

1 **Resilience to drought in a dry forest: insights from demographic** 2 **rates**

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27 **Abstract**

28 Concern is rising on whether forest function and structure will recover from drought-related
29 impacts, which are expected to increase under global warming. Understanding demographic
30 mechanisms underlying resilience (i.e. capacity of a system or individual to restore its
31 structure and function prior to a disturbance) is critical for properly assessing forest
32 vulnerability to drought. The simultaneous estimation of resilience of the main demographic
33 rates governing tree population dynamics (growth, recruitment and survival) allows for a
34 comprehensive assessment of forest response capacity. We evaluate the resilience of a large
35 *Pinus pinaster* forest (approx. 7,500 ha) in Southern Europe to one of the driest decades of the
36 last 70 years (i.e. 1942-52). As forest structure and management influence demographic rates,
37 their effects were removed prior to calculating resilience values for growth, recruitment and
38 survival. The extremely dry conditions negatively impacted tree growth and recruitment
39 during drought and slightly decreased survival in the decade after drought. Resilience values
40 were mostly high, despite some low values for recruitment or survival in some forest sections,
41 which indicate a general recovery of growth and recruitment and an absence of widespread
42 reductions in survival after drought. A joint analysis of the Demographic Resilience Index
43 (calculated by combining growth, recruitment and survival resilience; DRI) and resilience
44 values of each rate allows to detect demographic compensation effects. High DRI values,
45 even in sections where resilience in recruitment or survival was low, indicate that low
46 resilience values in a given rate were compensated by high resilience in the remaining rates.
47 Recorded resilience could allow the long-term persistence of the studied forest, although
48 increased frequency and intensity of droughts might exceed the critical threshold of system's
49 resilience. Our approach provides a step toward an exhaustive resilience assessment;
50 however, further research should consider potential resilience thresholds arising from more
51 complex non-linear dynamics.

52 **Keywords:** extreme climatic events, forest dynamics, forest management, vulnerability,
53 ecosystem functioning, demographic compensation.

54

55 **Introduction**

56 There is an increasing interest in predicting and quantifying potential impacts of climate
57 change on forest ecosystems, as they provide important ecological, societal and climatological
58 benefits (MEA, 2005; FAO, 2012; Gamfeldt *et al.*, 2013). Drought is a chief climatic-type
59 disturbance that constrains tree growth (Martínez-Vilalta *et al.*, 2012; Herrero & Zamora,
60 2014; Brienen *et al.*, 2015), reduces recruitment (Floyd *et al.*, 2009; Mendoza *et al.*, 2009;
61 Matías *et al.*, 2012) and increases mortality (Williamson *et al.*, 2000; Koepke *et al.*, 2010;
62 Herrero *et al.*, 2013a). The expected rise in the frequency of droughts for many regions
63 (including Southern Europe), along with more intense droughts due to warming conditions
64 (IPCC, 2013; Trenberth *et al.*, 2014), can spread and exacerbate drought-related impacts on
65 forests. Changes in species composition and dominance in forest ecosystems can occur
66 through species-specific drought-induced reductions in growth, recruitment and survival
67 (Allen & Breshears, 1998; Peñuelas *et al.*, 2007; Suárez & Kitzberger, 2008). However, the
68 persistence of these changes and the ability of forests to recover from drought-related impacts
69 remain largely untested in the absence of solid empirical evidence based on demographic
70 responses in the long run.

71 Shifts in forest structure and composition in response to drought could alter ecosystem
72 functions profoundly, affecting hydrological processes (Allen, 2007; Adams *et al.*, 2012),
73 nutrient cycling (Hughes *et al.*, 2006; Xiong *et al.*, 2011) and land-surface properties (Royer
74 *et al.*, 2011; Anderegg *et al.*, 2013). In this context, resilience is an important concept that is
75 gaining unprecedented attention in ecology (e.g. Reyer *et al.*, 2015). Resilience is the capacity
76 of an ecosystem, community or individual to restore pre-disturbance structure and function

77 after a disturbance (analogous to ‘engineering resilience’, see Holling 1996; see also Lloret *et*
78 *al.*, 2011). Thus, the assessment of forest resilience to climatic disturbances, such as extreme
79 droughts, provides critical information about the capacity of forests to maintain their structure
80 and to continue providing valuable ecosystem services. Furthermore, the analysis of resilience
81 using multiple demographic rates allows us to detect key vulnerabilities to drought in tree
82 population dynamics, such as reductions in recruitment or survival, which can prompt a
83 decline in dominant species shaping forest structure.

84 Although recurrent and extreme droughts can change forest structure and composition,
85 demographic compensation can boost forest resilience and allow ecosystem functions to be
86 maintained (Doak & Morris, 2010). For example, tree mortality after an extreme drought may
87 be compensated by enhanced growth and recruitment due to the release of competition with
88 established vegetation and to the beneficial effect of new conditions derived from global
89 warming and climatic variability (Lloret *et al.*, 2012). In this sense, global warming can
90 benefit tree growth lengthening the growing season (Peñuelas & Filella, 2001) and boosting
91 growth under relatively wet conditions (Juday *et al.*, 2015). In addition, sporadic rainy events
92 can also enhance tree recruitment in drought-prone areas (Matías *et al.*, 2012). Furthermore,
93 even if dry conditions prevent recruitment, dominant species could persist due to high
94 survival ability (García & Zamora, 2003). However, the evaluation of resilience in forest
95 ecosystems often focus on a single demographic rate, usually growth (Lloret *et al.*, 2011;
96 Herrero & Zamora, 2014; Merlin *et al.*, 2015) or recruitment (Jakovac *et al.*, 2015, Standish *et*
97 *al.*, 2015). Using only one demographic process provides an incomplete estimation of
98 resilience capacity that precludes the detection of synergies or trade-offs between
99 demographic rates. The simultaneous evaluation of resilience in terms of growth, recruitment
100 and survival will provide an overall assessment of forest response capacity and allow explore
101 relationships between the main demographic rates in tree population dynamics.

102 In the present study, we analyzed forest resilience to one of the driest decades of the
103 last 70 years in a large forested area in Southern Europe. Resilience in tree growth,
104 recruitment and survival was simultaneously assessed in a *Pinus pinaster* Ait. dry forest using
105 demographic data for a 30-year period before, during and after the extreme drought event. As
106 forest structure and management might influence demographic rates, their effects were
107 removed prior to the evaluation of resilience for each demographic rate. This integrated
108 evaluation of resilience through main demographic rates governing tree population dynamics
109 provides valuable information about the ability of forests to persist and to supply ecosystem
110 services in the near future under increased aridity. Also, it offers the possibility to identify
111 coupled demographic patterns during and after an extreme drought event.

112

113 **Material and Methods**

114 *Study Area*

115 The study was conducted in a managed dry forest ecosystem of approx. 7,500 ha located at
116 841 m a.s.l. in the central Iberian Peninsula (41°19'N – 4°12'W; see Fig. A.0). *Pinus pinaster*
117 is the dominant tree species, although other pines (*P. sylvestris* L., *P. nigra* Arnold) and oaks
118 (*Quercus ilex* L., *Q. faginea* Lam. and *Q. pyrenaica* Willd.) are marginally present in the
119 nearby seasonal streams or located in depressions. *P. pinaster* is a widespread-dominant pine
120 species in the Western Mediterranean basin, growing in a variety of substrates, elevations and
121 climate types (Barbéro *et al.*, 1998). The forest understory is mostly occupied by disperse
122 vegetation dominated by dwarf shrubs, annual plants and soil lichens. This forest occupies a
123 large, homogeneous territory across inland dunes in Central Spain, with sandy and highly
124 unconsolidated soils displaying low nutrient content and very low water retention capacity
125 (Gómez-Sanz & García-Viñas, 2011). Forest management is a shelterwood cutting, defined as
126 a progression of forest cuttings leading to the establishment of a new generation of seedlings

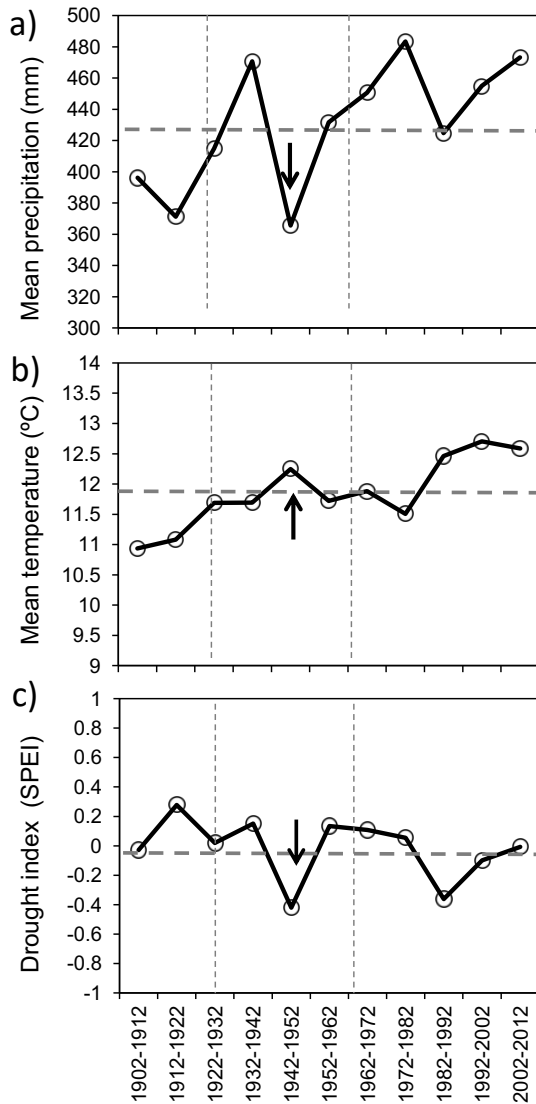
127 of a particular species or group of species (see Smith *et al.*, 1997 for further descriptions).
128 Shelterwood cutting is performed in permanent plots with moderate thinning and natural
129 regeneration over a 100-year rotation period. Alongside wood harvesting, resin extraction
130 constituted an important activity in the study area since the nineteenth century. The resin
131 extraction system employed was the Hughes method, performed forming concave resin faces
132 by extracting a part of the wood, which requires specialized labor (Rodríguez *et al.*, 2008).
133 The climate is continental Mediterranean, characterized by cold winters and hot and dry
134 summers (see Fig. A.1). Annual total precipitation is 430 mm and annual mean temperature is
135 11.9 °C. Average minimum temperature is below 0 °C in winter (December-March) and
136 average maximum temperature is above 30 °C in summer (June-September).

137

138 *Climatic data*

139 The Standardized Precipitation-Evapotranspiration Index (SPEI) was used to summarize
140 differences in moisture conditions among decades (Vicente-Serrano *et al.*, 2010). This global
141 database uses monthly total precipitation and mean temperature data from version 3.20 of the
142 CRU database for the period 1901-2011. SPEI values were calculated for a 12-month period
143 (from previous September to current August) and then averaged for each decade of study. The
144 1942-52 decade in particular was one of the driest periods of the last 70 years as shown by the
145 high negative average SPEI value, which is indicative of moisture deficit (Fig. 1).

146



147

148 **Figure 1.** Mean precipitation (a), temperature (b) and Standardized Precipitation-Evapotranspiration Index
 149 (SPEI) (c) per every decade during period 1902-2012 in the study area. Mean SPEI summarizes differences in
 150 moisture conditions among decades. Negative SPEI values indicate a moisture deficit. Vertical broken lines
 151 delimit the three decades of study and the arrows highlight the extremely dry and hot decade of 1942-52. The
 152 horizontal broken line marks the mean values for precipitation and temperature for the whole period, and a zero
 153 value for SPEI (i.e. no moisture deficit).

154

155 The studied decade was characterized by recurrent droughts (seven years with
 156 negative SPEI values), with three of them being exceptionally intense (under the 10th
 157 percentile for SPEI during the last 100 years; see Fig. A.2). On the contrary, the previous

158 (1932-42) and the following (1952-62) decades correspond to the mean moisture conditions
159 of the study area (see drought index, Fig. 1).

160

161 *Growth, recruitment and survival*

162 Growth, recruitment and survival data were recorded in a historical archive and accessed with
163 the permission of the regional agency for environmental management located in Segovia
164 (Spain). This archive contains detailed information about forest management (e.g.
165 shelterwood cutting, moderate thinning and natural regeneration), product exploitation (e.g.
166 hunting, wood and resin extraction), and stocks (e.g. number of trees and wood volume)
167 gathered every ten years since 1912 until its latest update in 2002 (see details in Madrigal-
168 González *et al.*, 2015). For administrative reasons, the forest was subdivided into 10 spatial
169 units (hereafter forest section) which represent smaller replicates (approx. 750 ha each) of the
170 whole forest in the sense that, in all of them, stocks and resources were similarly managed
171 following the same methodology and purpose.

172 Growth, recruitment and survival were calculated for the three decades of study (1932-
173 62). Growth of adult trees (i.e. ≥ 20 cm diameter at breast height, d.b.h.) was calculated as the
174 difference between wood volumes measured in consecutive inventories plus wood stocks
175 removed during the decade for each forest section (Madrigal-González *et al.*, 2015) and
176 expressed as wood volume increment relative to initial wood stock per hectare and year (%
177 $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$). Tree recruitment was quantified as the number of trees (No. trees) per hectare
178 that reach 20 cm d.b.h. every decade and was made relative to the number of adult trees in the
179 initial inventory. After that, recruitment was expressed as a percentage relative to hectare and
180 year (% No. trees $\text{ha}^{-1} \text{yr}^{-1}$). Tree survival was calculated subtracting the number of dead adult
181 trees due to natural causes (i.e. insect diseases, drought, windstorms) from the total number of

182 adult trees and was expressed relative to the number of adult trees in the initial inventory per
183 hectare and decade (% No. trees ha⁻¹ yr⁻¹).

184

185 *Data analysis*

186 To assess the impact of the extreme drought and the posterior resilience in growth,
187 recruitment and survival, data for the three decades of study were used: before-drought (1932-
188 42), during-drought (1942-52) and after-drought decade (1952-62). Firstly, we fitted Linear
189 Mixed-Effects models to explore the explanative contribution of structural and management
190 factors to each response variable (growth, recruitment and survival). Mean tree size (m³),
191 wood thinning (m³ ha⁻¹) and resin extraction (Mg ha⁻¹) were the structural and management
192 factors considered. Forest section was considered as a random factor affecting the intercept
193 parameter of the model, under the assumption that inventories conducted on the same forest
194 section are not mutually independent. A backward model selection starting with a maximal
195 model and removing one predictor at a time was applied for model selection. We considered
196 the Akaike Information Criterion corrected for small sample size (AICc) to test the
197 contribution of each predictor to the maximal model, following the rule that an increment of
198 at least 2 AICc units after the elimination of any given predictor variable from the maximal
199 model indicates a significant effect of this predictor on the dependent variable (Burnham and
200 Anderson, 2002). We tested for collinearity in the final models using the Variance Inflation
201 Factor (VIF) assuming a threshold of 3 units where upper values imply troubled collinearity
202 (Zuur *et al.*, 2010).

203 Once the best model for each of the three dependent variables was achieved, Pearson's
204 residuals from the selected models were scaled to 0-1 values according to the following
205 formula:

$$206 \quad \text{scaled } x_i = [(x_i - \min(x_j))/(\max(x_j) - \min(x_j))] + 1$$

207 where x_i is the residual value for a given observation i , and $\max(x_j)$ and $\min(x_j)$ are the
208 maximum and minimum residual values for a given demographic variable j (growth,
209 recruitment and survival). These scaled residuals are values of growth, recruitment and
210 survival without the effects of forest structure and management, and were used to calculate
211 impact and resilience values. The employed scaling procedure allowed us to calculate impact
212 and resilience values avoiding negative and zero values (see below).

213 Impact and resilience were calculated applying the procedure of Lloret and others
214 (2011) on the scaled Pearson's residuals. Impact, defined as the reduction in performance
215 (growth, recruitment or survival) during disturbance (in this study the extremely dry decade of
216 1942-52), was calculated as follows:

$$217 \quad \text{Impact} = 1 - (\text{Dr} / \text{PreDr})$$

218 where Dr is the during-drought and PreDr the before-drought performance (expressed
219 as growth, recruitment or survival scaled residuals). Impact values represent the reduction in
220 performance per unit. Negative impact values represent cases where during-drought
221 performance was greater than before-drought performance. Resilience, the capacity to return
222 to performance levels prior to a disturbance, was calculated as the ratio between after- and
223 before-drought performance. While a resilience value of 1 indicates a total recovery for a
224 given variable (that is, after-drought performance is identical to before-drought performance),
225 values higher than 1 mean greater after- than before-drought performance, and values lower
226 than 1 lower performance. Note that zero values for before-drought scaled residuals prevent
227 the calculation of resilience and impact values. Also, negative values for residuals prevent the
228 correct calculation of impact values and can result in negative resilience values (hampering an
229 easy interpretation of resilience values). The residuals were scaled to 0-1 values in order to
230 avoid these troubles.

231 Coupled with the calculation of impact and resilience, we compared scaled residuals
232 between decades for each demographic rate. To do this, linear models were fitted to the scaled
233 residuals of growth, recruitment and survival separately against ‘decade’ as a predictor. The
234 adjusted models were compared with the three respective null models without ‘decade’ to test
235 for differences in the three demographic rates during and after the drought event. We kept the
236 before-drought decade as the intercept parameter in the model to directly evaluate the effects
237 of during-drought (associated with drought impact) and after-drought (associated with
238 resilience to drought) on the response variables. A t-value test conducted on parameter
239 estimates showed us whether differences between decades for the scaled residuals of each
240 demographic rate were significantly different from zero.

241 Finally, we calculated a Demographic Resilience Index (DRI) combining growth,
242 recruitment and survival resilience values weighting each demographic variable equally. First,
243 resilience for each demographic variable was scaled to 0-0.333 values (previously resilience
244 values higher than 1 were set to 1). Then, growth, recruitment and survival scaled resilience
245 values were summed to obtain the DRI, which estimates the overall resilience capacity of the
246 forest, which varies from 0 (absence of resilience) to 1 (high resilience). Impact, resilience
247 and DRI were calculated for each forest section using corresponding scaled residuals of each
248 section, and then, impact, resilience and DRI values from sections were averaged for the
249 whole forest. All the analyses were performed using lme4 (Bates *et al.*, 2015) and stats
250 packages in the R environment (R Development Core Team 2013).

251

252 **Results**

253 *Demographic rates*

254 Values of relative tree growth per hectare and year ranged from 0% to 50%. Both mean tree
255 size and resin extraction had significant negative effects on tree growth (Table 1); i.e. larger

256 mean tree size and resin yields led to lower relative wood volume increments (Fig. A.3).
 257 Similar to growth, recruitment ranged from 0% to 60% of the standing tree stock and larger
 258 mean tree size and resin yields led to lower tree recruitment (Fig. A.3). Tree survival ranged
 259 from 85% to 100% of tree stock, although the majority of values were higher than 97%.
 260

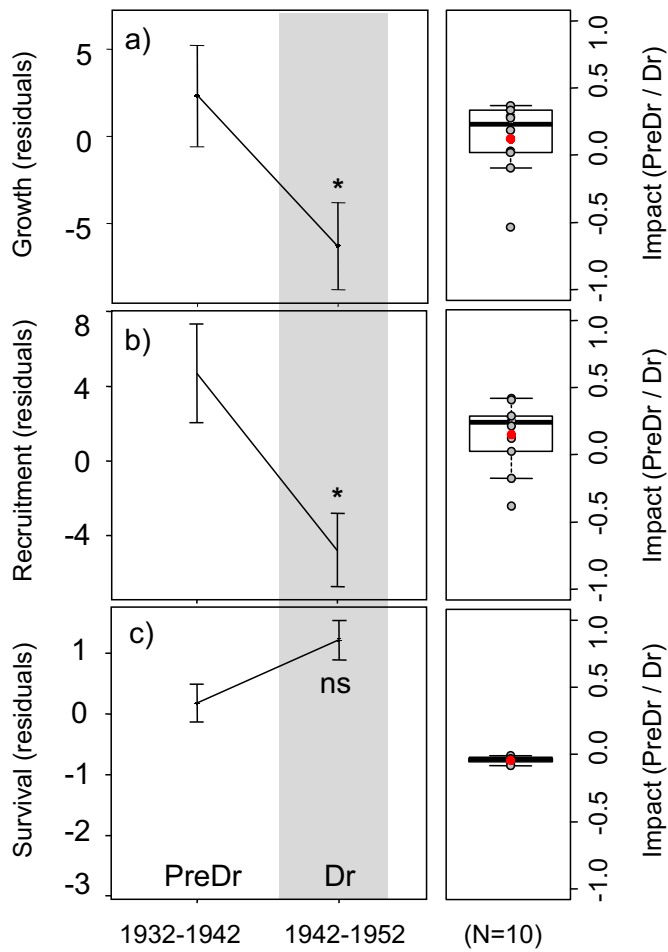
	Growth		Recruitment		Survival	
	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc
Full model	218.9502	0	224.2388	0	152.49	0
No MTS	227.06	8.1098	230.8799	6.6411	155.8186	3.3286
No Resin	224.1291	5.1789	227.6442	3.4054	151.8635	-0.6265
No Thinning	217.9241	-1.0261	223.9294	-0.3094	154.0485	1.5585
Null model	235.3782	16.428	237.7085	13.4697	162.7374	10.2474
Selected model	MTS + Resin		MTS + Resin		MTS	

261 **Table 1.** Backward selection of predictor variables separately for each demographic rate: growth, recruitment
 262 and survival. The Akaike Information Criterion corrected for small sample sizes (AICc) was used. Δ AICc is
 263 calculated as the AICc differences between the full model with the models ignoring the effects of mean tree size
 264 (No MTS), resin extraction (No Resin) and wood thinning (No Thinning) respectively. Models are assumed to be
 265 different whenever Δ AICc exceeds 2 units. Full model included mean tree size (MTS), wood thinning
 266 (Thinning) and resin extraction (Resin) as fixed factors.

267
 268 As shown by model selection, only mean tree size significantly affected survival with
 269 lower survival towards larger mean tree sizes (Table 1). The fitted models showed acceptable
 270 collinearity (maximum VIF = 1.07 for growth model and maximum VIF = 2.46 for
 271 recruitment).

272
 273 *Impact of drought*

274 The extremely dry decade of 1942-52 had a significant negative impact on both growth and
 275 recruitment (Fig. 2; see also model selection Tables 2), displaying averaged impact values of
 276 0.12 ± 0.08 and 0.15 ± 0.08 respectively (mean \pm SE).



278

279 **Figure 2.** Scaled Pearson's residual values (left column) for growth (a), recruitment (b) and survival (c) for
 280 before- (1932-42; PreDr) and during-drought decade (1942-52; Dr) and its associated impact (1-Dr/PreDr)
 281 values (right column). Residuals were obtained after fitting Linear Mixed-Effects models which included forest
 282 structure and management factors (mean tree size, resin yield and wood thinning). (*) indicates significant and
 283 (ns) non-significant differences between the two decades, respectively. The shaded area highlights values during
 284 the extremely dry decade and bars indicate the standard errors of calculated means (N=10 forest sections). In the
 285 box-plots grey circles indicate impact values for each forest section (approx. 750 ha each) and red circles
 286 represent the averaged impact value.

287 Therefore, growth and recruitment fell during drought by 12% and 15%, respectively.

288

Decade	Growth		Recruitment		Survival	
	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc
	210.6824	0	213.4737	0	150.993	0

Null model 221.8255 11.1431 224.1928 10.7191 154.333 3.0403

289 **Table 2.** Comparison of models fitted to scaled Pearson’s residual values for each demographic rate: growth,
 290 recruitment and survival. Models including decade as a predictor factor are compared to null models without any
 291 predictor variable and a fixed intercept parameter. The Akaike Information Criterion corrected for small sample
 292 sizes (AICc) was used. Models are assumed to be different whenever $\Delta AICc$ exceeds 2 units.

293
 294 The impact of drought varied between forest sections (i.e. sampling units) from no
 295 impact up to 37% and 42% reductions in growth and recruitment rates, respectively. Finally,
 296 no impact was detected for tree survival, with all the forest sections displaying very similar
 297 values (close to 0) and without significant differences in scaled residuals between before- and
 298 during-drought decades (Fig. 2).

	Growth		Recruitment		Survival	
	Estimate	Error	Estimate	Error	Estimate	Error
Intercept (before-drought 1932-42)	2.307	2.643	5.690	2.783	0.1749	0.8751
During-drought 1942-52	-8.611	3.738	-11.100	3.936	1.0381	1.2375
After-drought 1952-62	1.690	3.738	-5.970	3.936	-1.5627	1.2375

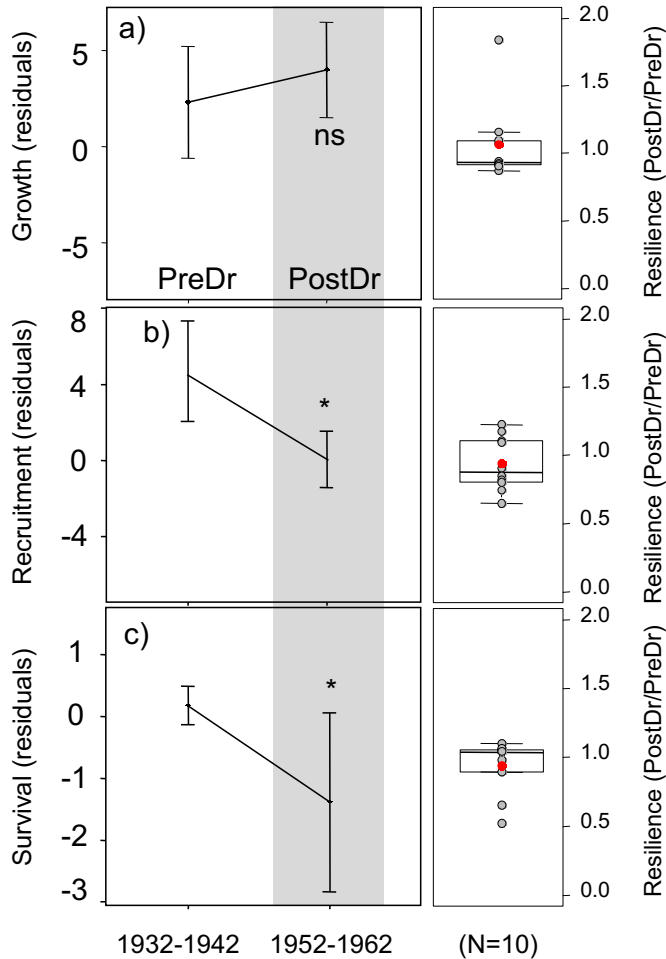
300 **Table 3.** Parameter estimates and associated error of models fitted to scaled Pearson’s residual values for each
 301 demographic rate: growth, recruitment and survival. Estimates significantly different from zero are highlighted
 302 in bold letters and indicate significant differences between decades for the scaled residuals. Note that differences
 303 between before- and during-drought decades are associated with the impact of drought and differences between
 304 before- and after-drought decades with the resilience to drought.

305
 306 However, survival declined the after-drought decade, suggesting a lagged impact of
 307 drought which affects the resilience in survival, although this lagged impact was noticeable in
 308 a few forest sections only (Fig. 3c).

309
 310 *Resilience to drought*

311 Averaged resilience values were high for the three demographic rates, with 1.06 for growth
 312 and 0.94 for recruitment and survival, which means there were similar after- and before-
 313 drought performance levels (Fig. 3).

314



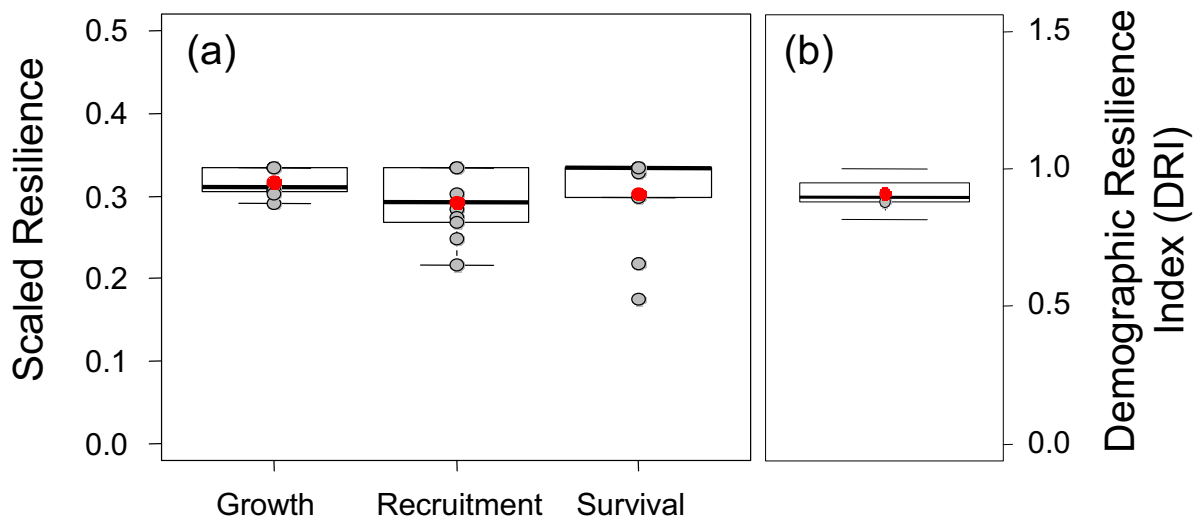
315

316 **Figure 3.** Scaled Pearson's residual values (left column) for growth (a), recruitment (b) and survival (c) for
 317 before- (1932-42; PreDr) and after-drought decade (1952-62; PostDr) and its associated resilience (Res.;
 318 PostDr/PreDr) values (right column). Residuals were obtained after fitting Linear Mixed-Effects models which
 319 included forest structure and management factors (mean tree size, resin yield and wood thinning). (*) indicates
 320 significant and (ns) non-significant differences between the two decades, respectively. The shaded area
 321 highlights values for after-drought decade and bars indicate the standard errors of calculated means (N=10 forest
 322 sections). In the box-plots grey circles indicate resilience values for each forest section (approx. 750 ha each) and
 323 red circles represent the averaged resilience value.

324

325 However, resilience values for the different forest sections revealed some differences
 326 between the demographic rates, especially with regard to minimum values. Growth displayed
 327 the highest resilience values (ranging from 0.87 to 1.84) and no significant differences were
 328 detected for the scaled residuals between before- and after-drought decades (Table 3, Fig. 3a).
 329 However, for recruitment (resilience ranging from 0.65 to 1.23) and survival (0.52-1.04) some
 330 forest sections displayed low resilience values (Table 3, Fig. 3b, c). Accordingly, scaled
 331 residuals were significantly lower after- than before-drought for recruitment and survival (Fig.
 332 3b, c), which indicate that some forest sections could not reach the before-drought
 333 performance levels.

334



335 **Figure 4.** Scaled resilience for growth, recruitment and survival (a) and the resulting Demographic Resilience
 336 Index (DRI) (b). Scaled resilience values are the resilience values scaled to a scale ranging from 0 to 0.333
 337 (previously resilience values higher than 1 were set to 1). DRI is the result of the sum of growth, recruitment and
 338 survival scaled resilience values and displays values ranging from 0 (absence of resilience) to 1 (high resilience).
 339 In the box-plots grey circles indicate values for each forest section (N=10; approx. 750 ha each) and red circles
 340 represent the averaged values.

342

343 Averaged DRI was 0.91, with little variation between values of forest sections (Fig. 4).
344 This indicates a compensation effect between demographic rates, as the lowest resilience
345 values for recruitment and survival (which occur at different forest sections) were balanced by
346 high resilience values in the remaining demographic rates. Therefore, low recruitment
347 resilience was compensated by high growth and survival resilience at some forest sections,
348 while low survival resilience was compensated by high growth and recruitment resilience at
349 other sections. This favored high DRI values in all cases (Fig. 4).

350

351 **Discussion**

352 The present study shows empirical evidence of demographic mechanisms underlying forest
353 resilience in response to an extreme drought. The 1942-52 decade was one of the driest
354 periods of the last 70 years in the region, which significantly reduced tree growth and
355 recruitment during drought and survival one decade after drought. The impact of this dry
356 period was also noticeable in the extremely narrow tree rings recorded for several tree species
357 in Southern Europe (Martín-Benito *et al.*, 2008; Linares & Tíscar, 2011; Herrero *et al.*,
358 2013b). Although some forest sections displayed low resilience values for recruitment or
359 survival, the majority of the values were close to 1, which means similar performance after
360 and before the drought. In addition, low resilience in recruitment or survival was compensated
361 by high resilience in the remaining demographic rates in different forest sections. Recorded
362 overall high resilience suggests a remarkably high tolerance of dry pinewoods to extreme and
363 long dry periods, which could allow for its long-term persistence and sustainable provision of
364 ecosystem services under the current context of increasing aridity. The present study
365 highlights the importance of long-term demographic data to assess forest vulnerability to
366 drought, especially under a global warming scenario where increases in drought-related
367 impacts in forests are expected (Allen *et al.*, 2015).

368 The high resilience to drought observed could be due to multiple factors. Local
369 adaptation could minimize the negative impact of drought on plant performance, for example,
370 thanks to a high root-shoot ratio that allows plants to access deeper water sources (Richter *et*
371 *al.*, 2012; Matías *et al.*, 2014). In this context, several studies suggest a high degree of local
372 adaptation for survival and growth across different *P. pinaster* provenances (Alía *et al.*, 1997,
373 González-Martínez *et al.*, 2002). Forest structure could also play a role in the observed
374 resilience capacity, with low tree densities avoiding strong inter-individual competition for
375 resources, especially water. Many studies point to strong competition for water between
376 individuals as one of the main causes for drought-related impacts in forest systems (Linares *et*
377 *al.*, 2009; Moreno-Gutiérrez *et al.*, 2011; Vilà-Cabrera *et al.*, 2011; Ruiz-Benito *et al.*, 2013).
378 Nevertheless, more studies are needed to clarify the role of other factors promoting tree
379 resilience, such as biotic interactions (e.g. mycorrhizae-plant interactions) or beneficial effects
380 of climate change (e.g. lengthening of the growing season; Peñuelas & Filella, 2001).

381 The extreme drought impacted the studied forest through reductions in growth,
382 recruitment and survival. Recorded decreases in growth could be due to the isohydric
383 behavior of *P. pinaster* in response to water stress, closing its stomata to avoid hydraulic
384 failure, which limits carbon uptake and photosynthesis (Ripullone *et al.*, 2007). This implies a
385 risk for carbon starvation-induced mortality during long dry periods, as a result of decreasing
386 non-structural carbohydrate availability (McDowell *et al.*, 2008). Although tree survival did
387 not decline during drought, it showed a significant reduction the decade after the drought,
388 suggesting a lagged impact of drought on survival. This lagged effect may be due to the
389 process of tree mortality, which could last several years (Pedersen, 1998a; McDowell *et al.*,
390 2008), or to the weakening of tree vigor, predisposing the tree to future stresses such as short-
391 term droughts or pathogen attacks (Manion 1981; Bigler *et al.*, 2006). However, this lagged
392 reduction in survival was remarkable only for a few forest sections and survival values never

393 dropped below 85%, with most of the values higher than 95%. Thus, although our results
394 demonstrate the potential deleterious effect of a prolonged and extreme drought, in general,
395 the critical threshold to cause adult tree mortality was barely reached. Finally, the observed
396 decline in recruitment could be explained by increases in seedling and sapling mortality,
397 reductions in sapling growth-rate and constraints in seed production. In fact, young trees
398 displayed great growth sensitivity to drought in the study area (Madrigal-González & Zavala,
399 2014). The assessment of forest resilience will provide information about how the forest
400 recovered for the mentioned drought-related impacts.

401 Despite the negative effects of drought, the target forest displayed an adequate
402 response capacity to restore its functions in the following ten years. Firstly, the high values of
403 growth resilience allowed for the recovery of tree growth potential and could be indicative of
404 increasing tree vitality after the disturbance (Dobbertin, 2005). The resilience values found
405 are comparable to those recorded in other studies conducted in water-limited areas (Herrero &
406 Zamora, 2014; Lloret *et al.*, 2011) and temperate climates (Merlin *et al.*, 2015). Thus, our
407 results suggest that tree growth in pine forests have the potential to recover from discrete
408 droughts and long dry periods. Secondly, despite low resilience in recruitment for some forest
409 sections, the overall recruitment resilience was high and would permit the self-replacement of
410 the individuals forming the canopy after the disturbance. Thirdly, even with the slight
411 reduction recorded in survival after drought, the rather high resilience values indicate the
412 absence of a widespread rise in adult tree mortality that could alter the structure of the forest.
413 Furthermore, we found a compensation effect between the different demographic rates,
414 allowing a high overall resilience capacity in all the forest sections sampled, as expressed by
415 consistently high DRI values. The lowest resilience values, recorded for recruitment or
416 survival, occurred separately at different forest sections along with high resilience values in
417 the remaining demographic rates. That is, while low recruitment was compensated by high

418 growth and survival, low survival was compensated by high growth and recruitment.
419 Therefore, the simultaneous assessment of resilience in main demographic rates allows
420 explore the relationship between them and detect key vulnerabilities to drought.

421 The employed methodology to estimate resilience in demographic rates (Lloret *et al.*,
422 2011) assumes linear changes in resilience capacity, while many theoretical models suggest
423 non-linear changes in ecosystem resilience based on threshold values between alternate states
424 (Carpenter *et al.*, 2001; Scheffer and Carpenter, 2003). However, the empirical detection of
425 these thresholds is complicated by the lack of detailed data about the multiple and interactive
426 factors influencing the resilience of a given ecosystem (e.g. temperature anomalies or soil
427 nutrient content). The proposed Demographic Resilience Index integrates growth, recruitment
428 and survival resilience and provides for the first time an empirical assessment of the overall
429 resilience capacity for dominant species shaping forest structure. The DRI index weights each
430 demographic rate equally, which may not be realistic, as some of the rates could be more
431 important than others for the persistence of the dominant tree population. Here, we encourage
432 the use of the index together with resilience values of each demographic rate separately, to
433 better acknowledge which rate is driving the resilience of the system and to explore the
434 potential existence of compensation mechanisms. The knowledge about the relative
435 importance of the different demographic rates for tree population dynamics, nowadays limited
436 due to the lack of long-term studies and the complex relationships between them, is critical to
437 properly integrate the different demographic rates when assessing resilience capacity. In this
438 context, tree survival could influence recruitment through a facilitative interaction, as the
439 shade provided by adult trees can ameliorate drought-stress for seedlings and saplings
440 (Rodríguez-García *et al.*, 2011; Ledo *et al.*, 2014). Likewise, high growth rates could allow
441 individuals to build a well-developed crown architecture and root system, which would favor
442 the subsequent investment in seed production. In conclusion, we provide a first approximation

443 to elaborate a more realistic index to be applied globally in order to assess the resilience
444 capacity of forest ecosystems.

445 To properly evaluate forest resilience capacity, it is also necessary to account for the
446 effects of forest structure and management on the main demographic rates. On the one hand,
447 tree size affects the main demographic rates, decreasing growth, survival and recruitment at
448 larger sizes, likely due to ageing effects (Day & Greenwood, 2011). However, rotation times
449 in managed forests for wood harvesting limits trees' maximum age, and, therefore, the
450 potential attribution to ageing effects. The observed growth reduction could also be due to
451 increasing hydraulic limitations with higher tree height (Magnani *et al.*, 2008). In the same
452 line, recruitment reduction could in addition be related to deeper shadow provided by bigger
453 trees, according to the light demanding nature of *P. pinaster* at young stages (Awada *et al.*,
454 2003). On the other hand, resin extraction also decreases both growth and recruitment,
455 probably caused by cambial damages (Bogino & Bravo, 2008) and by removing non-
456 structural carbohydrates that can be invested in growth or reproduction. Finally, the lack of
457 effects of thinning in tree growth and survival suggests that tree density was already low
458 enough to avoid strong inter-individual competition for resources. The knowledge of past and
459 current management activities is critical for the assessment of forest resilience. Most of the
460 forests of the northern hemisphere have been managed by humans for a long time, influencing
461 forest structure and composition (Kirby & Watkins, 1998). Thus, many ecological studies
462 deal with previously managed forests, but lack the information about past management
463 activities that can strongly influence the vulnerability of forests to drought stress (Camarero *et*
464 *al.*, 2011).

465 The present study disentangles the demographic mechanisms underlying the high
466 resilience capacity of a dry forest to an extreme drought event. However, forest resilience
467 could be diminished by recurrent droughts progressively weakening tree vigor leading to

468 mortality (Pedersen, 1998b; Bigler *et al.*, 2006), and/or by the increase in the intensity of
469 droughts, which could overwhelm the critical threshold of forest resilience. Other factors,
470 such as the beneficial effects of warming (Juday *et al.*, 2015) or adjustments in phenology
471 (Peñuelas & Filella, 2001), can play a role in forest resilience, counteracting in part the
472 detrimental effects of drought. Fire is another main disturbance in forest ecosystems, and the
473 expected increase in fire frequency in Southern Europe under different climate change
474 scenarios (Kovats *et al.* 2014 and references therein) represent a major threat for forest
475 resilience in these areas. Further, interactions between drought impacts and fire (e.g. drought-
476 induced tree mortality can increase fuel load; see also Allen, 2007; Brando *et al.*, 2016) could
477 additionally affect resilience capacity of forest ecosystems. The employed methodology,
478 considering the effects of forest structure and management on demographic rates, evaluating
479 resilience simultaneously in the main demographic rates, and combining resilience values in
480 an overall index, supposes a step toward a comprehensive resilience assessment in forest
481 ecosystems. Further research should be addressed to elucidate the actual role of each
482 demographic rate to properly integrate them in a more realistic resilience index to be applied
483 globally. The inclusion of information about resilience capacity in species distribution and
484 dynamic vegetation models would help to improve the accuracy of predictions concerning
485 tree species range shifts (Benito-Garzón *et al.*, 2011) and drought impacts on forests
486 (Steinkamp & Hickler, 2015), respectively. This information requires knowledge of the main
487 demographic rates for dominant species over extensive areas and long periods.

488

489 **Acknowledgements**

490 We thank Consejería de Medio Ambiente of the regional government of Castilla y León for
491 access to historical archives. This study was supported by VULPINECLIM (MINECO:
492 CGL2013-44553-R to M.A.Z), by the Basque Country Government post-doctoral grant (POS-

493 2014-1-88) to A.H, and by Plant Fellows (Grant Agreement No. PCOFUND-GA-2010-
494 267243) and Juan de la Cierva (FJCI-2014-19921) to P.R.B., which received funding from the
495 European Commission's Seventh Framework Programme (FP7/2007-2013) and The
496 Leverhulme Trust (No. IN-2013-004). The authors have declared that no conflicts of interests
497 exist. English language was edited by a professional editor of the Translation Editorial
498 Service of the University of Alcalá.

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- 714

715 **APPENDICES**

716 Additional supporting information may be found in the online version of this article:

717

718 **Figure A.1** Ombrotermic diagram displaying monthly mean temperature (solid line) and
719 monthly total precipitation (empty bars) for the period 1970-2010 in the study area.

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721 **Figure A.2** Standardized Precipitation-Evapotranspiration Index (SPEI) from 1912 to 2012.

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723 **Figure A.3** Growth, recruitment and survival relations with mean tree size, resin yield and
724 wood thinning.

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