

Highlights

- *A. pinsapo* response to climate change depends on stand structure and composition.
- Severe drought reduces the resistance and resilience of *A. pinsapo* to subsequent droughts.
- Competition reduced growth in *A. pinsapo*-*C. atlantica* mixed forests but not in *A. pinsapo*-*P. nigra* mixed forests.
- Climate severely influenced the structure and competition of *A. pinsapo* forests compromising their long-term persistence.

The Authors: Rafael M Navarro-Cerrillo, Rubén D. Manzanedo, Carlos Rodriguez, Antonio Gazol, Guillermo Palacios, J. Julio Camarero.

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2 **Competition modulates the response of growth to climate in pure and**
3 **mixed *Abies pinsapo* subsp. *maroccana* forests in northern Morocco**

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5 **Rafael M Navarro-Cerrillo^{1*}, Rubén D. Manzanedo^{2, 3}, Carlos Rodríguez¹, Antonio**
6 **Gazol^{4,5}, Guillermo Palacios¹, J. Julio Camarero⁵**

7 ¹Depto. Ingeniería Forestal, Grupo de Evaluación y Restauración de Sistemas Agrícolas y
8 Forestales – Lab, de Selvicultura, Dendrodat y Cambio climático. Universidad de Córdoba.
9 Campus de Rabanales, Crta. IV, km. 396, 14071 Córdoba. Spain. E-mail: rmnavarro@uco.es

10 ²Harvard Forest, Harvard University, Petersham, MA, 01366, USA

11 ³Biology Department, University of Washington, Seattle WA98195-1800, USA

12 ⁴Depto. Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, C/
13 Tulipán s/n, 28933, Móstoles, Spain.

14 ⁵Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza, Spain

15

16 *Author to whom correspondence should be addressed:

17 Rafael M Navarro Cerrillo

18 Departamento de Ingeniería Forestal-Universidad de Córdoba

19 Edf. Leonardo da Vinci, s/n

20 14071 Córdoba, Spain.

21 E-mail: rmnavarro@uco.es

23 **Abstract**

24 The effects of changes in structure and composition on the dynamics and responses of
25 secondary forests to climate change are understudied. Secondary forests of *Abies pinsapo*
26 var. *maroccana* are often a mosaic of patches of various development stages showing
27 different stand structures and successional stages. We hypothesise that the structure,
28 species composition and tree-to-tree competition of *A. pinsapo* stands in Talassemtane
29 National Park (Riff in northern Morocco) modulate the potential response of these
30 secondary forests to climate change. Nine plots representing three species mixtures were
31 established in *A. pinsapo*-dominated forests, and dendrometric and dendroecological
32 surveys were conducted. The two-parameter Weibull function was used to investigate the
33 diameter distributions of *Abies pinsapo*, *Pinus nigra* subsp. *mauritanica*, *Cedrus atlantica*,
34 *Acer opalus*, *Juniperus oxycedrus* and *Quercus ilex* for each site along the compositional
35 gradient. We quantified changes in radial growth, response to climate and drought, and
36 components of growth resilience. Finally, the influence of neighbourhood competition on
37 individual tree growth was evaluated using the a competition index. Diameter distributions
38 had an exponential, reverse-J character for *A. pinsapo* in pure and *C. atlantica* mixed
39 stands. By contrast, *A. pinsapo* presented a positively-skewed diameter distribution
40 dominated by small-sized trees in *P. nigra* mixed stands. There was a significant
41 correlation between tree growth and climate on all forest types, with differing magnitudes
42 per species. Significant precipitation-growth correlations were found for the previous
43 autumn and winter (October, December) in *A. pinsapo*. Drought events reduced *A.*
44 *pinsapo*'s resistance to subsequent droughts when growing in pure and mixed stands with
45 *C. atlantica*. This decline was statistically significant by the end of the studied period
46 (1999-2005). In contrast, mixed forests showed the highest recovery after drought.
47 Successive drought events consistently reduced *A. pinsapo*'s resilience to drought,
48 regardless of species composition. In pure *A. pinsapo* and in *A. pinsapo*-*C. atlantica* mixed

49 forests, competition reduced *A. pinsapo*'s growth, while in *A.pinsapo-P. nigra* mixed
50 forests increased competition with *P. nigra* seemed to have a positive-to-neutral effect on
51 *A. pinsapo* growth. Here, we showed that the response to climate and resilience of *A.*
52 *pinsapo* forests could be severely influenced by structure, species composition, and
53 competition, potentially influencing our expectations of long-term persistence of old-
54 growth coniferous trees in the Rif mountains. Understanding forest resilience and
55 response to changing climate has important implications towards managing and
56 safeguarding the productivity and health of these old growth forests.

57

58 **Keywords:** *Abies maroccana*; competition intensity; drought; radial growth; succession;
59 neighbourhood effects; regeneration; spatial pattern; stand structure.

61 **1. Introduction**

62 Secondary forests are often viewed as a mosaic of patches of various development stages,
63 stand structures and successional stages (Lira et al., 2012). Secondary forests display a
64 wide range of structures and ages, corresponding to different size distributions and a
65 diverse arrangement of individual trees within stands, thus the theoretical and practical
66 importance of understanding and managing secondary forests has taken more relevance in
67 a context of climate change (Lingua et al., 2008). Forest composition is another major
68 component of forest that may affect tree growth trajectories by modifying tree-to-tree
69 competition and growth responses to drought (Forrester and Bauhus, 2016; González de
70 Andrés et al., 2018; Grossiord, 2019). Forest structure and species diversity are shaped
71 directly by previous forest use and management practices, but they may also respond to
72 recent climate change (Keenan, 2015).

73 Structural and compositional changes modify neighbourhood competitive
74 interactions, which play an important role in tree growth and forest dynamics (D'Amato
75 and Puettmann, 2004; Coomes and Allen, 2007). For example, opening the canopy can
76 increase sun radiation and enhance carbon assimilation but can also lead to more water loss
77 through enhanced transpiration (Bréda et al., 2006), impacting radial tree growth and stand
78 development in drought-prone areas (Dobbertin, 2005). Additionally, structural diversity
79 (i.e. the variety of structural and species components within a forest) has been related to
80 higher resource diversity available to multiple species contributing to increased vertical
81 stratification and crown plasticity. The influence of structural diversity on productivity is
82 currently receiving a lot of attention (Dănescu et al., 2016; Juchheim et al. 2017; Forrester,
83 2019). Studies on how intra- and inter-specific competition affect growth in pure and
84 mixed stands provide a valuable assessment of how structural diversity affects the
85 responses of forests to climate; in particular, whether higher structural diversity may help

86 trees cope with higher drought stress (Bottero et al., 2017; Young et al., 2017; González de
87 Andrés et al., 2018).

88 Despite having been less studied, secondary forests provide an invaluable array of
89 ecosystem services that, in many areas, may be as important as those provided by fully-
90 natural forests (Gamfeldt et al., 2013). Recent dieback events in secondary mountain
91 conifer forests in North Africa raise the question of whether old-growth mountain conifers
92 may struggle more to adapt to climate change compared with lower elevation secondary
93 forests (Abel-Schaad et al., 2018; Navarro-Cerrillo et al., 2019). The structure and species
94 composition of these forests have been altered by centuries of traditional forest use and
95 harvesting. The resulting deforestation and agricultural extension (Barbero et al., 1990,
96 Taleb, 2016) have caused a loss of heterogeneity and structural diversity in most secondary
97 forests compared with the few remaining undisturbed stands, which often show more-
98 variable size distributions and random spatial patterns (Ajbilou et al., 2006). In the Riff
99 mountains of northern Morocco mixed conifer forests are dominated by pinsapo fir (*Abies*
100 *pinsapo* subsp. *maroccana* Trab.), black pine (*Pinus nigra* Arnold ssp. *salzmannii* (Dunal)
101 Franco var. *mauritanica* Maire & Peyereimh) and Atlas cedar (*Cedrus atlantica* (Endl.)
102 Carrière). Some populations of these three species are already showing growth declines at
103 drier sites related to recent warming and drying trends (M'hirit et al., 2006, Linares et al.,
104 2011). These relict forest ecosystems are highly sensitive to drought stress, and potentially
105 endangered by climate warming if drought severity increases (Sánchez-Salguero et al.,
106 2017). In areas where only small fragments of old-growth forests remain, locally adapted
107 species and phenotypes are at high risk of disappearing as a consequence of climate change
108 unless forest conservation strategies are implemented (Abel-Schaad et al., 2018). Although
109 growth responses to climate have been analysed previously in these species (Linares et al.,
110 2013; Camarero et al., 2013; Sánchez-Salguero et al., 2017), those assessments have
111 mainly focused on pure stands. Here, we compared pure and mixed pinsapo fir stands since

112 the first prerequisite for secondary forest conservation is an adequate understanding of the
113 structure and development of forests with different history, size structure and composition
114 (Pretzsch, 2014).

115 Although the diversity and variability of natural forests in North Africa have
116 recently been emphasised (Cheddadi et al., 2017), we still know very little about the
117 structural characteristics and, in particular, the differential response of secondary conifer
118 forests in this area (Navarro-Cerrillo et al., 2013). The factors governing competition may
119 differ markedly for secondary forests, where negligent management - in particular, illegal
120 harvesting and overgrazing - can reduce structural diversity, simplify tree spatial
121 distributions and affect tree growth. This is the case of some pinsapo fir forests in northern
122 Morocco, which form relict, fragmented and biogeographically-marginal populations
123 showing high sensitivity to climate and drought (Linares et al., 2013).

124 Current aridification trends in North Africa (Cook et al. 2016; Touchan et al., 2008,
125 2011) may adversely affect pinsapo fir forests, reduce their growth, and even lead to shifts
126 in the species distribution (Sánchez-Salguero et al., 2017). For these reasons, it is crucial to
127 continue improving our understanding of inter-species competition in secondary forests,
128 which may help contextualizing previous results on managed secondary conifer forests in
129 North Africa (Navarro-Cerrillo et al., 2013), and arrive to more general management
130 recommendations to preserve these ecosystems. Here, we analysed structural, competition
131 and dendrochronological data to examine how inter- and intra-specific interactions impact
132 the structure and radial growth in pure and mixed *A. pinsapo* stands in Talassemrane
133 National Park (Riff, northern Morocco). We hypothesized that the size structure, species
134 composition and tree-to-tree competition of these stands modulate the potential relation of
135 these secondary forests with climate change. Specifically, we tested three main hypotheses:
136 (i) the growth of the dominant species (pinsapo fir) does not only depend on climate and
137 drought, but also on competition between species and hence, species composition; (ii)

138 species and structure compositions influence post-drought resilience in pinsapo fir forests;
139 and (iii) the interaction between climatic factors and neighbourhood competition and
140 composition is stronger in mixed than in pure pinsapo fir stands, particularly its drought
141 tolerance. The results will provide insights into the interactions between the species-
142 specific effects and climate regarding structural and spatial responses of pure and mixed *A.*
143 *pinsapo* forests in North Africa, permitting better forecasts of their future dynamics under
144 warmer and drier conditions.

145

146 **2. Materials and methods**

147 *2.1 Study area*

148 We conducted this study in Talassemtane National Park (hereafter TLNP), located in the
149 southern area of the Riff calcareous ridge - which includes the highest summits of the
150 western Riff range in northern Morocco (35° 07' N - 5° 08' W; Figure S1, Table S1,
151 Supporting Information). TLNP covers an area of 58,000 ha, and two-thirds of the park is
152 located within the province of Chefchaouen and one-third belongs to the province of
153 Tetouan. The climate of TLNP is characterised by a mean monthly temperature ranging
154 from -1.3 °C in January to 26.5 °C in July (Talassemtane Meteorological Station, 1700 m
155 a.s.l), and a mean annual precipitation of 1939 mm with 46.4 mm falling between June and
156 August, resulting in summer drought. Pure and mixed forests of pinsapo fir, *P. nigra* var.
157 *mauritanica* and *C. atlantica* dominate between 1500 and 2000 m of elevation at slightly-
158 cold to extremely-cold temperatures (M'hirit et al., 2006), with the presence of other tree
159 species such as *Quercus ilex* L. subsp. *ballota* (Desf.) Samp., *Quercus faginea* Lam., *Acer*
160 *opalus* subsp. *granatense* (Boiss.) Font Quer & Rothm. and *Juniperus oxycedrus* L.
161 (Benabid 2000).

162

163 *2.2. Field data*

164 The forests in TLNP are spatially heterogeneous and can be classified along a gradient of
165 species composition ranging from pure to mixed pinsapo fir forests (Figure S2, Supporting
166 Information). The forest dynamics in TLNP seem to be governed through gap-phase
167 processes driven via tree mortality (Edman et al. 2007) and field observations confirm the
168 absence of legal logging, domestic wood collection and grazing within the reserve.
169 Although, there are reports of tree removal in the middle of the 20th century (Sevillano,
170 2009) and scattered stumps indicate occasional illegal logging.

171 In July 2011, nine 20 x 30 m plots representing three levels of species composition
172 were established in pinsapo fir stands, according to a stratified random design (Table S1;
173 Figure S2, Supporting Information): pure pinsapo fir forests, mixed pinsapo fir-black pine
174 forests and mixed pinsapo fir-cedar forests. The distances between plots ranged from 0.3 to
175 0.5 km and they were chosen in similar site conditions, with no recent history of logging
176 and a distance from roads sufficient to minimise other factors which could affect the
177 growth and provide noise in the establishment of the relationship with structural and
178 climatic conditions. Once a suitable stand was located, the first corner of the 20 × 30 m
179 plot was randomly located and laid out using a hand-held compass (Suunto KB-14/360R G
180 Compass; Finland) and a 50-m measuring tape (Lufkin®, Maryland-USA). To facilitate
181 tree measurements, each plot was divided into quadrants of approximately 10 × 15 m,
182 which were sampled in a fixed order. All living trees with diameter at breast height (dbh,
183 1.3 m above the ground) ≥ 5 cm were numbered, identified to the species level, mapped
184 and measured (dbh with a metric tape, with an accuracy of 0.1 cm). Tree height (H) was
185 measured using a Vertex III hypsometer (Haglöf, Sweden). Then, we calculated stand
186 density (N, trees ha⁻¹) and basal area (G, m² ha⁻¹). In three plots per stand type, the
187 structure of the seedling/sapling layer (dbh < 5 cm) was intensively sampled. Beginning
188 from a plot corner, all the sampled seedlings and saplings within each quadrant were
189 identified by species and height (±0.1 m) and classified in four size classes: seedlings (h <

190 50 cm), short saplings ($50 \text{ cm} \leq h < 130 \text{ cm}$), tall saplings ($h \geq 130 \text{ cm}$ and $\text{dbh} < 5 \text{ cm}$)
191 and juveniles ($5 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$) (Dobrowolska and Veblen, 2008) (Table 1; Figure S2,
192 Supplementary Material).

193 Due to its versatility and simplicity, the two-parameter Weibull shape parameter
194 (Bailey and Dell 1973) was used as an index of the reverse-J character of the diameter
195 distributions of *A. pinsapo*, *P. nigra* subsp. *mauritanica*, *C. atlantica*, *Acer opalus*, *J.*
196 *oxycedrus* and *Q. ilex* for each site, representing a different compositional gradient. The
197 two-parameter, left-truncated Weibull function has proven more suitable than some other
198 alternative functions for several species growing in the Mediterranean region (Palahí et al.,
199 2008; Navarro-Cerrillo et al., 2013). The fitting was carried out using the maximum
200 likelihood method provided by the “mle” R function in the “stats4” package (Mehtätalo et
201 al., 2011).

202

203 2.3. Dendrochronological methods

204 We used dendrochronology to estimate tree age and to quantify changes in radial growth
205 and responsiveness to climate and drought. In 2011, we extracted one or two increment
206 cores, at 1.3 m above the ground of mature living trees ($10 \leq \text{dbh} \leq 80 \text{ cm}$), in the direction
207 parallel to the slope contour, using increment borers and following standard
208 dendrochronological methods (Fritts 2001) (Table 1). The wood samples were air-dried
209 and polished in the laboratory with successively-finer grades of sandpaper. Visual cross-
210 dating for each sample was conducted under a binocular microscope and tree-ring widths
211 of dated samples were measured, using a LINTAB measuring system interfaced with the
212 Time Series Analysis Program (TSAP; Frank Rinntech, Heidelberg, Germany), to a
213 resolution of 0.01 mm. Cross-dating was conducted using the marker-year method of
214 Yamaguchi (1991), followed by statistical verification using COFECHA (Grissino Mayer,

215 2001). We produced three pinsapo fir chronologies (one for each forest type), one
216 chronology of *P. nigra* and one of *C. atlantica*.

217 We standardised and detrended the tree-ring width (TRW) data using common
218 dendrochronological procedures. We fitted negative exponential functions to the raw ring-
219 width data and obtained indices, followed by autoregressive modelling of the standardised
220 index series to remove temporal autocorrelation and to generate residual ring-width indices
221 (RWIs). Finally, a biweight robust mean was used to compute the mean residual
222 chronologies of the RWIs for each stand. In total, five residual site chronologies were
223 created.

224 To obtain a more-accurate representation of growth trends and to calculate the
225 resilience indices (see below), the tree-ring width data were converted into basal area
226 increment (BAI) data, assuming a circular shape of the stem. The BAI removes the
227 variation caused by adding volume to a circular stem (Biondi and Qaedan, 2008), thus
228 offering a more-accurate estimation of growth than TRW. We applied the following
229 formula:

$$230 \quad \text{BAI} = \pi (r_t^2 - r_{t-1}^2) \quad [1]$$

231 where r_t^2 and r_{t-1}^2 represent the squared radial increments at the end and beginning of a
232 given annual ring, corresponding to rings formed in years t and $t-1$, respectively. The dplR
233 library (Bunn et al., 2018) was used to calculate the dendrochronological statistics and
234 climate-growth correlations in the R statistical package version R-3.5.2 (R Development
235 Core Team 2016).

236

237 2.4. Climate–growth relationships

238 The meteorological stations nearest to TLNP, located 10 km away in Chefchaouen (630 m
239 a.s.l.) and at Forest Service Station (1700 m a.s.l.), have provided climate data since 1970.
240 Since those records are heterogeneous and contain numerous gaps, we used 0.5°-gridded

241 monthly data for the mean temperature and total precipitation available for the period
242 1901–2010 from the Climate Research Unit (CRU) TS4.0 datasets
243 (https://climexp.knmi.nl/selectfield_obs2.cgi?id=someone@somewhere). These data were
244 used to quantify trends in annual climatic variables and to assess the climate-growth
245 relationships. We also obtained monthly gridded (0.5° resolution) data of drought severity
246 using the Self-calibrating Palmer Drought Severity Index (scPDSI) for the period 1901–
247 2006, and for each site, based on the CRU TS 3.10. 01 dataset (van der Schrier et al.,
248 2013). The scPDSI was also used to select the five most-intense droughts in the study area
249 for the period 1990–2010 (Figure S3, Supplementary Material).

250 We calculated Pearson correlations using residual chronologies as response
251 variables and monthly climatic variables (mean maximum and minimum temperatures,
252 precipitation) and the scPDSI as predictors. We used the Treeclim package in the R
253 software to calculate correlation and response coefficients (Zang and Biondi, 2015). In the
254 analyses, the months considered run from October of the previous year to September of the
255 current year of growth. Correlations were obtained for the common period 1910–2006. The
256 significance of the correlations was estimated through bootstrapping. Site-specific moving
257 correlations were calculated by selecting those having significant response coefficients and
258 considering 20-year-long intervals shifted by one year for different periods.

259

260 *2.5. Quantification of drought resilience*

261 In order to understand the effects of droughts on the performance of the three species,
262 resilience components (Resistance, R_t ; Recovery, R_c ; Resilience, R_s) were calculated as in
263 Lloret et al. (2011). The resilience components are constructed by comparing the growth
264 previous to, during and after the occurrence of drought events. High resistance (R_t)
265 indicates a small reduction in growth during the drought year, whereas recovery (R_c)
266 quantifies the increase in growth after the drought and resilience (R_s) expresses the

267 persistence of the effect of the drought after it has ended (Lloret et al., 2011). Here, we
268 calculated the resilience components using the BAI and considering five droughts (1975,
269 1985, 1995, 1999 and 2005; Figure S3, Supplementary Material), according to:

$$270 \quad R_t = D_r / \text{Pre}D_r \quad [2]$$

$$271 \quad R_c = \text{Post}D_r / D_r \quad [3]$$

$$272 \quad R_s = \text{Post}D_r / \text{Pre}D_r \quad [4]$$

273 where D_r is the BAI in the year of the drought, $\text{Pre}D_r$ is the mean BAI calculated for the
274 previous period of up to three years before the drought and $\text{Post}D_r$ is the mean BAI
275 calculated for the period spanning three years after the drought. This avoids likely growth
276 overlap and also considers legacy effects that are mostly found up to 2-3 years after a
277 drought (Anderegg et al., 2015).

278

279 *2.6. Neighbourhood competition effects on tree growth*

280 The intensity of neighbourhood competition regarding individual tree growth was
281 evaluated using the Hegyi (1974) competition index (CI), which was calculated using
282 structure data measured in 2010. The CI includes information on tree–tree distance:

$$283 \quad \text{CI} = \sum D_j / D_i \times [1 / (L_{ij} + 1)] \quad [5]$$

284 where D_i is the dbh of subject tree i (cm); D_j is the dbh of competitor trees ($j \neq i$) (cm); and
285 L_{ij} is the distance of subject tree i from competitor j (m). We selected this CI based on its
286 previously-demonstrated success in characterising tree growth in other forest-structure
287 settings (D'Amato and Puettmann 2004). Competition was estimated at the individual tree
288 level, considering a variable radius of competition proportional to the dbh of the trees
289 present at the time of sampling. We avoided sampling trees that had tree stumps presents
290 within their radius of competition, as this could indicate that competition conditions would
291 have change substantially due to legal due to trees been harvested during our study period
292 (last 40 years). Trees may have been harvested and their remains completely rotted away,

293 in which case, we would underestimate competition. However, given the relatively short
294 period study, the study areas' inaccessibility (which would make extremely complex to
295 remove tree stumps), and the durability of the wood in these species, it is unlikely that the
296 number of 'missing trees' affect our calculation of competition. To further reduce this
297 potential confounding, we only include in our analyses trees with a dbh > 10 cm, to avoid
298 young or suppressed individuals that may not impact the growth of the target tree (cf.
299 Thorpe et al. 2010). Nevertheless, we assumed that the CI calculated for 2010 is a biased
300 representation of the competition 40 years ago.

301

302 *2.7. Patterns, trends and drivers of radial growth*

303 To quantify the variation in the relation with climate or growth between sites and whether
304 it was modulated by the stand type (pure and mixed) and the competition effects on growth
305 (the BAI of the last 40 years was studied), we applied linear mixed-effects models
306 (Pinheiro and Bates 2000). We used the following linear mixed-effects model:

$$307 \quad Y_i = X_i\beta + Z_ib_i + \varepsilon_i \quad [6]$$

308 where Y_i is the response variable (BAI), β is the vector of fixed effects (type of forest, year,
309 age, dbh, type of forest: year interaction), b_i is the vector of random effects (tree species),
310 X_i and Z_i are, respectively, fixed- and random-effects regressor matrices and ε_i is the error
311 vector. In the models, "type of forest" represented the different populations and "year"
312 accounted for BAI trends through time. Tree age and dbh were included in the models to
313 allow for potential differences in growth trajectories among trees of different age and size.
314 However, due to strong collinearity, only tree height was retained in the models because it
315 had the strongest effect. The CI was calculated at different distances. Finally, the CI at 10
316 m was retained because it had stronger effects on BAI trends. The 7-month-long SPEI for
317 December was included in the model to account for the effect of drought on growth.
318 Further, we included the triple interaction between site, calendar year and CI to account for

319 the potential different patterns in growth trends among populations. Similarly, a triple
320 interaction between site, SPEI-12 and CI was included to account for the potential different
321 relation of growth with climate among populations. Tree identity was included as a random
322 factor to account for the fact that each tree sample represented repeated measurements on
323 the same individual. We included in the models a first-order autocorrelation structure
324 (AR1) to account for the dependency of the growth in year t on the growth in the previous
325 year $t-1$. BAI was log-transformed ($\log(\text{BAI}+1)$) prior to the analyses to achieve
326 normality. To quantify the strength of the model, we calculated a pseudo- R^2 (Nakagawa
327 and Schielzeth 2013). Lastly, a graphical examination of the residuals and fitted values was
328 carried out to detect the influence of outliers and to evaluate the general model fit. A multi-
329 model inference approach based on information theory was applied to identify the set of
330 covariates that best explained the tree growth trends (Burnham and Anderson, 2002). We
331 ranked all the potential models according to the second-order Akaike information criterion
332 (AICc) and selected the model showing the lowest value (Aho et al., 2014). All
333 computations were performed using R version 3.1.2 (R Core Team 2014) and the lme4
334 package (Bates et al., 2015).

335

336 **3. Results**

337 *3.1. Stand structure and composition*

338 Among adult trees, the *A. pinsapo*-*P. nigra* stands were dominated by *P. nigra*, while the
339 mixed stands with *C. atlantica* were dominated by *A. pinsapo* (Table 1). The density of *A.*
340 *pinsapo* individuals ($\text{dbh} \geq 5$ cm) ranged from 466 (88% of total tree density) in pure
341 stands to 122 (17%) trees ha^{-1} in fir-pine mixed stands, being significantly higher in the
342 pure fir and fir-cedar mixed stands. However, the density of *A. opalus*, the other species
343 present in the three types of forest, was significantly higher in the *A. pinsapo*-*P. nigra* and
344 *A. pinsapo* stands (122 and 61 trees ha^{-1}), respectively. *Pinus nigra* and *C. atlantica* were

345 only present in mixed stands, reaching a density of 161 and 233 trees ha⁻¹, respectively, but
346 were completely absent from the pure fir stand. *Juniperus oxycedrus* was also present,
347 reaching a maximum density of 255 trees ha⁻¹ in the fir-black pine mixed stand, and *Q. ilex*
348 had a residual presence in the cedar-mixed stand. Consequently, the total live basal area of
349 *A. pinsapo* ranged widely, from 18.4 to 121.1 m² ha⁻¹. In pure *A. pinsapo* forests, *A.*
350 *pinsapo* accounted for over 98% of the basal area, being highly represented in the other
351 two forest types also (40% and 62%, respectively). Black pine and cedar reached values of
352 20.3 and 23.6 m² ha⁻¹, respectively, in mixed forests. Small trees (*A. opalus*, *J. oxycedrus*,
353 and *Q. ilex*) comprised only small fractions of the total basal area.

354 The mean dbh of *A. pinsapo* ranged from 27.4 cm (black pine-mixed) to 39.3 cm
355 (pure stands) (Figure 1). The dbh-class Weibull distribution had an exponential, reverse-J
356 character for *A. pinsapo* in pure and *C. atlantica* mixed stands, with many large individuals
357 and a long tail ($c=1.0$). By contrast, *A. pinsapo* presented a positively-skewed Weibull *pdf*
358 distribution dominated by small-sized trees (dbh \leq 20 cm) ($c=1.3$) in *P. nigra* mixed stands
359 (Figure 1). *Abies pinsapo* seedlings, short saplings and tall saplings were abundant in all
360 three forest types, showing a very-good regeneration status with a rapid decline in the
361 number of individuals in larger-size classes. *Abies pinsapo* juveniles were more abundant
362 in pure and *P. nigra*-mixed stands (139 and 66 trees ha⁻¹, respectively), but the differences
363 were not significant (Table 1).

364 The mean dbh of *P. nigra* trees was 39.7 cm in the *A. pinsapo*-*P. nigra* mixed
365 stands, with a low abundance of individuals in all size classes ($c>3.7$, Figure 1). This
366 indicates a negatively-skewed distribution of the age with few young individuals compared
367 to the individuals of average age; in fact, the regeneration density of *P. nigra* was very low
368 and tall saplings were non-existent (Table 1). The distributions show a plateau with a small
369 negative slope among the largest dbh classes. Above a tree diameter of approximately 65
370 cm, tree frequency declined rapidly. Finally, the mean dbh of *C. atlantica* trees was 37.1

371 cm in the *A. pinsapo-C. atlantica* mixed stands, with a high abundance of individuals in
372 the smaller size classes (Figure 1). The dbh class distribution has an exponential, reverse-J
373 character and indicates that there are abundant young individuals in the stands and that the
374 regeneration status of the species is good ($c=1.0$, Figure 1), with medium values of tall
375 saplings and juveniles but higher values of seedlings (45 seedlings ha⁻¹; Table 1).

376 Among the secondary tree species, *A. opalus* had a unimodal mound-shaped
377 distribution in pure and mixed stands, with a slightly-higher density of intermediate-sized
378 trees in pure and *A. pinsapo-P. nigra* stands (20 cm<dbh≤30 cm) ($c>3.7$), being less
379 present in *A. pinsapo-C. atlantica* mixed stands. *Juniperus oxycedrus* also had a positively-
380 skewed Weibull *pdf* distribution dominated by small-sized trees (dbh≤20 cm) ($c=1.3$),
381 showing abundant young individuals and good regeneration status (Figure 1). The pure fir
382 stands had the highest regeneration density of *A. opalus* (494 seedlings ha⁻¹). On the other
383 hand, *J. oxycedrus* regeneration (372 seedlings ha⁻¹; 238 saplings ha⁻¹) was highest in *A.*
384 *pinsapo-P. nigra* stands. In *A. pinsapo-C. atlantica* stands, the regeneration density was
385 similar for all small tree species

386

387 3.2. Characteristics of the tree-ring chronologies

388 For each forest type, separate chronologies were produced for fir, black pine and cedar.
389 The statistical parameters indicated that our chronologies were in general well-replicated,
390 captured a big proportion of the local growth variability, and showed high tree-to-tree
391 coherence in interannual growth variability and the time span for the chronologies dated
392 back to the 18th century in all types of forest, with a best common period of analysis
393 between 1910 and 2010 (Table 2; Figure S4, Supplementary Material). The mean age of
394 the trees sampled was higher than 100 years; *A. pinsapo* was younger in pure stands, but
395 older than *P. nigra* and *C. atlantica* in mixed forests. The mean TRW for the best-

396 replicated periods was significantly different among the species and forest types (Table 2),
397 as was the mean growth (BAI and BAI₄₀, $P < 0.001$).

398 For the 1850–2010 period, the *A. pinsapo* BAI chronologies in pure fir and fir-
399 cedar stands showed similar radial growth with noticeable growth increases during the
400 1910s, 1930s, early 1960s and late 1970s to early 1980s, and reductions in 1990-1995,
401 1999, 2005 and 2012 (corresponding to dry periods) (Figure 2). However, *A. pinsapo*
402 growth in fir-black pine stands deviated noticeably from the common pattern described
403 above. The mean BAI values of *A. pinsapo* were significantly higher ($P < 0.05$) in pure *A.*
404 *pinsapo* and *A. pinsapo-C. atlantica* stands than in *A. pinsapo-P. nigra* stands during the
405 selected time span (1970–2010) (Figure 2; Figure S6, Supplementary Material).

406

407 3.3. Climate-growth relationships

408 There was a significant relation between the growth (TRW) of the tree species and climate
409 for all forest types, but with different magnitudes (Figure 3). We found a negative and
410 significant relationship with mean temperature of the current February (*C. atlantica*, *P.*
411 *nigra*), May (*A. pinsapo-C. atlantica* forest) and June (*A. pinsapo-P. nigra* forest), but in
412 particular for September, for all types of forest. This negative effect on growth of warm
413 spring and autumn conditions was more noticeable in mixed than in pure forests. On the
414 other hand, a positive effect of higher August temperatures was observed for mixed forests
415 (*A. pinsapo-C. atlantica* and *A. pinsapo-P. nigra*).

416 Significant precipitation-growth correlations were found for the previous autumn
417 and winter (October, November, December); they were stronger in *A. pinsapo* regardless
418 of whether the trees were in pure or mixed forests (Figure 3). Significant correlations were
419 also found between growth and current February, May and July precipitation, but they
420 were particularly consistent across forest types for September conditions. *P. nigra* showed

421 a strong to precipitation in February precipitation. *Cedrus atlantica* showed a positive
422 relation with May precipitation, of the current year.

423

424 3.4. Post-drought resilience indices

425 The three drought indices calculated for *A. pinsapo* described the effect of each forest type
426 on the responses to five droughts between 1975 and 2005 (Figure 4, Table S3,
427 Supplementary Material). The influence on the resistance (R_t), recovery (R_c) and resilience
428 (R_s) growth indices calculated for *A. pinsapo* was different for the three forest types.
429 Drought events seem to reduce the resistance (R_t) to subsequent drought conditions when
430 *A. pinsapo* grew in pure and *A. pinsapo*-*C. atlantica* stands, a decline that was statistically
431 significant at the end of the studied period (1999-2005). In contrast, recovery (R_c) after
432 drought was facilitated more in those types of forest (with the most-highly-significant
433 positive effects) (Figure 4). The resilience (R_s) to drought of *A. pinsapo* was consistently
434 reduced by successive drought events, regardless of the stand species composition.

435

436 3.5. Effects of competition intensity and species composition on drought responses

437 Among the forest types, competition was higher in mixed forests with *C. atlantica*, being
438 lowest in pure forests (Figure S6, Supplementary Material). The linear regression fitted to
439 the relationship between BAI (1970-2010) and CI showed a negative effect of competition
440 on BAI in pure forests (Figure S7, Supplementary Material).

441 The linear mixed model developed for the forest types and BAI describes the effect
442 of each forest type on the growth responses (Table 3). The significant ($P<0.05$) factors
443 were tree height, competition index (CI_10), site, year and SPEI_7, as well as the two- and
444 three-way interactions (Table 3). The influence of the species mixtures on the growth
445 responses was different for the three forest types. The BAI trends for *A. pinsapo* differed in
446 time and were influenced by the other species (CI_10). The growth of *A. pinsapo* increased

447 with increasing height and declined with increasing competition, particularly in *A.*
448 *pinsapo*-*P. nigra* forests (Table 3, Figure 5). It also showed several positive interactions: *A.*
449 *pinsapo* growth was mostly increased by competition in mixed forests and in particular
450 years. However, the competition-forest type-year interaction negatively affected *A.*
451 *pinsapo*. Its growth was mostly reduced in mixed *A. pinsapo*-*P. nigra* forests in particular
452 dry years (with the most-significant negative effect) (Figure 5). *A. pinsapo* growth was
453 reduced by competition, although once again there was little effect and the differences
454 among the trends were complex and context-dependent (Figure 6). In both pure *A. pinsapo*
455 and *A. pinsapo*-*C. atlantica* mixed forests; competition reduced *A. pinsapo* growth, while in
456 *A. pinsapo*-*P. nigra* mixed forests increased competition with *P. nigra* seemed to have a
457 positive-to-neutral effect on *A. pinsapo* growth (Figure 6). These relationships seemed to
458 be changing in recent decades. Monospecific competition in pure stands had smaller
459 effects on *A. pinsapo* growth in recent years, while interspecific competition with *C.*
460 *atlantica* and *P. nigra* became more limiting for *A. pinsapo* growth as climate became
461 drier. The growth-climate interaction shows a more-plastic response to the SPEI in pure
462 forests; meanwhile, growth decreased in *A. pinsapo*-*P. nigra* forests, which could indicate
463 increased competition under wetter conditions. The mixture effect, calculated for a
464 simulated composition of equal shares between the three forest types, showed consistently-
465 negative effects of interspecific competition for *A. pinsapo* growth, particularly when
466 mixed with *P. nigra*.

467

468 **Discussion**

469 The results presented in this study highlight that the relation of *A. pinsapo* radial growth
470 with climate in the Riff Mountains is modulated by stand structure and neighborhood
471 competition. We found a marked sensitivity of pinsapo fir growth to competition in pure
472 stands in which larger basal area was also found, suggesting the strong impact of intra-

473 specific competition on growth response to climate. However, in mixed stands opposite
474 results were found with negative impacts on *P. nigra*-pinsapo fir stands and neutral ones in
475 *C. atlantica*-pinsapo fir stands, indicating that the potential positive effect of species
476 mixing on growth depends on the species identity. All together, these results indicate the
477 importance of considering stand structure and composition to understand the response of
478 tree growth to changing climate even in mountainous, long-lived conifer forests, where
479 climate has been regularly considered the main limiting factor to tree growth (e.g. Ettinger
480 et al., 2011).

481

482 *4.1. Forest structure and composition*

483 In the investigated forest stands, *A. pinsapo* is the major component in terms of both
484 density and basal area. Several authors have studied the population structure of *A. pinsapo*
485 communities in similar ecological situations and have confirmed the successional
486 convergence towards fir-dominated stands (Baumer, 1977; Melhaoui, 1990, Boukil, 1998,
487 Benabid, 2000). The density values measured for this species (range 466–122 trees ha⁻¹)
488 are higher than in previous findings for *A. pinsapo* forests in the Riff (63–115 trees ha⁻¹,
489 Baumer, 1977) but lower than those measured in southern Spain (807 trees ha⁻¹, Linares et
490 al., 2011a). Basal area was significantly higher in pure *A. pinsapo* forests (121.1 m² ha⁻¹,
491 98% of total basal area) compared with mixed forests (18.4 m² ha⁻¹, 40% and 43.4 m² ha⁻¹,
492 62% respectively), showing high structural within-stand variability in tree species
493 composition, and freeing more resources for secondary trees to thrive. *Acer opalus* and *J.*
494 *oxycedrus* appeared in higher densities in diverse forests. The presence of these species in
495 secondary *A. pinsapo* forests has also been reported by other researchers (Boukil, 1998,
496 Benabid, 2000), who suggested that, in the absence of perturbations (e.g., fire, over-
497 grazing or harvesting), the proportion of conifers increases due to the absence of large-
498 scale canopy disturbances. Comparatively less abundant secondary tree species represented

499 between 8% (fir-cedar forest) and 58% (fir-black pine forest) of the stand's total density.
500 The high density of *J. oxycedrus* and *A. opalus*, is particularly important, because they are
501 potential substitute species in *A. pinsapo* forests (Navarro-Cerrillo et al., 2014a). This
502 appears to be related to the absence of perturbations, which facilitates the recruitment of
503 these species, but also it could be promoted by climatic change (Gómez-Aparicio et al.,
504 2005).

505 Tree-size distributions varied considerably among forest types and tree species.
506 Uneven-aged stands of *A. pinsapo* exhibited reverse-J dbh frequency distributions
507 characteristic of old-growth stands as a result of late-successional stand dynamics or of
508 stands that have undergone slow, long-term establishment after catastrophic stand
509 mortality (Oliver and Larson, 1996), similar to those previously documented for old-
510 growth *A. pinsapo* forests in northern Morocco (Boukil, 1998). The stands are scattered
511 with tall, mature *A. pinsapo* that comprises 91% of the total stem density in pure forests
512 versus 17% in fir-black pine and 52% in fir-cedar forests. Such structural heterogeneity is
513 characteristic of Mediterranean fir forests, whose disturbance regime is dominated by
514 small-scale gap dynamics (Fyllas et al., 2010). The numbers of *A. pinsapo* seedlings and
515 saplings were higher in pure fir and mixed fir-black pine stands than in mixed fir-cedar
516 forests, which allows regeneration and the maintenance of a mixed tree composition, even
517 in old-growth forests (Aafi, 2000). In contrast, the regeneration of *A. pinsapo* was poorer
518 in *C. atlantica* mixed forests, probably because of the absence of gap disturbances. This
519 suggests that *A. pinsapo* becomes established as a dense cohort following a severe
520 disturbance (e.g., fire or forest harvesting) and continues to regenerate in large tree-fall
521 gaps (Sevillano, 2009). Even though *A. pinsapo* is traditionally considered a “late
522 successional” species, it can colonise and persist within old-growth stands, due to its
523 prolific seed-producing ability, combined with the availability of suitable microsites
524 (Arista, 1995). The high densities of saplings and juveniles in all forest types reflect the

525 ability of *A. pinsapo* to undergo rapid recruitment in disturbed forest areas due to episodic
526 high seed inputs from old trees, probably linked to mating events (Arista, 1995), although
527 its ability to become established below the canopy may depend on microhabitat factors,
528 such as soil resources, light levels, temperature or grazing - rather than factors associated
529 with fruit production, germination or seedling mortality (Arista, 1995; Arista et al., 1997;
530 Benavides et al., 2016). The recruitment rate of *A. pinsapo* juveniles seems adequate to
531 maintain the existing adult population in these areas, without the bottleneck in recruitment
532 between the seedling and sapling stages observed in other fir forests (Aussenac, 2002).
533 This is consistent with other studies that have observed successful *A. pinsapo* regeneration
534 in populations in southern Spain (Arista, 1995, Navarro-Cerrillo et al., 2014a).

535 On the other hand, *C. atlantica* and *P. nigra* showed poor regeneration status,
536 which could be attributable to the effect of low regeneration ability (Baumer, 1977; Tiscar
537 and Linares, 2011). The high density of regeneration by secondary tree species (such as *A.*
538 *opalus*, *J. oxycedrus* and *Q. ilex*) on the understory may indicate the potential of those
539 species to substitute the dominant species in the near future (Navarro-Cerrillo et al.,
540 2014a). Although human influence in study sites is currently very limited, these forests
541 have traditionally suffered unregulated harvesting and illegal logging up to the 20th
542 century, which could have affected the current forest structure or influence forest
543 disturbance regimes (Sevillano, 2009). The recent absence of silvicultural treatments has
544 favoured trees in the mid-diameter classes, and the understory, resulting in a greater range
545 of tree sizes in pure stands compared to mixed ones (Crow and Perera, 2004). Recent
546 efforts to control illicit logging in the area may have also increased the number of young
547 trees. It is, therefore, unclear the degree of influence of human intervention in the current
548 successional patterns of the Riff coniferous forests. However, the abundant regeneration
549 consistently observed in mature *A. pinsapo* forests suggests that increased by continue
550 reducing human influence and allowing forest to mature, Riff mountain conifer forests will

551 tend in the future to naturally transition to mixed forests. These results agree with the
552 regeneration strategies of *A. pinsapo* (Arista et al., 1997) as well as the dynamic models
553 proposed for mountain, old-growth conifer forests characterised by an elevated vertical
554 heterogeneity (van Pelt and Franklin, 2000). Nevertheless, there is much debate over the
555 level of perturbation necessary to maintain *A. pinsapo* forests and the mechanisms
556 involved in a context of global change (Navarro-Cerrillo et al., 2014a, 2016).

557

558 4.2 Growth responses to climate

559 The dendroclimatic potential of *A. pinsapo*, *P. nigra* and *C. atlantica* has been investigated
560 before (e.g., Till and Guiot, 1990; Camarero et al., 2013; Sánchez-Salguero et al. 2017;
561 Navarro-Cerrillo et al., 2019). However, the chronologies presented in this study are new
562 for the three species studied together in the Riff Mountains. The *A. pinsapo* chronologies
563 in pure and *C. atlantica* stands showed similar radial growth patterns and noticeable
564 differences from those in *A. pinsapo*-*P. nigra* stands. The dendrochronological data
565 indicate that *A. pinsapo* trees in pure and *C. atlantica* mixed forests had experienced
566 periods of juvenile suppression followed by rapid and sustained growth once they were
567 released, in particular by human influence (see Figure 2). Growth patterns of mature
568 individuals also seemed to show a vigorous response to the appearance of large gaps
569 related to harvesting in the 1950s (Sevillano, 2009).

570 Our results indicate a species-specific seasonal difference in radial growth relation
571 with temperature and/or precipitation across *A. pinsapo* forest types. We observed low
572 responsiveness of the usually climate-sensitive *P. nigra* and *C. atlantica* in the wet and
573 cool sites studied. However, the results suggest that these species growth were broadly
574 influenced by the winter and spring temperatures in water-limited stands. Warmer springs
575 may enhance tree radial growth in mountainous areas by increasing tree vigour via earlier
576 growth onset and higher photosynthetic rates under warmer later-spring conditions

577 (McDowell et al. 2011). However, the benefits of a longer growing season may be
578 counteracted by an increase in the risk of frost damage cause by extreme cold events
579 occurring during periods when the plants are now photosynthetically active and thus, more
580 vulnerable (Liu et al. 2018). Moreover, temperature rises affect coniferous carbon storage
581 because they may lead to an increased rate of respiration and carbohydrate consumption,
582 required to maintain cell metabolism (respiration), thus depleting the food reserves for the
583 following year (McDowell et al. 2011).

584 The relation of *A. pinsapo*, *P. nigra* and *C. atlantica* with precipitation are
585 consistent with those reported in nearby populations (Génova, 2007; Linares et al., 2011b;
586 2013, Sánchez-Salguero et al., 2012), while we present here the first correlation and
587 response function analysis for *A. pinsapo* forests at its southern limit of distribution.
588 Overall, the main climatic factors influencing *A. pinsapo* growth were precipitation during
589 the previous, as well as with winter, spring and early-autumn conditions of the year of tree-
590 ring formation. The *P. nigra* radial growth was more sensitive to the precipitation and
591 temperature during early spring of the year of tree-ring formation, similar to that observed
592 in nearby Iberian populations of *P. nigra* (Camarero et al., 2013) and *C. atlantica* (Linares
593 et al., 2013). Drought stress had a strong effect on growth, as shown by the strong positive
594 relationship between growth and May, July and September precipitation. Overall, our
595 results indicated that *A. pinsapo* is the most sensitive species of the dominant conifers in
596 the Riff Mountains to previous wet and cold late-winter conditions, while the
597 responsiveness of *P. nigra* and *C. atlantica* was unexpectedly lower, given that the growth
598 of these shade-intolerant species is usually constrained by water shortage (e.g., Sangüesa-
599 Barreda et al., 2019).

600 The climate response of *A. pinsapo*, *P. nigra* and *C. atlantica* can be better
601 understood in terms of ecophysiological adaptations to the extreme site conditions in the
602 Riff Mountains ecosystems. Cool-wet conditions during spring are likely to enhance the

603 synthesis of carbohydrates that can increase growth and the production of earlywood
604 (Camarero et al., 2010, Gimeno et al., 2012). Winter and early summer precipitation may
605 replenish soil water before spring and early-summer growth, critical for Mediterranean
606 conifer species in drought-prone areas with short springs and shallow soils (Camarero et
607 al., 2013). Wet autumns, in combination with warmer conditions, have been suggested to
608 extend the growing season, thus increasing growth (Camarero et al., 2010). The unstable
609 relationships between climate and growth observed for *P. nigra* and *C. atlantica* indicate
610 divergent responses, particularly during the late 20th century (Figure S4, Supplementary
611 Material). These patterns reflect a decreased responsiveness to climate of those species
612 (Navarro-Cerrillo et al., 2014b; 2019). Our results suggests that current-year winter and
613 spring temperatures and precipitation, as well as drought severity, are particularly
614 important growth factors for *A. pinsapo* in northern Africa, but not for other drought-prone
615 conifers (*P. nigra*, *C. atlantica*), which seem less responsive to climate at these cool and
616 wet mountain sites, compared with drier populations in southern Spain. In fact, we have
617 observed a severe growth reduction in the last decade in *A. pinsapo* growth, likely related
618 to rising temperatures and diminishing rainfall, leading to an increase in drought stress and
619 growth decline (Camarero et al., 2013; Sánchez-Salguero et al., 2017)

620

621 4.3. Post-drought resilience indices

622 Drought years can play a very-important role in the determination of species composition
623 in forest ecotones (Touchan et al. 2017). Extreme events, such as drought, can have a
624 disproportionate effect on forest ecosystems (Altwegg et al. 2017). Given the long lifespan
625 of most forest tree species, they are likely resist under suboptimal average conditions for
626 decades or even centuries, however extreme events can trigger sudden changes in
627 ecosystem structure, composition and functioning (Bräuning et al. 2017 and references
628 therein). This is supported by the correspondence of periods of growth reduction with

629 documented drought events in the Riff Mountains (Touchan et al. 2017). In fact, the period
630 between 1980s and 2000s has been considered among the driest of the past 900 years in
631 North-Western Africa (Cook et al. 2016, Touchan et al. 2008, 2011). The decline in *A.*
632 *pinsapo* resistance (R_t) and resilience (R_s) with subsequence droughts in both pure and
633 mixed-*C. atlantica* stands. indicates an overall increase in the vulnerability of these forest
634 to future drought. Should the prediction of increasing frequency and severity of extreme
635 events to be realized (Jentsch and Beierkuhnlein 2008), *A. pinsapo* forests may be under
636 increased persistence threat. Recovery (R_c) after drought was mostly facilitated in all
637 studied forest types; as a consequence, maximum heterogeneity in habitat features and tree
638 communities have been associated with drought response. Drought has been strongly
639 suggested to influence *A. pinsapo* communities in the western Mediterranean mountain
640 forests (Sánchez-Salguero et al., 2015, 2017). Similarly, the accumulative effect of
641 subsequent drought has been pointed out for multiple coniferous species in drier sites of
642 southern Spain (Sánchez-Salguero et al., 2012; 2017; Navarro-Cerrillo et al., 2018).

643

644 *4.3 Competition and stand stability*

645 Non-climatic factors (e.g., competition, insect outbreaks, etc.) contribute directly to the
646 conditioning of tree growth. For instance, dendroclimatic studies of *A. pinsapo* in southern
647 Spain have documented that competition is a limiting factor in radial growth (Linares et
648 al., 2010). Moreover, previous studies in other mountain coniferous species have
649 demonstrated the influence of competition on radial growth, in addition to the dominant
650 relationship of the latter with climatic conditions, highlighting its importance as a major
651 determinant of drought-induced stress (Young et al., 2017).

652 In our study, the influence of competition (CI₁₀) on *A. pinsapo* growth was
653 different for the three forest types. The linear regression fitted to the relationship between
654 BAI (1970-2010) and the CI showed a negative effect of competition on BAI in pure

655 forests and *A. pinsapo*-*P. nigra* forests (Figures S6 and S7, Supplementary Material). This
656 suggests that differences in the availability of resources between pure and mixed-species
657 stands - related to crown architecture, vertical positioning within the canopy, root
658 morphology, differences in physiology and soils - may result in more-efficient utilisation
659 of water (Tiscar and Linares 2010; Forrester and Bauhus 2016). It has been shown that,
660 during favorable years, *A. pinsapo* in mixed forests reaches the maximum growth rate;
661 however, during droughts, the positive effect disappeared although it was related to the
662 intensity of thinning treatments (Navarro-Cerrillo et al., 2016). The effect of competition
663 was less pronounced in *A. pinsapo*-*C. atlantica* stands, which may be related to the
664 dominant crown position of *C. atlantica* in these mixtures. Additionally, the *A. pinsapo*
665 forests in the study area have historically been subject to different levels of legal and
666 illegal use, altering growth and tree competition (Boukil et al., 1998). Therefore,
667 competitive interactions in this type of forest are often difficult to discern when evaluating
668 the benefits and disadvantages of mixed-species forests.

669

670 *4.4. Implications for forest management*

671 Comparing structures and dynamics of pure and mixed *A. pinsapo* forests in the Riff
672 Mountains illustrates the importance of considering forest composition and close species
673 interactions to understand population dynamics and regeneration. Our results investigating
674 tree-growth responses to climate and drought of *A. pinsapo*, *P. nigra* and *C. atlantica*
675 growing in mixtures in North Africa has revealed a strong impact of forest structure,
676 climate, and competition on the growth performance of one of the most endangered conifer
677 in the Mediterranean mountain forests, *A. pinsapo*, and its associated coniferous species.
678 Those slow-growing conifers may not be able to keep pace with recent and future climate
679 change. Tree growth resistance and resilience to extreme drought events was influenced by
680 these microhabitat factors, but not their recovery. We showed that although *A. pinsapo* is

681 currently able to regenerate under the current climate, the lack of seedlings and small
682 saplings in some of the species mixtures (*A. pinsapo-C. atlantica*) may hint to regeneration
683 problems for this species in the future, which may require management to successfully
684 regenerate. Studying additional *A. pinsapo-C. atlantica* sites under different climate and
685 management conditions and considering species interactions and pinsapo fir regeneration
686 would offer valuable information to understand the possible mechanisms associated with
687 this situation. In particular, we think that more attention should be dedicated to the role
688 played by secondary tree species in *A. pinsapo* forests (e.g. *P. nigra*, *J. oxycedrus*, and *Q.*
689 *ilex*). These species have a great substitutional potential in case the effects of changing
690 climate or human disturbance dramatically affect these forests, ensuring the survival of the
691 ecosystem and maintaining the conditions for these forest to survive (discussed in Boukil,
692 1998; Navarro-Cerrillo et al., 2014a). These types of studies can support adaptive
693 silvicultural decisions.

694

695 **5. Conclusions**

696 Overall, our results emphasise the dynamic character of secondary *A. pinsapo* forests, the
697 variety of late-successional forest structures and growth relationships with climatic
698 conditions. The evidence obtained so far suggests that *A. pinsapo* forests show continuous
699 recruitment, which is also consistent with the diameter distributions presented. We found
700 abundant recruits of small tree species (*Acer opalus*, *Juniperus oxycedrus* and *Quercus*
701 *ilex*) in mixed *A. pinsapo* forests, which act as early-successional candidates to replace *A.*
702 *pinsapo*. Considering the dominant young structures of protected *A. pinsapo* forests, it is
703 especially important to focus on the conservation of old stands and old living trees, which
704 are rare, difficult to replace, and have a large biodiversity and ecosystem functioning
705 associated with them. The growth of *A. pinsapo* in the Riff Mountains appears to be
706 limited more by precipitation than by temperature, but it seems that sensitivity to extreme

707 drought events is becoming increasingly limiting for *A. pinsapo* forests in North Africa.
708 This contrasting climatic sensitivity may yield a significant impact on future *A. pinsapo*
709 forest dynamics in the Rif Mountains and at a regional scale, since both a trend towards
710 warming and a decline in precipitation have been forecasted for the coming decades.

711

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726

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Figures

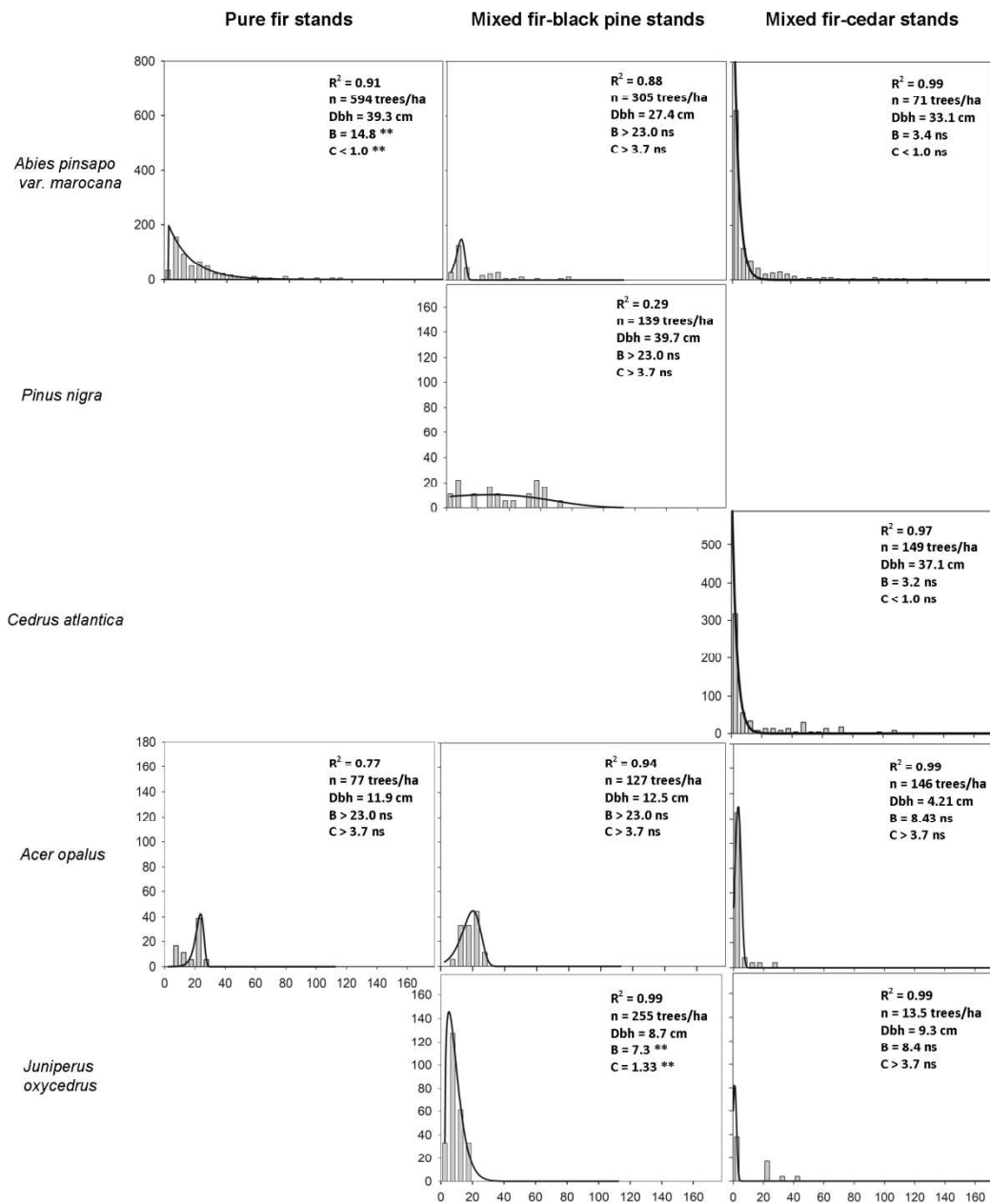


Figure 1. Number of trees per hectare in 5-cm diameter classes, and their corresponding fitted diameter (dbh) distributions (solid line) for four tree species along a management gradient in Talassemtane National Park (Rif, north Morocco). Data were pooled from all study plots. The parameters of each diameter distribution per species and per management gradient are included in Supporting Information; Table S1.

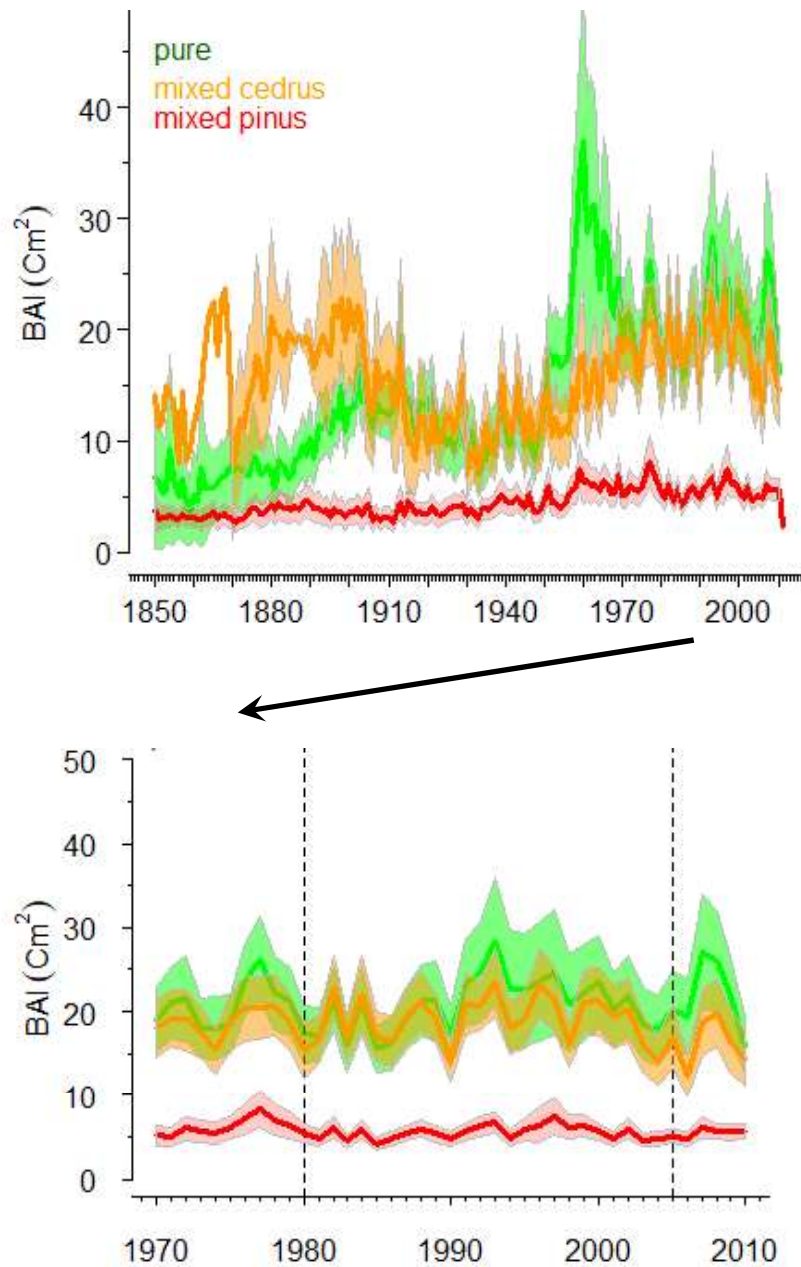


Figure 2. Growth data of *A. pinsapo* (BAI, basal area increment) in pure fir stands (black line and areas) and mixed stands (fir-black pine stands, dark grey line and areas; fir-cedar stands, grey line and areas) located in Talassemthane National Park. The lower plot shows a zoom for the 1970-2010 period and the vertical dashed lines indicate the 1980 and 2005 years. Shaded areas around each time series show standard errors.

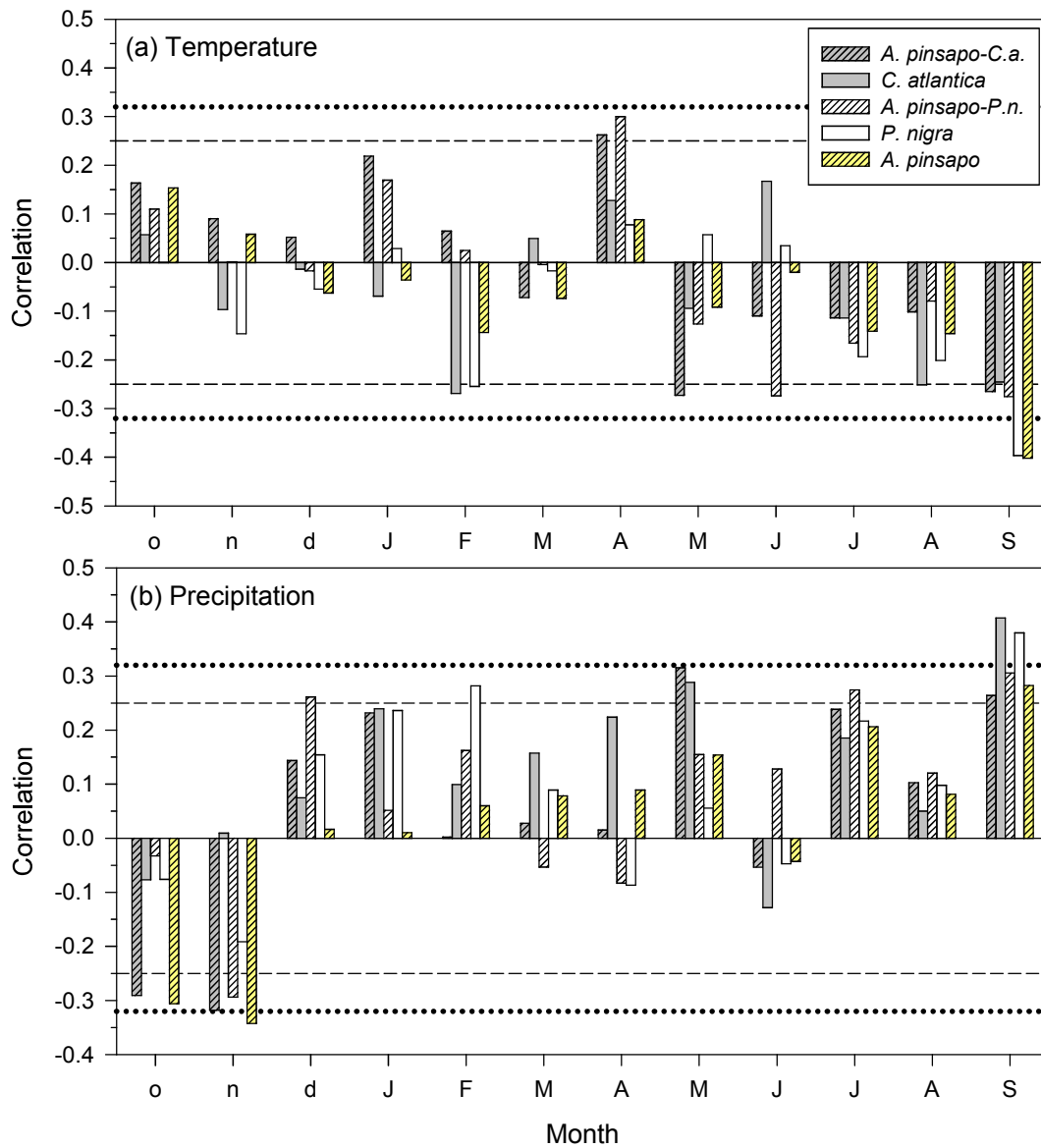


Figure 3. Climate-growth relationships (Pearson correlation coefficients) comparing radial growth (ring-width indices) and monthly mean temperature (a) and precipitation (b) for the study species and stand: *Abies pinsapo* subsp. *marocana* and *Cedrus atlantica* (*C.a.*) in mixed *A. pinsapo-C. atlantica* stands, *A. pinsapo* and *Pinus nigra* in mixed *A. pinsapo-P. nigra* stands, and *A. pinsapo* in pure stands. Monthly climatic variables go from the previous October to the current September and they are abbreviated by lowercase and uppercase letters, respectively. Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively.

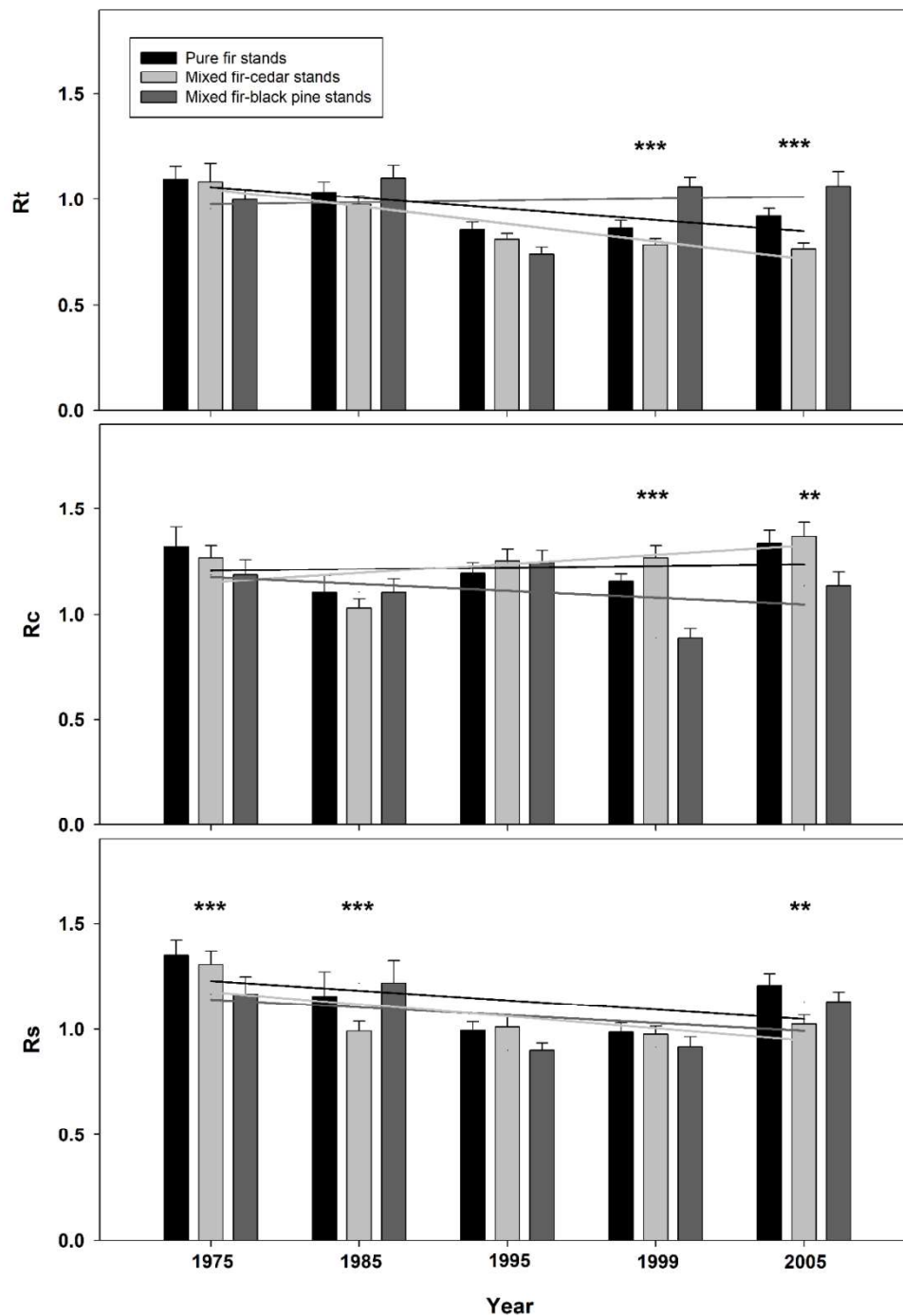


Figure 4. Resistance (R_T), recovery (R_C), and resilience (R_S) growth indices calculated for *Abies pinsapo* subsp. *marocana* in pure (black lines and areas) and mixed stands (*A. pinsapo-Pinus nigra*, grey lines and areas and *A. pinsapo-Cedrus atlantica*, dark grey lines and areas) located in Talassemtane National Park. Resilience indices were calculated considering five droughts (1975, 1985, 1995, 1999 and 2005). Lines of same color indicate trends of the indices for the three types of stands. Asterisks indicate significant differences in comparison between forest types each year at Student's t test: *** $P < 0.001$; ** $P < 0.01$ level. Values are means \pm SD. See Table S3.

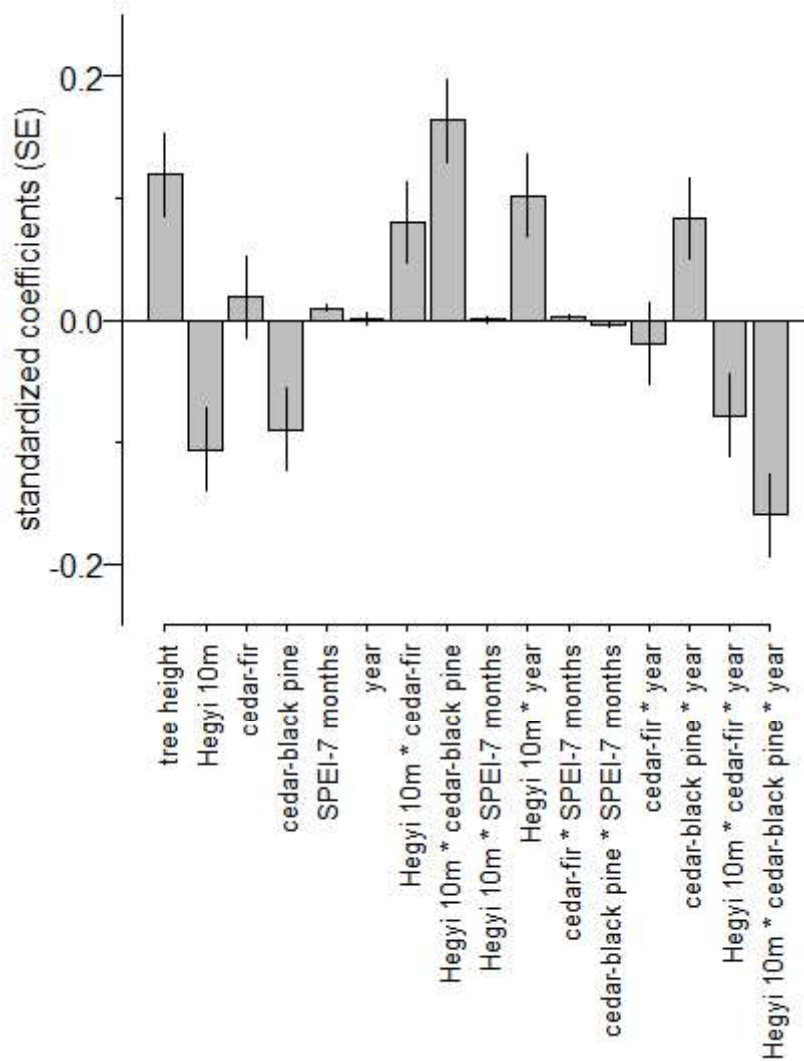


Figure 5. Variable importance in regression model of the six predictors used to predict growth in pure *Abies marocana* and mixed *A. marocana-Pinus nigra* and *A. marocana-Cedrus atlantica* forests in the Talassemtane National Park. High values indicate more important variables in the regression model. The six selected predictors were: tree height, 10 m-Hegyi's competition index (Hegyi_10), fir-cedar forest type (siteAmCe), fir-black pine forest type (siteAmPn), the 7-months Standardised Precipitation-Evapotranspiration Index (SEPI_7), year, and their interactions. Values are means \pm SE.

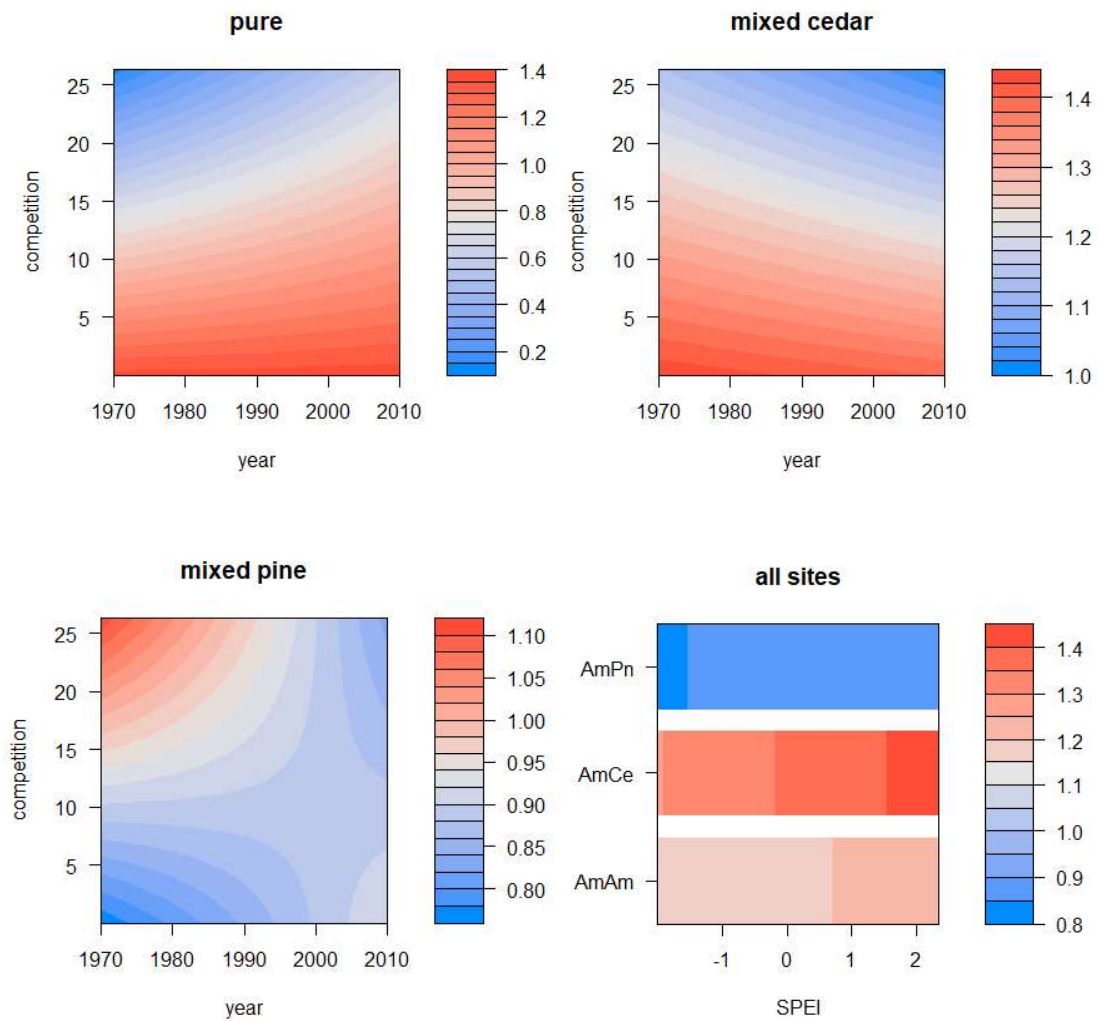


Figure 6. Interaction plots of Hegyi's competition index in pure *Abies pinsapo* and mixed *A. pinsapo-Pinus nigra* and *A. pinsapo-Cedrus atlantica* forests in the Talassemtane National Park (Rif, north Morocco) between 1970 and 2010. The final graph shows the effect of SPEI-7 on the BAI in each stands (i.e. interaction between SPEI and stand).

Tables

Table 1. Structural characteristics of the three stands types studied in the Talassemiane National Park, north Morocco. Values are means \pm SE. Different letters among columns indicate significant ($p < 0.05$) differences between forest types based on Tukey post-hoc tests or T-Student test * < 0.05 ** < 0.01 *** < 0.001

Forest type	Species	Adult density (stems ha ⁻¹)	Diameter (cm)	Height (m)	Basal area (m ² ha ⁻¹)	Reg < 0.50 m (pieds ha ⁻¹)	0.5 < Reg < 1.5 m (pieds ha ⁻¹)	Reg > 1.50 m (pieds ha ⁻¹)
Pure pinsapo fir	<i>Abies pinsapo</i> subsp. <i>marocana</i>	466.3 \pm 166.7 ab	33.8 \pm 5.2 a	11.9 \pm 1.4 a	121.1 \pm 2.3 a	405.56 \pm 200.08 a	144.44 \pm 56.38 b	138.89 \pm 65.5 ab
	<i>Acer opalus</i> subsp. <i>granatense</i>	61.0 \pm 30.8 ab	18.1 \pm 1.7 a	7.7 \pm 0.4 a	2.2 \pm 1.3 b	494.44 \pm 335.04 a	–	–
	<i>Juniperus oxycedrus</i>	–	–	–	–	–	11.11 \pm 11.11 b	–
	<i>Abies pinsapo</i> subsp. <i>marocana</i>	122.0 \pm 67.4 b	20.1 \pm 2.5 ab	6.4 \pm 0.8 b	18.4 \pm 3.2 c	416.67 \pm 160.7 a	283.33 \pm 67.36 a	66.67 \pm 41.94 ab
Mixed pinsapo fir-pine	<i>Acer opalus</i> subsp. <i>granatense</i>	122.0 \pm 67.4 ab	19.4 \pm 2.2 a	7.0 \pm 1.0 a	3.5 \pm 1.9 a	16.67 \pm 16.67 b	–	–
	<i>Juniperus oxycedrus</i>	255.3 \pm 139.1***	9.4 \pm 0.6	2.0 \pm 0.6 ns	2.4 \pm 1.4 ns	372.2 \pm 211.9**	238.89 \pm 29.4 a	72.22 \pm 29.4**
	<i>Pinus nigra</i>	161.0 \pm 38.7	34.1 \pm 3.9	13.5 \pm 1.6	20.3 \pm 4.0	5.56 \pm 5.56	11.11 \pm 11.11	–
	<i>Quercus ilex</i>	27.3 \pm 19.8	13.5 \pm 1.8	3.3 \pm 0.7	0.4 \pm 0.3	73.25 \pm 160.7	10.13 \pm 67.36	20.37 \pm 41.94
	<i>Abies pinsapo</i> subsp. <i>marocana</i>	311.0 \pm 80.6 ab	24.8 \pm 2.4 ab	7.8 \pm 0.6 b	43.4 \pm 4.1 b	54.63 \pm 160.7 b	37.63 \pm 67.36 c	29.88 \pm 41.94 b
Mixed pinsapo fir-cedar	<i>Acer opalus</i> subsp. <i>granatense</i>	16.0 \pm 3.5 b	10.8 \pm 4.6 b	7.3 \pm 0.8 c	0.5 \pm 0.2 c	45.00 \pm 16.67 b	–	–
	<i>Juniperus oxycedrus</i>	33.3 \pm 13.20	24.6 \pm 2.9***	1.88 \pm 0.6 ns	1.9 \pm 0.9 ns	21.75 \pm 211.9	0.50 \pm 29.4 c	0.50 \pm 29.4
	<i>Cedrus atlantica</i>	233.3 \pm 33.3	34.1 \pm 3.5	10.0 \pm 0.8	23.6 \pm 3.6	45.37 \pm 5.56	3.50 \pm 11.11	7.63 \pm 11.11

Table 2. Dendrochronological statistics of sampled trees in the three *A. pinsapo* forest types. Abbreviations: TRW, mean tree-ring width; AC1, first-order autocorrelation; r_m , mean correlation of individual series with master series. Values are means \pm SE. Different letters indicate significant ($P < 0.05$) differences between *A. pinsapo* stands according to forest type.

Forest type	Tree species	No. trees (No. cores)	Age at 1.3 m (years)	Timespan (best-replicated period)	TRW (mm)	AC1	r_m
Pure <i>A. pinsapo</i>	<i>A. pinsapo</i>	20 (40)	100 \pm 8a	1793-2010 (1910-2010)	1.77 \pm 0.12b	0.72 \pm 0.03	0.41 \pm 0.03a
Mixed <i>A. pinsapo</i> - <i>P. nigra</i>	<i>A. pinsapo</i>	14 (28)	148 \pm 10b	1776-2010 (1862-2010)	0.83 \pm 0.08a	0.73 \pm 0.03	0.37 \pm 0.02a
	<i>P. nigra</i>	14 (28)	133 \pm 9	1748-2010 (1878-2010)	1.19 \pm 0.08	0.71 \pm 0.03	0.44 \pm 0.03
Mixed <i>A. pinsapo</i> - <i>C. atlantica</i>	<i>A. pinsapo</i>	11 (19)	148 \pm 9b	1839-2010 (1920-2010)	2.30 \pm 0.15c	0.73 \pm 0.04	0.53 \pm 0.02b
	<i>C. atlantica</i>	11 (19)	133 \pm 10	1797-2010 (1877-2010)	1.78 \pm 0.10	0.84 \pm 0.02	0.47 \pm 0.02

Table 3. Statistical parameters of the evaluated fixed factors and selected interactions in linear mixed-effects models fitted to basal-area increment data for the period 1970-2010. Significant ($P<0.05$) factors are in bold characters. The six predictor variables were: Height is the height of the corresponding tree, 10 m-Hegyi's competition index (Hegyi_10), fir-cedar forest type (siteAmCe), fir-black pine forest type (siteAmPn), the 7-months Standardised Precipitation-Evapotranspiration Index (SPEI_7), and year.

variable	numDF	denDF	F-value	p-value
(Intercept)	1	1817	890.95	0.00
Tree height	1	39	58.99	0.00
CI_10	1	39	0.84	0.37
site	2	39	11.60	0.00
SPEI_7	1	1817	98.09	0.00
year	1	1817	2.09	0.15
Hegyi_10:site	2	39	5.04	0.01
Hegyi_10:year	1	1817	6.21	0.01
site:SPEI_7	2	1817	6.39	0.00
site:year	2	1817	3.03	0.05
Hegyi_10:site:year	2	1817	11.38	0.00

Conflicts of Interest: The authors declare no conflict of interest.

Author statement: Conceptualization, RMNC, RDM; Methodology, RMNC, RDM, AG, JJC; Formal Analysis, RMNC, CR, GPR, AG, RDM; Investigation, RMNC, RDM, AG, JJC; Resources, GPR and RMNC; Data Curation, RMNC, RDM, CR; Writing-Original Draft Preparation, RMNC, RDM, JJC; Writing-Review & Editing, RMNC and all the authors; Project Administration, RMNC and GPR.

Supplementary Material

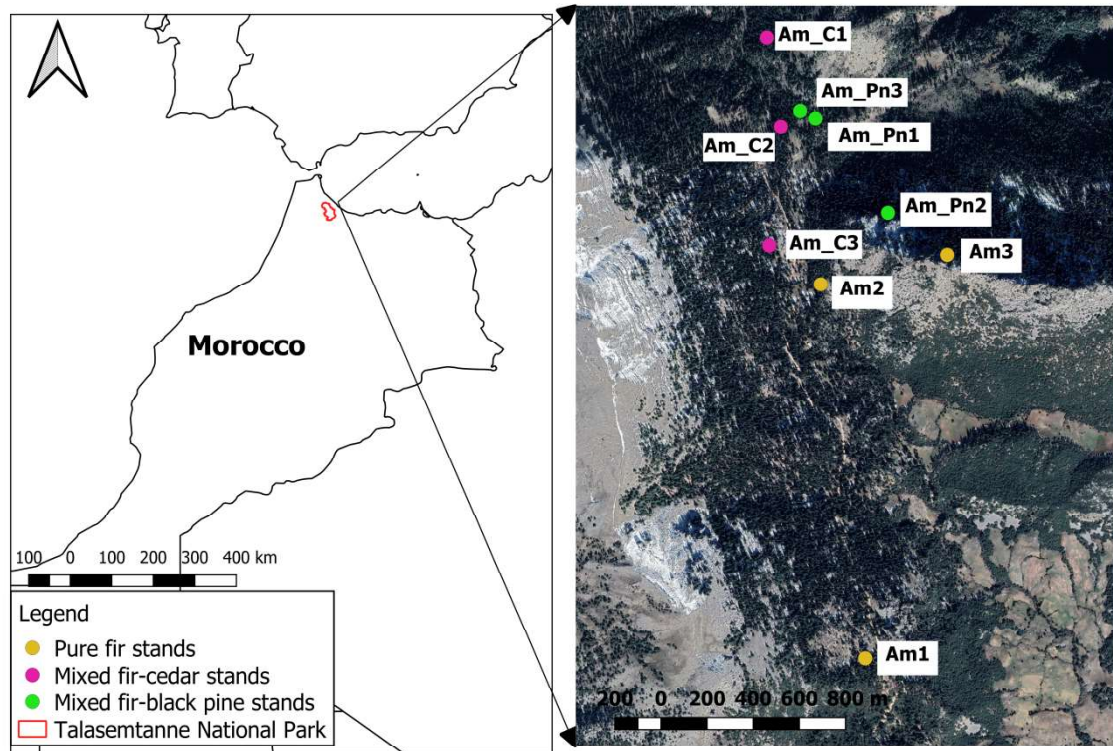


Figure S1. (a) Site locations in Talasemtane National Park (Rif, north Morocco) showing the distribution of pinsapo fir (*Abies pinsapo* subsp. *marocana* Trab.) in the western Mediterranean Basin and sampled plots corresponding to pure fir (green dots) and mixed fir-black pine (*Pinus nigra* Arnold ssp. *salzmannii* (Dunal) Franco var. *mauritanica* Maire & Peyerimh) (red dots) and fir-Atlas cedar (*Cedrus atlantica* (Endl.) Carrière.) forests (black dots).

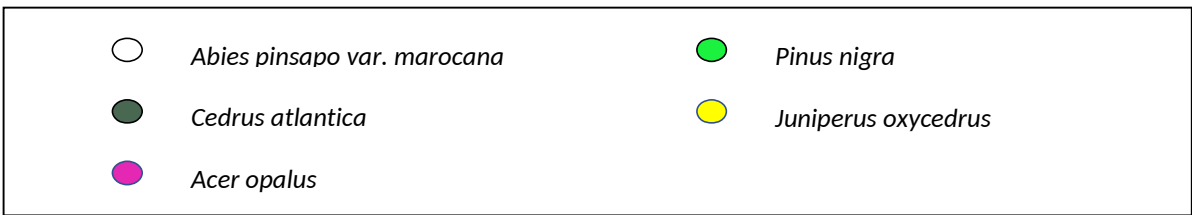
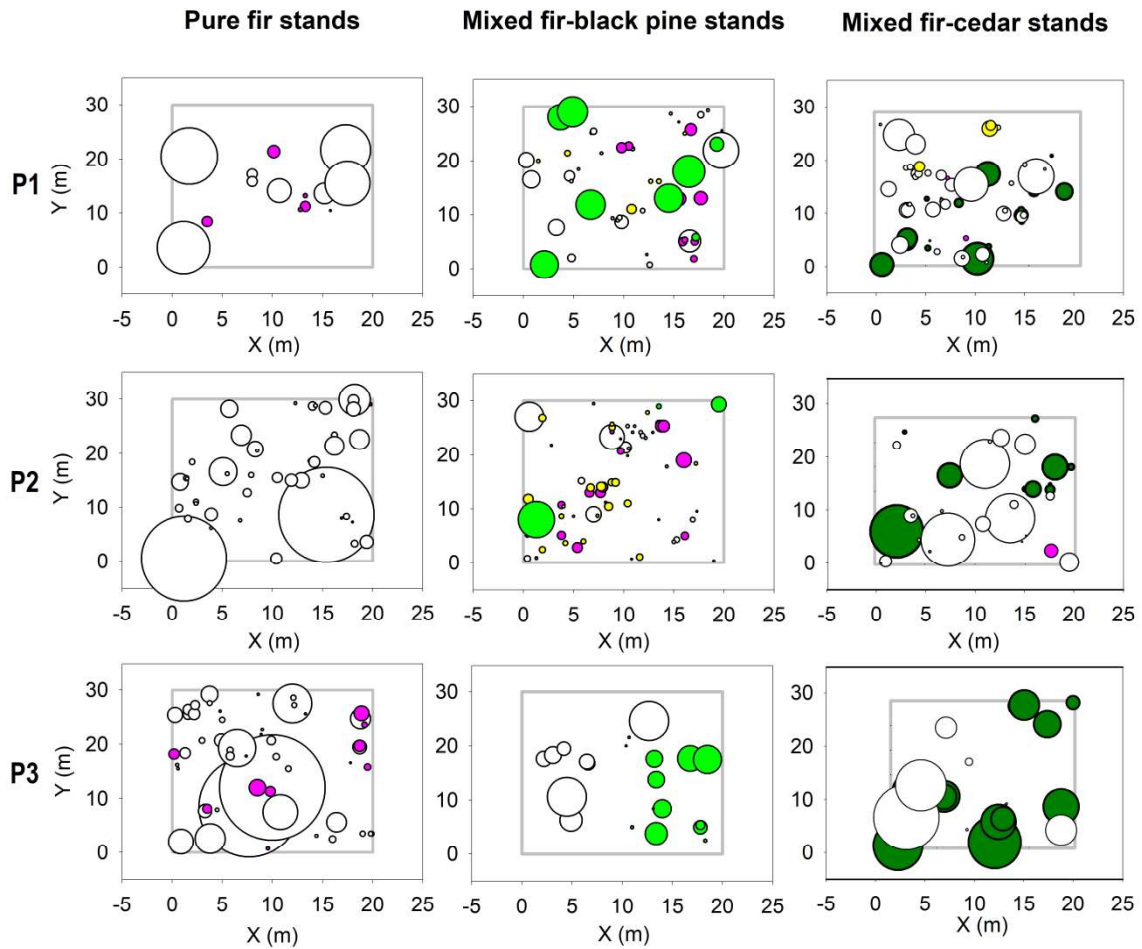


Figure S2. Projection map of tree crowns within three plots of each forest type (P1, P2, P3). The outer boundary (solid line) of plots (30 m x 40 m) is included to show crowns extending outside of the plots. The inner square (dashed line) indicates the 20 m x 30 m mapped plots. Species are indicated as follows: *Abies pinsapo* subsp. *marocana*, white symbols; *Pinus nigra*, green symbols; *Juniperus oxycedrus*, yellow symbols; and *Acer opalus* subsp. *granatense*, red symbols.

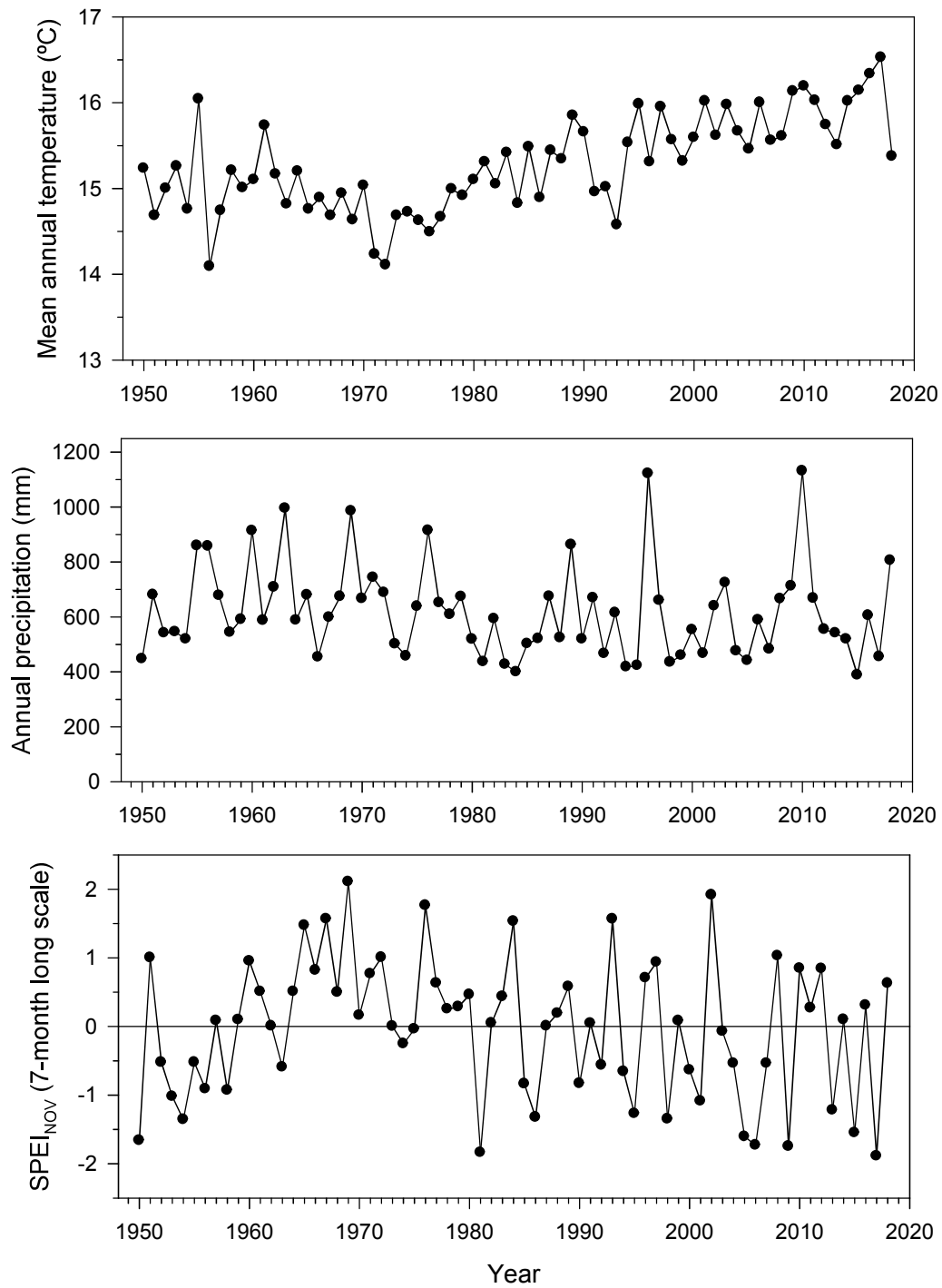


Figure S3. Climate trends in the study area considering mean annual temperature (a), annual precipitation (b) and Standardized Precipitation Evapotranspiration Index (SPEI) calculated at 7-month long scales for the 1950-2016 period.

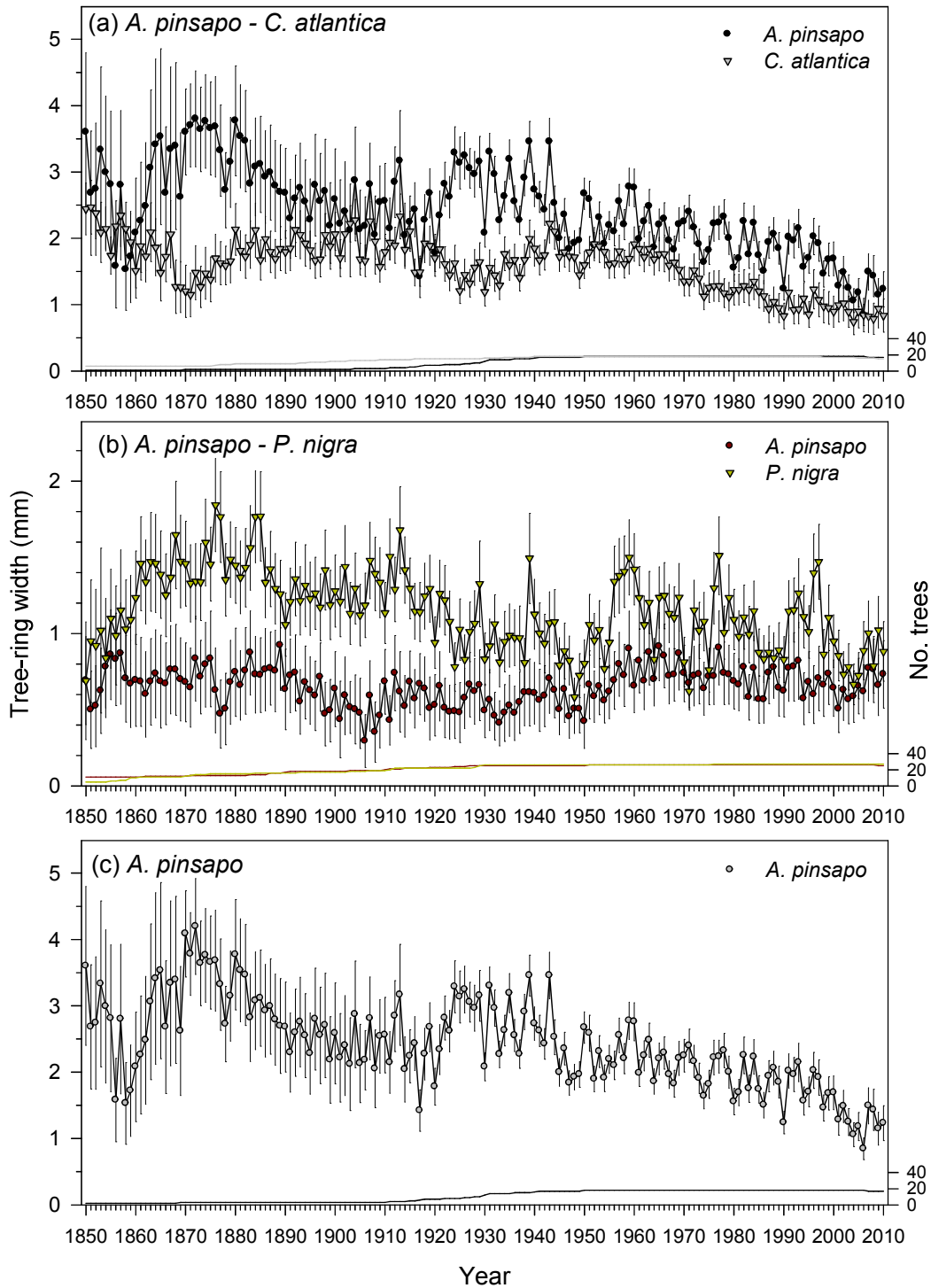


Figure S4. Tree ring width chronologies for *Abies pinsapo* subsp. *marocana* in pure (c) and *A. pinsapo*-*Pinus nigra* (b) and *A. pinsapo*-*Cedrus atlantica* (c) forests in the in Talassemtane National Park (Rif, north Morocco from 1850-2010. Values are means \pm SE.

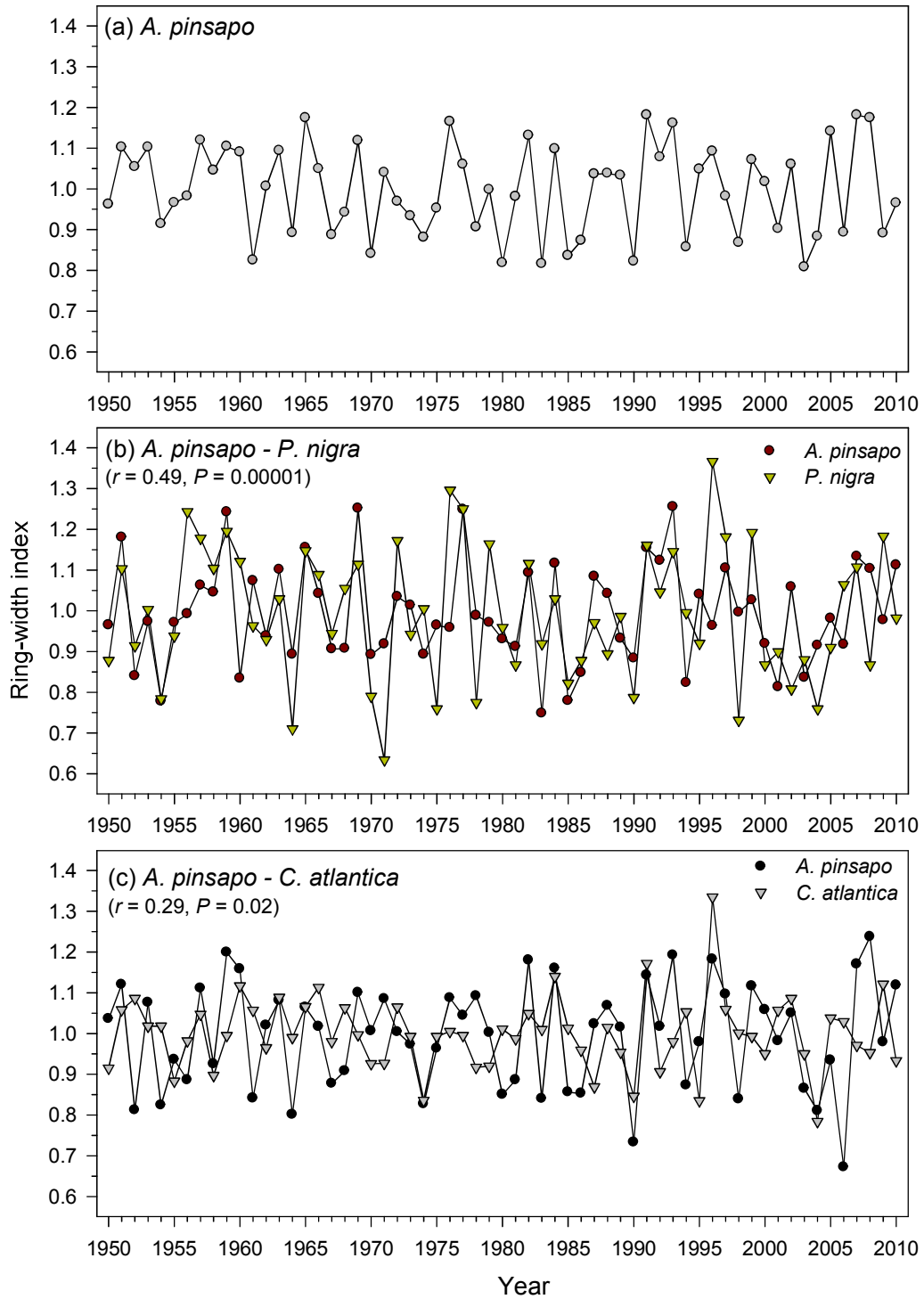


Figure S5. Variability and correlations between mean series of ring-width indices of *Abies pinsapo* subsp. *marocana* in mixed *A. pinsapo*-*Cedrus atlantica* (a) and *A. pinsapo*-*Pinus nigra* (b) stands in the Talassemtane National Park (north Morocco). The lowermost plot shows the mean series (chronology) for the pure stands.

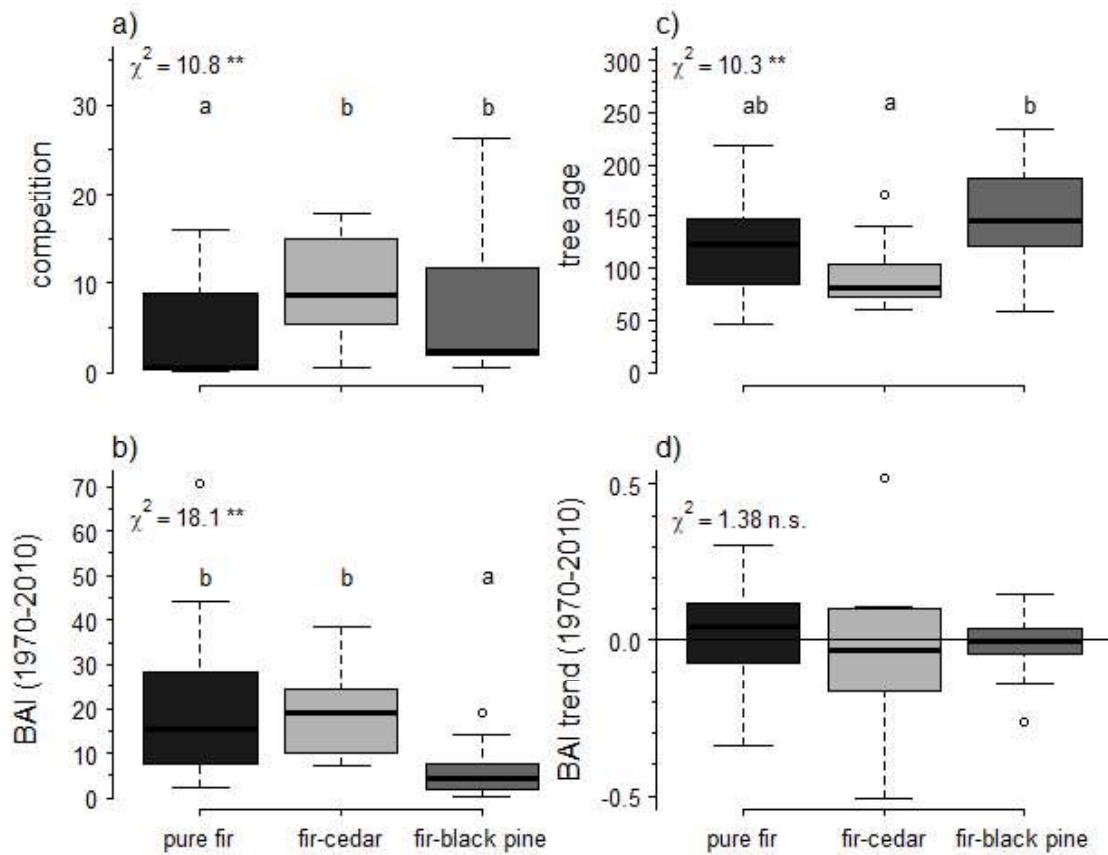


Figure S6. Response of the Hegyi's competition index, tree age, BAI and BAI trend for *Abies marocana* in pure (black) and *A. marocana-Pinus nigra* (dark grey) and *A. marocana-Cedrus atlantica* (light grey) forests in the in Talassemtane National Park (Rif, north Morocco from 1970-2010). Box represent the interquartile range (IQ) with a line in the median, whereas whiskers extend to 1.5*IQ. The chi-squared (χ^2) value indicates the existence of significant (*, $p < 0.05$; ** $p < 0.01$) differences between groups according to Kruskal-Wallis rank sum test. Letters indicate differences between pairwise comparisons according to a post-hoc Dunn's test. SE.

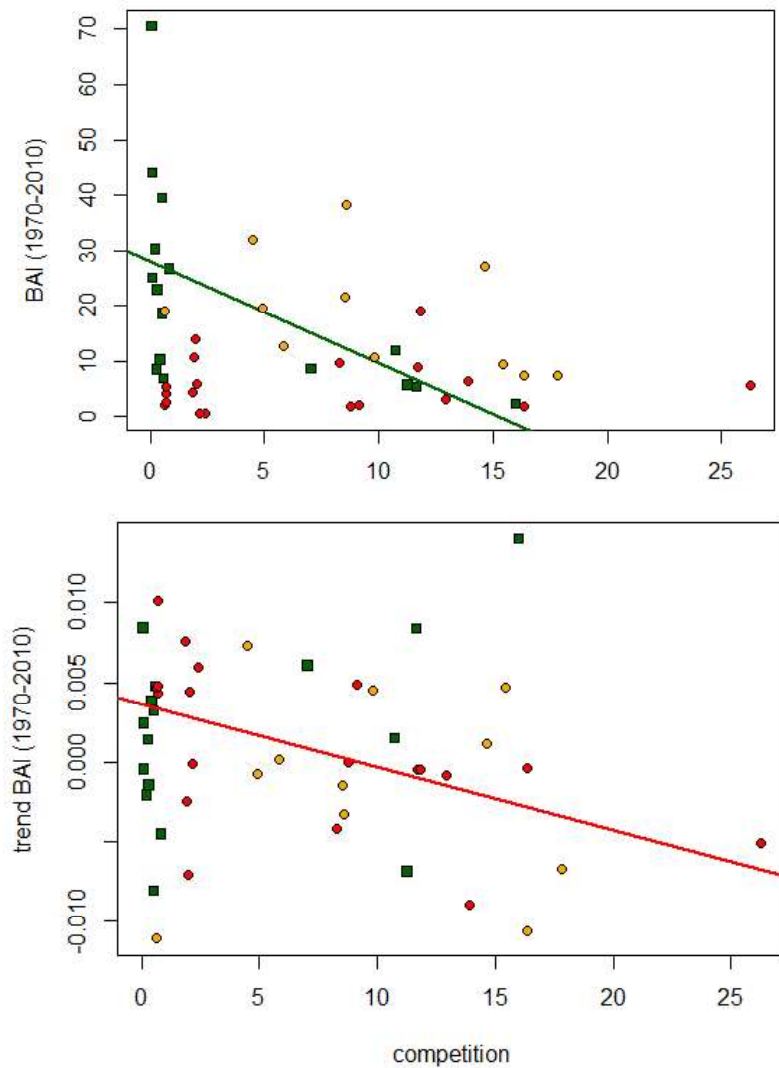


Figure S7. Fitted linear regression relationship between BAI and BAI trend (calculated for the period 1970-2010) and Hegyi's competition index (x axes) to test the effects of competition on annual growth for *Abies pinsapo* in pure (green symbols) and in mixed *A. pinsapo-Pinus nigra* (red symbols) and *A. pinsapo-Cedrus atlantica* (orange symbols) stands in the Talassemtane National Park.

Table S1. Descriptive information about the study plots of *Abies marocana*-*Pinus nigra* forests of Talassemtane National Park, N. Morocco.

Forest type	Plot	Elevation (m a.s.l.)	Coordinates	Slope (%)	Aspect (°)
Pure pinsapo fir (<i>Abies pinsapo</i> subsp. <i>marocana</i>)	1	1631	35° 07' 43'' N 5° 08' 14'' W	35	92 / SE
	2	1768	35° 08' 18'' N 5° 08' 30'' W	35	260 / SW
	3	1740	35° 00' 29'' N 5° 08' 09'' W	45	100 / SE
Mixed pinsapo fir-black pine (<i>A. pinsapo</i> - <i>P.</i> <i>nigra</i>)	1	1663	35° 08' 54'' N 5° 08' 34'' W	50	322 / NW
	2	1690	35° 08' 36'' N 5° 08' 16'' W	45	305 / NW
	3	1711	35° 08' 57'' N 5° 08' 38'' W	70	80 / NW
Mixed pinsapo fir-cedar (<i>A.</i> <i>pinsapo</i> - <i>C.</i> <i>atlantica</i>)	1	1719	35° 08' 40'' N 5° 08' 20'' W	38	232 / NW
	2	1727	35° 08' 26'' N 5° 08' 18'' W	40	210 / NW
	3	1753	35° 08' 17'' N 5° 08' 17'' W	55	180 / NW

Table S2. Main statistics of the ANOVAs calculated for the resistance (C_{RT}), recovery (C_{RC}) and resilience (C_{RS}) indices and mean growth (BAI_{20} , mean basal area increment calculated for the last 20 years). The ANOVAs compared the three indices for four droughts (1995, 1999, 2005 and 2012) and considering natural vs. planted *Pinus pinaster* stands (factor “stand type”) and non-declining and declining trees (factor “decline”). In each cell, the upper line is the F statistic and the lower line is its significance level (P). The last column shows the comparison of the BAI_{20} values (see also Table 2). Bold statistics correspond to significant F values ($P<0.05$).

	Stand	1975	1985	1994-95	1999	2005
Rt	Pure fir stands	1.10±0.06	1.03±0.05	0.86±0.04	0.86±0.04	0.92±0.04
	Mixed fir-cedar	1.08±0.09	0.98±0.04	0.81±0.03	0.79±0.03	0.77±0.03
	Mixed fir-black pine	0.99±0.05	1.10±0.06	0.74±0.03	1.06±0.05	1.06±0.07
Rc	Pure fir stands	1.32±0.09	1.10±0.08	1.19±0.05	1.15±0.04	1.34±0.06
	Mixed fir-cedar	1.27±0.06	1.03±0.04	1.25±0.06	1.27±0.06	1.37±0.07
	Mixed fir-black pine	1.18±0.08	1.10±0.06	1.24±0.05	0.89±0.05	1.13±0.06
Rs	Pure fir stands	1.34±0.08	1.16±0.11	0.99±0.04	0.98±0.04	1.21±0.05
	Mixed fir-cedar	1.30±0.06	0.99±0.05	1.01±0.05	0.98±0.04	1.02±0.04
	Mixed fir-black pine	1.17±0.08	1.22±0.11	0.90±0.04	0.92±0.05	1.13±0.05

Table S3. Drought and competence indices describing the responses to five droughts between 1975 and 2005 calculated for *Abies pinsapo* subsp. *Moroccana* forests of Talasemtane National Park (Morocco).

Height	Dm	Hegy1_10	site	SPEI_7	year	Hegy1_10:site	Hegy1_10:SPEI_7	Hegy1_10:year	site:SPEI_7	site:year	Hegy1_10:site:SPEI_7	Hegy1_10:site:year	df	logLik	AICc	Δ AICc
0.01	0.00	-0.95	+	0.02	0.00	+	NA	0.00	+	+	NA	+	20.00	1793.25	-	0.00
0.02	NA	-0.96	+	0.02	0.00	+	NA	0.00	+	+	NA	+	19.00	1791.43	-	1.58
0.01	0.00	-0.95	+	0.02	0.00	+	0.00	0.00	+	+	NA	+	21.00	1793.33	-	1.87
NA	0.00	-0.96	+	0.02	0.00	+	NA	0.00	+	+	NA	+	19.00	1791.27	-	1.91
0.02	NA	-0.96	+	0.02	0.00	+	0.00	0.00	+	+	NA	+	20.00	1791.52	-	3.45
NA	0.00	-0.96	+	0.02	0.00	+	0.00	0.00	+	+	NA	+	20.00	1791.36	-	3.78
0.01	0.00	-0.96	+	0.02	0.00	+	0.00	0.00	+	+	+	+	23.00	1794.21	-	4.22
0.02	NA	-0.96	+	0.02	0.00	+	0.00	0.00	+	+	+	+	22.00	1792.40	-	5.80
NA	0.00	-0.96	+	0.02	0.00	+	0.00	0.00	+	+	+	+	22.00	1792.23	-	6.12
0.01	0.00	-0.95	+	0.02	0.00	+	NA	0.00	NA	+	NA	+	18.00	1786.84	-	8.73
															3546.04	
															3544.46	
															3544.17	
															3544.13	
															3542.59	
															3542.26	
															3541.82	
															3540.24	
															3539.92	
															3537.31	