

1 **Title**

2 **Land use legacies drive higher growth, lower wood density and enhanced climatic**
3 **sensitivity in recently established forests**

4

5 **List of authors:**

6 Raquel Alfaro Sánchez¹, Alistair S. Jump^{1,2}, Joan Pino^{1,3}, Oihane Díez-Nogales³, Josep

7 Maria Espelta^{1,3}

8

9 **Institutional affiliations:**

10 ¹ CREAM, Centre de Recerca Ecològica i Aplicacions Forestals E08193 Bellaterra
11 (Cerdanyola de Vallès), Catalonia, Spain

12 ² Biological and Environmental Sciences, Faculty of Natural Sciences, University of
13 Stirling, Stirling, FK9 4LA, UK

14 ³ Universitat Autònoma de Barcelona, E08193 Bellaterra (Cerdanyola del Vallès),
15 Catalonia, Spain

16

17 **Corresponding author:** Raquel Alfaro Sánchez (r.alfarosanchez@gmail.com).

18 CREAM, Centre de Recerca Ecològica i Aplicacions Forestals E08193 Bellaterra
19 (Cerdanyola de Vallès), Catalonia, Spain. Tlf: +34 935814850

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22 **Abstract**

23 Europe is undergoing significant forest expansion due to the abandonment of rural areas
24 driven by economic and demographic changes. Recently established forests provide key
25 ecosystem services such as habitat provision and increased carbon stocks. However, we
26 lack understanding of whether past land use might alter their resilience to climate
27 change compared with long-established forests. Forests established in former
28 agricultural areas may benefit from land use legacies resulting in higher fertility, yet
29 such a benefit might turn into a disadvantage if it involves changes in functional
30 attributes that lower their ability to cope with negative climatic events (e.g. droughts).
31 Here we examined whether recently (post 1956) and long-established (pre 1956) beech
32 forests in Catalonia (NE Spain) differ in their growth patterns, wood density, sensitivity
33 to climate and response to extreme climatic events. Our results indicate higher growth
34 (32%) and lower wood density (3%) in trees from recently established forests, even
35 when controlling for tree age and competition. In addition, recently established forests
36 showed a higher sensitivity to Standardised Precipitation-Evapotranspiration Index
37 (SPEI), precipitation and temperature and to extreme negative and positive climatic
38 events. In particularly wet years, recently established forests show twice the number of
39 positive pointer years than long-established forests. Compensatory growth during
40 positive years in recently established forests, may be driving the similar or even higher
41 recovery and resilience detected after drought episodes. Nevertheless, the higher
42 climatic sensitivity of the recently established forests, together with their greater growth
43 and lower wood density indicates that they may be particularly vulnerable to future
44 droughts. Such enhanced vulnerability might question their ability to contribute to
45 carbon sequestration in the long term and emphasises the need to account for land use
46 legacies to better predict future forest function as climate changes.

47 **Keywords**

48 Forest expansion; land-use history; *Fagus sylvatica*; low latitude distribution;

49 dendroecology; extreme climatic events

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52 **1. Introduction**

53 The last decade (from 2008 to 2017) was the world's warmest, with global
54 average temperatures increasing at approximately 0.2°C per decade above pre-industrial
55 levels (EEA, 2017). In Europe, temperatures have risen above the global average and
56 climate models project further increases in temperature exceeding global average
57 projections over the 21st Century (EEA, 2017). In Southern Europe, the strongest
58 warming and decrease of precipitation is projected to occur in summer, together with
59 more frequent extreme heat waves and heavy precipitation events by 2100 (EEA, 2017).
60 Mitigation actions are vital to limit global warming of 1.5°C above pre-industrial levels
61 over the next decades (Masson-Delmotte et al., 2018). Land use and land-use change is
62 considered a critical feature of almost all mitigation pathways for the next decades
63 (Masson-Delmotte et al., 2018). For instance, the terrestrial carbon sink since the 1990s,
64 only from world's re-growing forests, equalled 24% of cumulative fossil carbon
65 emissions (Pan et al., 2011). However, it is uncertain whether this accelerated trajectory
66 of C sink will be sustained in the future.

67 In temperate forests, the increasing carbon sink detected during recent years has
68 been attributed to a transition recovery from past land use and natural disturbances
69 (Thom et al., 2018). Thus, in Europe the recent forest expansion is taking place mainly
70 on former agricultural lands as a consequence of the widespread abandonment of rural
71 landscapes (Keenan, 2015). New forests established in former agricultural lands can
72 show enhanced tree growth due to the legacies of the previous land-use (Gerstner et al.,
73 2014; Lambin and Meyfroidt, 2011; Leuschner et al., 2014). In comparison to forests
74 with a continuous land-use history, former agricultural soils tend to be deeper, more
75 basic, have higher N and P content and mineralization rates (Compton and Boone, 2000;
76 Fraterrigo et al., 2005), include a larger biomass of bacteria (Fichtner et al., 2014) and a

77 greater general decomposer activity (Freschet et al., 2014). Ultimately, these
78 characteristics may result in a positive and accelerated feedback between the
79 belowground and the aerial component leading to higher growth and productivity, e.g.
80 35% greater plant biomass (Freschet et al., 2014) or 25% higher growth (Vilà-Cabrera
81 et al., 2017). On the other hand, the initial advantage of higher growth might become a
82 disadvantage if it is accompanied by changes in functional traits. Changes in functional
83 traits can constrain the ability of trees to face unfavourable climatic conditions, such as
84 a reduction in wood density (i.e. greater number and area of conductive vessels) and in
85 water use efficiency. Indeed, lower wood density is associated with higher susceptibility
86 to drought and mortality responses (Greenwood et al., 2017). Lower wood density also
87 involves less resistance to wind forces (Anten and Schieving, 2010; Putz et al., 1983),
88 pathogen attacks (Augspurger, 1984), cavitation (because it's associated with larger
89 vessel diameter; Lambers et al., 2008) and implies less carbon storage for a given stock
90 of standing volume (Zeller et al., 2017). For example, Pretzsch et al., (2018) reported
91 faster stand and tree growth since 1870 in Europe for several dominant tree species.
92 However, this faster growth rate was associated with 8-12% decrease in wood density,
93 particularly on fertile sites (Pretzsch et al., 2018). Similarly, nitrogen fertilization
94 experiments have demonstrated a reduction in wood density with enhanced nitrogen
95 supplies for tree species (e.g. Cao et al., 2008; Mäkinen et al., 2002). These examples
96 imply that the effects of land use legacies in trees growing in recently established forests
97 may result in differences in functional attributes in comparison to more continuously
98 forested areas, potentially involving a different sensitivity to climate, and particularly to
99 extreme climatic events (e.g. drought episodes). Up to now, differences in the response
100 of forests to adverse climatic events has been mostly analysed from the perspective of
101 the previous climatic conditions experienced ('climate legacy effects', Lloret and

102 Kitzberger, 2018). Thus, it has been often reported that populations living in more
103 favourable climatic conditions would be more affected by adverse events than
104 conspecifics that had experienced harsher climates (Lloret and Kitzberger, 2018). In
105 fact, climatic legacies could contribute to explain why populations living in climatically
106 marginal areas of a species distribution can be more resistant to negative climatic events
107 than those in the core (see Cavin and Jump, 2017). Very few studies have addressed the
108 potential interactions among land use legacies and climate sensitivity (but see Mausolf
109 et al., 2018), although it is well known that soil nutrients and physical soil properties
110 can influence the growth sensitivity of temperate tree species (Lévesque et al., 2016).

111 We sought to determine whether recently established beech (*Fagus sylvatica* L.)
112 forests present differences in growth, wood density and climatic sensitivity, especially
113 when subject to extreme events, when compared to forests with a continuous land-use
114 history. Beech is one of the most abundant and extensively distributed broadleaf trees in
115 Europe (Ellenberg et al., 2010). This species is highly vulnerable to drought and
116 consequently it is expected to retreat from its current southern distribution limit
117 (Zimmermann et al., 2015). In fact, some studies have shown a decline in beech growth
118 in marginal distributional areas (Jump et al., 2007, 2006; Piovesan et al., 2008),
119 accompanied by the replacement by other more drought tolerant tree species (Peñuelas
120 et al., 2007; Zimmermann et al., 2015). In addition, tree populations within the species'
121 range can be affected differently by regional extreme events due to variation of local
122 climatic conditions or past history (Hampe and Petit, 2005). Populations at the southern
123 edge of distribution of *F. sylvatica* can be found in Northern Spain, where it occupies
124 8667 km² according to the Spanish Forest Inventory with almost 22% of the forest
125 surface established after 1950 (Vilà-Cabrera et al., 2017). Interestingly, this forest
126 expansion is occurring in a region where ongoing changes in climatic conditions are

127 predicted to result in its decline, raising the question of whether recently established
128 forests will cope with climate change in a similar way to long-established forests.
129 Consequently, these Southern *Fagus sylvatica* populations provide an important
130 opportunity to determine the response of growth and functional traits of recently
131 established forests to extreme climatic events. We hypothesise that 1) recently
132 established forests should show higher annual growth due to improved soil conditions
133 resulting from former agricultural or pasture land-use. 2) higher growth will be
134 accompanied by the production of lower density wood and 3) will result in a higher
135 sensitivity to climate and a poorer performance under extreme climatic events that
136 exacerbate limiting factors for the species, such as droughts. Ultimately, our results will
137 improve our understanding of whether beech forests established in former agricultural
138 areas will help the maintain of this species at low latitudes of its geographical
139 distribution. Alternatively, under harsher climatic scenarios, the positive effect of
140 forests growing in former agricultural areas could be transient, even predisposing such
141 forests to faster future decline.

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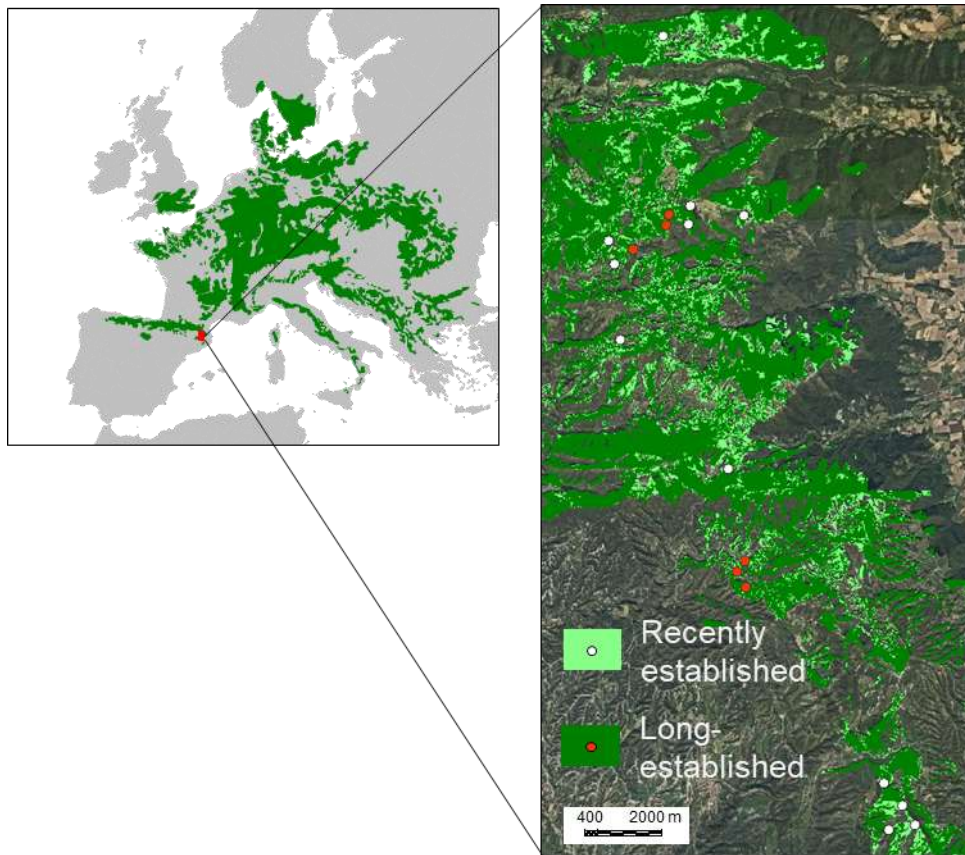
143 **2. Methods**

144 *2.1 Study area and sampling design*

145 This research was conducted in Catalonia, NE Spain, where *Fagus sylvatica* forests
146 occur at the south western (rear-edge) of this species distribution in Europe (Hultén and
147 Fries, 1986). In this area, detailed cartography of land use changes is available for the
148 second half of the twentieth century (Fig. 1).

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154 Figure 1. Natural distribution area of *Fagus sylvatica* distribution in Europe according
 155 to EUFORGEN (Pott, 2000; left panel) and location of the recently (light green) and
 156 long-established (dark green) beech forests in the study region (right panel). White and
 157 red circles in the right panel indicate the location of the studied recently and long-
 158 established forest patches, respectively (see Fig. S1 for details of patch selection).

159

160 Land-use change was identified by combining two land cover maps
 161 (<http://www.creaf.uab.cat/mcsc>) obtained through photo-interpretation of 1956-1957
 162 and 2005 orthoimages (Başnou et al., 2013). Current forest patches established in
 163 cropland/pastures abandoned after 1956 were considered as ‘recently established
 164 forests’, while forests that already existed in 1956, entailing a longer forest history,
 165 were classified as ‘long-established forests’. Notice that these two categories were not
 166 defined by the stand age, but by the age of the land use (see for similar criteria Mausolf
 167 et al., 2018). In fact, the two forest types could have a similar stand age and

168 physiognomy if long-established forests had been disturbed (e.g. logged) around the 50s
169 (Fig. S1). After field validation of the orthoimage photointerpretation, we selected six
170 patches of long-established forest and twelve patches of recently established forests in
171 similar topographic conditions. Maximum distance among patches was 45 km across an
172 elevation gradient from 831 to 1452 m asl (Fig. 1). From November 2017 to February
173 2018, 30 trees were randomly selected and geolocated per patch (511 trees were
174 included in the final analyses after discarding 29 trees with unreadable cores). Since one
175 of the main differences between trees growing in recently *vs.* long-established forests
176 could be their nutritional status owing to the positive land use legacies of previous
177 cropland/pastures (i.e. natural or artificial manuring; see Fraterrigo et al., 2005; Mausolf
178 et al., 2018), we previously analysed N content and $\delta^{15}\text{N}$ in a random sample of 10 fully
179 sun-exposed leaves per tree as a proxy of nutrient availability (Aerts and Chapin, 1999).
180 The measurement of $\delta^{15}\text{N}$ can provide evidence of the N source used by plants, with
181 more positive values expected in trees growing in former agricultural soils as a
182 consequence of past manuring or cattle raising (Treasure et al., 2016). After drying to
183 constant weight at 60°, all leaves per tree were pooled and ground and N and $\delta^{15}\text{N}$ were
184 analysed at the UC Davis Stable Isotope Facility (Univ. California, Davis, USA).
185 ANOVA tests were applied to test for differences in N and $\delta^{15}\text{N}$ between type of forests.

186

187 *2.2 Tree growth and wood density measurements*

188 Two increment cores were extracted per tree using a Pressler increment borer (46 mm)
189 at 50 cm above the ground level, to enable a more accurate estimation of tree age. Cores
190 were labelled and brought to the laboratory for subsequent analyses of tree-ring width
191 and wood density. Owing to the time-consuming nature of the analytical process, we
192 only determined wood density in a random sub-sample of 284 trees corresponding to 5

193 recently and 5 long-established forest patches. Wood density (g cm^{-3}) was calculated
194 using one of the two cores per tree as the dry weight of the core divided by its volume,
195 following Williamson and Wiemann (2010). Cores were first oven dried for at least two
196 hours at a temperature of 102°C and weighed to obtain the dry weight. Then, volume
197 was obtained by Archimedes' principle which is a reliable measurement for irregularly
198 shaped samples (Archimedes, 2009).

199 Once wood density was measured, cores were air dried, mounted on wood
200 supports, and sanded until rings were clearly visible with a stereomicroscope. For the
201 dendrochronological analyses, we used 935 cores from 511 trees from the 6 recently and
202 12 long-established forest patches. The two cores from the same tree were visually
203 crossdated with a stereomicroscope, scanned at 1600 d.p.i and ring widths measured to
204 an accuracy of 0.001 mm using the software CooRecorder v9.3 (Cybis Elektronik,
205 2018). Cross-dating of individual series was checked using CooRecorder and
206 COFECHA programs (Holmes, 1983). Whenever the pith was not reached in the core,
207 we estimated the distance from the innermost measured ring to the pith of the tree with
208 the software CooRecorder. Cambial age was also adjusted by adding the number of
209 rings to the pith estimated with CooRecorder, when none of the cores from a tree
210 reached the pith. Finally tree-ring width series were converted to basal area increment
211 (BAI) measurements ($\text{mm}^2 \text{ year}^{-1}$) using the R package 'dplR' (Bunn, 2008). For
212 climate-growth analyses, tree-ring width series were individually detrended with cubic
213 smoothing splines of 30 years to remove non-climatic growth trends related to the
214 increase in tree age and size (Cook and Kairiukstis, 1990). All tree-level indexed ring-
215 width series within recently or long-established forests were averaged to form a
216 chronology per type of forest by using a bi-weight robust mean. Average interseries
217 correlation and mean sensitivity were determined for each chronology with 'dplR'.

218

219 2.3 Forest structure and competition indices

220 In order to assess whether differences in competition in recently vs. long-established
221 forests influenced growth patterns, we calculated competition indices in a subsample of
222 140 focal trees (69 and 71 for recently and long-established forests, respectively). This
223 sampling included a minimum of three focal trees per patch from a range of ages
224 between 45 and 61 years. This range of ages was selected to avoid biases in subsequent
225 analyses due to tree age differences found between the two forest types (Fig. S2).

226 Neighbouring trees to the focal *F. sylvatica* individuals, including other tree species
227 (e.g. *Buxus sempervirens* L., *Quercus humilis* Mill., *Corylus avellana* L. and *Juniperus*
228 *communis* L.) were counted in circular subplots of 8 m of radius. Diameter at breast
229 height (DBH) of all trees (including the focal tree) larger than 5 cm DBH was measured
230 to calculate the basal area. To calculate the competition indices, we used a modification
231 of the index by Rozas and Fernández Prieto (2000), based on Lorimer (1983) and
232 defined as:

$$233 \quad CI = \sum_{j=1}^n \frac{BA_j}{BA_i}$$

234 Where CI is the competition index, BA_i is the basal area of the focal tree i , and BA_j is the
235 basal area of neighbouring trees j . In addition, tree density (trees ha⁻¹) and basal area
236 (m² ha⁻¹) was determined for each of the 18 forest patches. ANOVA tests were applied
237 to test for differences in tree density, basal area and mean DBH and mean raw ring
238 width between type of forests.

239

240 2.4 Climate data

241 We used monthly mean temperature and precipitation sum for the period 1950–2016
242 from the homogenized and quality-checked E-OBS v.17.0 dataset available on a 0.25°
243 grid (Haylock et al., 2008) from the KNMI Climate Explorer (<http://climexp.knmi.nl/>).
244 To assess drought severity at each location, the Standardised Precipitation-
245 Evapotranspiration Index (SPEI) was calculated using the R package ‘SPEI’ (Vicente-
246 Serrano et al., 2010) for a time scale of 1 month based on input data from E-OBS
247 v.17.0.

248 Our study plots are spatially distributed across four different E-OBS v.17.0 grid
249 cells and total annual precipitation and mean annual temperature range from 734 to 810
250 and 10.8 to 12°C, respectively. We averaged the climate data from these four grid cells
251 of 0.25° spatial resolution for subsequent analyses of climate sensitivity of study trees.
252 We then used the R package ‘treeclim’ (Zang and Biondi, 2015) to run *Pearson*
253 correlation analyses between monthly SPEI, precipitation and temperature data
254 (averaged for the four grid cells of climate data for the period 1950-2016) and the mean
255 tree-ring chronologies built for recently and long-established forests for the maximum
256 overlapping period (Table S1). A bootstrapping procedure was used to test for
257 significant correlations at $P < 0.05$ (Zang and Biondi, 2015).

258 These climate-growth analyses revealed that *F. sylvatica* forests showed the
259 highest response in growth during the months of June and July (see section 3).
260 Consequently, we focused on averaged June-July climate data for subsequent analyses
261 of climate sensitivity. To determine if climate variability is increasing over time in the
262 study area, we employed thirty-one years running variation for June-July SPEI,
263 precipitation and temperature data for the period 1950-2016. We also ran linear
264 regression models to determine if there is a significant rate of increase or decrease of

265 June-July precipitation and temperature from 1950 to 2016 in the study area
266 (significance level was set at $P < 0.05$).

267

268 *2.5 Events and pointer years*

269 Event years are defined as abrupt growth changes in individual tree-ring samples
270 (Schweingruber et al., 1990). To identify event years, we used the normalization in a
271 moving window method following Cropper (1979) and Schweingruber et al. (1990).
272 Annual ring width values for each individual tree were transformed into Cropper values
273 (Cropper, 1979) by using a 3 year window. A 13-year weighted low-pass filter (Fritts,
274 1976) was applied to tree-ring series prior to the calculation of event and pointer years.
275 This filter improves the detection of event and pointer years in complacent series, and
276 has little effect in sensitive series (Cropper, 1979). At the tree level, we identified a
277 negative (positive) event year when there is a significant decrease (increase) in growth
278 in the Cropper values.

279 A pointer year occurs when a higher proportion of tree-ring series from a group
280 show the same trend in a specific year (Schweingruber et al., 1990). The threshold in the
281 proportion of tree-ring series to identify a particular year as a pointer year is species and
282 site dependent. For instance, for coniferous trees a threshold value of 75% is often set
283 (e.g. Alfaro-Sánchez et al., 2018), whereas for deciduous trees, such as our target
284 species, *Fagus sylvatica*, lower threshold values are often considered to obtain a
285 reasonable number of pointer years, e.g Cavin and Jump (2017). Here, we set a
286 threshold value of 50% following Cavin and Jump (2017). Then, negative and positive
287 pointer years were identified when $\geq 50\%$ of the tree-ring series within a patch
288 presented an abrupt change in growth in a particular year; i.e. negative and positive
289 event years.

290 Pointer years can be associated with climatic and non-climatic events, such as
291 droughts or wildfires, respectively. Here we linked pointer years to extreme climatic
292 events, including extremely dry, wet, warm and cold years defined as the 90th or 10th
293 percentile values of the June-July SPEI, precipitation and temperature time series. The
294 period from 1970 to 2010 was used for the identification of pointer years. This period
295 covered a representative number of trees per patch and type of forest (after applying the
296 13-year low pass filter that truncates the tree-ring time series by 6 years at both ends).
297 Subsequently, pointer years were compared to June-July SPEI, precipitation and
298 temperature values, and classed as climatic-linked pointer years when the negative
299 (positive) pointer year fell below the 10th or 90th percentiles (above the 90th or 10th
300 percentiles) of the June-July precipitation or temperature climate time series during that
301 year, respectively.

302

303 *2.6 Resilience components*

304 The resilience components were calculated at the patch level for the climate-linked
305 pointer years with the R package ‘pointRes’ (van der Maaten-Theunissen et al., 2015)
306 following Lloret et al. (2011). The resilience components evaluated the recovery,
307 resistance and resilience of tree growth, here detrended growth values. To calculate the
308 resilience components, we considered a time window of 3 years before and after the
309 climate-linked pointer years. Therefore, the resistance index was calculated as the ratio
310 between the growth during the climate-linked pointer year and the averaged growth of
311 the 3 previous years. The recovery index was calculated as the ratio between the
312 averaged growth during the 3 years following the climate-linked pointer year and the
313 growth during that pointer year. Finally, the resilience index was calculated as the ratio
314 between the averaged growth during the 3 years following the climate-linked pointer

315 year and the averaged growth during the 3 years before the pointer year. ANOVA tests
316 were applied to test for differences in the resilience components between type of forests.

317

318 *2.7 Climate sensitivity, wood density and growth models*

319 The effects of forest type on the climate sensitivity of trees, wood density and growth
320 (BAI) were tested using Linear Mixed Effects Models (LMEMs; (Zuur, 2009). Two
321 LMEMs were performed for every response variable. The first one included all trees
322 sampled and the second one controlled any tree age effect by considering the range of
323 ages well represented in both recently and long-established forests, i.e. trees from 45 to
324 61 years (Fig. S2), hereafter referred to as ‘the comparable age subset’. Hence, we
325 focused on the results obtained using the comparable age subset and placed the analysis
326 carried out with all the sampled trees in the *Supplementary material*.

327 In order to study climate sensitivity, we used as the independent variable for the
328 LMEMs the slope coefficients obtained in linear regression models between detrended
329 ring-width series and June-July SPEI values at the tree level (the climatic variable
330 showing the highest correlation with tree growth in our study sites).

331 In the slope and wood density statistical models (LMEM or LM), the predictor
332 variables were: forest type, tree age, tree density obtained at the patch level (for all
333 sampled trees) or CI (for the comparable age subset between 45 and 61 years), tree
334 elevation (the elevation at which each tree is found), mean growth (only for the wood
335 density models) and the second order interactions among the factor type of forest and
336 the remaining variables. The patch was included in all the models as a random effect
337 (LMEM), with the exception of the WD models using the comparable age subset, where
338 the linear model (LM) showed a lower AIC and higher adjusted R^2 . The ‘lme4’ package

339 was used to fit the slope and wood density linear mixed effects models with the function
340 ‘lmer’ (Bates et al., 2015).

341 The effects of type of forest on growth (BAI) across the first 61 years of the life
342 of the trees (the period of time that trees from both type of forests shared in common)
343 were tested using LMEMs. The initial set of variables tested in the BAI LMEMs
344 included: forest type, tree density at the patch level (for all sampled trees) or CI (for the
345 comparable age subset between 45 and 61 years), June-July SPEI, and individual tree
346 variables such as the year of the tree life (considering only the first 61 years), tree
347 elevation, and the second order interactions among these variables and the factor type of
348 forest. We included the tree code as a random effect to account for the repeated
349 measures across an individual. A first-order autocorrelation structure (AR1) was also
350 included in the LMEMs to control for the temporal autocorrelation of BAI measures.
351 BAI, tree density and CI variables were transformed with a natural logarithm to
352 conform to normality. The influence of age across the first 61 years of the life of the
353 trees on BAI was modelled with a natural cubic spline with a B-spline basis with 5
354 equally spaced knots. The ‘nlme’ package was used to fit the BAI linear mixed effects
355 models with the function ‘lme’ (Pinheiro et al., 2018). The predictor variables were
356 standardized to eliminate differences in scale measurements.

357 The best model for each response variable, i.e. slope, wood density and BAI,
358 was chosen in a two-step procedure. First we identified the predictor variables with a
359 significant ecological or biological interest for the response variables by selecting the
360 LMEM or LM with the lowest AIC (Akaike Information Criterion), among sets of
361 alternative models fitted by maximum likelihood (for the LMEMs), and removing all
362 terms that were not significant according to likelihood ratio tests. Then, we tested
363 whether the variable of interest, type of forest, and its interaction with the remaining

364 variables improved the previous selected models in terms of AIC. We followed this
365 procedure to avoid possible collinearity effects of the variable type of forest with other
366 predictor variables such as the tree age. The final LMEMs were fitted using the
367 restricted maximum likelihood (REML) method (Zuur, 2009). We calculated marginal
368 (i.e. the proportion of variance explained by fixed effects) and conditional (i.e. the
369 proportion of variance explained by fixed and random effects) R^2 for the LMEMs with
370 the 'MuMIn' R package (Barton, 2018).

371

372 **3. Results**

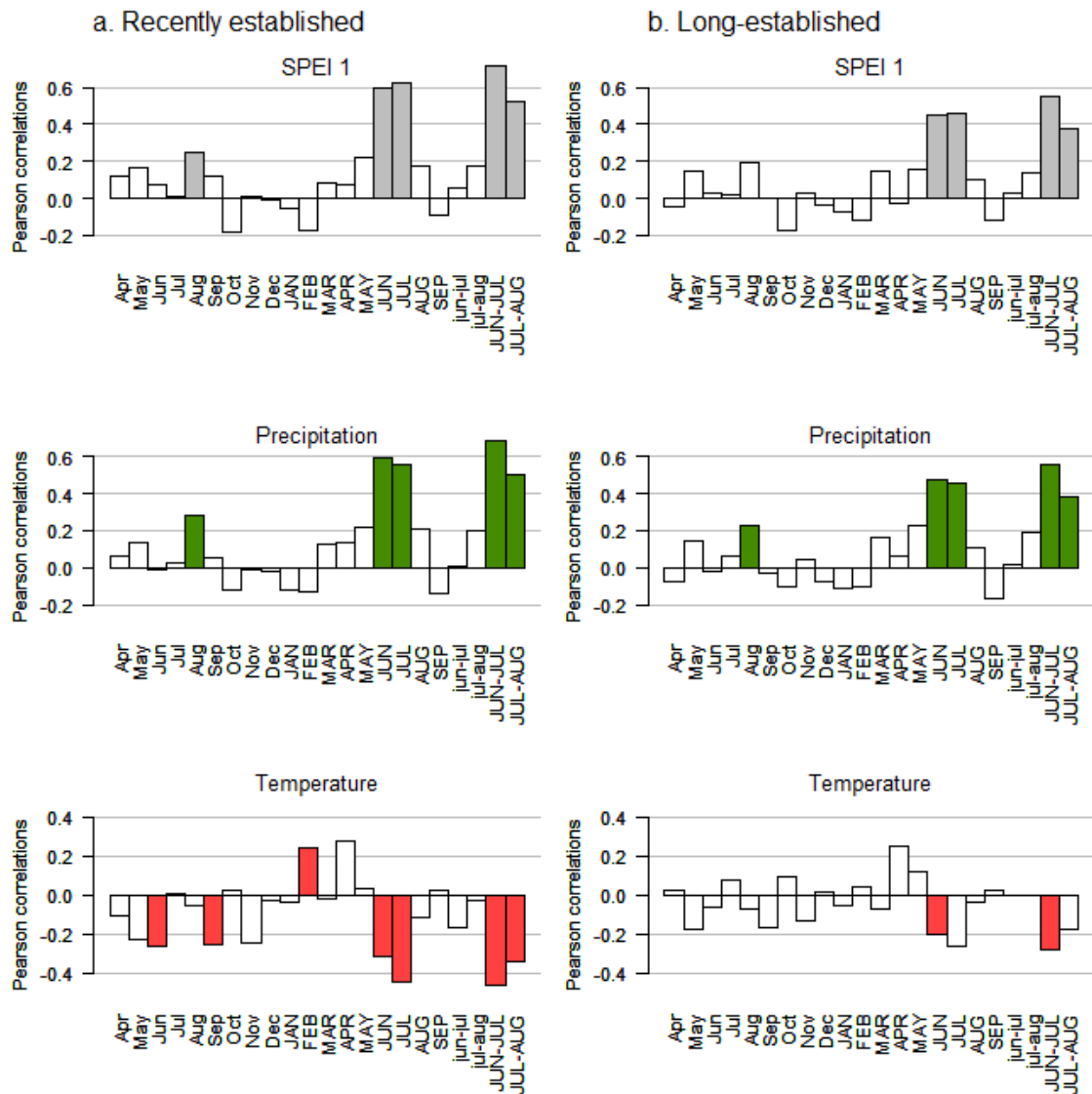
373 Mean tree age was significantly higher in long-established than in recently
374 established forests (65.2 ± 1.3 vs. 37.8 ± 0.6 years, respectively). Yet recently and long-
375 established forests showed similar forest structural characteristics, since no significant
376 differences were found in tree density, DBH and basal area (Table S1a). However, trees
377 in recently established forests have significantly higher N content and more positive leaf
378 $\delta^{15}\text{N}$ values than long-established forests (2.74 ± 0.03 vs. 2.46 ± 0.02 ‰ and $-3.14 \pm$
379 0.09 vs. -5.76 ± 0.08 ‰, respectively, Table S1a).

380

381 *3.1 Climate sensitivity*

382 Climate-growth *Pearson* correlations indicate that both types of forests are highly
383 sensitive to June-July (summer) conditions. However, recently established forests
384 displayed higher correlation values than long-established ones for the three climate
385 variables analysed: SPEI, precipitation and temperature (Fig. 2). This result is in line
386 with the higher mean sensitivity and higher interseries correlation found in the recently
387 established forests (Table S1b).

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392 Figure 2. Climate-growth relationships for recently (a) and long-established (b) forests.
393 SPEI, precipitation and temperature variables are considered for the period 1950-2016.
394 Previous and current year months are indicated in lowercase letters and uppercase
395 letters, respectively. The label 'SPEI 1' indicates that SPEI was calculated for a
396 timescale of 1 month, which gave higher correlations than timescales of 3, 6 and 12
397 months.

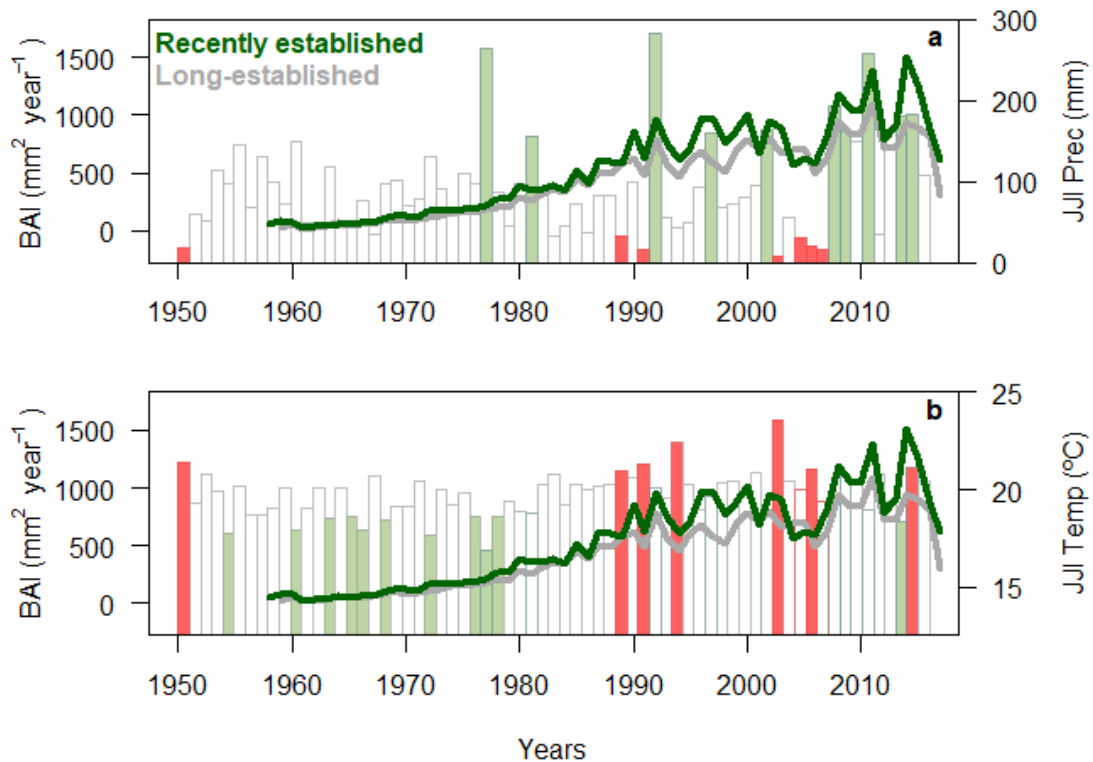
398

399 The study area has recorded an increase in summer (June-July) SPEI,
400 precipitation and temperature variability through time, and successive extreme wetter
401 and warmer summers since the early 1980s (Fig. S3). A significant increase in summer

402 temperature of 0.18°C per decade and an increase (although not significant) in summer
403 precipitation of 5.6 mm, has also been recorded for the period 1950-2017 (Fig. 3).

404

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408 Figure 3. Basal area increment (BAI) chronologies for recently and long-established
409 forests (green and grey lines, respectively) vs. June-July precipitation (a) or June-July
410 temperature (b) time series for the period 1950-2016. Only the comparable age subset
411 of trees between 45 and 61 years is considered. Green (pink) bars indicate extremely wet
412 or relatively cool (extremely dry or warm) summers, as those with June-July
413 precipitation and temperatures values above (below) the average plus (minus) 2 times
414 the standard deviation of the June-July climate time series.

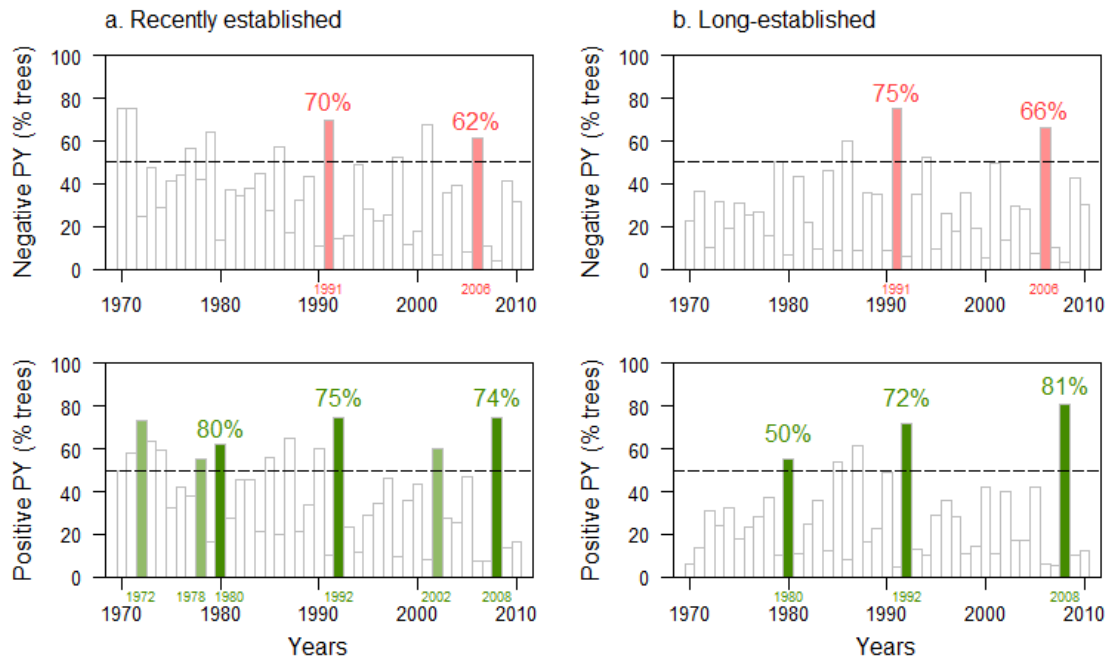
415

416 For the two types of forests, the drought years 1991 and 2006 (one of the
417 warmest years on record since 1950s) appeared as negative pointer years. Interestingly,
418 the recently established forests presented twice the number of positive pointer years (i.e.

419 years with a significant response to exceptional precipitation) compared to long-
420 established forests (Fig. 4).

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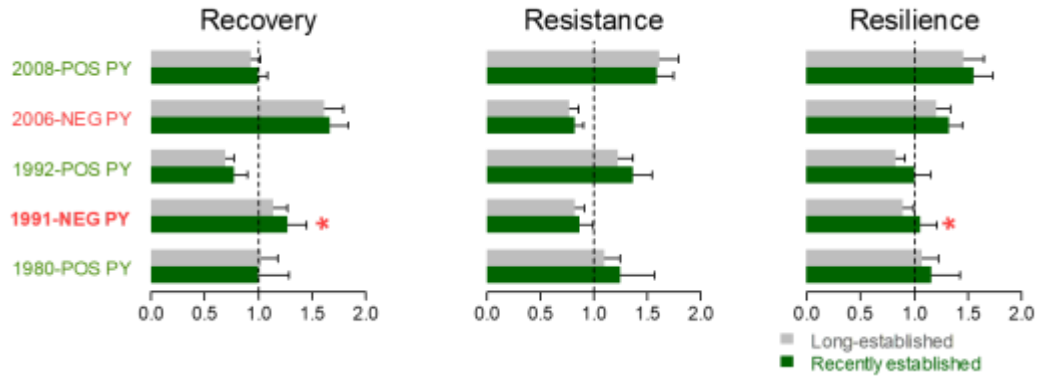
424

425 Figure 4. Climatic-linked negative (upper panels) and positive (lower panels) pointer
426 years for recently (a) and long-established forests (b). Red (green) bars denote negative
427 (positive) pointer years where more than 50% of the trees responded with a significant
428 decreased in growth. Positive pointer years in recent forests but absent in long-
429 established ones are indicated in light green.

430

431 In response to these pointer years, recently established forests presented
432 significant higher recovery, resistance and resilience values only for the negative pointer
433 year of 1991 (recovery and resilience, Fig. 5).

434



435

436

437 Figure 5. Mean \pm SE recovery, resistance and resilience values for the negative (red
 438 characters) or positive (green characters) pointer years identified in both, recently (dark
 439 green bars) and long-established (grey bars) forests (see Fig. 4). Asterisks denote
 440 significant differences among type of forests.

441

442 The higher climatic sensitivity of recently established forests was also confirmed
 443 by the significantly higher slope coefficient, obtained in linear regression models
 444 between detrended ring-width series and June-July SPEI, both when using all sampled
 445 trees (Table S2, Fig. S3a) or the comparable age subset between 45 and 61 years (Table
 446 1, Fig. 6a). In addition, climate sensitivity of growth increased with tree age in both type
 447 of forests, when using the comparable age subset (Table 1).

448

449 Table 1. LMEM and LM results for the effects of type of forest (recently or long-
 450 established), tree age and tree density on the slope and wood density (WD) variables,
 451 respectively. The slope coefficient was obtained in linear regression models between
 452 detrended ring-width series and June-July SPEI. Only the comparable age subset
 453 between 45 and 61 years is considered. Tree age and tree density were scaled in the
 454 models. The R^2_{adj} and R^2 due to fixed (R^2_m) and due to fixed and random effects (R^2_c)
 455 is also provided. Significance of the p values is indicated by: *** $P < 0.001$; ** $P < 0.01$ or
 456 * $P < 0.05$. The level type of forest: *recently established* is included in the intercept. n.a.
 457 not applied

458

459

460

	Slope				WD			
Fixed effects	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	-0.010	0.06	-0.17	0.862	0.506	0.016	30.88	<0.001***
Type of forest: <i>Long-established</i>	-0.044	0.020	-2.21	<0.05*	0.014	0.003	4.46	<0.001***
Tree age	0.0027	0.0011	2.46	<0.05*	0.0010	0.0003	3.04	<0.01**
Tree density	n.a.				-0.0036	0.0015	-2.46	<0.05*
Random effects	Std. Dev							
Patch	0.03							
Residual	0.06							
R^2_m / R^2_{adj}	0.10				0.32			
R^2_c	0.31							

461

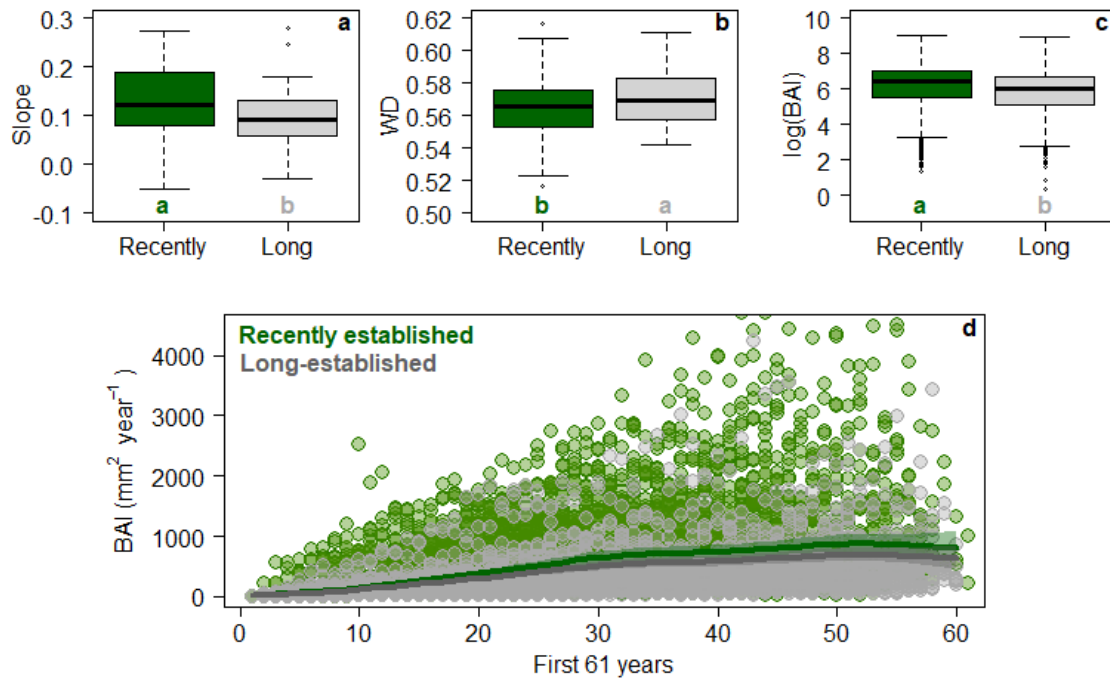
462

463 3.2 Wood density

464 The LMEM and LM results revealed a significant difference in wood density between
465 type of forests, i.e, higher wood density (3%) in long-established forests (Fig. 6b, Table
466 1) and a negative effect of tree density, both when using all sampled trees or the
467 comparable age subset (Table S2,1). Tree age also exhibited a positive effect on WD
468 when the comparable age subset was analysed, i.e. wood density increases with tree age
469 (Table 1).

470

471



472

473

474

475 Figure 6. Boxplots displaying slope coefficients obtained in linear regression models
 476 between detrended growth values and June-July SPEI (a), wood density (WD, g cm⁻³; b)
 477 and log-transformed BAI (c) differences between type of forest (recently or long-
 478 established). Lowercase coloured letters indicate significant differences found between
 479 type of forests (See Tables 1-2). Basal area increment (BAI) predictions across the first
 480 61 years of the life of the trees for recently (green line) and long-established (grey line)
 481 forests (d). The observed BAI values are indicated with green and grey circles, for
 482 recently and long-established forests, respectively. Only the comparable age subset
 483 between 45 and 61 years is considered.

484

485 3.3 Tree growth

486 Recently established forests displayed significant higher mean raw ring width (32%)
 487 than the long-established forests (Table S1b) and LMEMs indicated that during the first
 488 61 years of the trees' lifetime (i.e. the time period covered by both recently or long-
 489 established forests), trees growing in recently established forests also presented higher
 490 growth (BAI) rates, when using all the sampled trees (Table S3) and even when
 491 comparing a similar range of ages (Table 2, Fig. 6c-d).

492

493

494 Table 2. Results of basal area increment (BAI) using the comparable age subset, from
 495 45 to 61 years. Age is the year of the life of the tree. The R^2 due to fixed (R^2_m) and due
 496 to fixed and random effects (R^2_c) of each selected model is also provided. Significance
 497 of the p values is indicated by: *** $P < 0.001$; ** $P < 0.01$ or * $P < 0.05$.

498

499

BAI				
Fixed effects	Estimate	SE	t value	p value
(Intercept)	4.52	0.17	26.3	<0.001***
Age (0-10)	2.77	0.12	22.5	<0.001***
Age (10-20)	3.41	0.14	24.5	<0.001***
Age (20-30)	3.38	0.13	25.5	<0.001***
Age (30-40)	3.06	0.12	25.0	<0.001***
Age (40-50)	5.33	0.24	22.3	<0.001***
Age (50-60)	2.34	0.15	15.3	<0.001***
Type of forest: <i>Long-established</i>	-0.24	0.09	-2.8	<0.01**
Competition index (CI)	-0.47	0.05	-10.2	<0.001***
Jun-July SPEI	0.103	0.004	23.5	<0.001***
Random effects	Std. Dev			
Tree	0.39			
Residual	0.69			
R^2_m	0.57			
R^2_c	0.67			

500

501

502 Both LMEM BAI models presented a high explained variation; i.e. the LMEM
 503 using all the range of ages explained 41% of the variation (Table S3) whereas the model
 504 that accounted only for the trees between 45 and 61 years explained 57% of the
 505 variation (Table 2). Favourable June-July SPEI conditions exerted a positive influence
 506 on both growth LMEMs (Table 2; Table S3).

507 The LMEM that included all range of ages showed that tree elevation also
 508 exerted a positive influence on growth for both types of forests. Growth in the long-
 509 established forests was also less sensitive to climatic conditions, as reflected by the
 510 negative interaction between type of forest and June-July SPEI conditions (Table S3).

511 For the LMEM that used the comparable age subset, between 45 and 61 years, we
512 additionally included as a predictor variable a competition index calculated at the
513 individual level for that selection of trees. This competition index was significant in the
514 LMEM, showing a negative effect of tree competition on growth in both types of forests
515 (Table 2).

516

517 **4. Discussion**

518 This study stresses that recently established forests are more sensitive to climate. To the
519 best of our knowledge, our study is the first to highlight the importance that positive
520 climatic events may have in buffering the negative effects of drought episodes. In
521 addition, we noticed that the particular distribution of negative and positive climatic
522 extreme events can be crucial for forecasting the effects of climate change on forests,
523 particularly when conclusions about vulnerability are inferred only from resilience
524 components (*sensu* Lloret et al. 2011) across large geographical gradients.

525 In agreement with our first hypothesis, recently established beech forests grew
526 more than long-established ones even when controlling for tree age, i.e. running the
527 analyses with the common subset of trees aged between 45 and 61 years (Fig. 3, 6). For
528 this subset of trees, our analyses indicate that the recently established forests grew some
529 32% (in terms of mean raw ring width) more than long-established forests. Lower tree
530 competition during tree establishment might be invoked as a potential cause benefiting
531 trees growing in recently established forests. However, several pieces of evidence cast
532 doubts on this effect. First, no significant differences were found in patch structure
533 among the two types of forests, either in tree density or in basal area (Table S1).
534 Furthermore, competition at the individual level (CI) was included in the models and
535 although, as expected, it negatively affected tree growth (e.g. Zeller et al., 2017), no

536 significant interaction between CI index and the type of forest was observed. Second,
537 during the first years after establishment, growth was very similar in the two forest
538 types (i.e. see the period 1960-1970 in Fig. 3) and this trend persisted until some
539 unusual wet years occurred in the late 70s. In fact, recently established beech forests
540 only start demonstrating a clear advantage in their growth in recent decades when
541 negative, but also the majority of positive-climatic extreme years have occurred (from
542 the 90s onwards, see Fig. 3a).

543 These results, coupled with the higher N content observed in tree leaves in
544 recently established forests, suggest that legacies from a former agricultural or pastoral
545 use might be the main factor favouring a faster growth of trees in recently established
546 forests (see also Mausolf et al., 2018). Interestingly, the fact that differences in tree
547 growth between forest types become particularly high during wet years, is in line with
548 the paramount importance of water availability for nutrient uptake in Mediterranean
549 mountain ecosystems (Matías et al., 2011; He and Dijkstra, 2014). Thus, it is during
550 wetter years when the advantage of recently established forests, established in more
551 fertile soil, can be maximized. Furthermore, we cannot discard that due to this higher
552 soil fertility, recently established forests are obtaining an additional benefit in
553 comparison to long-established ones, from the overall positive physiological effects of
554 warming (see Fig. 3b), extension of the vegetative season and rising atmospheric CO₂,
555 reported for European forests during recent decades (Churkina et al., 2010; Pretzsch et
556 al., 2018).

557 Our second hypothesis was also confirmed with trees in recently established
558 forests showing a reduction in wood density of c.a. 3%, even after restricting the
559 analysis to the common 45-61 age class. This result is likely associated with the higher
560 growth detected in these recently established forests, which is also in line with previous

561 studies for beech in Central Europe (Pretzsch et al., 2018). However, a less pronounced
562 reduction in wood density was found in our study area, 3%, compared to the reduction
563 of 11% found by Pretzsch et al. (2018), possibly because of the different methodologies
564 used for wood density determination or in tree age (older trees in Pretzsch et al., 2018).
565 Reduced wood density implies a higher vulnerability to drought-induced cavitation
566 (Hacke et al., 2001) for the recently established forests, since low wood density is often
567 associated with wider vessels (Eilmann et al., 2014), that are more prone to suffer
568 cavitation at negative xylem pressures during drought episodes (Anderegg et al., 2015;
569 Hacke et al., 2001; Jump et al., 2017). Due to the decrease in mechanical stability, lower
570 wood density is also associated with less resistance to other disturbances such as wind
571 (Anten and Schieving, 2010) and pathogens (Augspurger, 1984), i.e., reduced stiffness
572 and strength (weaker wood in Pretzsch and Rais, 2016) and it implies less C
573 accumulation for similar tree volume (Zeller et al., 2017).

574 In our research, wood density also increased with tree age and decreased with
575 tree density. This positive relationship between wood density and tree age has been
576 previously reported (Diaconu et al., 2016) and attributed to the duraminization (or
577 heartwood formation) process, i.e. the chemical maturation of wood that increases the
578 density of the tree-rings over time (Bontemps et al., 2013).

579 In addition to differences in wood density, attention should be paid to the
580 consequences of a potential oversizing of canopies in trees growing in recently
581 established forests during their larger growth response in wetter years (Fig. 3a) for their
582 future vulnerability to increasing drought. A strong and positive relationship has been
583 reported between tree growth, mediated by favourable environmental conditions, and
584 canopy development and productivity (Fernández-Martínez et al., 2015), but also the
585 more negative effects that drought may have for larger trees for example due to the

586 higher evaporative demand of their larger crowns (Bennett et al., 2015; Jump et al.,
587 2017).

588 Both forest types showed a drought sensitive response of growth, i.e, positive
589 correlations with summer precipitation and SPEI and negative correlations with summer
590 temperature. This general pattern of climate-growth relationships is in agreement with
591 previous studies covering a latitudinal gradient in Western Europe that included our
592 study area located at the climatic margin of the species (Cavin and Jump, 2017).
593 However, climate-growth correlations and the slope coefficients between detrended
594 growth series and June-July SPEI values confirmed our third hypothesis that recently
595 established forests were more sensitive than long-established forests to climate (summer
596 conditions). As for other tree species, intraspecific differences in climate sensitivity in
597 beech have been reported to stem from genotypic differentiation or phenotypic plasticity
598 (Nielsen and Jørgensen, 2003; Rose et al., 2009). Preliminary results suggests the lack
599 of genetic differences among recently and long-established beech forest in our study
600 area (M. Mayol, unpublished results), as might be expected from the moderate
601 geographical scale covered and the wind-pollination habit of this species (see Leonardi
602 and Menozzi, 1996). Aside from genotypic differences, past climate legacies (Lloret and
603 Kitzberger, 2018) or land use legacies (von Oheimb et al., 2014) have also been
604 identified as important influences on the current sensitivity of tree species to climate.
605 Historical climate legacies have been one of the most invoked causes to explain the
606 greater vulnerability to extreme events of climatic-core populations in comparison to
607 climatic-marginal ones (Clark et al., 2016; Jump et al., 2017; Rose et al., 2009),
608 although the geographical and temporal scale of our study does not support this
609 explanation. Rather, our results suggest the combination of higher growth and lower
610 wood density in recently established forests to be responsible of their higher sensitivity

611 to climate. This finding is in agreement with previous studies that have stressed the role
612 that land use legacies play in determining differences in tree sensitivity to climate
613 (Mausolf et al., 2018; von Oheimb et al., 2014). As for our study area, Mausolf et al.
614 (2018) also observed that recently established Central European beech forests were
615 more sensitive to climatic variations than forest with a continuous land use history.
616 Ultimately, this higher sensitivity to climate of trees established in richer soils from
617 former agricultural areas agrees with the findings of Lévesque et al., (2016) who
618 detected higher growth sensitivity in beech trees growing on richer soils in a study that
619 followed a gradient of different soil properties in Central Europe.

620 Despite the observed higher climatic sensitivity of recently established beech
621 forests, they showed a similar or even higher recovery, resistance and resilience
622 capacity than long-established forests when challenged with drought events. These
623 results disagree with the findings of Mausolf et al. (2018) for Northern Germany, where
624 the authors detected higher growth reductions under drought and less resistance in
625 recently than in long-established beech forests. Divergences might arise from
626 methodological differences among these studies, such as differences in tree age of
627 recently established forests (100-150 vs. 61 yrs, respectively,) or the length of the series
628 used to explore the link between land-use legacies and climate sensitivity (1994-2013
629 vs. 1956-2017, respectively). In addition, other local characteristics (e.g. forestry
630 practices, historic climatic legacies) may lead to divergent results among distant
631 latitudinal points. However, it should also be taken into account that recovery and
632 resilience indices rely on the climatic conditions after the studied event. For instance,
633 we found a recovery value around 1.5 after the drought event of 2006 which can be
634 associated to the extremely rainy years of 2008 and 2009 that fall in the 3 years range of
635 the resilience components calculations (Fig. 3a, 5). The fact that most severe drought

636 events in our study area were followed by extremely wet years (Fig. 3a), and that
637 recently established forests experienced twice the positive pointer years than long-
638 established ones (Fig. 4), may help to explain the divergence in the response of recently
639 established beech forests to drought between Mausolf et al. (2018) and the results
640 presented here.

641 Indeed, our results strongly suggest that the decrease in growth during negative
642 climatic events is probably overcompensated by a large increase in rainy years,
643 explaining why the recently established forests show a strong response to drought years
644 despite their higher climate sensitivity. Furthermore, the relevance of favourable years
645 diminishing the negative impacts of drought in our marginal-climate beech forests, is in
646 line with the evidence of highly locally variable drought-linked growth decline in this
647 dry range-edge beech populations, particularly for the youngest forests (Cavin and
648 Jump, 2017) or the lack of changes in growth after drought episodes observed for beech
649 forests in the Pyrenees (Gazol et al., 2018).

650

651 **5. Conclusions**

652 During the 20th Century, Europe has experienced substantial forest expansion because
653 of the widespread abandonment of rural landscapes, a trend expected to continue in the
654 future (Keenan, 2015). These recently established forests are already having a pivotal
655 role in providing ecosystem services such as habitat supply, landscape defragmentation
656 and increased net primary production and terrestrial carbon stocks (Bonan, 2008), while
657 contributing to compensation of fossil carbon emission (Pan et al., 2011, Vilà-Cabrera
658 et al. 2017). Based on our findings, the greater growth of recently established forests
659 resulting from agricultural and pastoral land abandonment can contribute significantly
660 to these services. However, previous studies highlighted the role of enhanced growth

661 during climatically more favourable periods in substantially elevating risk of dieback
662 during subsequent drought (Jump et al., 2017), and the greater drought vulnerability of
663 trees with lower wood density (Greenwood et al., 2017). Therefore, greater growth in
664 combination with changes in functional traits (i.e. lower wood density) and their higher
665 sensitivity to climate pose significant risks of vulnerability of recently established
666 forests when coupled with the projections of a strong decrease of summer precipitation
667 by 2100 across southern Europe (EEA, 2017). With the projected increase in aridity for
668 our study region during the next decades, there is a significant risk that these recently
669 established forests might be more negatively impacted by future drought than forests
670 with more continuous land-use history. Therefore, the ability of recently established
671 forests to contribute to carbon sequestration and other ecosystem services in the long
672 term could be threatened. Given these risks, better understanding of the function and
673 dynamics of forests established following land abandonment is essential to better
674 predict their response to the climates of the future.

675

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682

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945 **Supplementary Figures**

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a. Recently established forest



b. Long-established forest



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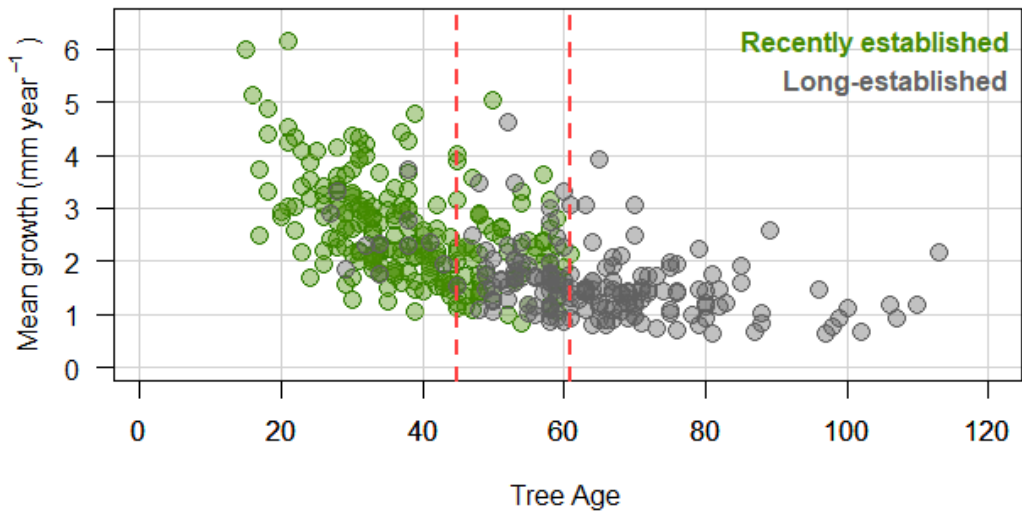
950 Figure S1. Orthoimages and descriptive pictures from recently and long-established

951 forests in 1956 and 2017-2018.

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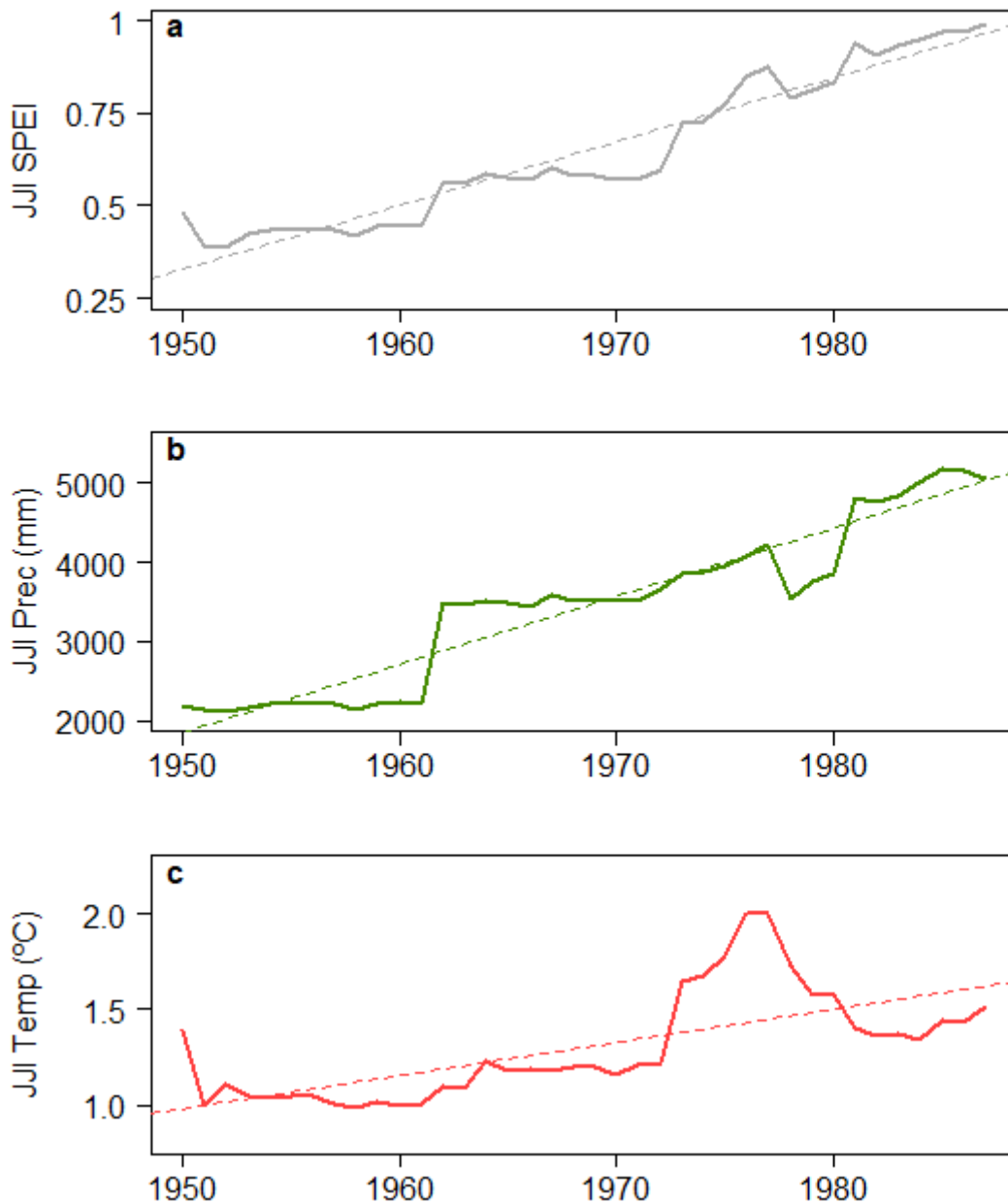
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957 Figure S2. Difference on tree ages in mean growth for both type of forests. Red dashed

958 lines indicate the comparable age subset between 45 and 61 years.

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Figure S3. Thirty-one years running variation for June-July SPEI (a) precipitation (b) and temperature (c) derived from E-OBS v.17.0 dataset for the period 1950-2016 and averaged over the four 0.25° spatial resolution grids covering the study region (2.125-2.625 E and 41.125-43.375 N). Dashed lines represent the trend obtained in linear regression models (significant at $P < 0.05$ in (a) and (b)).

969 **Supplementary Tables**

970 Table S1. Structural characteristics for recently and long-established forests. Mean \pm SE
 971 of tree age, tree density, DBH, basal area (BA), leaf nitrogen content and $\delta^{15}\text{N}$ values
 972 (a). Tree-ring statistics for Expressed Population signal (EPS) values above 0.85 for
 973 long-established forests, long-established forests younger than 62 years and recently
 974 established forests, and mean \pm SE raw tree-ring width and basal area increment (BAI,
 975 b). Asterisks denote significant differences among type of forests for these variables.

a.

Type of forest	Tree age (years)		Tree density (trees·ha ⁻¹)		DBH (cm)		BA (m ² ·ha ⁻¹)		N content (%)		Leaf $\delta^{15}\text{N}$ (‰)		Elevation (m)
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	range
Long-established	65.2*	1.3	1413	36	19.6	0.5	29.7	0.4	2.46	0.02	-3.14	0.09	831-1333
Recently established	37.8	0.6	1662	56	18.5	0.3	31.3	0.6	2.74	0.03	-5.76	0.08	1027-1452

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b.

Type of forest	Period	n trees	n cores	EPS	Interseries correlation	Mean sensitivity	Raw ring width (mm)		BAI (mm ² ·year ⁻¹)	
							mean	SE	mean	SE
Long-established	1917-2017	179	318	0.98	0.47	0.20	1.50	0.010	558	6
Long-established < 62 yrs	1959-2017	84	155	0.97	0.50	0.20	1.78	0.017	645	12
Recently established	1960-2017	332	617	0.99	0.52	0.30	2.35*	0.013	806*	8

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980 Table S2. LMEMs results for the predictive variable slope (obtained from the linear
 981 regression models between detrended growth values and June-July SPEI) and wood
 982 density (WD) using all range of ages. Tree density was scaled in the models. The R^2 due
 983 to fixed (R^2_m) and due to fixed and random effects (R^2_c) of each selected model is also
 984 provided. Significance of the p values is indicated by: *** $P < 0.001$; ** $P < 0.01$ or
 985 ** $P < 0.05$.

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	Slope				WD			
Fixed effects	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	0.135	0.010	14.25	<0.001***	0.5528	0.0024	7.10	<0.001***
Type of forest: <i>Long-established</i>	-0.045	0.016	-2.75	<0.05*	0.018	0.003	6.96	<0.01**
Tree density	n.a.				-0.0064	0.0017	7.13	<0.01**
Random effects	Std. Dev				Std. Dev			
Patch	0.03				0.004			
Residual	0.06				0.016			
R^2_m	0.09				0.28			
R^2_c	0.29				0.33			

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988 Table S3. Results of the LMEMs selected to study basal area increment (BAI) using all
 989 range of ages. In the models, age is the year of the life of the tree. Type of forest is a
 990 categorical variable to distinguish between recently and long-established forests. BAI
 991 and tree density variables were log-transformed to conform normality and tree elevation
 992 was scaled. The R^2 due to fixed (R^2_m) and due to fixed and random effects (R^2_c) of
 993 each selected model is also provided. Significance of the p values is indicated by:
 994 *** $P < 0.001$; ** $P < 0.01$ or * $P < 0.05$.

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	BAI			
	Estimate	SE	t value	p value
(Intercept)	3.58	0.07	54.5	<0.001***
Age (0-10)	2.86	0.07	42.4	<0.001***
Age (10-20)	3.34	0.08	41.2	<0.001***
Age (20-30)	3.27	0.09	38.1	<0.001***
Age (30-40)	2.94	0.10	29.4	<0.001***
Age (40-50)	5.35	0.15	36.5	<0.001***
Age (50-60)	2.22	0.14	16.1	<0.001***
Type of forest: <i>Long-established</i>	-0.46	0.09	-5.0	<0.001***
Tree elevation	0.14	0.04	3.7	<0.001***
Jun-July SPEI	0.127	0.003	39.2	<0.001***
Type of forest: <i>Long-established</i> × Jun-July SPEI	-0.030	0.007	-4.5	<0.001***
R^2_m	0.41			
R^2_c	0.69			

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