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**Full title:** Main biotic drivers of tree growth in a developing *Juniperus thurifera* stand in Central Spain

**Running title:** Tree growth patterns in reproductive and non-reproductive individuals of *Juniperus thurifera* in Central Spain

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## Abstract

Over the last few decades, abandonment of traditional management practices in Spain has led to widespread stand densification and has favoured the expansion of some forest species that previously exhibited more restricted ranges. Spanish juniper (*Juniperus thurifera* L.) woodlands are experiencing this phenomenon due to agricultural land abandonment and a decrease in the livestock pressure. Yet the main drivers underlying stand structure and dynamics at this novel scenario are poorly understood. In this study, we investigate the main biotic drivers of tree growth in a high-density stand of the dioecious *J. thurifera* at an early developmental stage (mean tree age of 32 years, 50 years after land abandonment). Tree growth was measured by coring 299 individuals of different reproductive classes (male, female and non-reproductive). Neighbourhood models were used to assess the relative importance of tree size and neighbourhood competition on tree growth of each reproductive class in the study plot. We found that tree size had the strongest effect on tree growth, whereas the effect of intraspecific competition was negligible. We observed differences in growth patterns among reproductive classes along trunk diameter sizes. Thus, at smaller sizes the three reproductive classes presented identical patterns of growth. However, at bigger sizes, females were the fastest growing individuals, followed by males and non-reproductive individuals. Overall, our results suggest that in young *J. thurifera* monospecific forests, where self-thinning processes may have not undergone yet, tree size and the reproductive class could play a relatively more important role than competition as drivers of tree growth. These findings constitute new information which contributes to understanding growth dynamics at early developmental stages in this dioecious species. Furthermore, our results provide guidelines for silvicultural managing; suggesting that at these young juniper stands thinning would likely not translate into enhanced growth on remnant trees.

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**Keywords:** dioecious, intraspecific competition, land use abandonment, Mediterranean forests, neighbourhood models, reproductive class, tree growth

43 **Introduction**

44 In Mediterranean countries human activities have shaped the structure and function of the  
45 forest ecosystem for ages (e.g. Thirgood 1981; Blondel and Aronson 1995; Urbieto et al.  
46 2008). Over the last few decades, abandonment of traditional management practices has led  
47 to a general stand densification and has favoured forest expansion (Matesanz et al. 2009;  
48 Olano et al. 2011; Vayreda et al. 2012). These relative novel conditions mostly appear  
49 confined either to unproductive marginal lands or to mountain areas, where abandonment of  
50 traditional agriculture and the decrease in livestock pressure have happened as a  
51 consequence of depopulation of rural areas (Thompson, 2005). Several studies have reported  
52 forest expansion and densification in different tree species (Poyatos et al. 2003; Gehrig-Fasel  
53 et al. 2007). For example, Améztegui et al. (2010) reported that *Pinus uncinata*, a mountain  
54 pine species, has increased its surface coverage in the Catalan Pyrenees (north-east Spain)  
55 by more than 16% in a period of 50 years.

56 Likewise, Spanish juniper (*Juniperus thurifera* L.) woodlands are experiencing a  
57 similar phenomenon (Blanco et al. 2005; Olano et al. 2011; Gimeno et al. 2012c). They are  
58 one of the dominant plant communities in the scarcely-populated mountain regions of the  
59 central Iberian Peninsula. In the past, juniper woodlands were largely shaped by livestock  
60 grazing and wood extraction pressures by the inhabitants of the area. As a consequence,  
61 recruitment, survival and growth rates of the species were arrested (De Soto et al. 2010,  
62 Olano et al. 2008). However, nowadays a process of densification is described due to the  
63 decline of these traditional activities. As a result of these novel conditions, these forests may  
64 undergo very different stand dynamics in relation to past forest dynamics.

65 Over the last decade several studies have focused on understanding the patterns of  
66 juniper growth in Spanish woodlands either as a consequence of land use changes (Olano et

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67 al. 2008b; DeSoto et al. 2010; Olano et al. 2011) or as a gender-specific response (e.g.  
68 Montesinos et al. 2006; Rozas et al. 2009; Montesinos et al. 2012; Gimeno et al. 2012a).  
69 Nevertheless, most of these studies have been conducted in mature stands, where average  
70 individual age was ~ 70-100 years (e.g. Rozas et al. 2008; Olano et al. 2008; DeSoto et al.  
71 2010, but see Gimeno et al. 2012ac). In contrast, the mechanisms driving population  
72 dynamics at earlier stages (age ~ 40 years), which are representative of these new juniper  
73 forests, have hardly been explored. In particular, we aimed to understand the role of  
74 intraspecific and intersexual competition in these new stands resulting from the release of  
75 traditional practices. Overall, this information could be crucial for establishing new scientific  
76 based management options for the future in this species.

77         Population structure results from a combination of abiotic and biotic factors, ranging  
78 from environmental conditions to inter- and intra-specific interactions (e.g. Hara 1984; Stoll  
79 et al. 1994; Coomes and Allen 2007). We hypothesize that three potentially important biotic  
80 factors might explain inter-individual differences in tree growth in high-density novel  
81 stands: (i) the reproductive class of the individual tree, (ii) tree size and (iii) neighbourhood  
82 competition. According to allocation theory (Chapin III et al. 1987) resources acquired by  
83 individual plants must be distributed among several competing functions, chiefly growth,  
84 maintenance and reproduction (Harper 1967). Consequently, the growth of non-reproductive  
85 individuals might be expected to differ from that of reproductive ones (Delph 1999).  
86 Specifically, we expect that non-reproductive individuals might invest a null amount of  
87 resources in reproduction, and hence show greater growth rates than reproductive  
88 individuals (Bazzaz et al. 1997). Moreover, in dioecious plant species, male and female  
89 individuals are expected to differ in their vegetative and reproductive strategies leading to  
90 differences in population structure and dynamics (Freeman et al. 1976). In general, males

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91 show relatively higher vegetative growth (Lloyd and Webb 1977; Cipollini and Whigham  
92 1994 but see Gimeno et al. 2012a) and survival rates than females (Doust et al. 1987; Allen  
93 and Antons 1993).

94         Size is one of the main determinants of a plant's interaction with its environment  
95 (Schulze 1982) and a common factor used to predict tree growth (Coomes and Allen 2007;  
96 Gómez-Aparicio et al. 2011). The relationship between size and growth rate arise both from  
97 internal and physiological causes (Gower et al. 1996), and because increasing size affects a  
98 tree's ability to acquire resources. The most common pattern for this relationship is a rapid  
99 increase of growth at small tree sizes until a maximum growth is reached at some  
100 intermediate size, and then a more or less sharp decline (depending on the species) in growth  
101 in larger size classes (Muller-Landau et al. 2006; Russo et al. 2007; Gómez-Aparicio et al.  
102 2011). Finally, competition at early stages of forest stand development constitutes a third  
103 critical factor influencing individual tree growth and determining future stand development  
104 patterns (Coomes and Allen 2007; Harper 1977; Kobe 1996). Furthermore, intra-specific  
105 competition is usually stronger than inter-specific competition (Tilman 1982; Stoll and  
106 Newbery 2005). This may be due to a higher competitive equivalence among individuals of  
107 the same species than among individuals of different species (Silvertown and Charlesworth  
108 2001). Within species, differences in resource allocation between reproductive classes might  
109 turn into dissimilarities in the competitive ability of males, females and non-reproductive  
110 individuals. Specifically we expect females to compete less strongly than males and non-  
111 reproductive individuals.

112         In this study, we aimed to explore tree growth patterns of the dioecious species  
113 *Juniperus thurifera* L. in a forest stand which is representative of new juniper forests  
114 resulting from agricultural and livestock farming abandonment (i.e. c.f 50 years) in the

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115 Iberian Peninsula. We used neighborhood models to predict tree growth for different  
116 reproductive classes (males, females and non-reproductive) as a function of size and  
117 intraspecific competition from neighbours (including interactions within and among the  
118 different reproductive classes). We specifically addressed the following hypotheses: (i) in a  
119 high density forest stand and at early stages of development, tree size is expected to be an  
120 important factor determining tree growth, (ii) intraspecific competition is expected to have a  
121 negative effect on tree growth, (iii) tree growth rates are expected to differ among different  
122 reproductive classes. Specifically, non-reproductive individuals are expected to grow faster  
123 than males and these in turn faster than females.

124

125 **Material and methods**

126 Study species and study area

127 *Juniperus thurifera* L. (Cupressaceae) is mainly a dioecious tree, though infrequently  
128 monoecious trees are found (Borel and Polidori, 1983, Lathuillière, 1994). In the Iberian  
129 Peninsula this species is mainly found in high plateaus and mountain regions of the central-  
130 east at a variety of altitudes (140-1,800 m a.s.l) in continental and cold Mediterranean  
131 climatic conditions (Gauquellin *et al.* 1999, Terrab *et al.* 2008, Fig. S1). It is usually the  
132 dominant species in low-density woodlands on poor, shallow, rocky soils (both acidic and  
133 calcareous, although more abundant in the latter) (Gauquelin *et al.* 1999). Juniper males and  
134 females flower at the end of the winter and wind-pollinated female cones mature during 20  
135 months. It is a masting species, that is, individuals present low or null reproduction for  
136 several years but every few years most individuals in a population present a massive  
137 reproduction event (Montesinos, 2007). It can also be considered a slow-growing species  
138 (Gómez-Aparicio *et al.* 2011).

139 The study area was located in Monte Pradenilla (Segovia, north-central Spain), near  
140 the Sierra of Guadarrama, at 1,120 m a.s.l. Soils are calcareous cambisols developed on  
141 Cretaceous dolomitic substrates. Climate in this region is continental Mediterranean, with  
142 hot and dry summers and cold and long winters. Mean annual rainfall is 572.41 mm (1957-  
143 1990, data from a close meteorological station Prádena C.F.: 41°08'20" N, 3°41'17" W,  
144 1,110 m a.s.l.). Mean annual temperature, mean minimum temperature and mean maximum  
145 temperature are 10.6 °C, 4.3 °C and 16.83 °C, respectively (1988-1992; all data provided by  
146 the Spanish Agencia Estatal de Meteorología). The study area was dominated by the species  
147 *J. thurifera* L., which forms even-aged monospecific forests with scatter presence of  
148 *Juniperus communis* L. subsp. *hemisphaerica* (K. Presl.) and a sparse understory of small

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149 calcicolous shrubs. Traditional management (livestock grazing and wood harvest) was  
150 abandoned in the late 70s; the stand is currently in an early development stage. Within this  
151 study area we selected a rectangular study plot of approximately 2,250 m<sup>2</sup>, with a high  
152 density of trees (0.71 trees m<sup>-2</sup>), fairly flat topography and homogenous in rockiness (J.  
153 Pavón-García, personal observation).

154

#### 155 *Data collection and reproductive class identification*

156 Data collection was conducted during the summer and fall of 1993. We selected this time of  
157 the year because it was adequate to visually identify the reproductive structures of  
158 individuals (when existing). We tagged all the individuals presented in the study plot, a total  
159 of 1604. The study plot was composed of 447 reproductive individuals (225 males, 215  
160 females and 7 monoecious individuals) and 1,157 non-reproductive individuals. Within  
161 reproductive individuals (males and females), 17 % presented multi-caulis structure, i.e.  
162 more than one stem. Within the non-reproductive class, 19% presented multicaulis structure.  
163 In the study plot, the reproductive: non-reproductive ratio was 0.39:1 and the sex ratio  
164 (male: female) was 1.05: 1. For each individual in the study plot, we recorded tree size by  
165 measuring the trunk perimeter at 10 cm from the ground, total height and the reproductive  
166 class (males, females and non-reproductive). Reproductive class assignation was based on  
167 the presence of reproductive structures. Accordingly to this criterion, the male class was  
168 composed of individuals with male cones; the female class was composed of individuals  
169 with either female cones or the existence of fruits; and the non-reproductive class was  
170 composed of those individuals without any reproductive structure in their branches yet.  
171 Reproductive class assignation was verified two more times, in 1994 and 1998. This

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172 verification helped us to assure that non-reproductive individuals were not a consequence of  
173 a non-masting year.

174 Wood cores were taken from a subsample of the individuals in each reproductive  
175 class (hereafter target trees) for characterization of growth rates and tree age. Target trees  
176 were selected following three main criteria (Pavón-García 2005): (i) trees should have a  
177 unique trunk in order to facilitate growth rate estimates, (ii) trees should have a minimum  
178 diameter of 25 mm (measured at 10 cm from the ground) in order to be able to core the trunk  
179 and to minimize serious damage after coring, and (iii) overlapping among neighbourhood  
180 areas should be avoided or minimized as much as possible. Overall, 115 males, 105 females  
181 and 79 non-reproductive individuals were selected (Table 1, Fig. 1). Wood cores were taken  
182 as close as possible to the ground, at approximately 10 cm, perpendicularly to the trunk and  
183 heading north east and reaching central trunk section by using a Pressler's increment borer.  
184 Cores were mechanically surfaced and then manually polished with a series of successively  
185 finer grades of sandpaper until the xylem cellular structure was clearly visible. In order to  
186 correctly visualize tree rings, a dissolvent (toluene) was added to remove traces or wood  
187 resins. Tree rings were visually dated following a standard procedure (Stokes and Smiley,  
188 1968) using a binocular regulated glass which helps to measure and count the tree rings. The  
189 double rings were scarce and easily detected. Radial growth of each target tree ( $\text{mm yr}^{-1}$ )  
190 was calculated by dividing the total length of the last ten tree-ring growth (mm) by the  
191 number of 10 years. Finally, we characterized the neighborhood of each target tree by  
192 recording the number, size and reproductive class of each neighbour tree within three  
193 different radii ( $R_i$ : 1 m, 2 m, 3 m) from the target tree (Table 2).

194

195 *Statistical analysis of growth models*

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196 We used a neighbourhood approach based on similar studies of tree growth (Canham and  
 197 Uriarte 2006; Gómez-Aparicio and Canham 2008) to predict recent tree growth (last ten  
 198 years) of the 299 target trees. Growth data were grouped in four subsets: one including all  
 199 individuals (i.e. without differentiation regarding the reproductive class); a second one  
 200 including only male individuals; a third one including only female individuals; and the  
 201 fourth one including only non-reproductive individuals. We predicted radial tree growth in  
 202 each subset (RG, mm yr<sup>-1</sup>) as a function of: (i) the potential growth of a hypothetical “free  
 203 growing” tree, i.e. without any competition effect (Pot RG, mm yr<sup>-1</sup>), (ii) the size (trunk  
 204 diameter) of the target tree and (iii) competition from neighbouring trees. The model takes  
 205 the form:

$$206 \quad \text{RG} = \text{Pot RG} \times \text{Size effect} \times \text{Competition effect} \quad \text{eqn 1}$$

207 where Pot RG is the parameter estimated from the data. The size and competition effects are  
 208 scalars ranging from 0 to 1, which act to reduce potential growth of a hypothetical “free  
 209 growing” tree. In this model, at a Competition effect of 0 (intense competition), growth is 0,  
 210 and at a Competition effect of 1, growth is no longer limited by this interaction. Similarly to  
 211 other studies (Canham et al. 2006; Coates et al. 2009, Gómez-Aparicio et al. 2011) we used  
 212 a lognormal function to shape the size effect (eqn 2).

$$213 \quad \text{Size effect} = \exp \left[ -\frac{1}{2} \left( \frac{\ln(D/X_0)}{X_b} \right)^2 \right] \quad \text{eqn 2}$$

214 where D is the trunk diameter (mm) of the target tree, X<sub>0</sub> is a parameter that represents the  
 215 trunk diameter (mm) of the target tree at which Pot RG occurs (i.e., the peak of the  
 216 lognormal shape), and X<sub>b</sub> is a parameter that determines the breadth of the function. The  
 217 lognormal function is flexible enough to be monotonically increasing (i.e., when X<sub>0</sub> is very

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218 large), decreasing (i.e., when  $X_0$  is very small), or to have a single “hump” and a skew to the  
219 left when  $X_0$  is within the normal range of trunk diameter.

220 The competition effect was modelled using a Neighbourhood Competition Index  
221 (NCI). This index takes into account the total basal area from neighbours contained in  
222 circumferences at different distances from the target tree. This type of indices has been  
223 shown to be generally sufficient to predict competition effects in relatively uniform even-  
224 aged stands (Lorimer 1983). Neighbours were defined as individuals growing within three  
225 different radii ( $R_i$ : 1 m, 2 m, 3 m) from target trees (Weiner 1984; Silander and Pacala 1985)  
226 within the study plot. We tried three different radii because the effects of local crowding can  
227 potentially vary depending on the radius used to define the local neighbourhood (Peterson  
228 and Squiers 1995; He and Duncan 2000). The NCI took the form:

$$229 \quad \text{NCI}_{R_i} = \sum_{j=0}^n BA_j \quad \text{eqn3}$$

230 where  $BA_j$  is the basal area of the neighbour trees ( $\text{cm}^2$ ) within one of the three influence  
231 areas tested, and  $R_i$  is the distance to the target tree (either 1 m, 2 m or 3 m).

232

233 We tested two forms of the NCI: (i) all neighbours were considered to be equivalent  
234 (eqn. 3), and (ii) the effect of neighbours was a function of their reproductive class (male,  
235 female and non-reproductive). The reproductive condition of the neighbour was included  
236 into the NCI by a new parameter ( $\lambda_k$ ) that ranges from 0 to 1 and allows for differences  
237 among sexual condition in their competitive effect on the target tree (eqn4):

$$238 \quad \text{NCI}_{R_i} = \sum_{i=0}^n \lambda_k \times BA_j \quad \text{eqn4}$$

239 The competition effect was assumed to decrease exponentially as a function of the NCI:



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264 likelihood (the Akaike Information Criterion corrected for small sample sizes,  $AIC_c$ ) to  
265 select the best growth model (Burnham and Anderson 2002). The absolute magnitude of the  
266 differences in AIC between alternate models ( $\Delta AIC$ ) provides an objective measure of the  
267 strength of empirical support for the competing models. The model with the strongest  
268 empirical support has the minimum AIC (Akaike 1992). Models with  $\Delta AIC$  between 0 and 2  
269 were considered to have equivalent and substantial empirical support,  $\Delta AIC$  between 4 and 7  
270 indicated less support, and models with  $\Delta AIC > 10$  were dismissed, as they had negligible  
271 empirical support (Burnham and Anderson 2002). As a measure of goodness-of-fit we used  
272 the  $R^2$  of the regression ( $1 - SSE/SST$ , SSE: sum of squares error, SST: sum of squares total)  
273 and as a measure of bias we used the slope of the regression with a zero intercept between  
274 observed and predicted radial growth (with an unbiased model having a slope of 1). We used  
275 asymptotic two-unit support intervals to assess the strength of evidence for individual  
276 maximum likelihood parameter estimates (Edwards 1992), which is roughly equivalent to a  
277 95% support limit defined using a likelihood ratio test (Hilborn and Mangel, 1997). A  
278 support interval is defined as the range of the parameter value that results in less than a two-  
279 unit difference in AIC. Residuals were normally distributed  $N \sim (0, 1)$ . All the analyses were  
280 done in the R environment (R Development Core Team 2013) using the likelihood package  
281 version 1.5 (Murphy, 2012).

282

283 **Results**284 **Biotic factors of tree growth assessed by model comparison and evaluation**

285 All of the best models produced unbiased estimates of growth (i.e. slopes of predicted versus  
286 observed growth were all very close to 1) and the percentage of variance explained by the  
287 best models ranged from 35% to 49% (Table 3, Fig. S2). On one hand, models that included  
288 the effect of target tree size on growth had in all cases a better fit to the data than the null  
289 model (Table 3). On the other hand, models that included the effect of competition on tree  
290 growth had larger support than the null model (i.e., lower AIC<sub>c</sub>) for all the trees together at R  
291 = 2 m and for female target trees at all the radii, but not for male or non-reproductive trees.  
292 However, bivariate models including size and competition were never a better fit to the data  
293 that univariate models considering only size (Table 3).

294

295 **Differential growth patterns between reproductive classes**

296 The three reproductive classes showed different patterns of variation in predicted radial  
297 growth as a function of target tree size (Fig. 2). At small sizes predicted radial growth of the  
298 three reproductive classes was similar and increased rapidly with trunk diameter. However,  
299 at a certain size non-reproductive individuals grew much more slowly than non-reproductive  
300 individuals. Non-reproductive individuals reached a growth peak at an intermediate size of  
301 trunk diameter and a slight decline afterwards. In contrast, reproductive individuals kept a  
302 monotonic growth curve, with female individuals of large size growing faster than males  
303 (Fig. 2).

304 Differences in growth rates among reproductive classes were also supported by the  
305 different values of the potential radial growth parameter (Pot RG), which measures the  
306 growth rate of a hypothetical “free growing tree” of optimal size (i.e. a target tree with D =

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307  $X_0$ , eqn 1). Predicted potential growth rates (Pot RG) were highest in females (2.56 [2.39-  
308 2.73] mm yr<sup>-1</sup>, mean [support interval]), followed by males (1.93 [1.83-2.03] mm yr<sup>-1</sup>) and  
309 non-reproductive individuals (0.99 [0.94-1.00] mm yr<sup>-1</sup>) (Table 4).

310

311 **Discussion**312 **Biotic factors influencing tree growth patterns**

313 Our results showed that *Juniperus* growth at early stages of stand development was largely  
314 governed by tree size and the reproductive class rather than by neighbourhood competition.  
315 Specifically, in agreement with our first hypothesis, size of the target tree was the main  
316 factor driving tree growth (e.g. Gimeno et al. 2012a; Lee et al. 2003; Mencuccini et al.  
317 2007). The size–growth curve showed a rapid increase of growth with size for the three  
318 reproductive classes (see also Gómez-Aparicio et al. 2011 for a similar result). However, the  
319 shape of the curves indicated that non-reproductive individuals have a lower growth  
320 potential than reproductive individuals, reaching a growth peak much faster than  
321 reproductive individuals. In fact, the shape of the size–growth curve for reproductive  
322 individuals suggests that such a peak would occur at larger sizes than those found in our  
323 study site. A plausible explanation for this would be the fact that our study forest is  
324 relatively young and the trees are relatively small, so our study population might not include  
325 reproductive individuals large enough to have reached their maximum growth yet.

326       Intraspecific competition did not constrain tree growth, neither when all neighbours  
327 were considered as equal competitors nor when they were separated into different  
328 reproductive classes. This result is contrary to our second hypothesis, which stated that  
329 neighbourhood competition may become a key driver of individual tree growth as previously  
330 reported for *Juniperus thurifera* (Gimeno et al. 2012c) and other dioecious tree species  
331 (Herrera 1988; Vasiliuskas and Aarssen 1992; Houle and Duchesne 1999; Zhang et al.  
332 2009). These studies have addressed the existence of intraspecific competition, and  
333 moreover, they have described inter- and intra-specific interaction between reproductive  
334 classes, although without finding consistent trends. For example, Vasiliuskas et al. (1992)

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335 showed for *Juniperus virginiana* (Cupressaceae) that the presence of neighbours decreased  
336 tree growth, independently of the reproductive class of the nearest neighbours. Meanwhile,  
337 Houle and Duchesne (1999) in *J. communis* suggested the existence of a moderate  
338 intraspecific competition only between males. These studies, however, focused on uneven  
339 aged populations that might already be experiencing self-thinning processes which could  
340 explain the existence of the observed competition interactions. On the contrary, in our young  
341 forest of study, the lack of canopy overlapping among young *Juniperus* (J. Pavón-García,  
342 personal observation), and the inherent slow-growing resource-conservative strategy of the  
343 species (García-Morote et al. 2012; Gómez-Aparicio et al. 2011) would help to explain the  
344 lack of competitive interactions among *Juniperus* individuals despite the high stand density.

345

#### 346 **Differential growth rates between reproductive classes**

347 Our results suggested that females **may** grow faster than males. This finding is confirmed by  
348 both the size-growth curves and the potential growth rates ( $\alpha$ ) estimated in the models. This  
349 result is in disagreement with our third hypothesis based on the fact that differences in  
350 resource investments to reproduction could result in different patterns of growth, with  
351 females showing slower growth rates than males and non-reproductive individuals (Herrera  
352 1988; Vasiliuskas and Aarssen 1992; Allen and Antons 1993). Previous studies with *J.*  
353 *thurifera* suggest the lack of a consensus about which gender grows faster than the other and  
354 why. For example, higher growth rates in males have been interpreted as the delayed cost of  
355 reproduction in females (Gauquelin et al. 2002; Montesinos et al. 2006). However, other  
356 studies have found no differences in growth rates between males and females of *Juniperus*  
357 *thurifera* (Gimeno et al. 2012a; Gimeno et al. 2012d), even in situations where the female  
358 reproductive effort was much greater than that of males (Ortiz 2002). Finally, some authors

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359 have found females to grow faster than males in individuals larger than those from our study  
360 plot (Rozas et al. 2009). Our results are in agreement with this last line of evidence. A higher  
361 female growth rate might be explained by the underlying mechanisms which offset female  
362 reproduction costs, e.g. photosynthetic reproductive structures, delayed reproduction,  
363 nutrient resorption from senescing organs or fallen fruits under the female's canopy, module  
364 specialization or higher photosynthetic rates in females (Delph 1990, Delph 1999; Obeso  
365 2002). In particular, Montesinos et al. (2012) suggested that female *J. thurifera* seem to have  
366 a long-term strategy which allows them to store and use their resources for future  
367 requirements, whilst males seem to have a short-term strategy which makes them adjust their  
368 growth and reproduction as a function of the current resource availability.

369       Lastly, and also contrary to our third hypothesis, our results showed that non-  
370 reproductive individuals had lower growth rates than male and female individuals. Our  
371 expectation was based on the idea that a lack of reproduction costs incurred by non-  
372 reproductive individuals would result in greater growth rates than reproductive individuals,  
373 as found in previous studies for the same species (Gimeno et al. 2012d). A plausible  
374 explanation to this finding could be related to the potential existence of small-scale spatial  
375 heterogeneity in environmental conditions (e.g. soil fertility), **with non-reproductive**  
376 **individuals being located in sub-optimal microsites that could limit their capacity to invest in**  
377 **both growth and reproduction. In fact, mean size of non-reproductive individuals was**  
378 **smaller than that of reproductive individuals despite having similar ages. Moreover, small**  
379 **junipers present higher sensitivity than large ones to stressful environmental conditions**  
380 **(Rozas et al. 2009), which might further limit their performance (i.e. lower growth rates and**  
381 **delayed reproduction). However, we cannot discard other alternative causes, such as the**

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382 existence of genetic variability or seed size effects, that might have prevented non-  
383 reproductive individuals from having a better performance,

384 Overall, our results suggest that in young *J. thurifera* monospecific forests, where  
385 self-thinning processes may have not undergone yet, tree size and the reproductive class  
386 could play a relatively more important role than competition as drivers of tree growth and  
387 stand dynamics. Female *Juniperus* apparently make a much more efficient use of their  
388 available resources allowing them to grow faster than males and non-reproductive  
389 individuals. The non-reproductive condition of individuals could be linked to specific  
390 microsite conditions or genetic variability effects which could hamper their development.  
391 Although competition is considered a major determinant of tree performance and population  
392 dynamics (Weiner 1984), intraspecific differences in growth patterns alone can also be of  
393 paramount importance in explaining population structure and dynamics (e.g. Zavala et al.  
394 2007).

395 In conclusion, this study contributes to understanding growth dynamics at early  
396 developmental stages in a dioecious tree species such as *Juniperus thurifera*. Additionally,  
397 our study provides guidelines to develop silvicultural recommendations in order to manage  
398 these new woodlands. Recently, juniper wood has aroused interest due to its quality for  
399 constructions (Crespo et al. 2006). Therefore, managers aim to seek both quantity and  
400 quality wood by controlling stand density throughout thinning (Nyland, 1996). Our results  
401 suggest that at this early successional stage, thinning would have little influence on the  
402 growth of remnant trees, as competition did not seem to limit growth of relatively young  
403 junipers.

404

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413

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415

416

417 **References**

- 418 Akaike H (1992) Information theory and an extension of the maximum likelihood principle.  
419 In Breakthroughs in statistics. Vol. 1. Edited by S. Kotz and N. Johnson. Springer-  
420 Verlag, London
- 421 Allen GA, Antons JA (1993) Sex ratio variation in the dioecious shrub *Oemleria*  
422 *cerasiformis*. *Am Nat* 141:537–553
- 423 Améztegui A, Brotons L, Coll L (2010) Land-use changes as major drivers of mountain pine  
424 (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Glob Ecol Biogeogr*. doi:  
425 10.1111/j.1466-8238.2010.00550.x
- 426 Bazzaz F (1997) Allocation of resources in plants: state of the science and critical questions.  
427 In: Bazzaz F, Grace J (ed) *Plant resource allocation*. Academic Press, San Diego, pp 1–  
428 37
- 429 Blanco E, Casado M, Costa M, et al. (2005) *Los bosques ibéricos: Una interpretación*  
430 *geobotánica*, 4a ed. Planeta, Barcelona
- 431 Blondel J, Aronson J (1995) Biodiversity and ecosystem function in the Mediterranean  
432 basin: human and non-human determinants. *Ecol Stud* 109:43–119
- 433 Borel A, Polidori JL (1983) Le Genévrier thurifère (*Juniperus thurifera* L.) dans le Parc  
434 National du Mercantour (Alpes-Maritimes). *Bulletin de la Société Botanique de France*  
435 130, *Lettres Bot.* (3): 227–242
- 436 Burnham K, Anderson D (2002) *Model selection and multimodel inference: a practical*  
437 *information-theoretic approach*, 2nd ed. Springer-Verlag, New York
- 438 Canham CD, Lepage PT, Coates KD (2004) A neighborhood analysis of canopy tree  
439 competition: effects of shading versus crowding. *Can J For Res* 34:778–787. doi:  
440 10.1139/X03-232
- 441 Canham CD, Uriarte M (2006) Analysis of neighborhood dynamics of forest ecosystems  
442 using likelihood methods and modeling. *Ecol Appl* 16:62–73
- 443 Chapin III FS, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple  
444 environmental factors. *Bioscience* 37:49–57. doi: 10.2307/1310177
- 445 Cipollini ML, Whigham DF (1994) Sexual dimorphism and cost of reproduction in the  
446 dioecious shrub *Lindera benzoin* (Lauraceae). *Am J Bot* 86:585–593

**Preprint submitted to Springer**

- 447 Coates KD, Canham CD, LePage PT (2009) Above-versus below-ground competitive  
448 effects and responses of a guild of temperate tree species. *J Ecol* 97:118–130. doi:  
449 10.1111/j.1365-2745.2008.01458.x
- 450 Coomes DA, Allen RB (2007) Effects of size, competition and altitude on tree growth. *J*  
451 *Ecol* 95:1084–1097. doi: 10.1111/j.1365-2745.2007.01280.x
- 452 Crespo A, Pinillos F, Lafuente E, Broto M, Alcalde F (2006) Aprovechamiento maderero de  
453 sabina en Castilla y León: Estudio de rendimientos en la fabricación de tarima de  
454 sabina. *Actas del III Coloquio Internacional sobre sabinas y enebrales Tomo II: 395–*  
455 *403. Junta de Castilla y León, Soria, Spain*
- 456 Delph LF (1990) Sex-differential resource allocation patterns in the subdioecious shrub  
457 *Hebe subalpina*. *Ecology* 71: 1342–1351
- 458 Delph L (1999) Sexual dimorphism in flowering plants. In: Geber MA, Dawson TE and  
459 Delph LF (ed) *Gender and sexual dimorphism in flowering plants*, Springer-Verlag,  
460 Berlin
- 461 DeSoto L, Olano JM, Rozas V, De la Cruz M (2010) Release of *Juniperus thurifera*  
462 woodlands from herbivore-mediated arrested succession in Spain. *Appl Veg Sci* 13:15–  
463 25. doi: 10.1111/j.1654-109X.2009.01045.x
- 464 Doust JL, Brien GO, Doust LL (1987) Effect of density on secondary sex ratio in *Silene alba*  
465 (Caryophyllaceae). *Am J Bot* 74:40–46
- 466 Edwards M (1992) *Likelihood*. Johns Hopkins. University Press, Baltimore, MD, USA
- 467 Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in  
468 seed plants. *Science* 295:1517–1520
- 469 Freeman DC, Klikoff LG, Harper KT (1976) Differential resource utilization by the sexes of  
470 dioecious plants. *Science* 193:597–599
- 471 García-Morote FA, López-Serrano FR, Andrés M, Rubio E, González-Jimenez JL, de las  
472 Heras J (2012) Allometries, biomass stocks and biomass allocation in the thermophilic  
473 Spanish juniper woodlands of Southern Spain. *For Ecol Manage* 270:85-93
- 474 Gauquelin T, Bertaudière V, Montès N, Badri W, Asmode JF (1999) Endangered stands of  
475 thuriferous juniper in the western Mediterranean basin: ecological status, conservation  
476 and management. *Biodiversity and Conservation* 8: 1479–1498

Preprint submitted to Springer

- 477 Gauquelin T, Bertaudière-Montès V, Badri W, Montès N (2002) Sex ratio and sexual  
478 dimorphism in mountain dioecious thuriferous juniper (*Juniperus thurifera* L.  
479 Cupressaceae). Bot J Linn Soc 138:237–244
- 480 Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps:  
481 Climate change or land abandonment? J Veg Sci 18:571–582
- 482 Gimeno TE, Camarero JJ, Granda E, et al. (2012a) Enhanced growth of *Juniperus thurifera*  
483 under a warmer climate is explained by a positive carbon gain under cold and drought.  
484 Tree Physiol 32:326–36. doi: 10.1093/treephys/tps011
- 485 Gimeno TE, Escudero A, Delgado A, Valladares F (2012b) Previous land use alters the  
486 effect of Climate Change and facilitation on expanding woodlands of Spanish juniper.  
487 Ecosystems 15:564–579. doi: 10.1007/s10021-012-9529-z
- 488 Gimeno TE, Pías B, Martínez-Fernández J, et al. (2012c) The decreased competition in  
489 expanding versus mature juniper woodlands is counteracted by adverse climatic effects  
490 on growth. Eur J For Res 131:977–987. doi: 10.1007/s10342-011-0569-2
- 491 Givnish T (1988) Adaptation to sun and shade: a whole-plant perspective. Aust J Plant  
492 Physiol 15:63–92. doi: 10.1071/PP9880063
- 493 Goffe WL, Ferrier GD, Rogers J (1994) Global optimization of statistical functions with  
494 simulated annealing. J Econom 60:65–69
- 495 Gómez-Aparicio L, Canham CD (2008) Neighbourhood analyses of the allelopathic effects  
496 of the invasive tree *Ailanthus altissima* in temperate forests. J Ecol 96:447–458. doi:  
497 10.1111/j.1365-2745.2007.01352.x
- 498 Gómez-Aparicio L, García-Valdés R, Ruiz-Benito P, Zavala MA (2011) Disentangling the  
499 relative importance of climate, size and competition on tree growth in Iberian forests:  
500 implications for forest management under global change. Glob Chang Biol 17:2400–  
501 2414. doi: 10.1111/j.1365-2486.2011.02421.x
- 502 Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline  
503 with stand age: potential causes. Trends Ecol Evol 11:378–382
- 504 Hara T (1984) A stochastic model and the moment dynamics of the growth and size  
505 distribution in plant populations. J Theor Biol 109:173–190
- 506 Harper J (1977) Population biology of plants. Academic Press, London
- 507 He F, Duncan R (2000) Density-dependent effects on tree survival in an old-growth Douglas  
508 Fir Forest. J Ecol 88:676–688

**Preprint submitted to Springer**

- 509 Herrera CM (1988) Plant size, spacing patterns, and host-plant selection in *Osyris*  
510 *quadripartita*, a dioecious hemiparasitic shrub. *J Ecol* 76:995–1006
- 511 Hilborn R, Mangel M (1997). The ecological detective: confronting models with data.  
512 Princeton University Press, Princeton, N.J.
- 513 Houle G, Duchesne M (1999) The spatial pattern of a *Juniperus communis* var. *depressa*  
514 population on a continental dune in subarctic Québec, Canada. *Can J For Res* 29:446–  
515 450. doi: 10.1139/cjfr-29-4-446
- 516 Kobe RK (1996) Intraspecific variation in sapling mortality and growth predicts geographic  
517 variation in forest composition. *Ecol Monogr* 66:181–201. doi: 10.2307/2963474
- 518 Lathuillière L (1994) Le Genévrier thurifère: monographie et études des différentes stations  
519 des Alpes. Mémoire de la F.I.F., Nancy et Conservatoire Botanique Gap-Charance
- 520 Lee WK, Gadow KV, Chung DJ, et al. (2003) DBH growth model for *Pinus densiflora* and  
521 *Quercus variabilis* mixed forests in central Korea. *Ecol Mod* 176:187–200
- 522 Lloyd D, Webb C (1977) Secondary sex characters in plants. *Bot Rev* 43:177–216
- 523 Murphy L (2012) Likelihood: Methods for maximum likelihood estimation. R package  
524 version 1.5. <http://CRAN.R-project.org/package=likelihood>
- 525 Lorimer CG (1983) A test of the accuracy of shade-tolerance classifications based on  
526 physiognomic and reproductive traits. *Can J Bot Can Bot* 61:1591–1598
- 527 Marion C, Houle G (1996) No differential consequences of reproduction according to sex in  
528 *Juniperus communis* var *depressa* (Cupressaceae). *Am J Bot* 83:480–488
- 529 Matesanz S, Escudero A, Valladares F (2009) Impact of three global change drivers on a  
530 Mediterranean shrub. *Ecology* 90:2609–2621
- 531 Mencuccini M, Martínez-Vilalta J, Hamid HA, et al. (2007) Evidence for age- and size-  
532 mediated controls of tree growth from grafting studies. *Tree Physiol* 27:463–473
- 533 Montesinos D. 2007. Resource availability and reproductive efficacy of the dioecious tree  
534 *Juniperus thurifera*. Dissertation thesis, Universitat de València, Valencia, Spain.
- 535 Montesinos D, de Luís M, Verdú M, et al. (2006) When, how and how much: gender-  
536 specific resource-use strategies in the dioecious tree *Juniperus thurifera*. *Ann Bot*  
537 98:885–9. doi: 10.1093/aob/mcl172
- 538 Montesinos D, Villar-Salvador P, García-Fayos P, Verdú M (2012) Genders in *Juniperus*  
539 *thurifera* have different functional responses to variations in nutrient availability. *New*  
540 *Phytol* 193:705–712. doi: 10.1111/j.1469-8137.2011.03982.x

**Preprint submitted to Springer**

- 541 Muller-Landau HC, Condit RS, Chave J, et al. (2006) Testing metabolic ecology theory for  
542 allometric scaling of tree size, growth and mortality in tropical forests. *Ecol Lett* 9:575–  
543 88. doi: 10.1111/j.1461-0248.2006.00904.x
- 544 Nyland RD (1996) *Silviculture: concepts and application*. McGraw-Hill Series in Forest  
545 Resources. McGraw-Hill, New York
- 546 Obeso JR (2002) The costs of reproduction in plants. *New Phytologist* 155: 321–348
- 547 Olano JM, Rozas V, Bartolomé D, Sanz D (2008) Effects of changes in traditional  
548 management on height and radial growth patterns in a *Juniperus thurifera* L. woodland.  
549 *For Ecol Manage* 255:506–512. doi: 10.1016/j.foreco.2007.09.015
- 550 Olano JM, Zavala MA, Rozas V (2011) Disruption of *Juniperus thurifera* woodland  
551 structure in its northwestern geographical range: potential drivers and limiting factors.  
552 *Eur J For Res* 131:563–570. doi: 10.1007/s10342-011-0531-3
- 553 Ortiz PL (2002) Sex ratio and reproductive effort in the dioecious *Juniperus communis*  
554 subsp. *alpina* (Suter) Celak. (Cupressaceae) Along an Altitudinal Gradient. *Ann Bot*  
555 89:205–211. doi: 10.1093/aob/mcf028
- 556 Pavón-García J (2005) *Biología vegetativa y reproductiva en los primeros estadios de*  
557 *crecimiento de Juniperus thurifera L.* Dissertation thesis, Universidad de Alcalá de  
558 Henares, Madrid, Spain
- 559 Peterson CJ, Squiers ER (1995) Competition and succession in an aspen–white-pine forest. *J*  
560 *Ecol* 83:449–457
- 561 Poyatos R, Latron J, Llorens P (2003) Land use and land cover change after agricultural  
562 abandonment - the case of a Mediterranean mountain area (Catalan Pre-Pyrenees). *Mt*  
563 *Res Dev* 23:362–368
- 564 R Core Team (2013). *R: A language and environment for statistical computing*. R  
565 Foundation for Statistical. Computing, Vienna, Austria. URL [http://www.R-](http://www.R-project.org/)  
566 [project.org/](http://www.R-project.org/).
- 567 Reich PB, Tjoelker MG, Machado J, Oleksyn J (2006) Universal scaling of respiratory  
568 metabolism, size and nitrogen in plants. *Nature* 439:457–461
- 569 Rozas V, Olano JM, De Soto L, Bartolome D (2008) Large-scale structural variation and  
570 long-term growth dynamics of *Juniperus thurifera* trees in a managed woodland in  
571 Soria , central Spain. *Ann For Sci*. doi: 10.1051/forest

**Preprint submitted to Springer**

- 572 Rozas V, DeSoto L, Olano JM (2009) Sex-specific, age-dependent sensitivity of tree-ring  
573 growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytol* 182:687–697.  
574 doi: 10.1111/j.1469-8137.2009.02770.x
- 575 Russo SE, Wiser SK, Coomes DA (2007) Growth-size scaling relationships of woody plant  
576 species differ from predictions of the metabolic ecology model. *Ecol Lett* 10:889–901.  
577 doi: 10.1111/j.1461-0248.2007.01079.x
- 578 Schulze ED (1982) Plant life forms and their carbon, water and nutrient relations. In:  
579 Springer Berlin Heidelberg (ed) *Physiol. Plant Ecol. II Encycl. Plant Physiol.* pp 615–  
580 676
- 581 Silander Jr JA, Pacala SW (1985) Neighborhood predictors of plant performance. *Oecologia*  
582 66:256–263
- 583 Silvertown J, Charlesworth D (2001) *Introduction to plant population biology*, 4th ed.  
584 Blackwell, London
- 585 Stokes MA, Smiley TL (1968) *An introduction to tree-ring dating*. University of Chicago  
586 Press, Chicago, IL
- 587 Stoll P, Newbery DM (2005) Evidence of species-specific neighborhood effects in the  
588 Dipterocarpaceae of a Bornean rain forest. *Ecology* 86:3048–3062
- 589 Stoll P, Weiner J, Schmid B (1994) Growth variation in a naturally established population of  
590 *Pinus sylvestris*. *Ecology* 75:660–670
- 591 Terrab A, Schönswetter P, Talavera S, et al. (2008) Range-wide phylogeography of  
592 *Juniperus thurifera* L., a presumptive keystone species of western Mediterranean  
593 vegetation during cold stages of the Pleistocene. *Mol Phylogenet Evol* 48:94–102
- 594 Thirgood J V (1981) *Man and the Mediterranean Forest. A history of resource depletion*.  
595 London
- 596 Thompson J (2005) *Plant evolution in the Mediterranean*. Oxford University Press, Oxford
- 597 Tilman D (1982) Some thoughts on resource competition and diversity in plant-communities.  
598 *Ecol Stud* 43:322–336
- 599 Urbietta I, Zavala M, Marañón T (2008) Human and non-human determinants of forest  
600 composition in southern Spain: evidence of shifts towards cork oak dominance due to  
601 last century management. *J Biogeogr* 35:1688–1700
- 602 Vasiliuskas SA, Aarssen LW (1992) Sex ratio and neighbor effects in monospecific stands  
603 of *Juniperus virginiana*. *Ecology* 73:622–632

**Preprint submitted to Springer**

- 604 Vayreda J, Martínez-Vilalta J, Gracia M, Retana J (2012) Recent climate changes interact  
605 with stand structure and management to determine changes in tree carbon stocks in  
606 Spanish forests. *Glob Chang Biol* 18:1028–1041. doi: 10.1111/j.1365-  
607 2486.2011.02606.x
- 608 Weiner J (1984) Neighbourhood interference amongst *Pinus rigida* individuals. *J Ecol*  
609 72:183. doi: 10.2307/2260012
- 610 Zavala MA, Angulo O, Bravo de la Parra R, López-Marcos JC (2007) An analytical model  
611 of stand dynamics as a function of tree growth, mortality and recruitment: the shade  
612 tolerance-stand structure hypothesis revisited. *J Theor Biol* 244:440–50. doi:  
613 10.1016/j.jtbi.2006.08.024
- 614 Zhang C, Zhao X, Gao L, Gadow KV (2009) Gender, neighboring competition and habitat  
615 effects on the stem growth in dioecious *Fraxinus mandshurica* trees in a northern  
616 temperate forest. *Ann For Sci* 66:812–812. doi: 10.1051/forest/2009068

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1 This manuscript includes 2 Figures, 4 Tables and 2 Supplementary material Figures.

2

3 **Table 1** Summary data from target trees. Number of individuals, age, growth rate, trunk  
4 diameter and height for each reproductive class are shown. Statistical differences between  
5 reproductive classes were tested using one way anova test in: Age, Growth rate\*, Trunk  
6 diameter\*\*, Height. SE means standard error.

7

8 **Table 2** Summary data of neighbourhood conditions for target trees in each reproductive  
9 class. Range, mean and standard error (SE) are shown for each variable. NCI (Neighborhood  
10 Competition Index) is the total basal area (cm<sup>2</sup>) from neighbours contained in  
11 circumferences at different distances (1, 2 and 3 m) from the target tree; and Aver. n° ind. is  
12 the average number of individuals contained in circumferences at different distances from  
13 the target tree. Differences between reproductive classes were tested using one way anova  
14 test in NCI and with generalized linear models (family= Poisson distribution) in Aver. n° ind.  
15

16 **Table 3** Comparison of alternate growth models analysing the effect of size and competition  
17 at three different distances for the whole population together and for each reproductive class  
18 of the target trees. The most parsimonious model (indicated in bold) is the one with the  
19 lowest AIC<sub>c</sub>. Slope and R<sup>2</sup> (the goodness of fit) are given for the best model.

20

21 **Table 4** Maximum likelihood parameter values with two unit support intervals (in  
22 parentheses) for the selected best models. PotRG: maximum potential radial growth (mm yr<sup>-1</sup>);  
23 X<sub>0</sub>: trunk diameter (mm) of the target tree at which PotRG occurs; X<sub>b</sub>: breadth of the  
24 function; sd: standard deviation.

25

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1 **Fig. 1** Observed frequency distribution of trunk diameter (stem diameter at 10 cm from the  
2 ground) for male, female and non- reproductive *Juniperus thurifera* individuals. Diameters  
3 are separated into 10 mm classes.

4

5 **Fig. 2** Predicted radial growth (mm yr<sup>-1</sup>) as a function of size (trunk diameter in mm) for  
6 each reproductive class in the absence of competition effects. See Table 4 for the estimated  
7 parameters of the fitted eqn 1. Confident intervals are represented by continuous lines.

8

9 **Fig. S1** Geographic distribution of *Juniperus thurifera*, indicating those areas where the  
10 species appears as dominant. This map has been drawn based on information from the Mapa  
11 Forestal de España 1:50,000 (Ministerio de Medio Ambiente and Banco de Datos de la  
12 Biodiversidad).

13

14 **Fig. S2** On the left panel, predicted vs observed growth data and the R<sup>2</sup> (percentage of  
15 variance explained of the best models). The solid lines represent linear regressions with a  
16 zero intercept and slope of one. On the right panel, residuals vs predicted data for the  
17 different reproductive classes and the whole dataset.

18 .

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1 **Table 1** Summary data from target trees. **Number of individuals, age, growth rate, trunk**  
 2 **diameter and height for each reproductive class are shown.** Statistical differences between  
 3 reproductive classes were tested using one way anova test in: Age, Growth rate\*, Trunk  
 4 diameter\*\*, Height. **SE means standard error.**

		Male trees	Female trees	Non-reproductive trees
Number of individuals		115	105	79
Age (yr)	range	23-41	26-42	23-41
	mean	33.14 a	34.19 a	31.27 b
	SE	0.33	0.35	0.4
Growth rate (mm yr <sup>-1</sup> )	range	0.17-1.85	0.26-2.78	0.22-1.43
	mean	0.77 a	0.84 a	0.50 b
	SE	0.05	0.05	0.04
Trunk diameter (mm)	range	28.97-165.50	31.19-176.70	25.46-84.35
	mean	71.86 a	81.04 a	45.02 b
	SE	3.37	3.43	2.59
Height (cm)	range	150.00-470.00	150.00-480.00	70.00-260.00
	mean	258.17 a	275.52 a	156.89 b
	SE	8.94	9.11	6.88

5 Different letters indicate significant differences between reproductive classes for the studied  
 6 variables at  $\alpha = 0.05$ .

7 \* Estimated at 10 cm from the ground

8 \*\* Measured at 10 cm from the ground

9

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1 **Table 2** Summary data of neighbourhood conditions for target trees in each reproductive  
 2 class. Range, mean and standard error (SE) are shown for each variable. NCI (Neighborhood  
 3 Competition Index) is the total basal area (cm<sup>2</sup>) from neighbours contained in  
 4 circumferences at different distances (1, 2 and 3 m) from the target tree; and Aver. n° ind. is  
 5 the average number of individuals contained in circumferences at different distances from  
 6 the target tree. Differences between reproductive classess were tested using one way anova  
 7 test in NCI and with genelarize linear models (family= Poission distribution) in Aver. n° ind.  
 8

		Male trees	Female trees	Non-reproductive trees
NCI (1m) (cm <sup>2</sup> )	range	0-281.62	0-266.00	0-358.10
	mean	52.44 a	47.47 a	57.35 a
	SE	6.34	8.24	8.39
NCI (2m) (cm <sup>2</sup> )	range	32.56-644.04	6.44-504.34	47.80-1045.13
	mean	164.65 a	172.87 a	203.58 a
	SE	14.10	18.31	18.66
NCI (3m) (cm <sup>2</sup> )	range	35.43- 914.65	140.89- 1191.94	158.38-1495.60
	mean	273.87 a	245.45 ab	293.64 b
	SE	19.62	25.48	25.97
Aver. n° ind. (1 m)	range	0-10	0-10	0-8
	mean	2.10 b	2.33 a	2.71 a
	SE	0.09	0.09	0.07
Aver. n° ind. (2 m)	range	2-24	1-19	3-24
	mean	8 b	9 c	10 a
	SE	0.05	0.05	0.03
Aver. n° ind. (3 m)	range	4-36	7-38	8-37
	mean	18 b	19 c	20 a
	SE	0.03	0.03	

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- 1 Different letters indicate significant differences between reproductive classes for the studied
- 2 variables at  $\alpha = 0.05$
- 3

4 **Table 3** Comparison of alternate growth models analysing the effect of size and  
 5 competition at three different distances for the whole population together and for each  
 6 reproductive class of the target trees. The most parsimonious model (indicated in bold)  
 7 is the one with the lowest AIC<sub>c</sub>. NP means the number of parameters of the model.  
 8 Slope and R<sup>2</sup> (the goodness of fit) is given for the best model.  
 9

		NP	AIC <sub>c</sub>	ΔAIC	Slope: R <sup>2</sup>
<i>All target trees</i>	Null	2	219.36	198.12	
	<b>Size</b>	<b>4</b>	<b>21.25</b>	<b>0.00</b>	<b>1.00 0.49</b>
	Competition (R=1 m)	4	223.34	202.09	
	Competition (R=2 m)	4	216.18	194.93	
	Competition (R=3m)	4	221.46	200.21	
	Gender competition (R=1 m)	10	223.40	202.15	
	Gender competition (R=2 m)	10	228.32	207.07	
	Gender competition (R=3 m)	10	228.59	207.34	
	Size + competition (R= 2 m)	6	25.28	4.03	
<i>Male trees</i>	Null	2	68.40	61.47	
	<b>Size</b>	<b>4</b>	<b>6.93</b>	<b>0.00</b>	<b>1.00 0.44</b>
	Competition (R=1 m)	4	71.08	64.16	
	Competition (R=2 m)	4	71.82	64.89	
	Competition (R=3 m)	4	70.40	63.48	
	Gender competition (R=1 m)	10	81.36	74.43	
	Gender competition (R=2 m)	10	75.55	68.62	
	Gender competition (R=3 m)	10	76.72	69.79	
	<i>Female trees</i>	Null	2	109.08	56.79
<b>Size</b>		<b>4</b>	<b>52.28</b>	<b>0.00</b>	<b>1.00 0.35</b>
Competition (R=1 m)		4	97.53	45.25	
Competition (R=2 m)		4	94.98	42.69	

	NP	AIC <sub>c</sub>	ΔAIC	Slope:	R <sup>2</sup>
Competition (R=3 m)	4	97.02	44.73		
Gender competition (R=1 m)	10	109.94	57.66		
Gender competition (R=2 m)	10	96.26	43.97		
Gender competition (R=3 m)	10	105.07	52.78		
Size + competition (R=1 m)	6	56.95	4.66		
Size + competition (R=2 m)	6	57.00	4.71		
Size + competition (R=3m)	6	57.02	4.73		
Size + gender competition (R=1 m)	10	381.08	328.80		
Size + gender competition (R=2 m)	10	380.43	328.15		
Size + gender competition (R=3 m)	10	377.65	325.37		
<i>Non-reproductive trees</i>					
Null	2	363.19	46.82		
<b>Size</b>	<b>4</b>	<b>316.37</b>	<b>0.00</b>	<b>0.99</b>	<b>0.48</b>
Competition (R=1 m)	4	366.07	49.70		
Competition (R=2 m)	4	367.57	51.20		
Competition (R=3 m)	4	367.56	51.18		
Gender competition (R=1 m)	10	381.08	64.71		
Gender competition (R=2 m)	10	380.43	64.06		
Gender competition (R=3 m)	10	377.65	61.28		

10

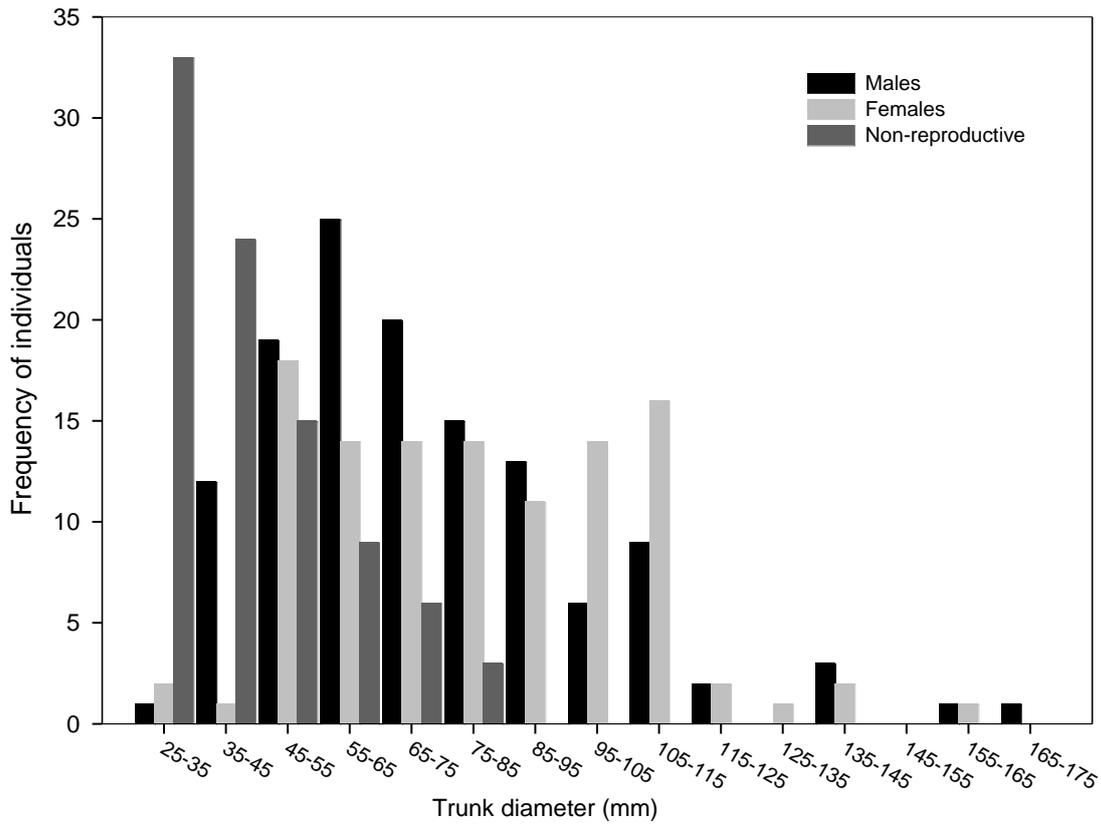
11

12 **Table 4** Maximum likelihood parameter values and 2-unit support intervals [in  
 13 brackets] for the selected best models. Pot RG: maximum potential radial growth mm  
 14 year<sup>-1</sup>; X<sub>0</sub>: trunk diameter (mm) of the target tree at which Pot RG occurs; X<sub>b</sub>: breadth  
 15 of the function; sd: standard deviation.

	<b>MODEL</b>	<b>Pot RG</b>	<b>X<sub>0</sub></b>	<b>X<sub>b</sub></b>	<b>sd</b>
<i>all trees</i>	<b>Size</b>	2.40	1000	1.76	0.25
		[2.33-2.47]	[960.40-1000]	[1.74-1.77]	[0.23-0.27]
<i>Male trees</i>	<b>Size</b>	1.93	616.34	1.61	0.24
		[1.83-2.03]	[579.96-662.38]	[1.56-1.65]	[0.22-0.27]
<i>Female trees</i>	<b>Size</b>	2.56	996.27	1.69	0.30
		[2.39-2.73]	[927.13-1000]	[1.64-1.74]	[0.26-0.34]
<i>Non-reproductive trees</i>	<b>Size</b>	0.99	158.11	1.10	1.70
		[0.94-1.00]	[146.30-169.90]	[1.05-1.17]	[1.47-2.00]

16

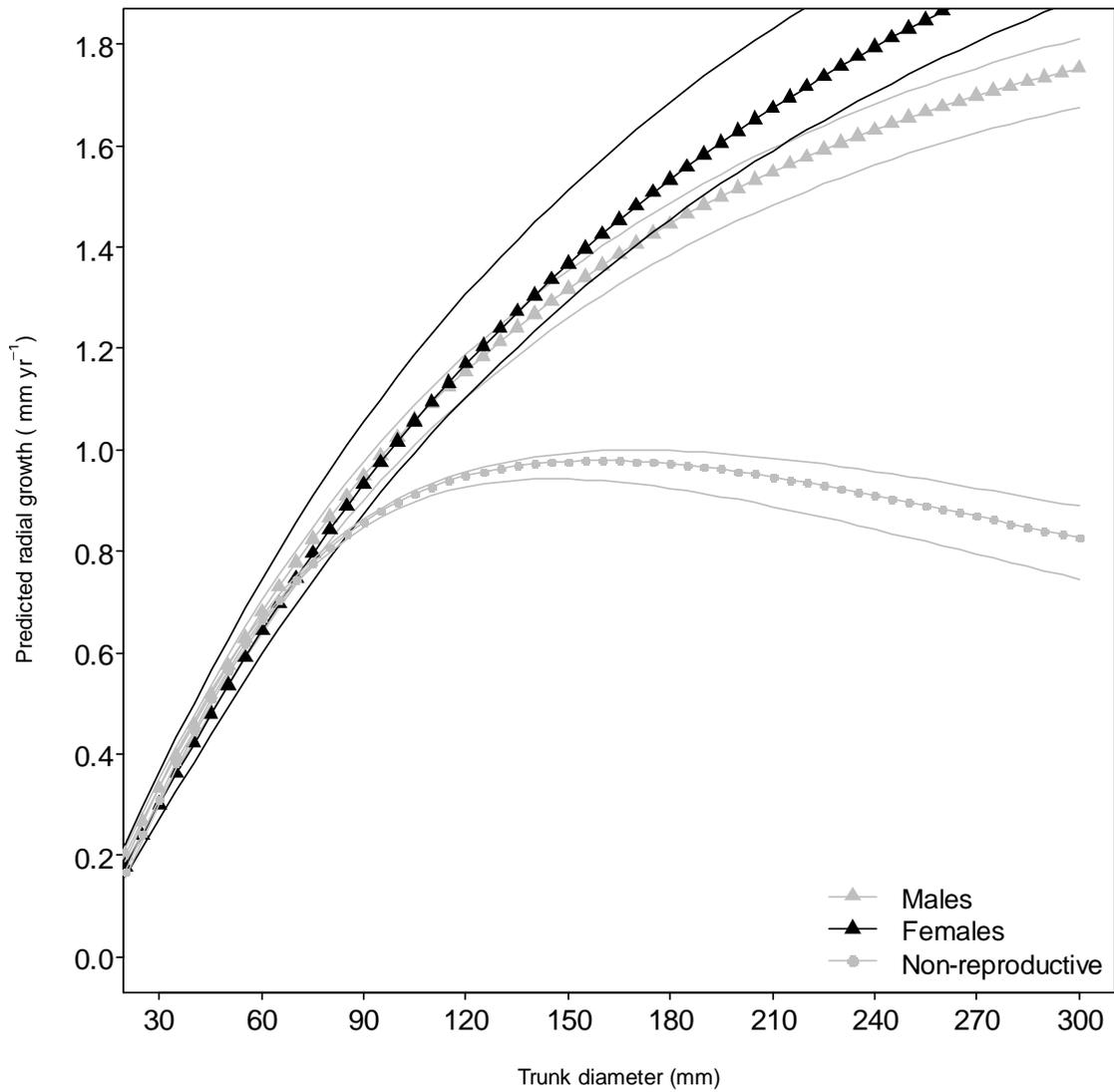
17



18

19 **Fig. 1** Observed frequency distribution of trunk diameter (stem diameter at 10 cm from  
 20 the ground) for male, female and non- reproductive *Juniperus thurifera* target  
 21 individuals. Diameters are separated into 10 mm classes.

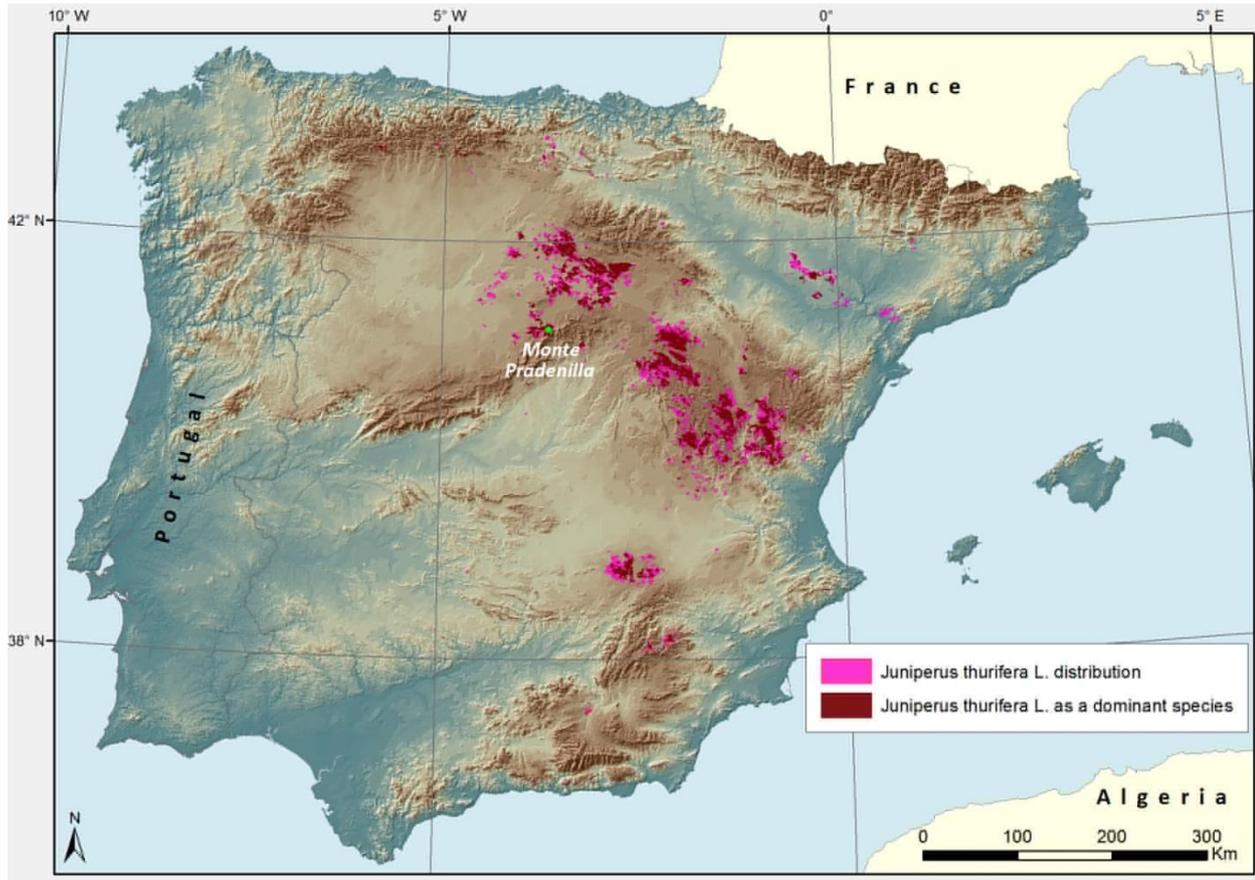
22



23

24 **Fig. 2** Predicted radial growth (mm yr<sup>-1</sup>) as a function of size (trunk diameter in mm) for  
 25 each reproductive class in the absence of competition effects. See Table 4 for the  
 26 estimated parameters of the fitted eqn 1. Confidence intervals are represented by  
 27 continuous lines.

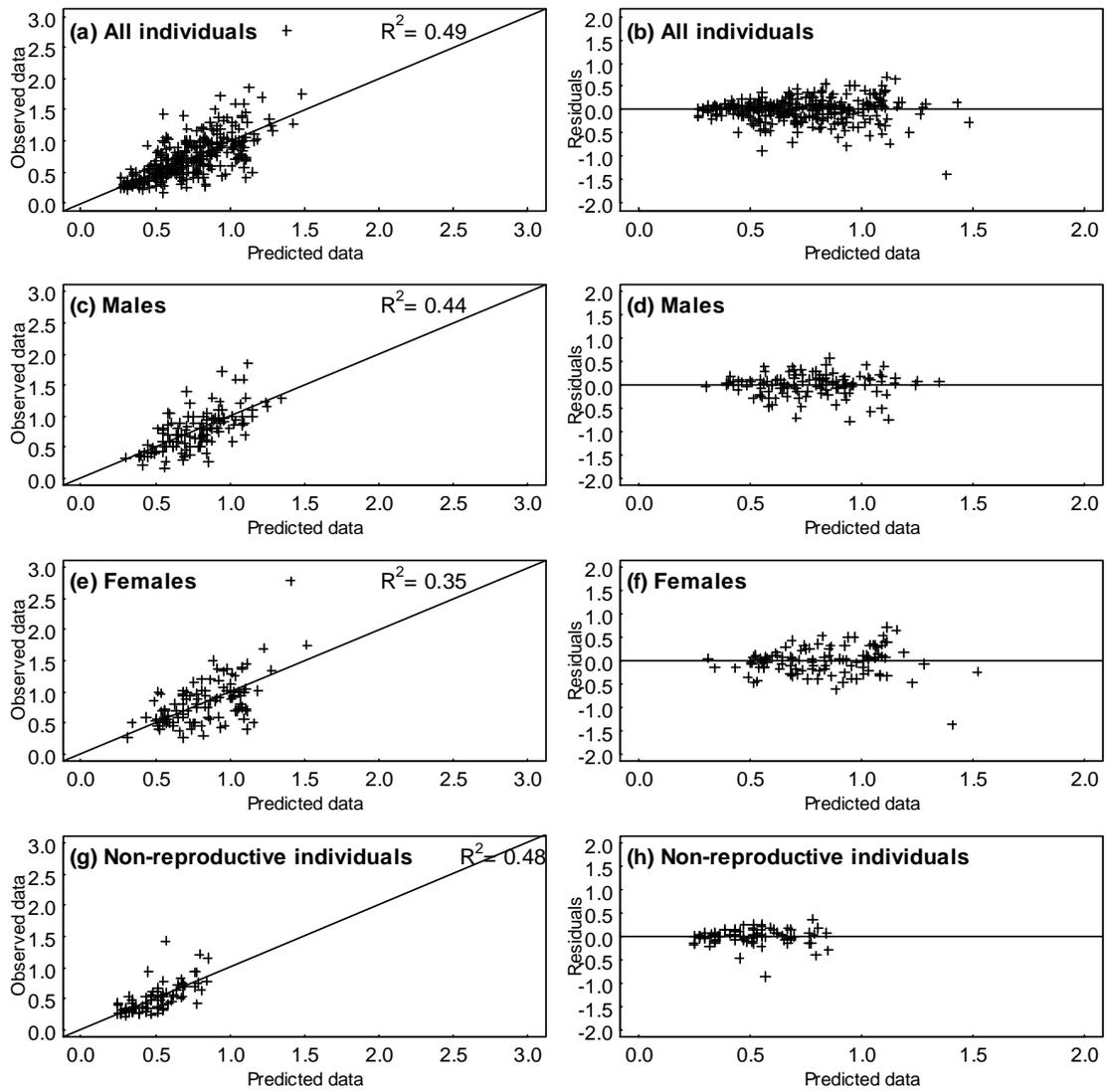
28



1

2 **Fig. S1** Geographic distribution of *Juniperus thurifera*, indicating those areas where the species  
3 appears as dominant. This map has been drawn based on information from the Mapa Forestal de  
4 España 1:50,000 (Ministerio de Medio Ambiente and Banco de Datos de la Biodiversidad).

5



1

2 **Fig. S2** On the left panel, predicted vs observed growth data and the  $R^2$  (percentage of  
 3 variance explained of the best models). The solid lines represent linear regressions with  
 4 a zero intercept and slope of one. On the right panel, residuals vs predicted data for the  
 5 different reproductive classes and the whole dataset.

6