



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

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## ABSTRACT

The effects of changes in structure and composition on the dynamics and responses of secondary forests to climate change are understudied. Secondary forests of *Abies pinsapo* var. *maroccana* are often a mosaic of patches of various development stages showing different stand structures and successional stages. We hypothesise that the structure, species composition and tree-to-tree competition of *A. pinsapo* stands in Talasemane National Park (Riff in northern Morocco) modulate the potential response of these secondary forests to climate change. Nine plots representing three species mixtures were established in *A. pinsapo*-dominated forests, and dendrometric and dendroecological surveys were conducted. The two-parameter Weibull function was used to investigate the diameter distributions of *Abies pinsapo*, *Pinus nigra* subsp. *mauritanica*, *Cedrus atlantica*, *Acer opalus*, *Juniperus oxycedrus* and *Quercus ilex* for each site along the compositional gradient. We quantified changes in radial growth, response to climate and drought, and components of growth resilience. Finally, the influence of neighbourhood competition on individual tree growth was evaluated using the a competition index. Diameter distributions had an exponential, reverse-J character for *A. pinsapo* in pure and *C. atlantica* mixed stands. By contrast, *A. pinsapo* presented a positively-skewed diameter distribution dominated by small-sized trees in *P. nigra* mixed stands. There was a significant correlation between tree growth and climate on all forest types, with differing magnitudes per species. Significant precipitation-growth correlations were found for the previous autumn and winter (October, December) in *A. pinsapo*. Drought events reduced *A. pinsapo*'s resistance to subsequent droughts when growing in pure and mixed stands with *C. atlantica*. This decline was statistically significant by the end of the studied period (1999–2005). In contrast, mixed forests showed the highest recovery after drought. Successive drought events consistently reduced *A. pinsapo*'s resilience to drought, regardless of species composition. In pure *A. pinsapo* and in *A. pinsapo*-*C. atlantica* mixed forests, competition reduced *A. pinsapo*'s growth, while in *A. pinsapo*-*P. nigra* mixed forests increased competition with *P. nigra* seemed to have a positive-to-neutral effect on *A. pinsapo* growth. Here, we showed that the response to climate and resilience of *A. pinsapo* forests could be severely influenced by structure, species composition, and competition, potentially influencing our expectations of long-term persistence of old-growth coniferous trees in the Riff mountains. Understanding forest resilience and response to changing climate has important implications towards managing and safeguarding the productivity and health of these old growth forests.

## 1. Introduction

Secondary forests are often viewed as a mosaic of patches of various development stages, stand structures and successional stages (Lira et al.,

2012). Secondary forests display a wide range of structures and ages, corresponding to different size distributions and a diverse arrangement of individual trees within stands, thus the theoretical and practical importance of understanding and managing secondary forests has taken

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more relevance in a context of climate change (Lingua et al., 2008). Forest composition is another major component of forest that may affect tree growth trajectories by modifying tree-to-tree competition and growth responses to drought (Forrester and Bauhus, 2016; González de Andrés et al., 2018; Grossiord, 2019). Forest structure and species diversity are shaped directly by previous forest use and management practices, but they may also respond to recent climate change (Keenan, 2015).

Structural and compositional changes modify neighbourhood competitive interactions, which play an important role in tree growth and forest dynamics (D'Amato and Puettmann, 2004; Coomes and Allen, 2007). For example, opening the canopy can increase sun radiation and enhance carbon assimilation but can also lead to more water loss through enhanced transpiration (Bréda et al., 2006), impacting radial tree growth and stand development in drought-prone areas (Dobbertin, 2005). Additionally, structural diversity (i.e. the variety of structural and species components within a forest) has been related to higher resource diversity available to multiple species contributing to increased vertical stratification and crown plasticity. The influence of structural diversity on productivity is currently receiving a lot of attention (Dănescu et al., 2016; Juchheim et al. 2017; Forrester, 2019). Studies on how intra- and inter-specific competition affect growth in pure and mixed stands provide a valuable assessment of how structural diversity affects the responses of forests to climate; in particular, whether higher structural diversity may help trees cope with higher drought stress (Bottero et al., 2017; Young et al., 2017; González de Andrés et al., 2018).

Despite having been less studied, secondary forests provide an invaluable array of ecosystem services that, in many areas, may be as important as those provided by fully-natural forests (Gamfeldt et al., 2013). Recent dieback events in secondary mountain conifer forests in North Africa raise the question of whether old-growth mountain conifers may struggle more to adapt to climate change compared with lower elevation secondary forests (Abel-Schaad et al., 2018; Navarro-Cerrillo et al., 2019). The structure and species composition of these forests have been altered by centuries of traditional forest use and harvesting. The resulting deforestation and agricultural extension (Barbero et al., 1990; Taleb, 2016) have caused a loss of heterogeneity and structural diversity in most secondary forests compared with the few remaining undisturbed stands, which often show more-variable size distributions and random spatial patterns (Ajbilou et al., 2006). In the Riff mountains of northern Morocco mixed conifer forests are dominated by pinsapo fir (*Abies pinsapo* subsp. *maroccana* Trab.), black pine (*Pinus nigra* Arnold ssp. *salzmannii* (Dunal) Franco var. *mauritanica* Maire & Peyerimh) and Atlas cedar (*Cedrus atlantica* (Endl.) Carrière). Some populations of these three species are already showing growth declines at drier sites related to recent warming and drying trends (M'Hirit and Benzyare, 2006; Linares et al., 2011b). These relict forest ecosystems are highly sensitive to drought stress, and potentially endangered by climate warming if drought severity increases (Sánchez-Salguero et al., 2017). In areas where only small fragments of old-growth forests remain, locally adapted species and phenotypes are at high risk of disappearing as a consequence of climate change unless forest conservation strategies are implemented (Abel-Schaad et al., 2018). Although growth responses to climate have been analysed previously in these species (Linares et al., 2013; Camarero et al., 2013; Sánchez-Salguero et al., 2017), those assessments have mainly focused on pure stands. Here, we compared pure and mixed pinsapo fir stands since the first prerequisite for secondary forest conservation is an adequate understanding of the structure and development of forests with different history, size structure and composition (Pretzsch, 2014).

Although the diversity and variability of natural forests in North Africa have recently been emphasised (Cheddadi et al., 2017), we still know very little about the structural characteristics and, in particular, the differential response of secondary conifer forests in this area (Navarro-Cerrillo et al., 2013). The factors governing competition may

differ markedly for secondary forests, where negligent management – in particular, illegal harvesting and overgrazing – can reduce structural diversity, simplify tree spatial distributions and affect tree growth. This is the case of some pinsapo fir forests in northern Morocco, which form relict, fragmented and biogeographically-marginal populations showing high sensitivity to climate and drought (Linares et al., 2013).

Current aridification trends in North Africa (Cook et al. 2016; Touchan et al., 2008, 2011) may adversely affect pinsapo fir forests, reduce their growth, and even lead to shifts in the species distribution (Sánchez-Salguero et al., 2017). For these reasons, it is crucial to continue improving our understanding of inter-species competition in secondary forests, which may help contextualizing previous results on managed secondary conifer forests in North Africa (Navarro-Cerrillo et al., 2013), and arrive to more general management recommendations to preserve these ecosystems. Here, we analysed structural, competition and dendrochronological data to examine how inter- and intra-specific interactions impact the structure and radial growth in pure and mixed *A. pinsapo* stands in Talassemtane National Park (Riff, northern Morocco). We hypothesized that the size structure, species composition and tree-to-tree competition of these stands modulate the potential relation of these secondary forests with climate change. Specifically, we tested three main hypotheses: (i) the growth of the dominant species (pinsapo fir) does not only depend on climate and drought, but also on competition between species and hence, species composition; (ii) species and structure compositions influence post-drought resilience in pinsapo fir forests; and (iii) the interaction between climatic factors and neighbourhood competition and composition is stronger in mixed than in pure pinsapo fir stands, particularly its drought tolerance. The results will provide insights into the interactions between the species-specific effects and climate regarding structural and spatial responses of pure and mixed *A. pinsapo* forests in North Africa, permitting better forecasts of their future dynamics under warmer and drier conditions.

## 2. Materials and methods

### 2.1. Study area

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

### 2.2. Field data

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

In July 2011, nine 20 × 30 m plots representing three levels of species composition were established in pinsapo fir stands, according to a stratified random design (Table S1; Fig. S2, Supporting Information): pure pinsapo fir forests, mixed pinsapo fir-black pine forests and mixed pinsapo fir-cedar forests. The distances between plots ranged from 0.3 to 0.5 km and they were chosen in similar site conditions, with no recent history of logging and a distance from roads sufficient to minimise other factors which could affect the growth and provide noise in the establishment of the relationship with structural and climatic conditions. Once a suitable stand was located, the first corner of the 20 × 30 m plot was randomly located and laid out using a hand-held compass (Suunto KB-14/360R G Compass; Finland) and a 50-m measuring tape (Lufkin®, Maryland-USA). To facilitate tree measurements, each plot was divided into quadrants of approximately 10 × 15 m, which were sampled in a fixed order. All living trees with diameter at breast height (dbh, 1.3 m above the ground) ≥ 5 cm were numbered, identified to the species level, mapped and measured (dbh with a metric tape, with an accuracy of 0.1 cm). Tree height (H) was measured using a Vertex III hypsometer (Haglöf, Sweden). Then, we calculated stand density (N, trees ha<sup>-1</sup>) and basal area (G, m<sup>2</sup> ha<sup>-1</sup>). In three plots per stand type, the structure of the seedling/sapling layer (dbh < 5 cm) was intensively sampled. Beginning from a plot corner, all the sampled seedlings and saplings within each quadrant were identified by species and height (± 0.1 m) and classified in four size classes: seedlings (h < 50 cm), short saplings (50 cm ≤ h < 130 cm), tall saplings (h ≥ 130 cm and dbh < 5 cm) and juveniles (5 cm ≤ dbh < 10 cm) (Dobrowolska and Veblen, 2008) (Table 1; Fig. S2, Supplementary Material).

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

### 2.3. Dendrochronological methods

We used dendrochronology to estimate tree age and to quantify changes in radial growth and responsiveness to climate and drought. In 2011, we extracted one or two increment cores, at 1.3 m above the ground of mature living trees (10 ≤ dbh ≤ 80 cm), in the direction parallel to the slope contour, using increment borers and following standard dendrochronological methods (Fritts 2001) (Table 1). The wood samples were air-dried and polished in the laboratory with successively-finer grades of sandpaper. Visual cross-dating for each sample was conducted under a binocular microscope and tree-ring widths of dated samples were measured, using a LINTAB measuring system interfaced with the Time Series Analysis Program (TSAP; Frank RinnTech, Heidelberg, Germany), to a resolution of 0.01 mm. Cross-dating was conducted using the marker-year method of Yamaguchi (1991), followed by statistical verification using COFECHA (Grissino-Mayer, 2001). We produced three pinsapo fir chronologies (one for each forest type), one chronology of *P. nigra* and one of *C. atlantica*.

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

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

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

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

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

## 2.4. Climate-growth relationships

The meteorological stations nearest to TLNP, located 10 km away in Chefchaouen (630 m a.s.l.) and at Forest Service Station (1700 m a.s.l.), have provided climate data since 1970. Since those records are heterogeneous and contain numerous gaps, we used 0.5°-gridded monthly data for the mean temperature and total precipitation available for the period 1901–2010 from the Climate Research Unit (CRU) TS4.0 datasets ([https://climexp.knmi.nl/selectfield\\_obs2.cgi?id=someone@somewhere](https://climexp.knmi.nl/selectfield_obs2.cgi?id=someone@somewhere)). These data were used to quantify trends in annual climatic variables and to assess the climate-growth relationships. We also obtained monthly gridded (0.5° resolution) data of drought severity using the Self-calibrating Palmer Drought Severity Index (scPDSI) for the period 1901–2006, and for each site, based on the CRU TS 3.10. 01 dataset (van der Schrier et al., 2013). The scPDSI was also used to select the five most-intense droughts in the study area for the period 1990–2010 (Fig. S3, Supplementary Material).

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

## 2.5. Quantification of drought resilience

In order to understand the effects of droughts on the performance of the three species, resilience components (Resistance,  $R_r$ ; Recovery,  $R_c$ ; Resilience,  $R_s$ ) were calculated as in Lloret et al. (2011). The resilience components are constructed by comparing the growth previous to, during and after the occurrence of drought events. High resistance ( $R_r$ ) indicates a small reduction in growth during the drought year, whereas recovery ( $R_c$ ) quantifies the increase in growth after the drought and resilience ( $R_s$ ) expresses the persistence of the effect of the drought after it has ended (Lloret et al., 2011). Here, we calculated the resilience components using the BAI and considering five droughts (1975, 1985, 1995, 1999 and 2005; Fig. S3, Supplementary Material), according to:

$$R_r = D_r / \text{Pr } eD_r \quad (2)$$

$$R_c = \text{Post}D_r / D_r \quad (3)$$

$$R_s = \text{Post}D_r / \text{Pr } eD_r \quad (4)$$

where  $D_r$  is the BAI in the year of the drought,  $\text{Pr } eD_r$  is the mean BAI calculated for the previous period of up to three years before the

drought and  $\text{Post}D_r$  is the mean BAI calculated for the period spanning three years after the drought. This avoids likely growth overlap and also considers legacy effects that are mostly found up to 2–3 years after a drought (Anderegg et al., 2015).

## 2.6. Neighbourhood competition effects on tree growth

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

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

where  $D_i$  is the dbh of subject tree  $i$  (cm);  $D_j$  is the dbh of competitor trees ( $j \neq i$ ) (cm); and  $L_{ij}$  is the distance of subject tree  $i$  from competitor  $j$  (m). We selected this CI based on its previously-demonstrated success in characterising tree growth in other forest-structure settings (D'Amato and Puettmann, 2004). Competition was estimated at the individual tree level, considering a variable radius of competition proportional to the dbh of the trees present at the time of sampling. We avoided sampling trees that had tree stumps presents within their radius of competition, as this could indicate that competition conditions would have change substantially due to legal due to trees been harvested during our study period (last 40 years). Trees may have been harvested and their remains completely rotted away, in which case, we would underestimate competition. However, given the relatively short period study, the study areas' inaccessibility (which would make extremely complex to remove tree stumps), and the durability of the wood in these species, it is unlikely that the number of 'missing trees' affect our calculation of competition. To further reduce this potential confounding, we only include in our analyses trees with a dbh > 10 cm, to avoid young or suppressed individuals that may not impact the growth of the target tree (cf. Thorpe et al. 2010). Nevertheless, we assumed that the CI calculated for 2010 is a biased representation of the competition 40 years ago.

## 2.7. Patterns, trends and drivers of radial growth

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

$$Y_i = X_i \beta + Z_i b_i + e_i \quad (6)$$

where  $Y_i$  is the response variable (BAI),  $\beta$  is the vector of fixed effects (type of forest, year, age, dbh, type of forest: year interaction),  $b_i$  is the vector of random effects (tree species),  $X_i$  and  $Z_i$  are, respectively, fixed- and random-effects regressor matrices and  $e_i$  is the error vector. In the models, "type of forest" represented the different populations and "year" accounted for BAI trends through time. Tree age and dbh were included in the models to allow for potential differences in growth trajectories among trees of different age and size. However, due to strong collinearity, only tree height was retained in the models because it had the strongest effect. The CI was calculated at different distances. Finally, the CI at 10 m was retained because it had stronger effects on BAI trends. The 7-month-long SPEI for December was included in the model to account for the effect of drought on growth. Further, we included the triple interaction between site, calendar year and CI to account for the potential different patterns in growth trends among populations. Similarly, a triple interaction between site, SPEI-12 and CI was included to account for the potential different relation of growth with climate among populations. Tree identity was included as a random factor to account for the fact that each tree sample represented repeated measurements on the same individual. We included in the models a first-order autocorrelation structure (AR1) to account for the



dependency of the growth in year  $t$  on the growth in the previous year  $t-1$ . BAI was log-transformed ( $\log(\text{BAI} + 1)$ ) prior to the analyses to achieve normality. To quantify the strength of the model, we calculated a pseudo- $R^2$  (Nakagawa and Schielzeth 2013). Lastly, a graphical examination of the residuals and fitted values was carried out to detect the influence of outliers and to evaluate the general model fit. A multi-model inference approach based on information theory was applied to identify the set of covariates that best explained the tree growth trends (Burnham and Anderson, 2002). We ranked all the potential models according to the second-order Akaike information criterion (AICc) and selected the model showing the lowest value (Aho et al., 2014). All computations were performed using R version 3.1.2 (R Core Team, 2014) and the lme4 package (Bates et al., 2015).

### 3. Results

#### 3.1. Stand structure and composition

Among adult trees, the *A. pinsapo*-*P. nigra* stands were dominated by *P. nigra*, while the mixed stands with *C. atlantica* were dominated by *A. pinsapo* (Table 1). The density of *A. pinsapo* individuals ( $\text{dbh} \geq 5$  cm) ranged from 466 (88% of total tree density) in pure stands to 122 (17%) trees  $\text{ha}^{-1}$  in fir-pine mixed stands, being significantly higher in the pure fir and fir-cedar mixed stands. However, the density of *A. opalus*, the other species present in the three types of forest, was significantly higher in the *A. pinsapo*-*P. nigra* and *A. pinsapo* stands (122 and 61 trees  $\text{ha}^{-1}$ ), respectively. *Pinus nigra* and *C. atlantica* were only present in mixed stands, reaching a density of 161 and 233 trees  $\text{ha}^{-1}$ , respectively, but were completely absent from the pure fir stand. *Juniperus oxycedrus* was also present, reaching a maximum density of 255 trees  $\text{ha}^{-1}$  in the fir-black pine mixed stand, and *Q. ilex* had a residual presence in the cedar-mixed stand. Consequently, the total live basal area of *A. pinsapo* ranged widely, from 18.4 to 121.1  $\text{m}^2 \text{ha}^{-1}$ . In pure *A. pinsapo* forests, *A. pinsapo* accounted for over 98% of the basal area, being highly represented in the other two forest types also (40% and 62%, respectively). Black pine and cedar reached values of 20.3 and 23.6  $\text{m}^2 \text{ha}^{-1}$ , respectively, in mixed forests. Small trees (*A. opalus*, *J. oxycedrus*, and *Q. ilex*) comprised only small fractions of the total basal area.

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

The mean dbh of *P. nigra* trees was 39.7 cm in the *A. pinsapo*-*P. nigra* mixed stands, with a low abundance of individuals in all size classes ( $c > 3.7$ , Fig. 1). This indicates a negatively-skewed distribution of the age with few young individuals compared to the individuals of average age; in fact, the regeneration density of *P. nigra* was very low and tall saplings were non-existent (Table 1). The distributions show a plateau with a small negative slope among the largest dbh classes. Above a tree diameter of approximately 65 cm, tree frequency declined rapidly. Finally, the mean dbh of *C. atlantica* trees was 37.1 cm in the *A. pinsapo*-*C. atlantica* mixed stands, with a high abundance of individuals in the smaller size classes (Fig. 1). The dbh class distribution has an exponential, reverse-J character and indicates that there are abundant young individuals in the stands and that the regeneration status of the species is good ( $c = 1.0$ , Fig. 1), with medium values of tall saplings and juveniles but higher values of seedlings (45 seedlings  $\text{ha}^{-1}$ ;

Table 1).

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

#### 3.2. Characteristics of the tree-ring chronologies

For each forest type, separate chronologies were produced for fir, black pine and cedar. The statistical parameters indicated that our chronologies were in general well-replicated, captured a big proportion of the local growth variability, and showed high tree-to-tree coherence in interannual growth variability and the time span for the chronologies dated back to the 18th century in all types of forest, with a best common period of analysis between 1910 and 2010 (Table 2; Fig. S4, Supplementary Material). The mean age of the trees sampled was higher than 100 years; *A. pinsapo* was younger in pure stands, but older than *P. nigra* and *C. atlantica* in mixed forests. The mean TRW for the best-replicated periods was significantly different among the species and forest types (Table 2), as was the mean growth (BAI and  $\text{BAI}_{40}$ ,  $P < 0.001$ ).

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

#### 3.3. Climate-growth relationships

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

Significant precipitation-growth correlations were found for the previous autumn and winter (October, November, December); they were stronger in *A. pinsapo* regardless of whether the trees were in pure or mixed forests (Fig. 3). Significant correlations were also found between growth and current February, May and July precipitation, but they were particularly consistent across forest types for September conditions. *P. nigra* showed a strong to precipitation in February precipitation. *Cedrus atlantica* showed a positive relation with May precipitation, of the current year.

#### 3.4. Post-drought resilience indices

The three drought indices calculated for *A. pinsapo* described the effect of each forest type on the responses to five droughts between

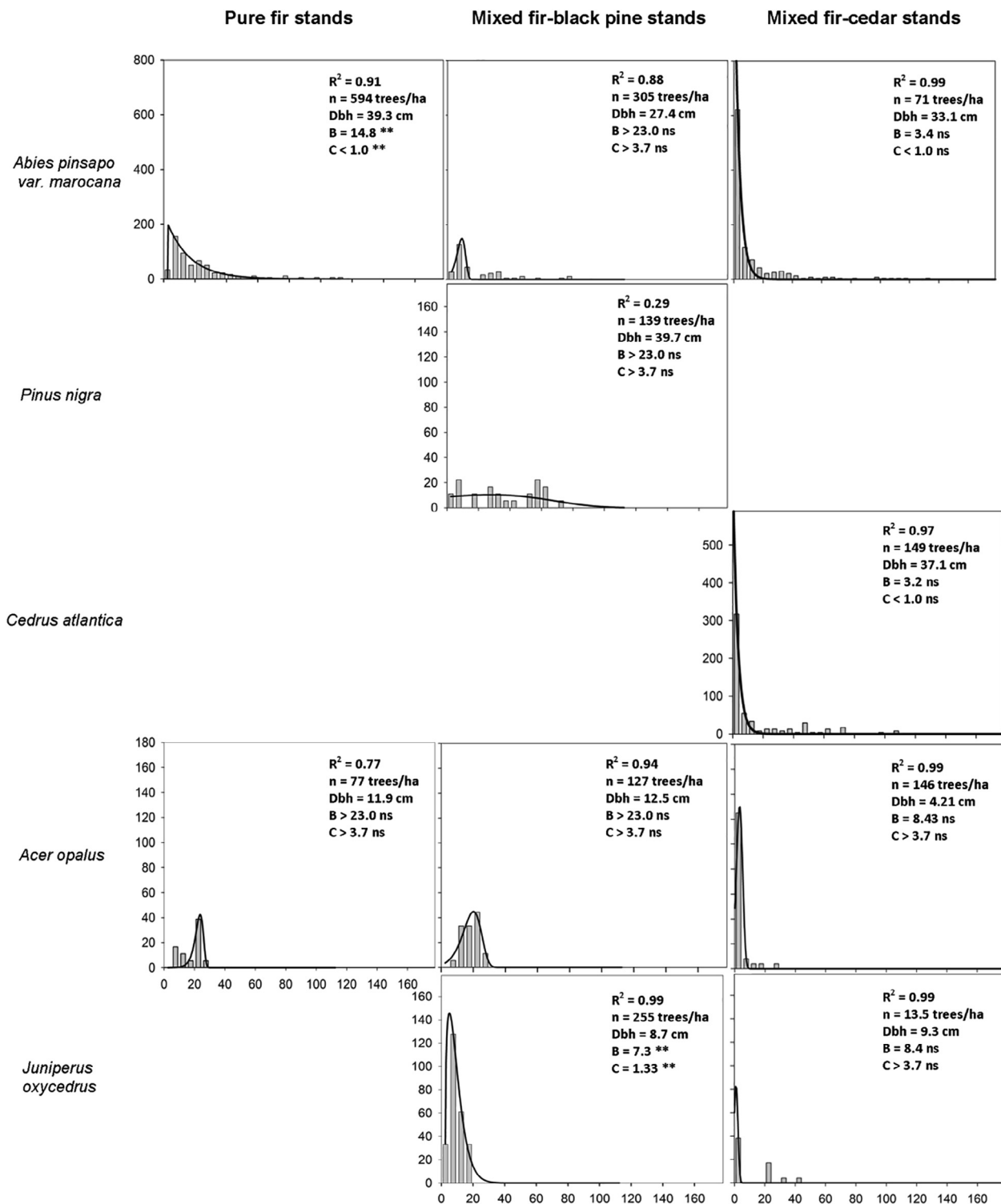


Fig. 1. Number of trees per hectare in 5-cm diameter classes, and their corresponding fitted diameter (dbh) distributions (solid line) for four tree species along a management gradient in Talassemtane National Park (Rif, north Morocco). Data were pooled from all study plots. The parameters of each diameter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

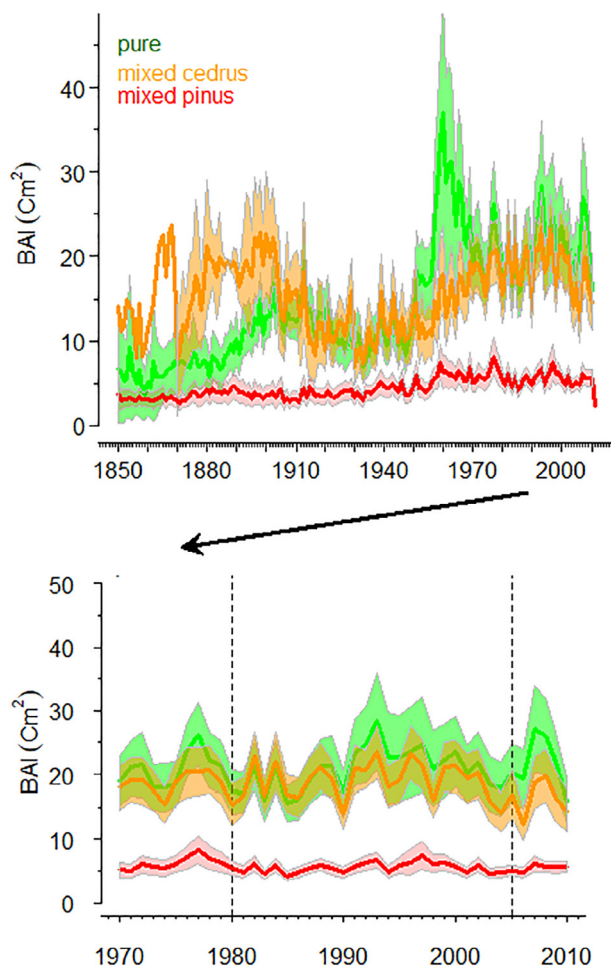
1975 and 2005 (Fig. 4, Table S3, Supplementary Material). The influence on the resistance ( $R_i$ ), recovery ( $R_c$ ) and resilience ( $R_r$ ) growth indices calculated for *A. pinsapo* was different for the three forest types. Drought events seem to reduce the resistance ( $R_i$ ) to subsequent drought conditions when *A. pinsapo* grew in pure and *A. pinsapo*–*C. atlantica* stands, a decline that was statistically significant at the end of the studied period (1999–2005). In contrast, recovery ( $R_c$ ) after drought

was facilitated more in those types of forest (with the most-highly-significant positive effects) (Fig. 4). The resilience ( $R_r$ ) to drought of *A. pinsapo* was consistently reduced by successive drought events, regardless of the stand species composition.

**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



**Fig. 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 Talasemane 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.

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

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

The linear mixed model developed for the forest types and BAI describes the effect of each forest type on the growth responses (Table 3). The significant ( $P < 0.05$ ) factors were tree height, competition index (CI<sub>10</sub>), site, year and SPEI<sub>7</sub>, as well as the two- and

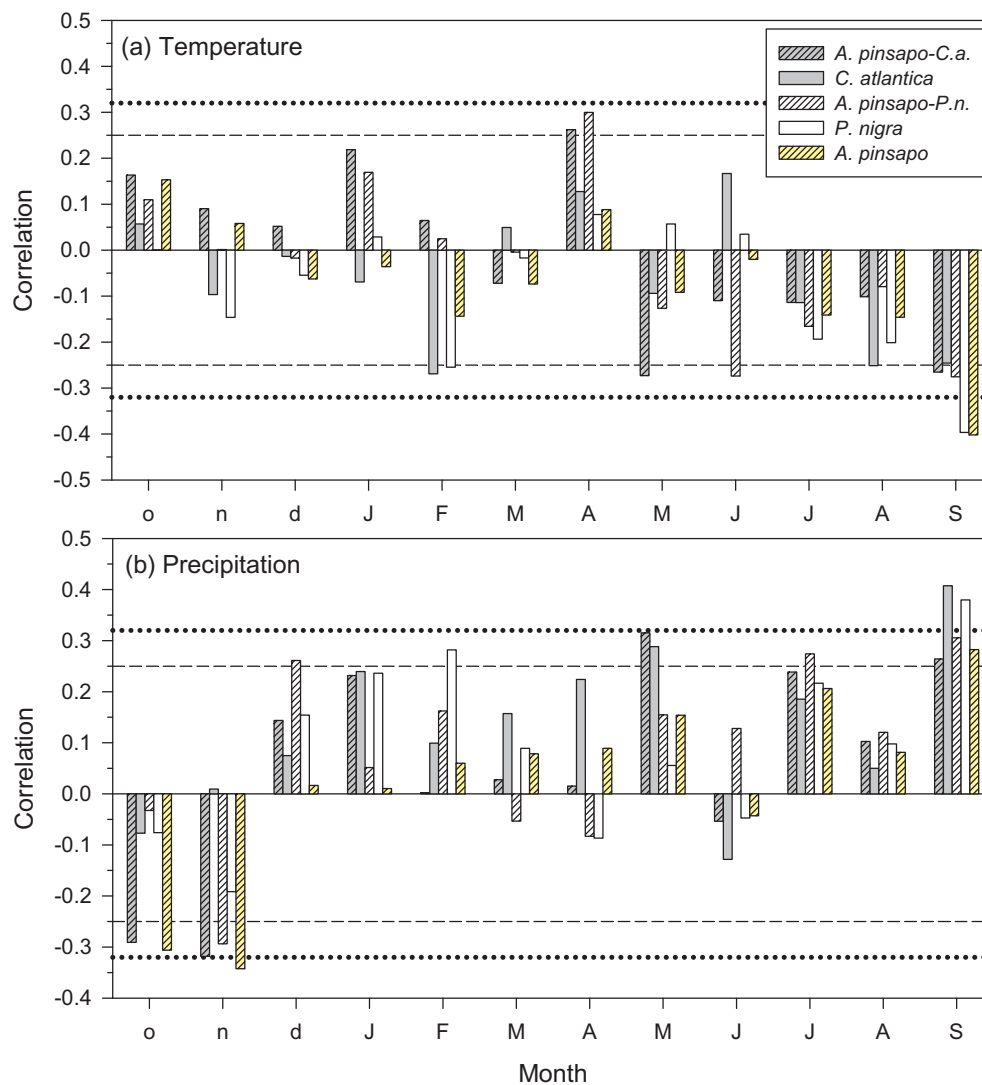
three-way interactions (Table 3). The influence of the species mixtures on the growth responses was different for the three forest types. The BAI trends for *A. pinsapo* differed in time and were influenced by the other species (CI<sub>10</sub>). The growth of *A. pinsapo* increased with increasing height and declined with increasing competition, particularly in *A. pinsapo*–*P. nigra* forests (Table 3, Fig. 5). It also showed several positive interactions: *A. pinsapo* growth was mostly increased by competition in mixed forests and in particular years. However, the competition-forest type-year interaction negatively affected *A. pinsapo*. Its growth was mostly reduced in mixed *A. pinsapo*–*P. nigra* forests in particular dry years (with the most-significant negative effect) (Fig. 5). *A. pinsapo* growth was reduced by competition, although once again there was little effect and the differences among the trends were complex and context-dependent (Fig. 6). In both pure *A. pinsapo* and *A. pinsapo*–*C. atlantica* mixed forests; competition reduced *A. pinsapo* growth, while in *A. pinsapo*–*P. nigra* mixed forests increased competition with *P. nigra* seemed to have a positive-to-neutral effect on *A. pinsapo* growth (Fig. 6). These relationships seemed to be changing in recent decades. Monospecific competition in pure stands had smaller effects on *A. pinsapo* growth in recent years, while interspecific competition with *C. atlantica* and *P. nigra* became more limiting for *A. pinsapo* growth as climate became drier. The growth-climate interaction shows a more-plastic response to the SPEI in pure forests; meanwhile, growth decreased in *A. pinsapo*–*P. nigra* forests, which could indicate increased competition under wetter conditions. The mixture effect, calculated for a simulated composition of equal shares between the three forest types, showed consistently-negative effects of interspecific competition for *A. pinsapo* growth, particularly when mixed with *P. nigra*.

## 4. Discussion

The results presented in this study highlight that the relation of *A. pinsapo* radial growth with climate in the Riff Mountains is modulated by stand structure and neighborhood competition. We found a marked sensitivity of pinsapo fir growth to competition in pure stands in which larger basal area was also found, suggesting the strong impact of intra-specific competition on growth response to climate. However, in mixed stands opposite results were found with negative impacts on *P. nigra*–pinsapo fir stands and neutral ones in *C. atlantica*–pinsapo fir stands, indicating that the potential positive effect of species mixing on growth depends on the species identity. All together, these results indicate the importance of considering stand structure and composition to understand the response of tree growth to changing climate even in mountainous, long-lived conifer forests, where climate has been regularly considered the main limiting factor to tree growth (e.g. Ettinger et al., 2011).

### 4.1. Forest structure and composition

In the investigated forest stands, *A. pinsapo* is the major component in terms of both density and basal area. Several authors have studied the population structure of *A. pinsapo* communities in similar ecological situations and have confirmed the successional convergence towards fir-dominated stands (Baumer, 1977; Melhaoui, 1990; Boukil, 1998,



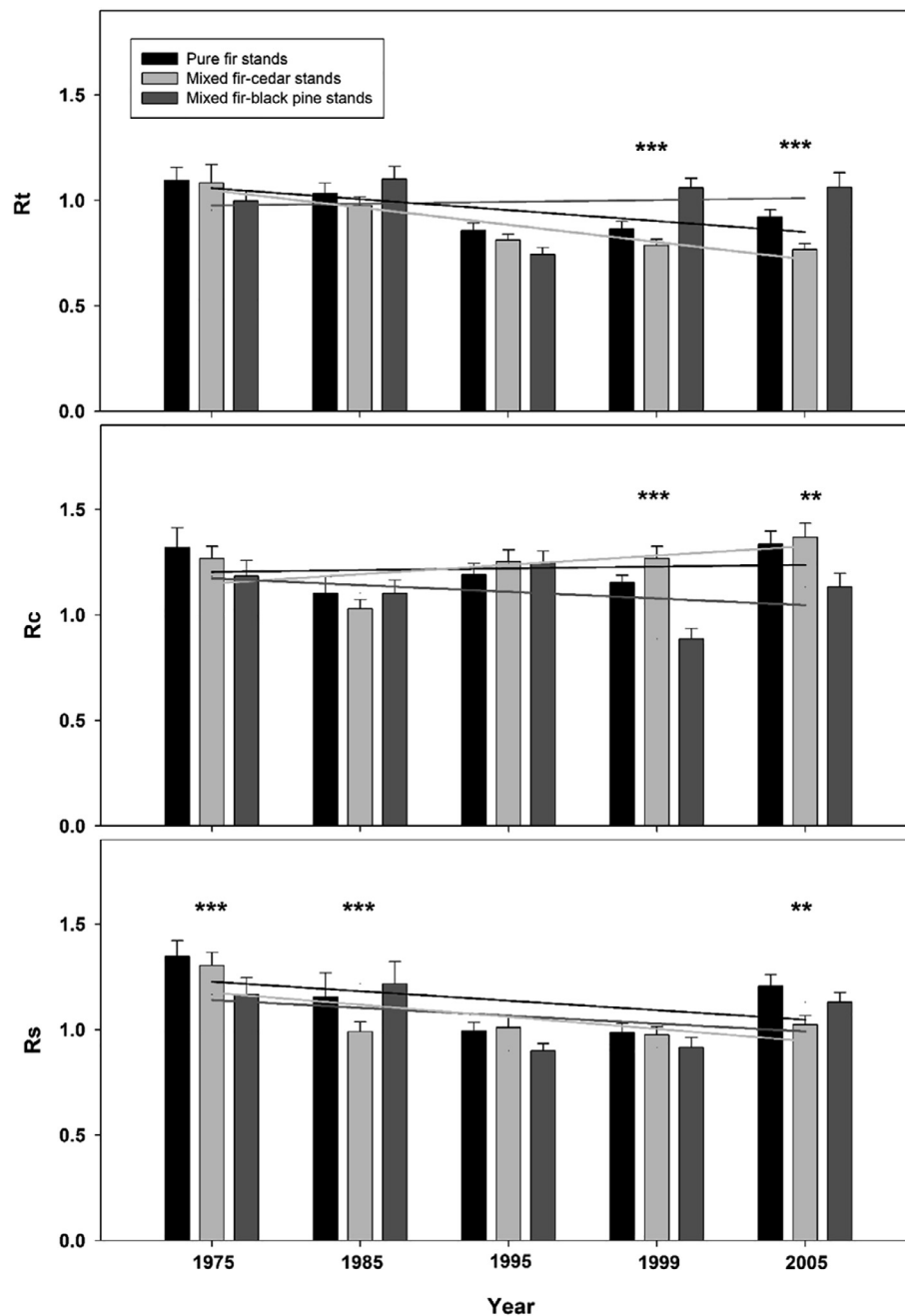
**Fig. 3.** Climate-growth relationships (Pearson correlation coefficients) comparing radial growth (ring-width indices) and monthly mean temperature (a) and precipitation (b) for the study species and stand: *Abies pinsapo* subsp. *marocana* and *Cedrus atlantica* (C.a.) in mixed *A. pinsapo*–*C. atlantica* 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.

Benabid, 2000). The density values measured for this species (range 466–122 trees  $\text{ha}^{-1}$ ) are higher than in previous findings for *A. pinsapo* forests in the Rif (63–115 trees  $\text{ha}^{-1}$ , Baumer, 1977) but lower than those measured in southern Spain (807 trees  $\text{ha}^{-1}$ , Linares et al., 2011a). Basal area was significantly higher in pure *A. pinsapo* forests (121.1  $\text{m}^2 \text{ha}^{-1}$ , 98% of total basal area) compared with mixed forests (18.4  $\text{m}^2 \text{ha}^{-1}$ , 40% and 43.4  $\text{m}^2 \text{ha}^{-1}$ , 62% respectively), showing high structural within-stand variability in tree species composition, and freeing more resources for secondary trees to thrive. *Acer opalus* and *J. oxycedrus* appeared in higher densities in diverse forests. The presence of these species in secondary *A. pinsapo* forests has also been reported by other researchers (Boukil, 1998, Benabid, 2000), who suggested that, in the absence of perturbations (e.g., fire, over-grazing or harvesting), the proportion of conifers increases due to the absence of large-scale canopy disturbances. Comparatively less abundant secondary tree species represented between 8% (fir-cedar forest) and 58% (fir-black pine forest) of the stand's total density. The high density of *J. oxycedrus* and *A. opalus*, is particularly important, because they are potential substitute species in *A. pinsapo* forests (Navarro-Cerrillo et al., 2014a). This appears to be related to the absence of perturbations, which facilitates the recruitment of these species, but also it could be

promoted by climatic change (Gómez-Aparicio et al., 2005).

Tree-size distributions varied considerably among forest types and tree species. Uneven-aged stands of *A. pinsapo* exhibited reverse-J dbh frequency distributions characteristic of old-growth stands as a result of late-successional stand dynamics or of stands that have undergone slow, long-term establishment after catastrophic stand mortality (Oliver and Larson, 1996), similar to those previously documented for old-growth *A. pinsapo* forests in northern Morocco (Boukil, 1998). The stands are scattered with tall, mature *A. pinsapo* that comprises 91% of the total stem density in pure forests versus 17% in fir-black pine and 52% in fir-cedar forests. Such structural heterogeneity is characteristic of Mediterranean fir forests, whose disturbance regime is dominated by small-scale gap dynamics (Fyllas et al., 2010). The numbers of *A. pinsapo* seedlings and saplings were higher in pure fir and mixed fir-black pine stands than in mixed fir-cedar forests, which allows regeneration and the maintenance of a mixed tree composition, even in old-growth forests (Aafi, 2000). In contrast, the regeneration of *A. pinsapo* was poorer in *C. atlantica* mixed forests, probably because of the absence of gap disturbances. This suggests that *A. pinsapo* becomes established as a dense cohort following a severe disturbance (e.g., fire or forest harvesting) and continues to regenerate in large tree-fall gaps (Sevillano





**Fig. 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 Talasemtane 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.

Queipo de Llano, 2009). Even though *A. pinsapo* is traditionally considered a “late successional” species, it can colonise and persist within old-growth stands, due to its prolific seed-producing ability, combined with the availability of suitable microsites (Arista, 1995). The high densities of saplings and juveniles in all forest types reflect the ability of *A. pinsapo* to undergo rapid recruitment in disturbed forest areas due to episodic high seed inputs from old trees, probably linked to mating events (Arista, 1995), although its ability to become established below the canopy may depend on microhabitat factors, such as soil resources, light levels, temperature or grazing – rather than factors associated with fruit production, germination or seedling mortality (Arista, 1995; Arista et al., 1997; Benavides et al., 2016). The recruitment rate of *A. pinsapo*

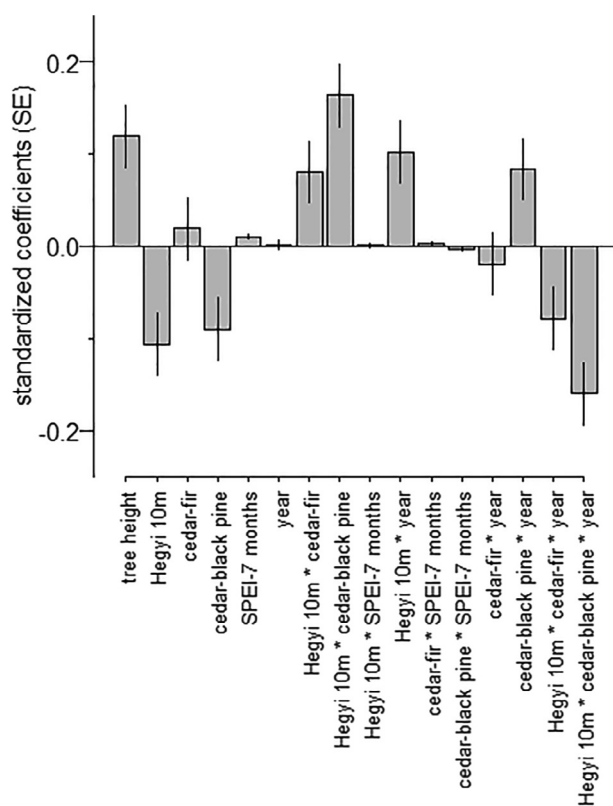
juveniles seems adequate to maintain the existing adult population in these areas, without the bottleneck in recruitment between the seedling and sapling stages observed in other fir forests (Aussenac, 2002). This is consistent with other studies that have observed successful *A. pinsapo* regeneration in populations in southern Spain (Arista, 1995; Navarro-Cerrillo et al., 2014a).

On the other hand, *C. atlantica* and *P. nigra* showed poor regeneration status, which could be attributable to the effect of low regeneration ability (Baumer, 1977; Tíscar and Linares, 2011). The high density of regeneration by secondary tree species (such as *A. opalus*, *J. oxycedrus* and *Q. ilex*) on the understory may indicate the potential of those species to substitute the dominant species in the near future

**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-Hegy's competition index (Hegy10), fir-cedar forest type (siteAmCe), fir-black pine forest type (siteAmPn), the 7-months Standardised Precipitation-Evapotranspiration Index (SPEI7), and year.

variable	numDF	denDF	F-value	p-value
(Intercept)	1	1817	890.95	0.00
<b>Tree height</b>	<b>1</b>	<b>39</b>	<b>58.99</b>	<b>0.00</b>
Cl_10	1	39	0.84	0.37
<b>site</b>	<b>2</b>	<b>39</b>	<b>11.60</b>	<b>0.00</b>
<b>SPEI7</b>	<b>1</b>	<b>1817</b>	<b>98.09</b>	<b>0.00</b>
year	1	1817	2.09	0.15
Hegy10:site	2	39	5.04	0.01
Hegy10:year	1	1817	6.21	0.01
site:SPEI7	2	1817	6.39	0.00
site:year	2	1817	3.03	0.05
Hegy10:site:year	2	1817	11.38	0.00



**Fig. 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-Hegy's competition index (Hegy10), fir-cedar forest type (siteAmCe), fir-black pine forest type (siteAmPn), the 7-months Standardised Precipitation-Evapotranspiration Index (SPEI7), year, and their interactions. Values are means  $\pm$  SE.

(Navarro-Cerrillo et al., 2014a). Although human influence in study sites is currently very limited, these forests have traditionally suffered unregulated harvesting and illegal logging up to the 20th century, which could have affected the current forest structure or influence forest disturbance regimes (Sevillano Queipo de Llano, 2009). The recent absence of silvicultural treatments has favoured trees in the mid-diameter classes, and the understory, resulting in a greater range of tree sizes in pure stands compared to mixed ones (Crow and Perera, 2004).

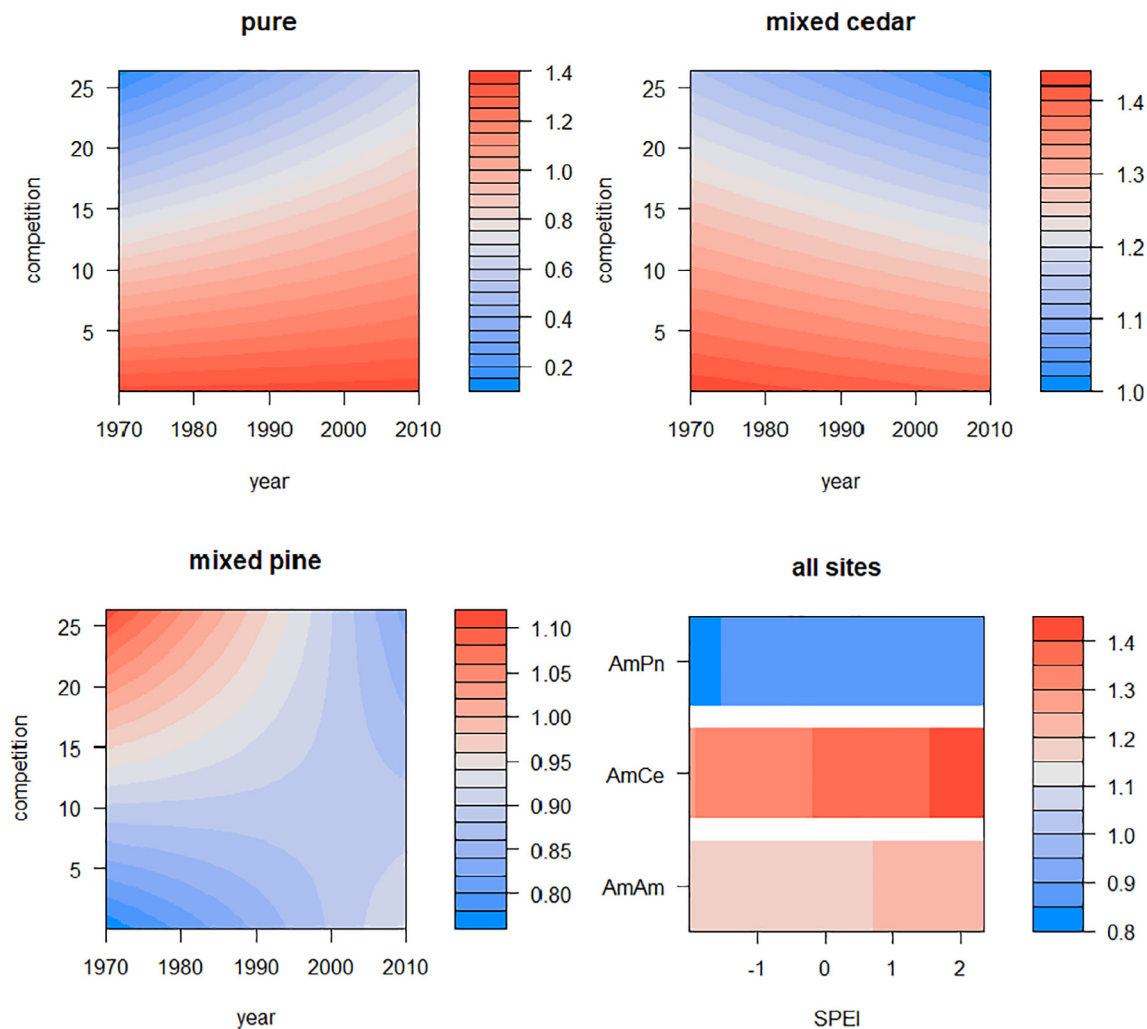
Recent efforts to control illicit logging in the area may have also increased the number of young trees. It is, therefore, unclear the degree of influence of human intervention in the current successional patterns of the Riff coniferous forests. However, the abundant regeneration consistently observed in mature *A. pinsapo* forests suggests that increased by continue reducing human influence and allowing forest to mature, Riff mountain conifer forests will tend in the future to naturally transition to mixed forests. These results agree with the regeneration strategies of *A. pinsapo* (Arista et al., 1997) as well as the dynamic models proposed for mountain, old-growth conifer forests characterised by an elevated vertical heterogeneity (van Pelt and Franklin, 2000). Nevertheless, there is much debate over the level of perturbation necessary to maintain *A. pinsapo* forests and the mechanisms involved in a context of global change (Navarro-Cerrillo et al., 2014a, 2016).

#### 4.2. Growth responses to climate

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

Our results indicate a species-specific seasonal difference in radial growth relation with temperature and/or precipitation across *A. pinsapo* forest types. We observed low responsiveness of the usually climate-sensitive *P. nigra* and *C. atlantica* in the wet and cool sites studied. However, the results suggest that these species growth were broadly influenced by the winter and spring temperatures in water-limited stands. Warmer springs may enhance tree radial growth in mountainous areas by increasing tree vigour via earlier growth onset and higher photosynthetic rates under warmer later-spring conditions (McDowell et al. 2011). However, the benefits of a longer growing season may be counteracted by an increase in the risk of frost damage cause by extreme cold events occurring during periods when the plants are now photosynthetically active and thus, more vulnerable (Liu et al. 2018). Moreover, temperature rises affect coniferous carbon storage because they may lead to an increased rate of respiration and carbohydrate consumption, required to maintain cell metabolism (respiration), thus depleting the food reserves for the following year (McDowell et al. 2011).

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



**Fig. 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 Talassemrane 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).

given that the growth of these shade-intolerant species is usually constrained by water shortage (e.g., Sangüesa-Barreda et al., 2019).

The climate response of *A. pinsapo*, *P. nigra* and *C. atlantica* can be better understood in terms of ecophysiological adaptations to the extreme site conditions in the Rif Mountains ecosystems. Cool-wet conditions during spring are likely to enhance the synthesis of carbohydrates that can increase growth and the production of earlywood (Camarero et al., 2010; Gimeno et al., 2012). Winter and early summer precipitation may replenish soil water before spring and early-summer growth, critical for Mediterranean conifer species in drought-prone areas with short springs and shallow soils (Camarero et al., 2013). Wet autumns, in combination with warmer conditions, have been suggested to extend the growing season, thus increasing growth (Camarero et al., 2010). The unstable relationships between climate and growth observed for *P. nigra* and *C. atlantica* indicate divergent responses, particularly during the late 20th century (Fig. S4, Supplementary Material). These patterns reflect a decreased responsiveness to climate of those species (Navarro-Cerrillo et al., 2014b; 2019). Our results suggests that current-year winter and spring temperatures and precipitation, as well as drought severity, are particularly important growth factors for *A. pinsapo* in northern Africa, but not for other drought-prone conifers (*P. nigra*, *C. atlantica*), which seem less responsive to climate at these cool and wet mountain sites, compared with drier populations in southern Spain. In fact, we have observed a severe growth reduction in the last

decade in *A. pinsapo* growth, likely related to rising temperatures and diminishing rainfall, leading to an increase in drought stress and growth decline (Camarero et al., 2013; Sánchez-Salguero et al., 2017)

#### 4.3. Post-drought resilience indices

Drought years can play a very-important role in the determination of species composition in forest ecotones (Touchan et al. 2017). Extreme events, such as drought, can have a disproportionate effect on forest ecosystems (Altwegg et al. 2017). Given the long lifespan of most forest tree species, they are likely resist under suboptimal average conditions for decades or even centuries, however extreme events can trigger sudden changes in ecosystem structure, composition and functioning (Bräuning et al. 2017 and references therein). This is supported by the correspondence of periods of growth reduction with documented drought events in the Rif Mountains (Touchan et al. 2017). In fact, the period between 1980s and 2000s has been considered among the driest of the past 900 years in North-Western Africa (Cook et al. 2016; Touchan et al. 2008, 2011). The decline in *A. pinsapo* resistance ( $R_c$ ) and resilience ( $R_s$ ) with subsequence droughts in both pure and mixed-*C. atlantica* stands. indicates an overall increase in the vulnerability of these forest to future drought. Should the prediction of increasing frequency and severity of extreme events to be realized (Jentsch and Beierkuhnlein 2008), *A. pinsapo* forests may be under increased

persistence threat. Recovery ( $R_c$ ) after drought was mostly facilitated in all studied forest types; as a consequence, maximum heterogeneity in habitat features and tree communities have been associated with drought response. Drought has been strongly suggested to influence *A. pinsapo* communities in the western Mediterranean mountain forests (Sánchez-Salguero et al., 2015, 2017). Similarly, the accumulative effect of subsequent drought has been pointed out for multiple coniferous species in drier sites of southern Spain (Sánchez-Salguero et al., 2012, 2017; Navarro-Cerrillo et al., 2018).

#### 4.4. Competition and stand stability

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

In our study, the influence of competition (CI<sub>10</sub>) on *A. pinsapo* growth was different for the three forest types. The linear regression fitted to the relationship between BAI (1970–2010) and the CI showed a negative effect of competition on BAI in pure forests and *A. pinsapo*–*P. nigra* forests (Figs. S6 and S7, Supplementary Material). This suggests that differences in the availability of resources between pure and mixed-species stands – related to crown architecture, vertical positioning within the canopy, root morphology, differences in physiology and soils – may result in more-efficient utilisation of water (Linares et al., 2010; Forrester and Bauhus 2016). It has been shown that, during favorable years, *A. pinsapo* in mixed forests reaches the maximum growth rate; however, during droughts, the positive effect disappeared although it was related to the intensity of thinning treatments (Navarro-Cerrillo et al., 2016). The effect of competition was less pronounced in *A. pinsapo*–*C. atlantica* stands, which may be related to the dominant crown position of *C. atlantica* in these mixtures. Additionally, the *A. pinsapo* forests in the study area have historically been subject to different levels of legal and illegal use, altering growth and tree competition (Boukil, 1998). Therefore, competitive interactions in this type of forest are often difficult to discern when evaluating the benefits and disadvantages of mixed-species forests.

#### 4.5. Implications for forest management

Comparing structures and dynamics of pure and mixed *A. pinsapo* forests in the Riff Mountains illustrates the importance of considering forest composition and close species interactions to understand population dynamics and regeneration. Our results investigating tree-growth responses to climate and drought of *A. pinsapo*, *P. nigra* and *C. atlantica* growing in mixtures in North Africa has revealed a strong impact of forest structure, climate, and competition on the growth performance of one of the most endangered conifer in the Mediterranean mountain forests, *A. pinsapo*, and its associated coniferous species. Those slow-growing conifers may not be able to keep pace with recent and future climate change. Tree growth resistance and resilience to extreme drought events was influenced by these microhabitat factors, but not their recovery. We showed that although *A. pinsapo* is currently able to regenerate under the current climate, the lack of seedlings and small saplings in some of the species mixtures (*A. pinsapo*–*C. atlantica*) may hint to regeneration problems for this species in the future, which may require management to successfully regenerate. Studying additional *A. pinsapo*–*C. atlantica* sites under different climate and management conditions and considering species interactions and *pinsapo* fir regeneration would offer valuable information to understand the possible mechanisms associated with this situation. In particular, we think that

more attention should be dedicated to the role played by secondary tree species in *A. pinsapo* forests (e.g. *P. nigra*, *J. oxycedrus*, and *Q. ilex*). These species have a great substitutional potential in case the effects of changing climate or human disturbance dramatically affect these forests, ensuring the survival of the ecosystem and maintaining the conditions for these forest to survive (discussed in Boukil, 1998; Navarro-Cerrillo et al., 2014a). These types of studies can support adaptive silvicultural decisions.

## 5. Conclusions

Overall, our results emphasise the dynamic character of secondary *A. pinsapo* forests, the variety of late-successional forest structures and growth relationships with climatic conditions. The evidence obtained so far suggests that *A. pinsapo* forests show continuous recruitment, which is also consistent with the diameter distributions presented. We found abundant recruits of small tree species (*Acer opalus*, *Juniperus oxycedrus* and *Quercus ilex*) in mixed *A. pinsapo* forests, which act as early-successional candidates to replace *A. pinsapo*. Considering the dominant young structures of protected *A. pinsapo* forests, it is especially important to focus on the conservation of old stands and old living trees, which are rare, difficult to replace, and have a large biodiversity and ecosystem functioning associated with them. The growth of *A. pinsapo* in the Riff Mountains appears to be limited more by precipitation than by temperature, but it seems that sensitivity to extreme drought events is becoming increasingly limiting for *A. pinsapo* forests in North Africa. This contrasting climatic sensitivity may yield a significant impact on future *A. pinsapo* forest dynamics in the Riff Mountains and at a regional scale, since both a trend towards warming and a decline in precipitation have been forecasted for the coming decades.

## 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.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117847>.

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