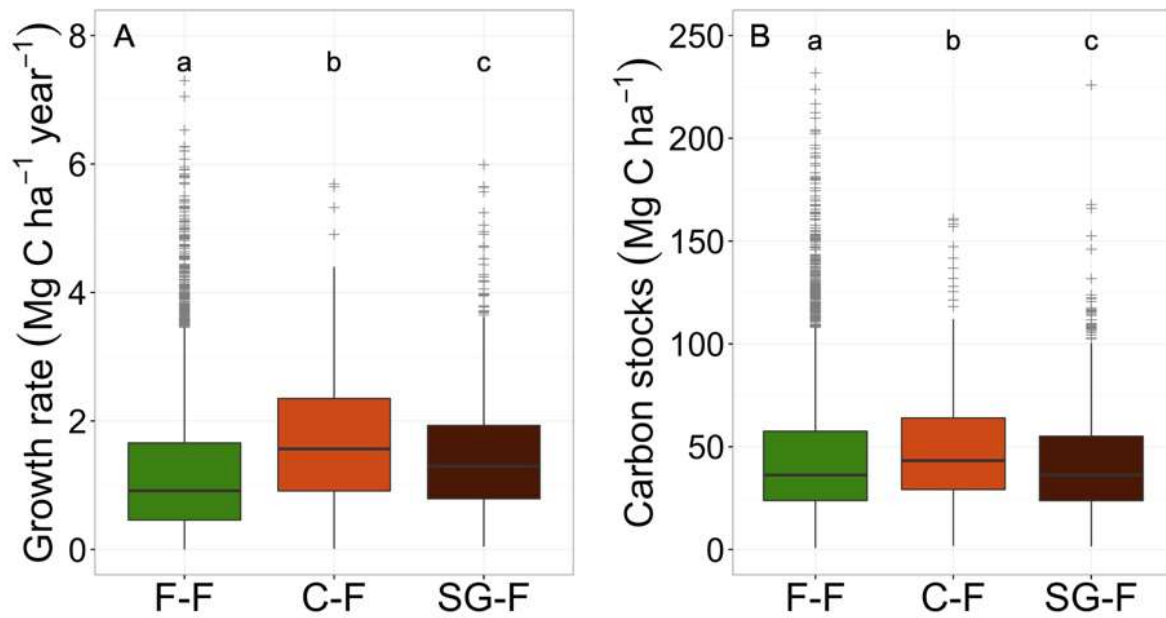831

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834    **Figure 2**

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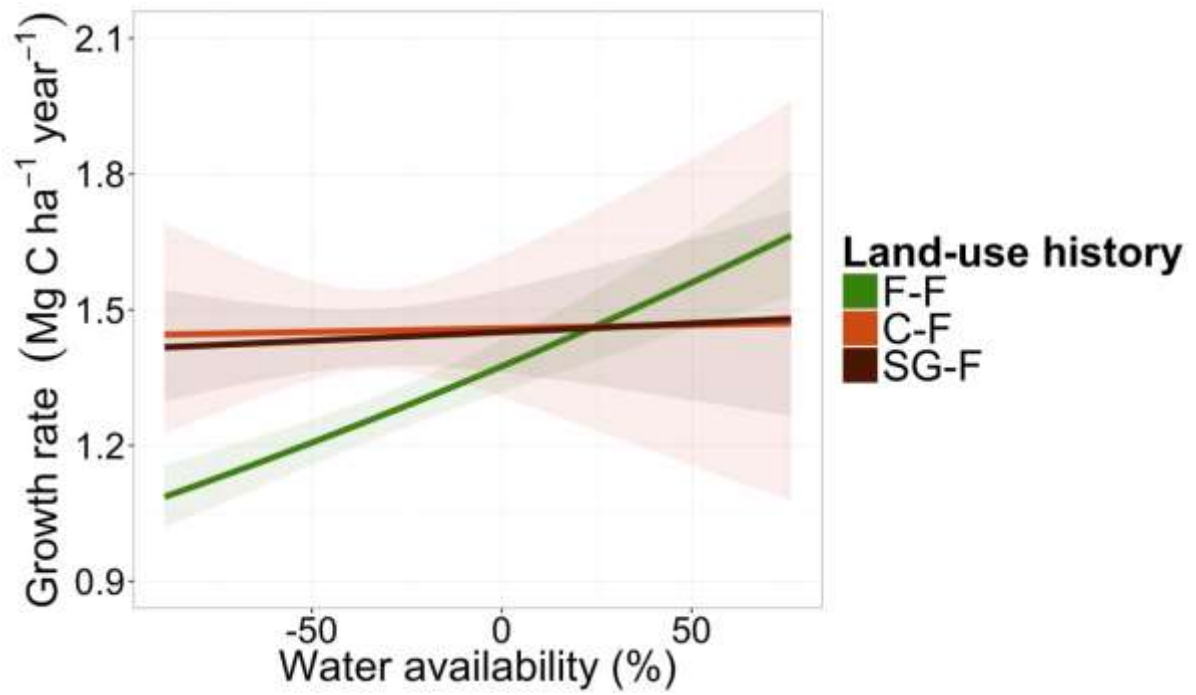
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850   **Figure 3**

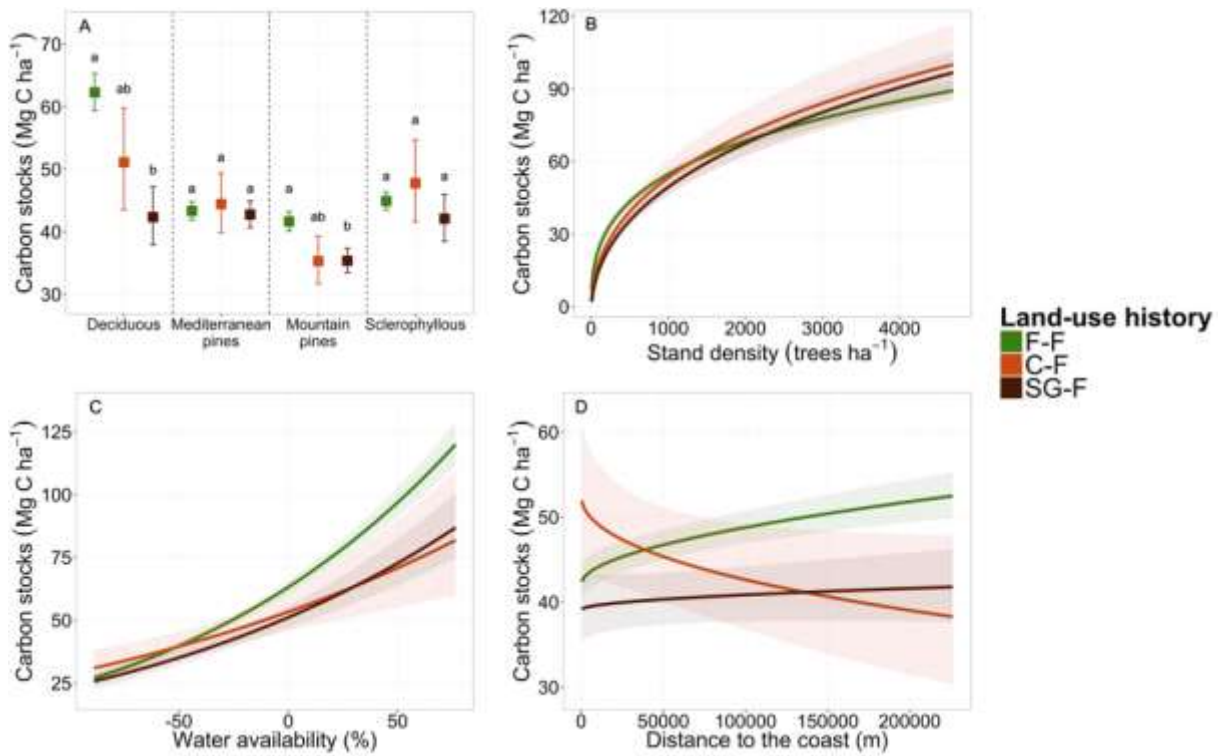851

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**Figure 4**