



## Differential growth responses in *Pinus nigra*, *P. pinaster* and *P. sylvestris* to the main patterns of climatic variability in the western Mediterranean

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### ABSTRACT

Large-scale climate indices, such as the Atlantic Multidecadal Oscillation (AMO), the East-Atlantic pattern (EA), the North-Atlantic Oscillation (NAO) and the Western Mediterranean Oscillation (WeMO), are recognized as important drivers of tree growth and forest productivity in south-western Europe. However, it is still poorly understood whether species respond to these climatic influences differently. Do different pine tree species respond similarly to the main climatic patterns in south-western Europe? If not, will the species respond according to what should be expected from their biogeographical character? Here we analyse the paper of climatic patterns on tree growth in a mountainous Mediterranean environment where three contrasting pine species cohabit (*Pinus nigra*, *P. pinaster* and *P. sylvestris*). We first identified the climatic patterns that most influence temperature and precipitation variability during the coldest months of the year. Secondly, we evaluated the role of these climatic patterns as drivers of Basal Area Increments (BAI) using mixed-effect models separately for each of the three pines considered. A backward model selection was applied using AICc. Only two out of the four climatic patterns analysed were supported as potential drivers of temperature and precipitation variability in our study site. Specifically, EA correlated positively with temperatures and precipitation, whereas NAO correlated negatively with precipitation. Model selection supported both EA and NAO as important drivers of BAI in *P. nigra* and *P. sylvestris*, while *P. pinaster* was sensitive to EA. Our results highlight EA as the most influential climatic driver of tree growth in this area. Furthermore, and according to the biogeographical characters of the species studied, the models show how high temperatures influence *P. pinaster* the most, while *P. sylvestris* is the most sensitive species to precipitation variability. Our findings show the existence of clear species-specific differences in tree growth responses to climatic variability patterns.

### 1. Introduction

Ongoing climate change might jeopardize the current energy and mass exchanges in Mediterranean forests according to the differential sensitivity of tree species to the increased intensity and frequency of drought and other extreme climatic events. It is currently thought that tree species well adapted to dry or seasonally dry environments will replace drought-intolerant tree species northwards in the Northern Hemisphere (Bertrand et al., 2016). At the same time, tree species intolerant to drought may disappear locally over the coming century, affecting forest functioning beyond taxonomical and functional biodiversity losses (García-Valdés et al., 2018). To address such challenges, the study of the climatic components driving tree growth is a common

procedure within dendrochronological methodologies. However, climatic variability is complex in the context of trees growing in temperate latitudes, as these areas experience short- to long-term patterns of temperature and precipitation oscillations. Specifically, recurrent and persistent large-scale variability in atmospheric and oceanic circulation influences meteorological conditions (i.e. temperature, humidity, precipitation) at local and regional scales on continents (Stoner et al., 2009), which affect ecological processes such as primary productivity, plant growth and animal behaviour (Bastos et al., 2016; Hallett et al., 2004; Hódar et al., 2012). Nevertheless, little is known about whether large-scale climatic patterns can influence tree species individually and if species are responding in accordance with their biogeographical character. If true, understanding how these complex patterns of climatic

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variability influence tree functioning may help to predict the potential consequences of climatic warming, and to establish the necessary measures for mitigation and adaptation in extensive diverse forests in the Mediterranean Basin.

South-western Europe is a mid-latitude transitional region where orography and the influence of two large water bodies, namely the Atlantic Ocean and the Mediterranean Sea, determine complex climatic patterns (Martin-Vide and Lopez-Bustins, 2006). The North-Atlantic Oscillation (NAO) controls the amount of winter precipitation and temperature in the western European continent (Comas-Bru & McDermott, 2014; Gallego et al., 2005; Trigo et al., 2002). NAO is defined as the sea-level pressure (SLP) dipole between Azores and Iceland and depicts two opposing phases. In southern Europe, the NAO negative phases are linked to warm-wet winters whereas positive phases correlate to dry winters with a high continental influence, owing to the blockage of westerlies by the Azores high (Trigo et al., 2002). Another large-scale climatic pattern is the Atlantic Multidecadal Oscillation (AMO). This pattern is composed of periodic fluctuations of sea surface temperatures (SSTs) and is associated with the magnitude of boreal summers and heat waves (Sutton & Hodson, 2005) on both sides of the Atlantic Ocean (Knight et al., 2006; Wettstein & Mearns, 2002). The East-Atlantic (EA) pattern in turn is located in the North-Atlantic basin and is based on a north-south dipole displaced southward from NAO. The EA pattern is known to influence climatic elements across the westernmost European coast (Moore & Renfrew, 2012; Rodriguez-Puebla et al., 1998) and recent research has highlighted the importance of the EA-NAO composite on climatic elements over the Iberian Peninsula (Comas-Bru & McDermott, 2014; Sánchez-López et al., 2016). In addition, new climatic patterns have been recently proposed for those regions in which the previous patterns do not adequately explain climatic elements variability. In south-western Europe, the Western Mediterranean Oscillation (WeMO) has been proposed to drive rainfall variability in areas of the Iberian Peninsula where NAO has proven to be less influential (Martin-Vide and Lopez-Bustins, 2006). Despite what is known about these phenomena, predicting climatic patterns presents certain difficulties under the future climate change scenarios (Shepherd, 2014).

Singular or coupled influences of atmospheric and oceanic circulation patterns on climatic elements – and therefore on biosphere – have been seriously debated by ecologist over the last few decades. For instance, climatic patterns can explain tree growth on both large and local scales (Camarero, 2011; Camisón et al., 2016). In addition, it has been confirmed that couplings like AMO-NAO can explain many different types of forest ecological processes (Carnicer et al., 2019; Madrigal-González et al., 2017, 2018). Other less studied couplings, such as the EA-NAO, have been recently shown to drive the carbon sink role of vegetation across Europe (Bastos et al., 2016). Nevertheless, information on how these large-scale climate variability patterns influence species differently is scarce in the literature, which is critical to upscaling biotic responses from communities to whole ecosystems and biomes (Galván et al., 2014; Marqués et al., 2016; Sánchez-Salguero et al., 2012).

In this work we studied how AMO, EA, NAO and WeMO affect tree growth on three different pine species in south-western Europe. Our initial aim was to determine which climatic patterns better explain temperature and precipitation variability in the central-western Iberian Peninsula. Then, tree growth was modelled as a function of climatic variability by separately applying mixed-effect models on tree ring data taken from the following pine species: *Pinus nigra* ssp. *salzmannii*, *Pinus pinaster* and *Pinus sylvestris* (hereafter *P. nigra*, *P. pinaster* and *P. sylvestris*). We hypothesized that the species would respond to climatic patterns as has already been shown by previous studies carried out in the Central Iberian Peninsula (Bastos et al., 2016; Carnicer et al., 2019; Madrigal-González et al., 2018, 2017). If true, climatic patterns could be useful to feed up predictive models in which variability of both long-term large-scale patterns as well as intra-annual climatic extreme events are taken into account. Nonetheless, and bearing in mind the

contrasted biogeographic character of the three species considered, we expected to find differential growth responses, or even specific-species responses, to certain climatic patterns and not the others. As such, the findings of this study would help to establish new research lines headed to generate predictive tools for analysing forest functioning according to tree species composition and structural features.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the Sierra de Gredos mountain range (Central sector of the Spanish Central System range), where three dominant pine tree species (namely, *Pinus pinaster* Aiton., *Pinus sylvestris* L. and *Pinus nigra* Arnold) coexist in restored seminatural forests (Fig. 1). The mean annual temperature is 11.0 °C, with cold winters, and the mean annual precipitation is 514.8 mm. As all Mediterranean climates, a chronic dry-warm period is characteristic in our study area (see Fig. S1 for details). Cambisols are the most extended soil type in the slopes.

### 2.2. Sampling and tree ring data

A total of 10 square shaped sampling plots (900 m<sup>2</sup> area) were selected, ranging from 1075 to 1325 m a.s.l., where pine species were

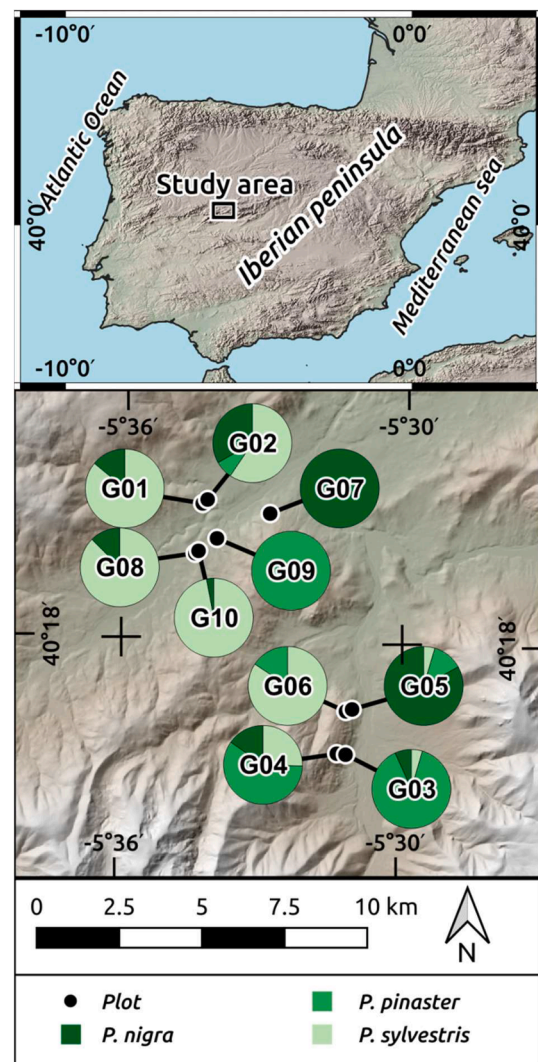


Fig. 1. Location of the study area showing the stands and the specific stand composition (pie charts), indicated as the proportion (%) of living adult pines.

dominant and have not been thinned since the 1960s. In each plot we sampled living adult trees with a Pressler increment borer (Häglof, Sweden). In case the number of adult trees inside the plot was lower than the fixed number (45 individuals), the next closest trees were then sampled until 45 cores were reached. Trees were considered adults when diameter at breast height (DBH)  $\geq 5.0$  cm and height  $\geq 2.0$  m. Cores were extracted at a height of 0.3–0.4 m above the ground level to record as many rings as possible (Veblen, 1992). One core per tree was taken, since the reduction in error in growth estimates generally depends more on the number of trees than on the number of cores sampled from each tree, and it is generally enough to characterize growth trends (Fritts, 1976; Woodall, 2008; Camarero et al., 2015). Cores were always taken parallel to elevation contours of the gentle slopes that characterized these sites. Additionally, we measured DBH of each sampled tree (Fig. 2b). The samples were recorded between March 2017 and May 2018. Increment cores were mounted and sanded following the procedure established by Stokes and Smiley (1968) and scanned at a resolution of 2400 dpi (Perfection V550, Epson, Japan). We measured tree-ring widths on scanned JPG images to the nearest 0.01 mm using the software CooRecorder 7.6 (Cybis, Sweden). Afterwards, we proceeded to do visual and statistical cross-dating using Cofecha (Holmes, 1986). Next, we converted every single year ring-width to Basal Area Increment (BAI) (Fig. 2a) using the ‘dplr’ R library (Bunn, 2008). For analytical reasons we only considered those cores with a minimum length of 50 years, eliminating the individuals established after 1968. Subsequently, a total of 202 cores were analysed: 61 for *P. nigra*; 56 for *P. pinaster*; and 85 for *P. sylvestris*.

### 2.3. Climatic data

Since the closest meteorological station did not provide a sufficient amount of information on temperature and precipitation, this data was obtained from the three closest long-term (1954–2019 period) climate stations (Cáceres (39°28'25"N 6°22'33" W; 425 m a.s.l.), Matacán airport (40°56'23"N 5°30'02"W; 790 m a.s.l.) and Ávila (40°39'19"N 4°41'27"W; 1135 m a.s.l.), AEMET, see Fig. S2 for details). The mean values from November of the previous year to May were determined for each variable, year and station. Then, we interpolated each station values by calculating its mean, and to ensure the validity of the procedure, we estimated Pearson correlation coefficients between the interpolated values and those obtained from the closest weather station at El Barco de Ávila (40°21'34"N 5°31'36"W; period 1994–2019, AEMET, see Fig. S1 for details). The resulting correlation values were 0.778 ( $p < 0.001$ ) for temperature and 0.908 ( $p < 0.001$ ) for precipitation. We covered four climatic patterns widely recognized as being important drivers of climatic elements (Bastos et al., 2016; Martin-Vide

and Lopez-Bustins, 2006; Steinman, Mann & Miller, 2015) and tree growth (Camisón et al., 2016; Madrigal-González et al., 2017): AMO EA, NAO and WeMO. Data for AMO and EA patterns were retrieved from [www.esrl.noaa.gov/](http://www.esrl.noaa.gov/), NAO data were obtained from [www.cru.uea.ac.uk/](http://www.cru.uea.ac.uk/) and WeMO data were downloaded from [www.ub.edu/gc/es/](http://www.ub.edu/gc/es/). We calculated the mean indices for November of the previous year to May timeframe from monthly data. We decided to use such timeframe during the period occurring from November of the previous year to May because the climatic patterns considered have less influence on climatic elements during the summer season

### 2.4. Statistical analysis

First, we standardized into z-scores all explanatory variables, i.e. climatic elements and climate pattern indices as well as tree size. Then we performed simple linear models to evaluate which climatic patterns significantly influenced the local climatic elements; namely, annual precipitation and temperature. Second, we applied linear mixed-effects models using the ‘nlme’ R library (Pinheiro et al., 2012, R Core Team, 2020). BAI was modelled as a linear function of those climatic patterns that were supported in the previous step. We also included tree size as a fixed effect, because it is known to be one of the major variables driving individual growth (Dănescu et al., 2017) in conjunction with climatic variables. Furthermore, we included individual trees and plots as random effects, and evaluated the best temporal autocorrelation structure to be adjusted in each case. A different model was fitted for each species separately. The full model ( $M_{full}$ ) can be written as follows:

$$Y_{ij} = \alpha + a_j + \beta z_{ij} + \varepsilon_{ij}$$

where  $Y_{ij}$  is the response variable (square-rooted(BAI + 1) transformed) for the individual tree  $i$  and the year  $j$ ;  $\alpha$  is the intercept;  $a_j$  is the random intercept (tree individual/plot);  $\beta$  is the vector containing general slopes;  $z_{ij}$  is the vector containing fixed effects, and finally  $\varepsilon_{ij}$  is the error with the first- and second-order temporal autocorrelation function. For each of the three models we carried out a backward model selection starting with the full model ( $M_{full}$ ), and generating new simpler models by removing one climatic variable at a time ( $M_1, M_2 \dots M_i$ ). Then, each resulting model was compared with the full model using the Akaike Information Criterion corrected for small sample size (AICc, Burnham & Anderson, 2002) and those predictor variables were considered relevant when  $\Delta AICc_{M_i - M_{full}} \geq 2.0$  units (Burnham & Anderson, 2002). Each best model was finally compared with a null model ( $M_{null}$ ) using  $\Delta AICc_{M_{null} - M_{best}}$ . Null models were set by removing fixed terms, keeping the random components and temporal autocorrelation structures intact.

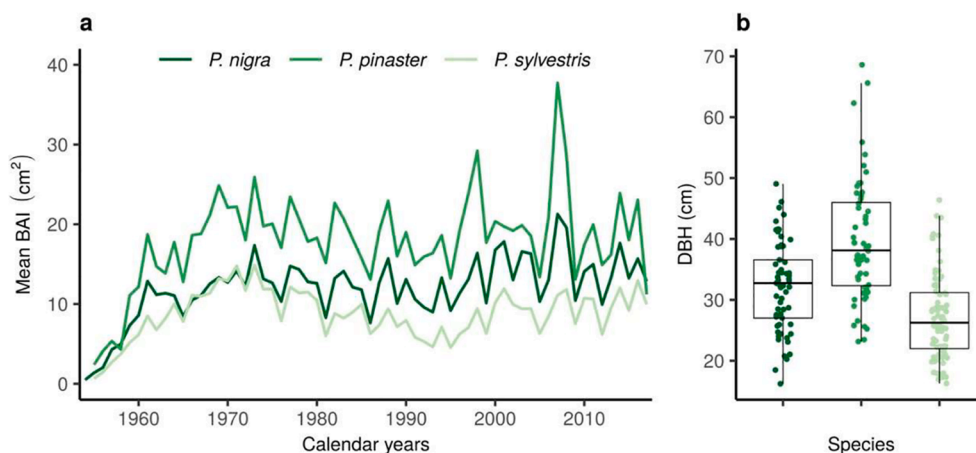


Fig. 2. (a) Mean growth chronologies and (b) box plot of tree size (dots show measured values, boxes hold the interquartile range (IQR), solid lines indicate the median, and whiskers depict the maximum and minimum 1.5 IQR).

## 3. Results

### 3.1. Tree growth and size at tree and species level

These values showed that *P. pinaster* had the highest mean BAI values of the three species (Table 1, Fig. 2a) followed by *P. nigra* and *P. sylvestris*. DBH values presented similar results, indicating that *P. pinaster* has the highest DBH and size variability with some extremely high values (Table 1, Fig. 2b).

### 3.2. Effects of climatic patterns on climatic elements

Linear models supported only EA and NAO climatic patterns as relevant drivers of climatic elements in this area (Table 2). EA pattern was positively related to both temperature ( $F = 13.570$ ,  $p < 0.001$ ) and precipitation ( $F = 5.446$ ,  $p = 0.023$ ) (Table 2; Fig. 3f and b). NAO-precipitation relationship appeared in turn as a solid negatively connection, as shown by  $F = 18.740$ ,  $p < 0.001$  and  $R^2 = 0.222$  (Fig. 3c). None of the results shown gave enough support to AMO and WeMO patterns for them to be considered as drivers of the climatic elements in the study area (Table 2; Fig. 3).

### 3.3. Model selection and effects of climatic patterns on BAI

As a result of the previous analysis, only EA and NAO were considered for the model selection process. Thus, only the following models were included in the backward selection:  $M_1$  as  $M_{full}$  without NAO variable, and  $M_2$  as  $M_{full}$  without EA variable.  $\Delta AICc_{Mi - M_{full}}$  supported the full models ( $M_{full}$ ) for *P. nigra* and *P. sylvestris*, and the  $M_1$  as the best model for *P. pinaster* (Table 3). The comparison using the null model gave adequate support for accepting the fixed variables as drivers of BAI. For all the three species, EA was the climatic pattern that most explained the variance observed in the tree growth, showing a positive relationship among them (Table 4; Fig. 4). Furthermore, EA explained the variability even more than tree size for both *P. nigra* and *P. pinaster* (Table 4). NAO, excluded from the *P. pinaster* best model, presented a negatively proportional influence on BAI of the other species, which was even greater in the case of *P. sylvestris* (Table 4; Fig. 4).

## 4. Discussion

Our results show the EA pattern has a strong influence on the growth of the three pine species studied; in some cases, even more than endogenous factors like tree size (Table 4). The NAO pattern in turn appears as a secondary climatic mode, less decisive for tree growth but still important. EA was revealed as the main driver of the mean temperature with a lesser role on controlling precipitation, whereas NAO appeared as the main driver of precipitation (Table 2). Taken together these findings suggest temperature has a slightly more significant impact on tree growth during the colder months than the amount of precipitation, and support the idea of the coupled EA-NAO patterns as a major controller of primary productivity in south-western Europe (Bastos et al., 2016). The role of AMO in terms of explaining the variability of the climatic elements in our study area was found to be inconclusive (Table 2) despite its influence on both temperature and precipitation

**Table 1**

Summary of the BAI and tree size data. For each species, mean values  $\pm$  standard error (SE) are shown (the maximum measured value (Max. value) is only shown for tree growth).

Species	Tree growth (BAI cm <sup>2</sup> )			Tree size (DBH cm)	
	Mean value	SE	Max. value	Mean value	SE
<i>Pinus nigra</i>	12.87	0.17	84.16	32.24	0.94
<i>Pinus pinaster</i>	19.15	0.29	139.36	39.67	1.35
<i>Pinus sylvestris</i>	9.30	0.10	67.23	27.19	0.75

**Table 2**

Summary of the linear models in relation to climatic elements and patterns. For each model,  $F$  statistic, the associated probability ( $*p$ -value  $< 0.05$ ,  $***p$ -value  $< 0.001$ ) and multiple  $R^2$  (only indicated for the significant results) are shown.

	$F$	$R^2$
<i>Precipitation</i>		
AMO	0.543	
EA	*5.446	0.082
NAO	***18.740	0.235
WeMO	0.328	
<i>Temperature</i>		
AMO	0.427	
EA	***13.570	0.128
NAO	0.624	
WeMO	0.835	

during the winter and spring seasons (Knight et al., 2006; Steinman et al., 2015; Sutton & Hodson, 2005). Reasons for such results are likely due to the time span covered by our climatic elements database and tree cores age, being that AMO periodicity is relatively larger in comparison with our data. Should exist or not an AMO influence over tree growth in our study area, our results did not support a relationship between this climatic pattern and temperatures and/or precipitation, even though research demonstrated a control of AMO on shifting drought regimes and drought indices in the Iberian Peninsula (Carnicer et al., 2019; Madrigal-González et al., 2017) and other zones of the Mediterranean region (Gray et al., 2004). Finally, the WeMO pattern was found to be uncorrelated with the local climatic elements (Table 2) notwithstanding of being reported to modulate tree growth in the western Mediterranean region (Camisón et al., 2016; Pasho et al., 2011). Moreover, references to WeMO support are rather weak with the climatic elements in the western Iberian Peninsula, where the Atlantic Ocean has a prevailing role (Martin-Vide and Lopez-Bustins, 2006).

It is well-known that NAO controls rainfall in winter in western Europe (Martin-Vide and Lopez-Bustins, 2006; Scaife et al., 2008; Trigo et al., 2002; Tsimplis & Josey, 2001). When the Azores high weakens, NAO turns to a negative phase that allows the westerlies to access southern Europe through the Iberian Peninsula; thus increasing the amount of precipitation to above average (Table 2; Fig. 3c). The opposite is true when the Azores high is strengthened, and NAO turns to positive phases. In addition, recent research has established how EA, and especially the EA-NAO composite, can explain temperature and rainfall variations in Europe (Comas-Bru & McDermott, 2014; Comas-Bru et al., 2016; Moore et al., 2013; Rodriguez-Puebla et al., 1998; Sánchez-López et al., 2016), and thus primary productivity (Bastos et al., 2016). In the Iberian Peninsula, the positive EA phases, as shown by our results (Table 2; Fig. 3f, b), are associated with warm-wet winters, but combinations with NAO+ phases lead to insufficient meteorological conditions for primary productivity during January to May across Europe (Bastos et al., 2016). Moreover, the worst conditions for primary productivity are expected in EA-NAO+, which in turn corresponds to lower-than-average temperature and precipitation anomalies (Bastos et al., 2016). The best scenario for the enhancement of primary production is expected in EA+NAO- phases, when heat and water-vapour transport values are higher-than-average and, therefore, the soil water content and temperatures become more favourable for photosynthesis (Bastos et al., 2016) and, consequently, tree growth (Table 4).

Iberian pines tend to dominate in mountainous areas where angiosperm competitiveness is weaker. This occurs, in part, due to low temperatures conditions during winter in which conifers are less sensitive to suffer freeze-thaw-like embolisms (Carnicer et al., 2013; Gómez-Aparicio et al., 2011). We found that tree growth is mainly improved in EA+ phases when temperatures, and to a lesser extent precipitation, increase. Thus, warm-wet winters, and especially mild spring conditions, appear to promote the early activation of photosynthesis and the lengthening of the growing season (Carnicer et al., 2013; Gómez-Aparicio et al., 2011;

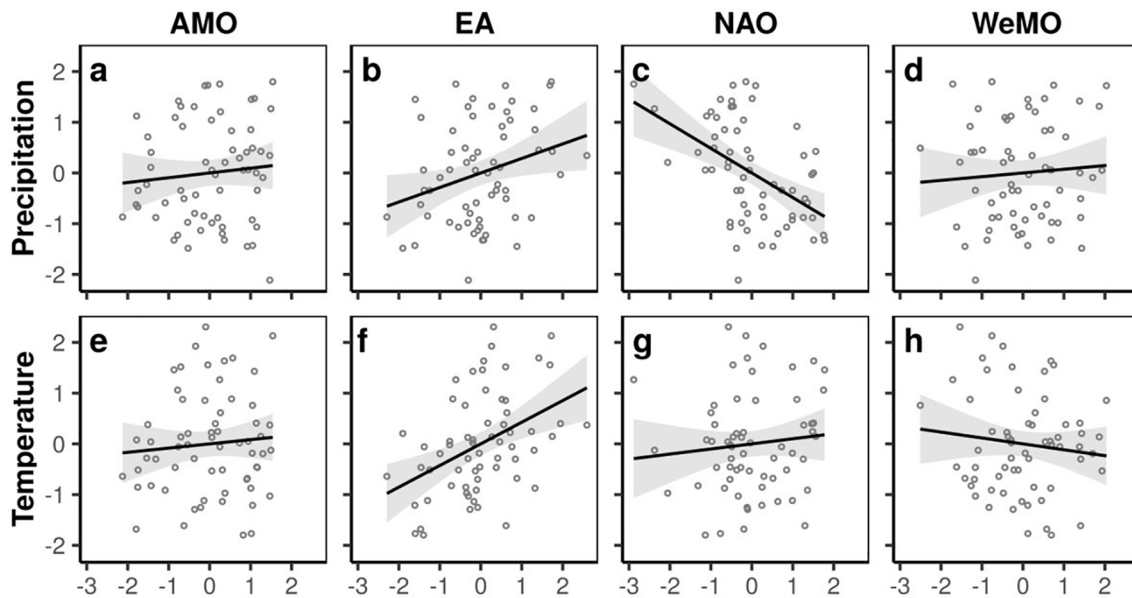


Fig. 3. Plots of the linear models of the climatic elements as a function of climatic patterns (Table 2), showing regression lines (in black) and 0.95 level confidence intervals (grey areas).

Table 3

Backward  $\Delta$ AICc model selection. Full models ( $M_{full}$ ) included tree size, NAO and EA as predictor variables;  $M_i$  models are composed as  $M_{full}$  but ignoring the effect of NAO ( $M_1$ ) and EA ( $M_2$ ).

	<i>P. nigra</i>		<i>P. pinaster</i>		<i>P. sylvestris</i>	
	AICc	$\Delta$ AICc	AICc	$\Delta$ AICc	AICc	$\Delta$ AICc
$M_{full}$	5659.40		6381.75		6149.99	
$M_1$	5672.23	12.83	6373.06	-8.69	6281.89	131.6
$M_2$	6174.28	514.88	6961.34	579.59	6969.61	819.62
$M_{best}$	$M_{full}$		$M_1$		$M_{full}$	
$M_{null}$	6202.05	542.65	6973.25	591.5	7061.63	911.64

Table 4

Parameter estimates and goodness of fit (conditional  $R^2$ ) of best supported models.

Species		Estimate	SE	$R^2$
<i>P. nigra</i>	Intercept	3.464	0.187	0.424
	Tree size	0.209	0.046	
	EA	0.211	0.009	
	NAO	-0.039	0.008	
<i>P. pinaster</i>	Intercept	4.525	0.508	0.579
	Tree size	0.184	0.064	
	EA	0.270	0.010	
<i>P. sylvestris</i>	Intercept	3.024	0.219	0.310
	Tree size	0.273	0.043	
	EA	0.187	0.006	
	NAO	-0.069	0.006	

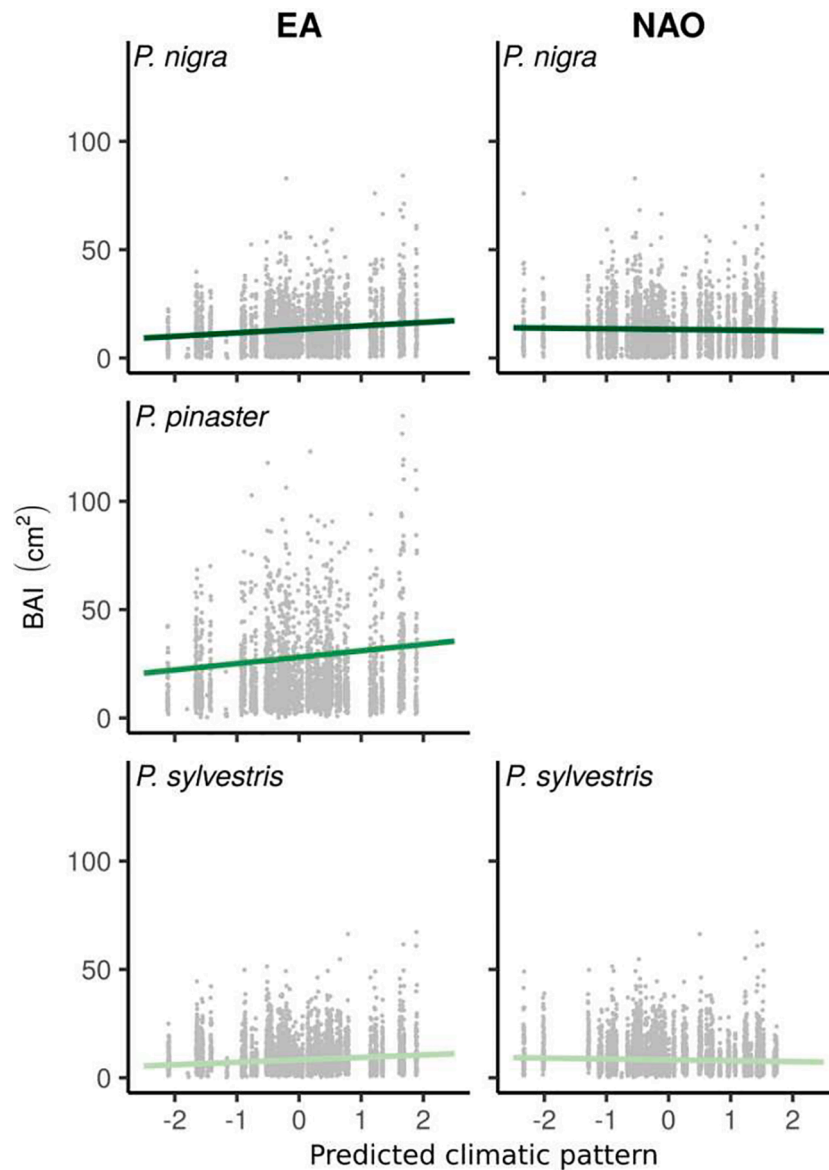
Maselli et al., 2014). Nevertheless, each species tends to respond differently to climate depending on its particular biogeographical characters; i.e., Mediterranean pines are more sensitive to lower temperatures than continental pines.

The presence of the Eurasian pine species *P. sylvestris* is circumscribed to mountains in the Mediterranean Basin where summer water deficit is attenuated upwards (Matías & Jump, 2012). The results obtained in this work indicate that *P. sylvestris* is the species most sensitive of all pines studied to NAO (Table 4; Fig. 4) which highlights the greater water demands. Surprisingly, EA relative role was revealed more important than NAO, which promote growth during EA+NAO- when

winters are mild and moist. Although it is well known that tree growth is comparatively higher in years with warm winters (Fajardo et al., 2012; Michelot et al., 2012), this positive influence can also represent a major threat to tree growth if unusually warm temperatures extend throughout the summer and/or autumn (Matías & Jump, 2012). Unsatisfied water demands during EA-NAO+ phases are not only adverse for tree growth, but cause dieback and trigger decline events in *P. sylvestris* in its southernmost range limit (Matías & Jump, 2012; Sánchez-Salguero et al., 2012; Vilà-Cabrera et al., 2014; Voltas et al., 2013).

In contrast, *P. pinaster* is a dominant pine species in the western Mediterranean, and is characterized by a wide ecological tolerance ranging from sea level to 2000 m a.s.l. Since our analysis did not support NAO as a relevant explanatory variable of *P. pinaster* growth (Table 3), we presume that cold-wet conditions in this mountain fulfil this species water requirements. Therefore, temperature seems to be the main limiting factor causing EA to be the most influential variable with regard to BAI (Fig. 4). The stimulation of photosynthesis by higher winter-spring temperatures also increases the demand for water (Medlyn et al., 2002), which corresponds with EA+ phases when both temperature and precipitation are higher-than-average. Many authors have shown that *P. pinaster* is more dependent on soil water availability than temperature during winter (Bogino & Bravo, 2008; Sánchez-Salguero et al., 2018). Nevertheless, other authors have found higher winter temperatures to be essential for early wood formation and photosynthesis (Kurz-Besson et al., 2016; Vieira et al., 2014), which is in accordance with our results.

Finally, *P. nigra* is situated in an intermediate position, being comparatively less responsive to NAO than *P. sylvestris*, and less responsive to EA than *P. pinaster*. Interestingly, the relative role of EA on *P. nigra* growth is five times greater than that of NAO (Table 4; Fig. 4). Moreover, *P. nigra* growth is influenced by climatic patterns in accordance with its biogeographical character like being a circum-Mediterranean mountain pine species (Morales-Molino et al., 2017). Thus, *P. nigra* is a more water-demanding species than *P. pinaster* and less sensitive to temperature than *P. sylvestris*. The results obtained with the model suggest that the growth of *P. nigra* increases during EA+NAO- phases when warm-wet pre-growth season conditions prevail, as reported in a number of other studies (Camarero et al., 2013; Martín-Benito et al., 2008; Sánchez-Salguero et al., 2013; Sangüesa-Barreda et al., 2019).



**Fig. 4.** Model predictions for climatic patterns calculated using the best supported models (Table 4) showing measured BAI values as a function of the EA and NAO patterns (points) and the regression lines of the predicted BAI values (solid lines).

Vulnerability to summer drought, winter and summer water demands, and lower tree growth put *P. sylvestris* populations at risk of local disappearance according to the predicted climate change scenarios within the Iberian Peninsula. Marqués et al. (2016) proposed that *P. sylvestris* would undergo an altitudinal dominance shift, becoming less abundant in low lands, to the benefit of *P. nigra*. However, the long term biogeographic approximations at the rear edge, like those proposed by Sánchez-Salguero et al. (2012), indicate a risk of decline in the isolated forests of both mountainous pine species. The struggle of mountainous pines for survival could benefit more water-drought resistant species like *P. pinaster* that are more likely to perform better under the predicted warmer and drier conditions.

The use of climate-tree growth models to assess forest vulnerability to climate warming is one of the key elements for helping in the decision making. Forest adaptation to the upcoming weather conditions demands a thorough evaluation of climatic sensitivities of tree species to address how they will be exposed to global change (Keenan, 2015; Kolström et al., 2011; Sánchez-Salguero et al., 2017). The species-specific responses to climatic patterns shown here can open new possibilities for enhancing these climate-tree growth models at the mid-term owing to

the control of climatic anomalies on local climatic elements variability.

## 5. Conclusions

We have shown the role of climatic patterns on the relationship between climatic elements and tree growth. In addition, our results shed light on how climatic patterns differentially influence tree species in relation to their biogeographical and climatic affinities. An increase in the recurrence and strength of extreme climatic events is expected under the ongoing climate change scenarios but, nevertheless, predictions for intra-annual temperature and precipitation variability are difficult to estimate. In this regard, the implementation of large-scale climatic patterns in forest productivity models, which account for inter-annual and decadal climate variability, can help to understand and predict regional geographical shifts, and so it can be helpful for forest ecosystem planning.

## Credit authorship contribution statement

**Héctor Hernández-Alonso:** Sampling design, Field work,

Resources, Formal analysis, Writing - original draft, Writing - review & editing. **Jaime Madrigal-González**: Conceptualization, Formal analysis, Writing - review & editing. **Fernando Silla**: Sampling design, Formal analysis, Writing - review & editing.

## 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 material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.118921>.

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