

**Disparate effects of global-change drivers on mountain conifer forests:  
warming-induced growth enhancement in young trees vs. CO<sub>2</sub> fertilization  
in old trees from wet sites**

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Running head: CO<sub>2</sub> and tree growth in subalpine forests

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## 1 **Abstract**

2 Theory predicts that the post-industrial rise in the concentration of CO<sub>2</sub> in the atmosphere ( $c_a$ )  
3 should enhance tree growth either through a direct fertilization effect or indirectly by  
4 improving water use efficiency in dry areas. However, this hypothesis has received little  
5 support in cold-limited and subalpine forests where positive growth responses to either rising  
6  $c_a$  or warmer temperatures are still under debate. In this study we address this issue by  
7 analyzing an extensive dendrochronological network of high-elevation *Pinus uncinata* forests  
8 in Spain (28 sites, 544 trees) encompassing the whole biogeographical extent of the species.  
9 We determine if the basal-area increment (BAI) trends are linked to climate warming and  
10 increased  $c_a$  by focusing on region- and age-dependent responses. The largest improvement in  
11 BAI over the past six centuries occurred during the last 150 years affecting young trees and  
12 being driven by recent warming. Indeed, most studied regions and age classes presented BAI  
13 patterns mainly controlled by temperature trends, while growing-season precipitation was  
14 only relevant in the driest sites. Growth enhancement was linked to rising  $c_a$  in mature (151-  
15 300 years old trees) and old mature trees (301–450 years old trees) from the wettest sites only.  
16 This finding implies that any potential fertilization effect of elevated  $c_a$  on forest growth is  
17 contingent on tree features that vary with ontogeny and it depends on site conditions (for  
18 instance water availability). Furthermore, we found widespread growth decline in drought-  
19 prone sites probably indicating that the rise in  $c_a$  did not compensate for the reduction in water  
20 availability. Thus, warming-triggered drought stress may become a more important direct  
21 driver of growth than rising  $c_a$  in similar subalpine forests. We argue that broad approaches in  
22 biogeographical and temporal terms are required to adequately evaluate any effect of rising  $c_a$   
23 on forest growth.

24 *Keywords:* basal area increment, climate warming, dendroecology, Generalized Additive  
25 Mixed Models, subalpine forests, *Pinus uncinata*.

## 26 **Introduction**

27 The post-industrial planet has experience a steep increase in  $c_a$  which is linked to warmer air  
28 temperatures (IPCC, 2013). However, current  $c_a$  does not suffice to saturate photosynthesis of  
29  $C_3$  tree species (Norby & Zak, 2011). Therefore, future growth trends of those tree species  
30 will depend on how forests respond to a rapidly  $CO_2$ -enriched and warmer world (Bonan,  
31 2008). Short-term experiments based on young trees growing under high  $c_a$  levels do not  
32 allow a full understanding how mature trees will respond to elevated  $c_a$  in the field where  
33 growth is mediated by ontogeny and limited by temperature oscillations and water availability  
34 (Körner, 2013). For example, rising  $c_a$  stimulates photosynthesis and decreases stomatal  
35 conductance through an improved intrinsic water-use efficiency (iWUE), i.e. the carbon gain  
36 per unit of water lost (Norby *et al.*, 1999). However, such improved iWUE does not  
37 necessarily translate into enhanced growth in the field (Peñuelas *et al.* 2008, 2011; Linares &  
38 Camarero, 2012).

39 The questions of whether, where, and when tree growth is influenced by post-  
40 industrial  $c_a$  still remain open and controversial. Numerous field studies performed in  
41 different biome and forest types worldwide have found either positive (e.g., LaMarche *et al.*,  
42 1984; Hari & Arovaara, 1988; Graybill & Idso, 1993; Idso & Kimball, 1993; Nicolussi *et al.*,  
43 1995; Soulé & Knapp, 2006; Voelker *et al.*, 2006, Wang *et al.*, 2006; Martinez-Vilalta *et al.*,  
44 2008; Cole *et al.*, 2010, Koutavas, 2013), or neutral to negative (Kienast & Luxmoore, 1988;  
45 Graumlich, 1991; Tognetti *et al.*, 2000, Gedalof & Berg, 2010; Andreu-Hayles *et al.*, 2011;  
46 Girardin *et al.*, 2011; Nock *et al.*, 2011; Lévesque *et al.*, 2014) growth responses to higher  $c_a$ .  
47 A possible explanation for these contrasting findings can be that the influence of  $c_a$  on tree  
48 growth depends either on local site conditions or on tree ontogeny.

49 Local conditions modulate the effect of recent rising temperature on growth since  
50 post-industrial temperature trends vary in space (Hättenschwiler *et al.*, 1997; Rolland *et al.*,

51 1998, Hember *et al.*, 2012). Such spatial variability of long-term climate warming may be a  
52 more important driver of tree growth than changing  $c_a$  in cold mountain forests (Salzer *et al.*,  
53 2009). Direct warming effects on growth could thus confound indirect effects due to rising  $c_a$   
54 *per se* since growth is more sensitive to temperature than photosynthesis across the expected  
55 range of temperatures in montane environments (Körner, 2003). Several authors speculate that  
56 such fertilization effect of rising  $c_a$  on growth would happen in dry sites where iWUE should  
57 be mainly improved (Huang *et al.*, 2007), whereas others regard mesic sites with high N  
58 deposition rates as being the most sensitive sites to any  $c_a$ -enhanced growth (Knapp *et al.*,  
59 2001; McMahon *et al.*, 2010; Silva & Anand, 2013).

60         The consideration of ontogeny is also critical to detect any fertilization effect on  
61 growth since trees are organisms continuously adjusting to changing environmental  
62 conditions ( $c_a$  and climate) through aging and changing size (Luysaert *et al.*, 2008; Phillips *et*  
63 *al.*, 2008; Voelker, 2011). Under experimental conditions, trees subjected to warming allocate  
64 more carbon to primary than to secondary growth being taller and skinnier than control trees  
65 (Way & Oren, 2010). Such allocation rules can shift through ontogeny because young trees  
66 tend to display growth stimulation under controlled CO<sub>2</sub> concentrations while mature trees do  
67 not (Körner *et al.*, 2005; Norby *et al.*, 1999, 2010; Battipaglia *et al.*, 2013). Consequently, it is  
68 essential to consider the individual responses of trees to changing  $c_a$  across wide climatic and  
69 biogeographical gradients and encompassing long temporal frameworks (Johnson & Abrams,  
70 2009; Carrer *et al.*, 2010). Dendrochronology may allow tackling these questions, once its  
71 shortcomings are adequately treated. First, the ability to detect potential influences of rising  $c_a$   
72 on tree growth may be limited by the use of detrending techniques that remove long-term  
73 growth trends (Briffa & Melvin, 2011; Bowman *et al.*, 2013). Second, a biased sampling of  
74 big or fast-growing (small or slow-growing) trees could produce spurious rising (declining)  
75 growth rates (Cherubini *et al.*, 1998; Brien *et al.*, 2012). Therefore, it is important to sample

76 coexisting trees of diverse sizes, growth rates and ages. Finally, rising  $c_a$  and temperatures  
77 may also exert nonlinear influences on growth (Lloyd *et al.*, 2013) by stimulating them up to  
78 certain site- or age-dependent thresholds (Fig. 1).

79 Here we evaluate these ideas by quantifying the long-term growth responses of *Pinus*  
80 *uncinata* trees to rising  $c_a$  and air temperature. These trees were sampled in 28 forests  
81 subjected to different climatic conditions across the entire distribution area of the species in  
82 Spain. Specifically, we test two hypotheses: (i) pre-industrial trees (age > 150 years) present  
83 lower juvenile growth rates than post-industrial trees (age ≤ 150 years) established later and  
84 subjected to higher  $c_a$ , and (ii) tree growth will be enhanced in the driest sites where iWUE is  
85 improved and growth is not so constrained by low temperatures. Thus, we expect growth  
86 stimulation by rising  $c_a$  being more noticeable either in young trees (cf. Voelker *et al.*, 2006)  
87 or in relatively dry and mild sites (cf. Huang *et al.*, 2007).

88

## 89 **Material and methods**

### 90 *Study site and species*

91 *Pinus uncinata* Ram. is a long-lived and shade intolerant conifer occurring in subalpine  
92 forests from the Alps, the Vosges, the Pyrenees and the Iberian System. Across the study area  
93 in NE Spain, *P. uncinata* is subjected to a wide range of topographical and soil conditions and  
94 the southernmost limit of its distribution is located in this area (Ceballos & Ruiz de la Torre,  
95 1979). In this species wood formation mainly occurs from May to October (Camarero *et al.*,  
96 1998). We used data of 544 *P. uncinata* trees with complete topographic and size data (see  
97 below) selected among 642 living trees sampled from 1994 to 2010 (see details in Galván *et*  
98 *al.*, 2012, 2014). These trees were sampled in 28 forests located throughout the entire  
99 geographic range of the species in northern Spain (Supporting Information, Table S1; for a  
100 complete description of the studied regions see Galván *et al.*, 2012, 2014). Most sampled sites

101 (25 out of 28) were located in the Pyrenees where the species is dominant and forms the  
102 alpine treeline ecotone, while 2 sites were sampled in the Iberian System and another one in  
103 the Pre-Pyrenees. The climate of the sampled populations is continental but varied from sub-  
104 Mediterranean (relatively dry summers) to temperate conditions (wet-cool summer)  
105 (Supporting Information, Fig. S1). The macroclimate of the study area is strongly influenced  
106 by east–west and north–south gradients with increasing warmer conditions eastwards and  
107 southwards, whereas dry and continental conditions prevail in the Central Pyrenees (Galván *et*  
108 *al.*, 2012). In the Central Pyrenees mean annual temperatures range between 3.0 and 3.5 °C,  
109 whereas total precipitation vary between 1150 and 1280 mm (Supporting Information, Figure  
110 S1). Across the Spanish Pyrenees total precipitation amounts increase westwards (about 1500-  
111 2500 mm), whereas the driest sites are located southwards either in the Pre-Pyrenees or in the  
112 Iberian System (1100-1200 mm). During the past century, the whole study area has  
113 experienced a significant warming trend (on average +0.015 °C yr<sup>-1</sup>; see Galván *et al.*, 2014)  
114 but no evident changes in the amount of precipitation have been observed (Supporting  
115 Information, Fig. S2).

116

### 117 *Tree dataset*

118 We reconstructed growth trends for 544 living *P. uncinata* individuals. In each sampled site  
119 10 to 65 dominant trees representative of the population size and age distributions were  
120 sampled. Trees that were at least 10 m apart from each other were randomly selected.  
121 Topographic (elevation, slope, and aspect) and biometric (dbh, diameter at breast height  
122 measured at 1.3 m, and tree height) variables were recorded for each tree. From each sampled  
123 tree, two or three cores were taken at 1.3 m height using increment borers. The diameter,  
124 excluding bark, was converted to basal area assuming a circular shape of the stem. Cores were  
125 visually cross-dated and measured to a precision of 0.01 mm using a LINTAB measuring

126 device (Rinntech, Heidelberg, Germany). We evaluated the cross-dating and measurement  
127 accuracy with the program COFECHA, which calculates cross correlations between  
128 individual series of each core and a master chronology, obtained by averaging all measured  
129 series in each site except the one being checked (Holmes, 1983).

130         In the cases of cores without pith, the distance to the pith was estimated by fitting a  
131 template of concentric circles with known radii to the curve of the innermost rings (Norton *et*  
132 *al.*, 1987). This allowed the estimation of the missing radius length to transform it into the  
133 number of missing rings. In those trees in which the central core section could not be  
134 estimated because the innermost rings did not curve, we used the dbh of each tree to estimate  
135 the tree radius without bark. The conversion of the radius length into missing rings was  
136 carried out using a subset of cores with pith ( $n = 41$ ), and considering the innermost 40 rings,  
137 by using a regression calculating the mean number of rings ( $y$ ) for the estimated distance to  
138 the pith ( $x$ ):  $y = 0.0109 x$  ( $R^2 = 0.99$ ,  $P < 0.001$ ). After calculating the missing rings to the  
139 pith, we estimate the cambial age (at 1.3 m) adding the number of calculated rings to the total  
140 number of measured rings. We estimated tree age at 1.3 m following three criteria depending  
141 on the method used and the suitability of each core in assessing the tree age: (a) when the  
142 innermost part of the core lacks a tree-ring curvature and hence the pith locator method cannot  
143 be used, we estimated age as a function of the dbh; (b) when both methods (dbh-age  
144 regression and pith locator) have been applied to different cores of the same tree we  
145 considered the age estimated by using the pith locator method; and (c) when the pith locator  
146 method was used, we chose the age assessed from the core with a smaller estimated distance  
147 to the pith. At the same time, we followed three criteria to establish a scale of uncertainty in  
148 age estimation: (i) low uncertainty, when the core includes the pith or when the core has an  
149 estimated distance to the theoretical pith smaller than 1.5 cm; (ii) medium uncertainty, when  
150 cores with estimated distance to the pith was longer than 1.5 cm, and (iii) high uncertainty,

151 when the innermost tree rings of the core did not curve and tree age was estimated as a  
152 function of dbh. On average, *P. uncinata* trees take 20 years to reach a height of 1.3 m  
153 (Camarero, 1999). Therefore we added 20 years to the estimated age at 1.3 m to estimate the  
154 age in the base of the trunk.

155

#### 156 *Climate and atmospheric CO<sub>2</sub> data*

157 We used homogeneous and interpolated monthly climate data corresponding to the CRU TS  
158 3.1 database produced by the Climate Research Unit for the period 1901-2009 at a 0.5° spatial  
159 resolution (Harris *et al.*, 2014). We selected 0.5° grids including the study sites and the  
160 monthly climatic variables which most growth variability of *P. uncinata* explain, namely  
161 previous mean maximum November temperature (hereafter abbreviated as *pTMx11*), current  
162 mean minimum May temperature (hereafter abbreviated as *TMi5*) and June precipitation  
163 (hereafter abbreviated as *P6*) (see Tardif *et al.* 2003; Galván *et al.*, 2014). Annual *c<sub>a</sub>* values  
164 were computed from monthly values taken from the Mauna Loa (Hawaii) observatory from  
165 1958 onwards (see <http://www.esrl.noaa.gov/gmd/ccgg/trends/>).

166

#### 167 *Growth models*

168 The use of measurements such as basal area increment (BAI) partially avoids the problem of  
169 removing long-term growth trends since BAI captures the sigmoid trajectory of tree growth  
170 (Biondi & Qaedan, 2008). The dynamics of BAI usually display a young phase of exponential  
171 growth and a stable phase when trees age and reach height and BAI plateaus (Fritts, 2001). To  
172 model tree growth accurately, individual tree-ring width series were converted into BAI,  
173 which allows removing the geometrical constraint of adding a volume of wood to a stem of  
174 increasing radius (Biondi & Qaedan, 2008) as:

$$175 \quad \text{BAI} = \pi (r_t^2 - r_{t-1}^2) \quad (1)$$



176 where  $r_t^2$  and  $r_{t-1}^2$  are the squared stem radial increments corresponding to rings formed in  
177 years  $t$  and  $t-1$ , respectively.

178 Since we expect that BAI trends and response to  $c_a$  are age dependent, trees were  
179 classified in four groups according to their age: young trees (individuals with age  $\leq 150$   
180 years), mature trees (151–300 years old trees), old mature trees (301–450 years old trees) and  
181 old trees (individuals with age  $\geq 451$  years). Age classes were defined to represent different  
182 life stages and environmentally contrasting periods (e.g., pre- vs. post-industrial periods) but  
183 keeping a robust enough sample size for each class. Given that BAI trajectories vary strongly  
184 among individuals and within populations flexible statistical methods can be used to represent  
185 growth such as Generalized Additive Mixed Models (GAMM; Wood, 2006). This approach  
186 allows describing how BAI varies with the additive increase of cambial age or calendar year.  
187 BAI depends on site conditions as well as on the particular growth conditions to which each  
188 individual tree is subjected along its ontogeny (e.g., Pokharel & Froese, 2009). In order to  
189 avoid underrepresentation of some age- (4 classes) and site (28 levels) replications, sites were  
190 grouped into regions with similar growth characteristics based on a previous study by Galván  
191 *et al.* (2012). They considered five regions showing coherent geographical, topographical and  
192 growth conditions (similar growth trends and responses to climate) shared by trees inhabiting  
193 each region (see Table 1).

194 The GAMM we fitted was of the form:

$$195 \quad \text{BAI}_i = s(\text{dbh}_i) + s(\text{tree age}_i) + s(\text{cambial age}) + Z_i B_i + \nu_i \quad (2)$$

196 where the BAI of a tree  $i$  is modelled as smooth functions ( $s$ ) of three predictors (dbh,  
197 tree age, cambial age of tree-ring formation) and tree identity ( $Z_i B_i$ ) considered a random  
198 effect since multiple measurements were performed for each individual tree along its life.

199 Since BAI of year  $t$  depends on the previous-year ( $t-1$ ) BAI we also included in the model an  
200 error term ( $\nu_i$ ) with an AR1 ( $p=1, q=0$ ) correlation structure. The smooth terms were

201 represented using thin plane regression splines (Wood, 2006). The degree of smoothness is  
 202 determined through an iterative fitting process (see Wood, 2003). Cambial age refers here to a  
 203 variable which represents tree ageing from its establishment (*age 0*) to the date in which the  
 204 annual ring was formed (*age n*), whereas tree age is a fixed value representing the age of the  
 205 tree. Therefore, cambial age varies within each tree along time, whereas tree age is a fixed  
 206 value which changes between trees. Since BAI has a skewed distribution, we first log (BAI  
 207 +1) - transformed this variable. To test if BAI depends on the particular time period in which  
 208 each individual tree was established separated models were performed for the trees grouped in  
 209 different age classes. In addition, BAI trends were characterized for each study region and age  
 210 class, and also since the 1950s when  $c_a$  started steeply rising.

211 To reveal whether recent trends in *P. uncinata* growth are only due to biological  
 212 features (e.g., tree ageing) or, alternatively, they are mainly influenced by climate and  $c_a$ , we  
 213 correlated age- and site-specific growth trends over the period 1958-1994 with selected  
 214 climatic variables (*pTMx11*, *TMi5*, *P6*) and annual values of  $c_a$ . Since we expect age-  
 215 dependent growth responses to climate, separate analyses were performed for each age class.  
 216 In addition, we also considered site-mediated growth responses to  $c_a$ . For each age class, the  
 217 following model was proposed to study the influence of year-to-year variability in climate  
 218 variables on BAI after removing mid-term fluctuations not related to climate:

$$219 \quad \text{BAI}_{res} = pTMx11s + TMi5 + P6 + c_a + Z_i B_i + \varepsilon_i \quad (3)$$

220 where  $\text{BAI}_{res}$  represent BAI residuals after extracting biological trends (i.e. after  
 221 removing the influence of dbh and tree age), and *pTMx11*, *TMi5* and *P6* are climatic  
 222 variables.

223 Separate analyses were carried out for each site by following a multi-model inference  
 224 approach based on information theory (Burnham & Anderson, 2002). This approach  
 225 calculates the probability that a given model is more appropriate than other competing models

226 in explaining the response variable. Multi-model inference is recommended for analysing  
227 large-scale datasets across broad geographical ranges (Zuur *et al.*, 2009). We ranked all the  
228 potential models that could be generated with the different explanatory variables according to  
229 the second-order Akaike information criterion (AICc). For each model, we considered its  
230  $\Delta\text{AICc}$  (i.e. the difference between AICc of each model and the minimum AICc found for all  
231 models). After selecting the set of best candidate models (those having a  $\Delta\text{AIC} < 2$ ) we  
232 selected the coefficients for the model with the lowest  $\Delta\text{AIC}$ . We evaluated the fit of the  
233 model by graphical examination of the residual and fitted values (Zuur *et al.*, 2009). All  
234 statistical analyses were performed using the R statistical software (R Development Core  
235 Team, 2014). The *mgcv* package was used to calculate the GAMMs (Wood, 2006) and the  
236 *MuMIn* package to perform multi model selection (Barton, 2013).

237

## 238 **Results**

239 The most abundant age classes were formed by trees with 251 up to 300 years old (Fig. 2).  
240 During the first years of the tree life BAI values showed a marked increase with cambial age,  
241 being larger for young trees, followed by mature, old mature and old trees (Fig. 3a; see also  
242 Supporting Information, Table S2). In general, BAI decreased as trees aged, but the slope of  
243 the decrease was lower for the old mature and old trees. For instance, at the age of 40 and 80  
244 years, trees in the youngest age class (< 150 years) display significantly larger values of BAI  
245 than trees in the rest of age classes (Fig. 3a).

246 We observed both accelerating and decelerating BAI trends in the first and second  
247 halves of the past century, respectively, which mainly corresponded to improved growth of  
248 young trees in response to the warm 1940s and 1950s (Fig. 3b). Such growth enhancement  
249 seems to be exceptional when compared with other age classes in the context of the past seven

250 centuries. A slight growth deceleration was observed in all age classes during the second half  
251 of the 20<sup>th</sup> century but it was more noticeable in young trees.

252 The models proposed to study the long-term BAI dynamics showed different patterns  
253 depending on the age class, site and time periods considered (Figs. 4 and 5). For example,  
254 BAI of young trees is best represented by an exponential function that reaches an asymptote  
255 and decreases at age varying from 80 (e.g., Central Pyrenees) to 60 years (e.g., Iberian System  
256 and Pre-Pyrenees). Trees in the remaining three classes also show a constant exponential BAI  
257 trend that reaches an asymptote, although in several cases (e.g., Central Western Pyrenees) the  
258 trend was represented by a straight line. An important part of the BAI variance was accounted  
259 for by tree size (dbh) and age (Supporting Information, Table S2). However, the relevance of  
260 tree size on determining growth decreased with tree age.

261 Significant BAI increases were only observed since 1950 in old-mature and mature  
262 trees from the Western and Central-Western Pyrenees, and also in old-mature trees from the  
263 Iberian System and Pre-Pyrenees (Fig. 5). Negative or low BAI trends were common among  
264 the oldest trees and also in all age classes of the Central and Eastern Pyrenees. We found a  
265 positive influence of temperature on BAI in the different analysed age classes, particularly in  
266 the Central and Eastern Pyrenees (Table 2). Precipitation also enhanced BAI of young and  
267 mature trees from the driest sites in the Iberian System and Pre-Pyrenees region.  
268 Contrastingly, we only found a significant and positive influence of rising  $c_a$  on BAI in old  
269 mature trees from the wet Western Pyrenees (Table 2), where the highest BAI enhancement  
270 since 1950 was also observed (Fig. 5).

271

## 272 **Discussion**

273 We found that tree growth responds more to other factors (ontogeny, temperature, water  
274 availability) than to rising  $c_a$ . We detected little evidence of widespread growth enhancement

275 in subalpine *Pinus uncinata* forests in response to increasing  $c_a$  and a related fertilization  
276 effect. The much higher growth rates of post-industrial young trees than pre-industrial old  
277 trees for the same age confirm our first hypothesis, namely that pre-industrial trees present  
278 lower juvenile growth rates than post-industrial trees subjected to higher  $c_a$ . This must be  
279 interpreted with caution since higher post-industrial growth rates could be also the result of  
280 age-related selection against fast growing individuals irrespective of  $c_a$  trends (Voelker,  
281 2011). The resurgence in radial growth was observed in old mature trees from the wettest  
282 study region (Western Pyrenees) and not in young trees from the driest areas (Iberian System  
283 and Pre-Pyrenees), where iWUE should be the most benefitted because of rising  $c_a$ , thus  
284 contradicting our second hypothesis. Thus, the rapid growth increase of young or post-  
285 industrial trees, mostly established in the 19<sup>th</sup> and 20<sup>th</sup> centuries, seems to be a response to  
286 rising air temperatures across the study area. These findings have several implications for  
287 studies of forest growth as related to global-change drivers such as climatic warming and  
288 increasing  $c_a$ .

289         Firstly, long-term growth stimulation in response to rising  $c_a$  is unlikely in the field  
290 because tree growth is more constrained by low temperatures or by low water availability than  
291 by accessible carbon (Körner *et al.*, 2005; Körner, 2013). Along these lines, reviews of free-  
292 air CO<sub>2</sub> enrichment experiments also reveal that the initial CO<sub>2</sub> stimulation of tree growth  
293 under optimal nutrient conditions disappears after one or two decades suggesting ontogenetic  
294 limitations (Kimball *et al.*, 2007; Norby & Zak, 2011). Secondly, trees showing higher iWUE  
295 values or increments do not necessarily have to present growth enhancement resulting from  
296 rising  $c_a$  as has been evidenced at local (Silva *et al.*, 2010; Nock *et al.*, 2011; Linares &  
297 Camarero, 2012; Gómez-Guerrero *et al.*, 2013; Lévesque *et al.*, 2014) and global scales  
298 (Peñuelas *et al.*, 2011; Silva & Anand, 2013). In the eastern Pyrenees the iWUE reconstructed  
299 from carbon isotopic ratios of *P. uncinata* wood doubled during the 20th century whereas

300 radial growth declined at a mean rate of  $0.002 \text{ mm yr}^{-1}$  (Andreu-Hayles *et al.*, 2011). These  
301 authors interpreted such iWUE rise as a response to significant increases in leaf intercellular  
302  $\text{CO}_2$  concentration ( $c_i$ ), but it did not suffice to enhance tree growth. Overall, our results do  
303 not support any  $c_a$ -enrichment effect even if we studied trees growing at high elevations  
304 where low partial pressures of  $\text{CO}_2$  could make it more limiting than at lower elevations  
305 (Körner *et al.*, 1991). Our findings suggest long-term anatomical and physiological  
306 adaptations for adjusting  $c_i$  to increasing  $c_a$  such as changing stomatal density or  
307 photosynthetic rates (Ward *et al.*, 2005). Such adjustments could explain why rising  $c_a$  might  
308 modify climate sensitivity of trees, but not overall growth rates (Gerhart *et al.*, 2012).

309         The interactions between temperature and water availability can determine the tree  
310 growth responses to rising  $c_a$  (Norby *et al.*, 2010). Rising  $c_a$  should enhance growth as long as  
311 water is not limiting; but we found negative correlations between  $c_a$  and basal area increment  
312 among all assessed age classes, particularly in old trees. Our findings agree with observations  
313 in boreal black spruce (*Picea mariana*) forests where old trees also responded negatively to  
314 rising  $c_a$  (Girardin *et al.*, 2014). Elevated  $\text{CO}_2$  conditions increased the maximal  
315 photosynthetic rate and iWUE of *Pinus mugo* at the alpine treeline where soil water  
316 availability was high (Streit *et al.*, 2014). Consequently, the amount of carbon available to  
317 sinks (growth, storage, root exudation, metabolic respiration) increased under those  
318 conditions but again this did not translate into enhanced basal area growth (Handa *et al.*,  
319 2006; Dawes *et al.*, 2011, 2013). In fact warming could also induce drought stress and  
320 override any potential effect of rising  $c_a$  and improved iWUE on carbon supply and growth if  
321 water supply is not adequate to sustain sink demand (Lévesque *et al.*, 2014). This could  
322 explain the growth enhancement observed in the Western Pyrenean *P. uncinata* forests, where  
323 climate conditions are wet. In addition, in that area warming was more pronounced in those  
324 months most strongly related to growth (Supporting Information, Fig. S2).

325           The postulated CO<sub>2</sub> fertilization was observed in old mature trees but this effect could  
326 be mediated by other features than tree ontogeny *per se* such as tree height, leaf or sapwood  
327 area. In old trees the efficiency of water transport is maintained because xylem elements grow  
328 progressively larger with tree age and only in very tall trees the hydrostatic gradient induces  
329 limits on xylem functionality towards the top of the tree (Ryan & Yoder, 1997). Since *P.*  
330 *uncinata* is a shade-intolerant species, tree height and competition for light play minor roles as  
331 drivers of growth in these open forests (Supporting Information, Fig. S3). Accordingly, tree  
332 size was not a significant factor controlling growth in older age classes confirming that once  
333 those old trees reach a senescent phase their BAI rates do not depend on tree size. Regarding  
334 ontogenic processes, young or small trees could also preferentially assimilate respired CO<sub>2</sub>  
335 when growing in closed canopies altering the isotopic composition of their wood and biasing  
336 inferred iWUE trends (Bert *et al.*, 1997), but this effect seems to be unlikely since most of the  
337 study sites are open stands. Thus, other size-related constraints related to leaf and sapwood  
338 production could explain recent BAI trends (Galván *et al.*, 2012). Nevertheless, future growth  
339 and iWUE assessments should consider the whole range of tree sizes and ages (Nehrbass-  
340 Ahles *et al.*, 2014).

341           Regarding the roles played by  $c_a$ , temperature and water availability as drivers of long-  
342 term growth trends, a survey of studies reporting positive growth responses to rising CO<sub>2</sub>  
343 suggests either a potential fertilization effect in fast-growing hardwood species growing in  
344 moist sites such as *Populus* trees (Cole *et al.*, 2010; Battipaglia *et al.*, 2013) or improved  
345 growth due to improved iWUE, particularly in dry sites (Soulé & Knapp, 2006). In the first  
346 case the presumed stimulation of growth has been poorly discussed and could represent initial  
347 stimulatory (ontogenetic) effects of growth in rapidly-growing sprouting *Populus* species. In  
348 the second case, recent results dismiss the generality of this pattern since declining growth  
349 trends have been described in the same conifer species coexisting either in xeric or in mesic

350 sites (Lévesque *et al.*, 2014). Despite a reduction in stomatal conductance in response to higher  
351  $c_a$  has been observed in broadleaf species drought-induced stomatal closure diminishes  
352 growth in the long term (Lévesque *et al.*, 2014). Still, in these discussed cases the effects of  
353 low temperatures on growth are minor compared with those described in this and other cold-  
354 limited forests (Salzer *et al.*, 2009; Silva & Anand, 2013). Our findings also imply  
355 considering warming-related drought stress as a major driver of growth in old trees from  
356 mountain forests (Bellassen *et al.*, 2011). In the Pyrenees a warming trend has characterized  
357 the past 700 years (Bünten *et al.*, 2008). Due to the rise in air temperature, young trees  
358 experience longer seasons nowadays than older trees did when they were in their juvenile  
359 phase, resulting in large growth rates nowadays (Way & Oren, 2010). Finally, we only  
360 considered one tree species so future studies should investigate several coexisting tree species.  
361 Those species could grow differently in response to rising  $c_a$  as a function of different  
362 photosynthetic and phenological adjustments affecting carbon uptake and wood production.

363         To conclude, we show that forest growth responses to rising  $c_a$  and climate warming  
364 depend on site conditions and tree ontogeny and are nonlinear. Our results illustrate how  
365 growth of post-industrial *P. uncinata* trees has improved during the past 150 years. Such  
366 growth improvement was linked to climate warming, while a positive response of tree growth  
367 to rising  $c_a$  was only detected in relatively old trees from wet sites. We argue that growth,  
368 stemwood production and productivity will increase as  $c_a$  rises in those wet sites, whereas  
369 climate warming can directly enhance growth in other sites or even lead to growth decline if  
370 rising temperatures amplify water shortage in the most xeric sites. Our findings emphasize the  
371 need of using broader perspectives in temporal (ontogeny), biogeographic (site conditions)  
372 and also functional (e.g., comparing conifers and broadleaf species) terms to comprehensively  
373 evaluate long-term  $c_a$  effects on forest growth.

374



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## Tables

**Table 1.** Number of trees per age class studied in each region and site. See additional site information in Supporting Information, Table S1.

Region (code)	Site	No. trees				
		Total	Age classes (age)			
			Young trees ( $\leq 150$ years)	Mature trees (151–300 years)	Old mature trees (301– 450 years)	Old trees ( $\geq 451$ years)
Western Pyrenees (WP)	Contienda-Larra	20	0	5	13	2
	Atxerito	12	0	5	2	5
Central-Western Pyrenees (CWP)	Respomuso	14	1	8	4	1
	Pic d'Arnousse	6	1	3	2	0
Central Pyrenees (CP)	Mirador del Rey	17	1	16	0	0
	Las Cutas	10	10	0	0	0
	Bielsa	10	1	7	1	1
	Senda de Cazadores	32	2	14	9	7
	Sobrestivo	38	1	9	19	9
Eastern Pyrenees (EP)	Airoto	14	0	9	3	2
	Amitges	24	0	7	13	4
	Conangles	20	1	7	10	2
	Corticelles	23	0	2	7	14
	Estanys de la Pera	19	0	10	5	4
	Estany Gerber	28	1	6	11	10
	Barranc de Llacs	31	1	12	6	12
	Lladres	7	0	2	3	2
	Mata de València	8	0	6	2	0
	Mirador	31	1	7	14	9
	Monestero	25	0	9	12	4
	Estany Negre	40	0	14	10	16
	Ratera	2	1	1	0	0
	Sant Maurici	20	0	20	0	0
	Tessó del Son	9	0	5	1	3
Mulleres	10	0	3	2	5	
Iberian System and Pre-Pyrenees (IS-PP)	Vinuesa	22	1	7	7	7
	Teruel	30	14	8	7	1
	Guara	13	4	9	0	0

**Table 2.** Influence of climatic variables and atmospheric CO<sub>2</sub> concentrations on basal area increment from different regions and considering five age classes (period 1958-1994). For each region, the influence of the annual increment in CO<sub>2</sub> is shown by the *t* statistic and its associated probability (*P*). Coefficients were only considered for regions with more than 5 trees per age class. Abbreviations of climatic variables: *pTMx11*, previous mean maximum November temperature; *TMi5*, current mean minimum May temperature; *P6*, current June precipitation. Significant levels: \**P* ≤ 0.05; \*\* *P* ≤ 0.01. Grey cells show significant positive effects of CO<sub>2</sub> on basal area increment.

Age class (age)	Region	<i>pTMx11</i>	<i>TMi5</i>	<i>P6</i>	CO <sub>2</sub>	No. models	Relative weight
Young trees (≤ 150 years)	Western Pyrenees	–	–	–	–	–	–
	Central-Western Pyrenees	–	–	–	–	–	–
	Central Pyrenees	0.056**	0.019**	–0.018**	–	1	1
	Eastern Pyrenees	–	–	–	–	–	–
	Iberian System and Pre-Pyrenees	0.057**	–	0.037**	–0.006*	1	1
Mature trees (151–300 years)	Western Pyrenees	0.036**	–0.006	0.013*	0.006	6	0.98
	Central-Western Pyrenees	0.031**	0.042**	–0.014	0.003	3	0.99
	Central Pyrenees	0.058**	0.015*	0.012*	–0.008**	1	1
	Eastern Pyrenees	0.056**	0.044**	0.018*	–0.005**	1	1
	Iberian System and Pre-Pyrenees	0.044**	0.022*	0.020**	–0.007**	1	1
Old mature trees (301–450 years)	Western Pyrenees	0.009	0.018*	0.009	0.013**	6	0.99
	Central-Western Pyrenees	0.021*	0.027*	–0.005	–	6	0.99
	Central Pyrenees	0.049**	0.029**	–0.007	–0.008**	2	0.99
	Eastern Pyrenees	0.044**	0.043**	0.012*	–0.003**	1	1
	Iberian System and Pre-Pyrenees	0.030**	0.036**	0.003	0.003	3	0.99
Old trees (≥ 451 years)	Western Pyrenees	0.011	0.018	0.011*	–	5	1
	Central-Western Pyrenees	–	–	–	–	–	–
	Central Pyrenees	0.041**	0.007	–0.018*	–0.012*	2	0.99
	Eastern Pyrenees	0.034**	0.042**	–0.002	–0.002*	2	0.99
	Iberian System and Pre-Pyrenees	0.037**	0.034**	–0.007	–	2	0.99

## Figure legends

**Figure 1.** Expected responses of photosynthetic rates (a) and growth or basal area increment (b, c, d) to rising atmospheric CO<sub>2</sub> concentrations ( $c_a$ ) and temperatures as a function of either tree ontogeny (cambial age) or time. (c) Postulated ontogenetic trajectories of growth as a function of temperature for three levels of tree performance (low –clear grey–, mid –dark grey– and high performance –black line). Symbols indicate the trajectories of warming-induced growth increase for different performance levels. (d) We expect a departure of the observed basal area increment (BAI) (red continuous lines, circles) as compared with ontogenetically expected BAI (dashed blue line, triangles) in response to rising  $c_a$  (grey area). Panels a, b and c are adapted and modified from Sage & Kubien (2007), Phillips *et al.* (2008), and Way & Oren (2010).

**Figure 2.** Age structure of *Pinus uncinata* trees sampled in the Iberian Peninsula. The age classification was based on 25-year age classes considering three levels of uncertainty in age estimation (see *Material and Methods*).

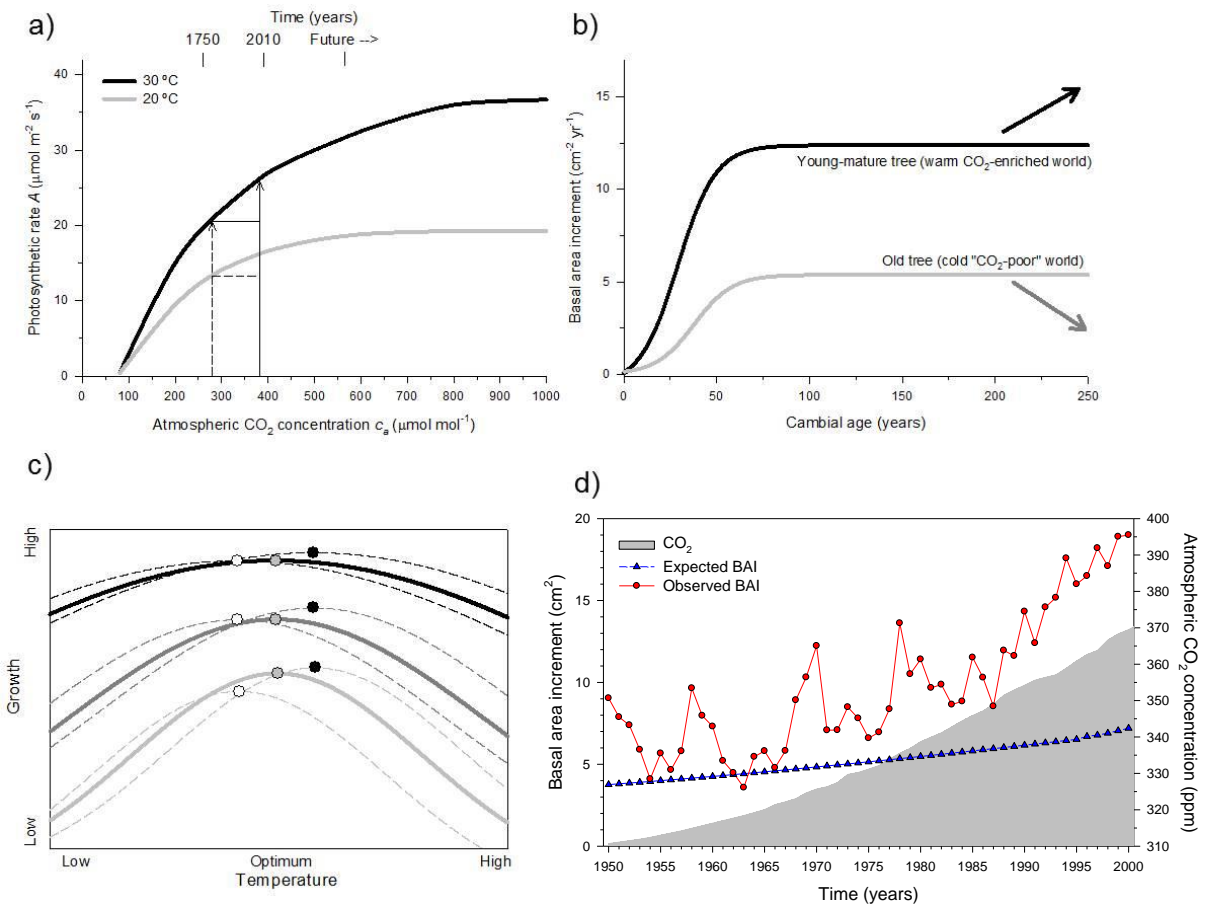
**Figure 3.** Basal area increment (mean  $\pm$  SE) as a function of cambial age (a) and calendar year (b) for the trees in the four age classes considered. The upper and lower insets show basal area increment trends from 20 up to 100 years and for the 20<sup>th</sup> century, respectively. Different colours of lines indicate different age classes: red lines, young trees (individuals with age  $\leq$  150 years); green lines, mature trees (151–300 years old trees); blue lines, old mature trees (301–450 years old trees); and black lines, old trees (individuals with age  $\geq$  451 years).

**Figure 4.** Long-term trends in basal area increment (BAI, y axes) displayed as a function of cambial age (x axes) for trees grouped in four age classes (rows) and five study regions (columns; see regions' abbreviations in Table 1). The lines show the fitted GAMMs used to model age-dependent trends in BAI while dots show raw values (the darker the point fills the larger the tree diameter).

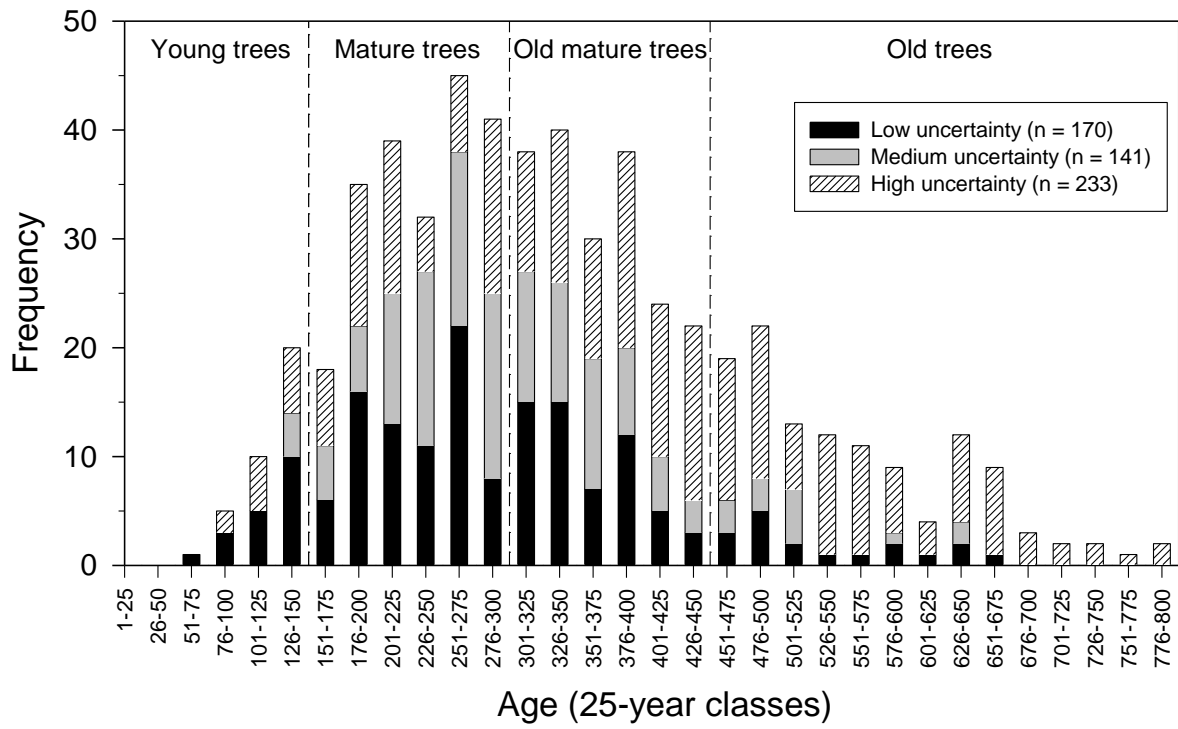
**Figure 5.** Recent trends in basal area increment (BAI, y axis) of *Pinus uncinata* as a function of year grouped in four age classes (rows) and considering the five study regions (columns; see Table 1). The continuous and dotted lines indicate the observed and fitted BAI trends, while the vertical line shows the first year with data of atmospheric CO<sub>2</sub> concentration used in BAI models. In each graph the correlations show the associations between mean BAI values (black lines) and year (significant trends are written in bold characters). Dots show raw BAI values (the darker the point fills the larger the tree diameter). Note that the fact that the observed BAI exceeds that modelled by GAMMs is an artefact since GAMMs were fitted to a longer period than the most recent 50 years presented in the figure.

# Figures

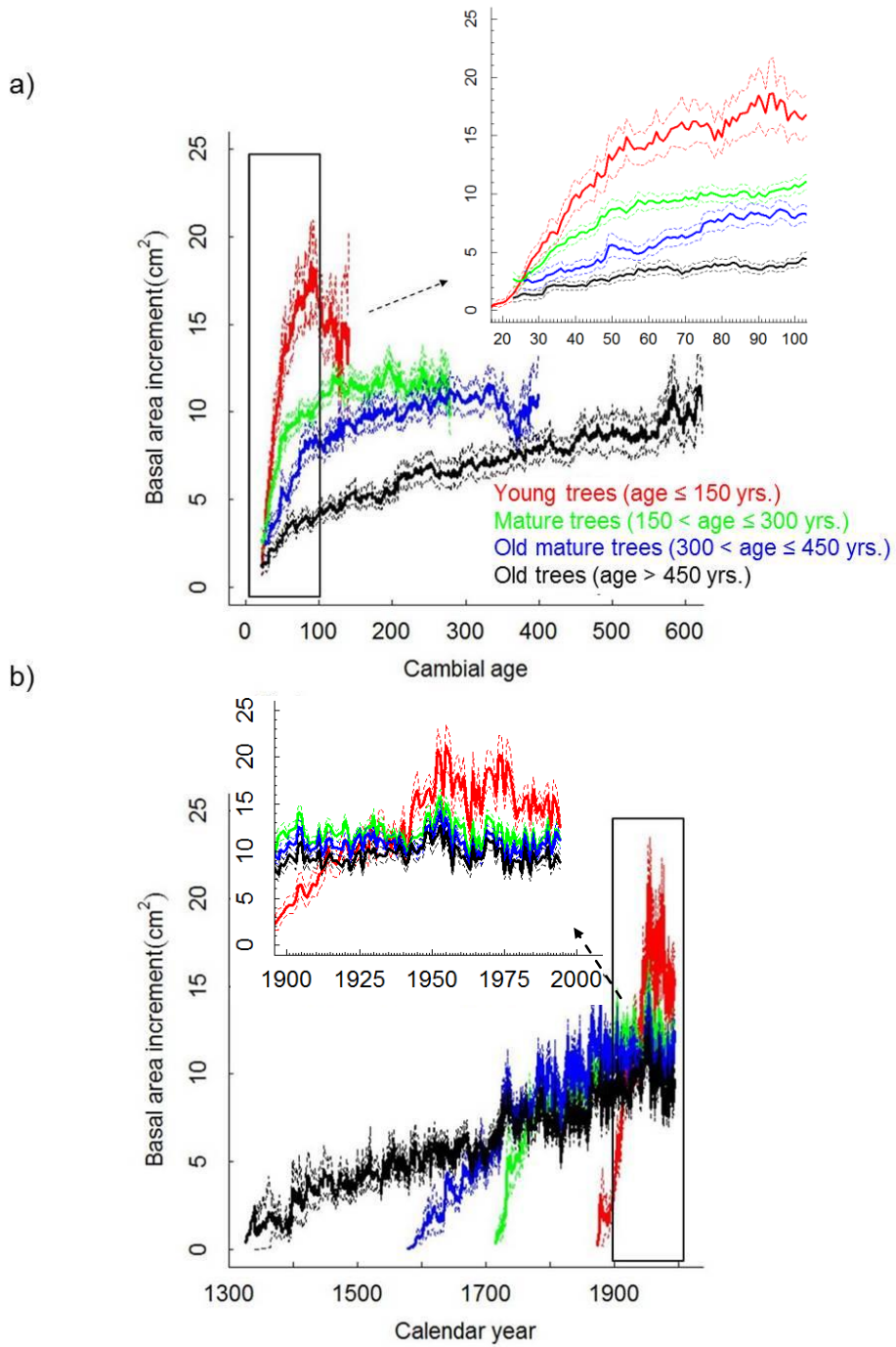
## Figure 1







**Figure 2**



**Figure 3**

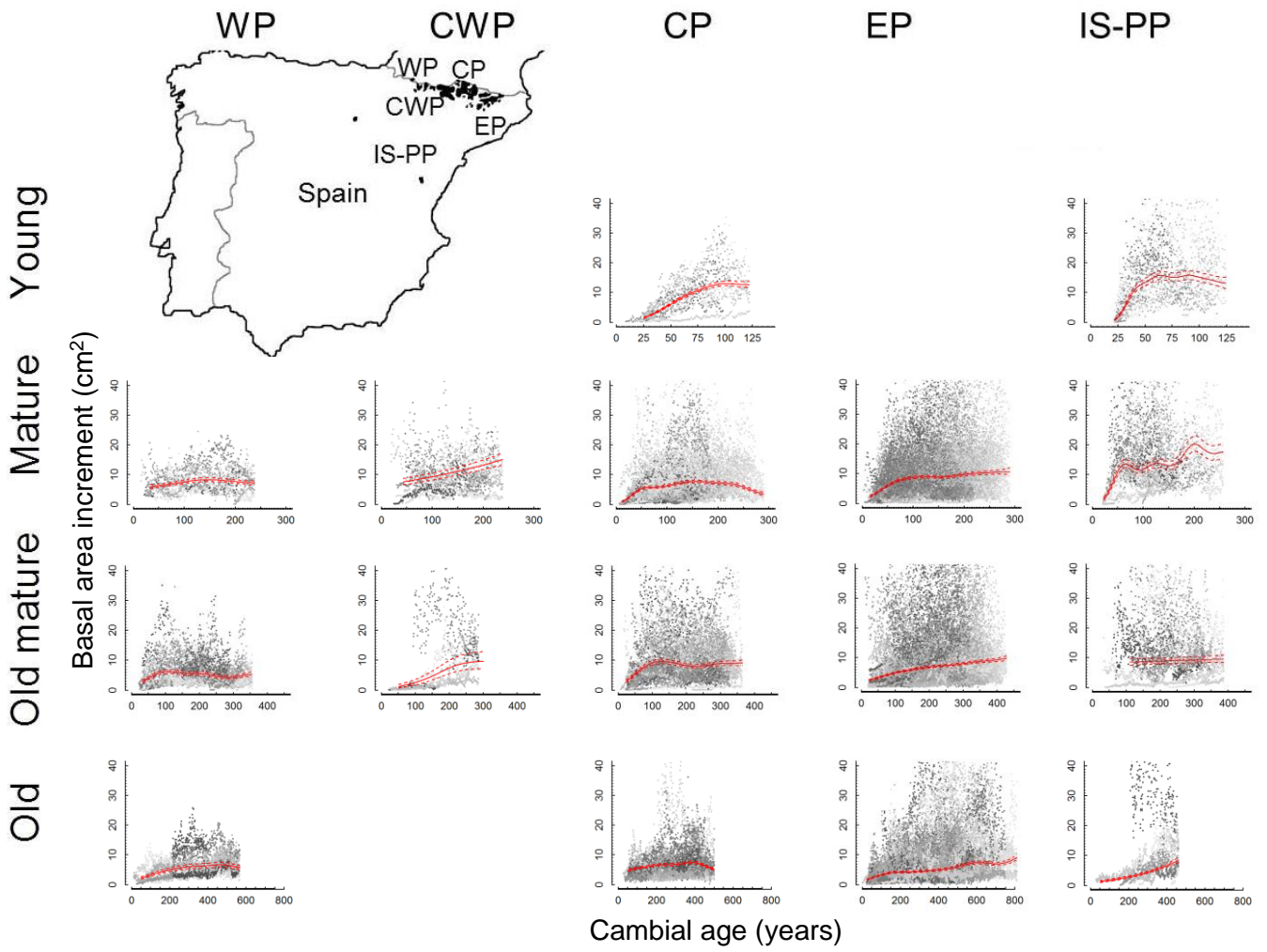


Figure 4

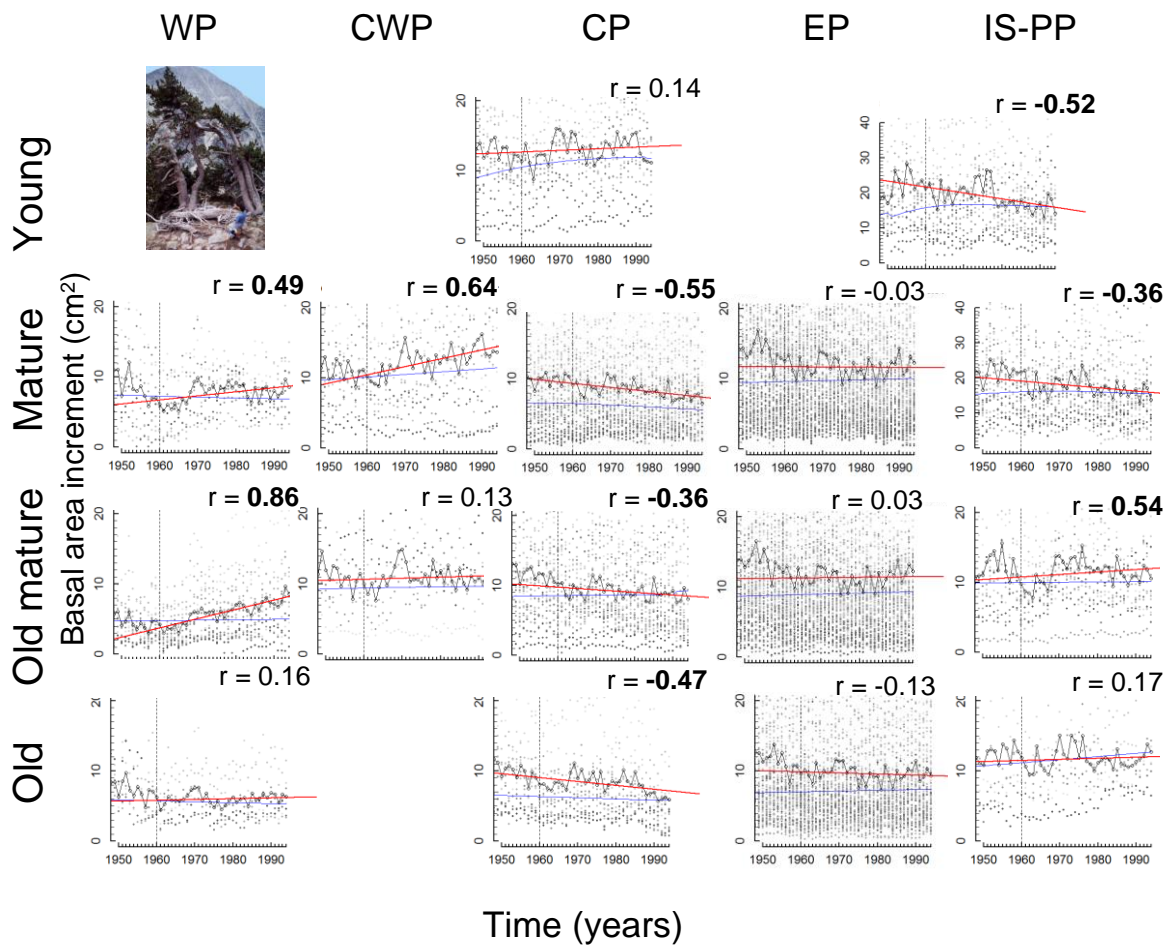


Figure 5