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ARTICLE

Climate Ecology

Positive effects of warming do not compensate growth reduction due to increased aridity in Mediterranean mixed forests

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Abstract

Increased winter and early spring temperatures due to climate change can enhance forest productivity due to earlier growth onset in temperate regions. However, drought-prone forests can be highly vulnerable to the combined effect of high summer temperatures and water stress. Understanding how water stress and rising temperatures along the growing season control tree growth in co-occurring species with contrasting drought tolerances is key to project climate change effects on forest dynamics. Here, we evaluated the interactive effect of seasonal temperature and water availability on annual radial growth and climate–growth instability over six decades (1951–2015) in three pine species with contrasting drought tolerances (*Pinus pinaster*, *Pinus nigra*, and *Pinus sylvestris*). For this, we retrospectively observed radial tree growth using dendroecological methods and evaluated seasonal temperature and water availability effects by using linear mixed models. Early growing season temperature and water availability had a positive effect on tree growth, but the positive effect of late season temperature was modulated by water availability. Moving time-window analyses revealed temporal instability in climate–growth relationships. Since the 1980s, pine species showed a higher growth sensitivity to both seasonal temperatures and annual water availability. Furthermore, growth reductions were more pronounced due to increased summer temperatures and reduced precipitation. Our results were similar for the three studied pine species despite their contrasting tolerance to drought. Overall, climate warming effects on pine growth are contingent upon water availability in Mediterranean continental forests. Synchronization among species, climate–growth instability, and negative growth trends suggests an increased vulnerability to drought of Mediterranean pine species in response to ongoing climate change.

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KEYWORDS
basal area increment, climate change, climate–growth instability, dendroecology, drought, early growing season temperature, tree rings

INTRODUCTION

Drought-prone Mediterranean forests are one of the most vulnerable ecosystems to climate change (Lindner et al., 2010). During the past century, mean annual temperature increased in the Mediterranean basin by 1.4°C (Cramer et al., 2018). Furthermore, climatic projections point to an increase of 2–5°C by the end of the 21st century, a decrease in precipitation of up to 30%, and increased frequency and intensity of extreme heat waves and drought events (IPCC, 2021). The combined effect of increased temperatures and water stress might compromise the carbon sink capacity of these forests (Astigarraga et al., 2020; Ruiz-Benito et al., 2014). However, winter warming may enhance tree growth by enlarging the growing season (Gimeno et al., 2012; Granda et al., 2013; Lindner et al., 2010), which in combination with increased CO_2 atmospheric concentrations could also enhance water use efficiency (Martínez-Vilalta et al., 2008). Thus, the net outcome of warming on tree growth might rely on water availability (Babst et al., 2019), but also on species' drought tolerance. Understanding differences between the climate response of co-occurring tree species to the interactive effect of increased temperatures and water scarcity is key to forecast forest dynamics and compositional shifts under climate change scenarios.

Drought-induced mortality events and growth reductions, despite being common across a variety of functional groups (Druckenbrod et al., 2019), are high in conifers, which has been linked to their low resistance to drought and lower wood density (Gazol, Camarero, Vicente-Serrano, et al., 2018; Greenwood et al., 2017). Some economically important conifer tree species have their southern distribution limit in the Iberian Peninsula where an increased vulnerability to drought has been already reported at the beginning of the 21st century (e.g., Camarero et al., 2015; Sánchez-Salguero et al., 2017). Such is the case of *Pinus sylvestris*, which has shown a high vulnerability to climate change in its rear edge (Galiano et al., 2010; Hereş et al., 2014; Matías & Jump, 2015; Pellizzari et al., 2016). While Mediterranean pine species are typically segregated along environmental and altitudinal gradients according to their drought tolerance (Ruiz-Benito et al., 2012), they can form mixed forests in extensive areas of the Iberian Peninsula (Sánchez de Dios et al., 2019). For instance, in Mediterranean mountains, *P. sylvestris* L. can co-occur at mid-altitude locations next to more drought-tolerant pine species such as *Pinus nigra* J.F. Arnold and *Pinus pinaster* Ait. (Herrero & Zamora, 2014; Marqués et al., 2016; Martin-Benito et al., 2013; Salazar-Tortosa et al., 2018). These species also have contrasting intra-annual growth patterns: Mediterranean species such as *P. pinaster* can present facultative bimodal growth patterns (Valeriano et al., 2021) as opposed to *P. sylvestris*, which presents an unimodal growth (Camarero et al., 2010). The evaluation of tree species response to environmental factors in mixed forests is key to understand current species segregation and to project species performance under ongoing climate change.

In the Mediterranean biome, water scarcity may compromise tree species performance along altitudinal and latitudinal gradients, especially at low-elevation sites and for isohydric species (Camarero et al., 2015; Gazol, Camarero, Vicente-Serrano, et al., 2018; Marqués et al., 2016; Serra-Maluquer et al., 2018). The species performance to drought across climatic gradients (see Sánchez-Salguero et al., 2017) can lead to differential responses of coexisting species under increased drought stress (e.g., Andivia et al., 2020; Marqués et al., 2016). Increased drought stress at southern range limits can speed up range contraction (e.g., *P. sylvestris*), which could, in turn, lead to dominance shifts toward more drought-tolerant tree species (e.g., *P. pinaster*, Hampe & Petit, 2005; Ruiz-Benito et al., 2017). For example, Gazol, Camarero, Sangüesa-Barreda, et al. (2018) reported growth decline and lack of recruitment capacity for *P. sylvestris* at its rear edge, which ultimately lead to their replacement by more drought-tolerant species such as *Juniperus thurifera*. In this context, increased frequency and magnitude of extreme drought events might exceed species-specific drought tolerance (Andivia et al., 2020; Serra-Maluquer et al., 2018), compromising the persistence of these valuable forest ecosystems and posing new challenges for its management (e.g., Andivia et al., 2018).

As trees and other woody species form growth rings annually, the retrospective quantification of tree growth is widely used as a functional proxy of tree vigor (e.g., Fritts, 1976). Radial growth series allow evaluating tree responses to past climatic variability and to the occurrence of extreme events such as droughts and heat waves (e.g., Dobbertin, 2005; Gazol, Camarero, Vicente-Serrano, et al., 2018; Sánchez-Salguero et al., 2015), which is key to evaluate how tree growth will respond to climate change. In addition, as climate changes, the response of tree growth to such drivers can also change leading to nonstationary relationships, which need to be accounted for (Peltier & Ogle, 2020; Wilmking et al., 2020). Since climate change is expected to increase temperature and water deficit, its net effect on tree secondary growth at a certain site would rely on the interaction between both limiting factors (Babst et al., 2019; Boisvenue & Running, 2006) and the plasticity of tree species to adapt their growth responses to the change in such factors. High early season temperatures promote earlier wood development and a higher intensity of cell production (Gimeno et al., 2012; Rossi et al., 2014). However, higher late spring temperatures and heat waves during dry periods may exacerbate the negative effects of water shortage on forests (Allen et al., 2015; Marqués et al., 2018; Vicente-Serrano et al., 2011). Under such scenario, drought-tolerant species such as *P. pinaster* could be favored over drought sensitivity species such as *P. nigra* and *P. sylvestris*. The evaluation of tree growth responses for co-occurring species is key to better understand differential vulnerability to climate and forecasting forest dynamics under climate change. However, few studies have evaluated growth vulnerability to extreme drought events in co-occurring pine species with contrasting drought tolerances (Andivia et al., 2020; Granda et al., 2018; Herrero & Zamora, 2014; Marqués et al., 2016). Moreover, to the best of our knowledge, there is a lack of studies comparing temporal trends in growth sensitivity to climate due to the interactive effect of warming and water stress in Mediterranean mixed forests.

In this study, we assessed tree growth response to the interactive effect of seasonal temperature (early and late season) and water availability for three co-occurring pine species with contrasting drought tolerances (*P. pinaster*, *P. nigra*, and *P. sylvestris*). In addition, we evaluated temporal instability in growth response to seasonal temperature and water availability over the study period, because of potential effects through time due to recent warming and increased drought frequency. For this, we retrospectively observed tree growth for the period 1951–2015 using dendroecological methods. We selected continental dry Mediterranean forests in the Iberian Northern Plateau as a representative case study of extensive areas where tree growth is strongly limited by both the delay in growth onset due to low winter temperatures and growth cessation due to summer drought (Camarero et al., 2010). We hypothesized that: (1) tree growth is enhanced by high temperatures during the early season and by water availability; (2) recent warming and more frequent droughts increase growth sensitivity to low water availability and high late season temperatures; thus, positive effects of high early season temperatures would not compensate the negative effects of increased aridity on tree growth; and (3) *P. sylvestris* is the most vulnerable species to increased aridity due to its location in the rear edge of its distribution range and its lower tolerance to drought compared with *P. pinaster* and *P. nigra*.

MATERIALS AND METHODS

Study area

The study area is an extensive pine forest of approximately 7500 ha within a protected area of the European Nature Network (LIC-ES4180070) in the Iberian Northern Plateau (41°19′ N–4°12′ W; 841 m above sea level). The forest is dominated by *P. pinaster*, which can be found in large mixed stands with *P. nigra* and *P. sylvestris*. It is one of the few extensive forests with mixed stands with three native pine species in the Iberian Peninsula. The climate is continental Mediterranean, characterized by cold winters and hot and dry summers. Mean annual temperature is 12.1°C (minimum mean temperature is 4.0°C in January and maximum mean temperature is 21.7°C in July) and mean annual precipitation is 454 mm mainly occurring in autumn, with a summer drought period of about 4 months (from June to September) for the period 1951–2015. These climatic conditions can be considered the dry climatic edge of *P. sylvestris* (see climatic marginality in Changenet et al., 2021). The study forest is on inland sand dunes with a sand layer of about 10–15 m in depth (García Fernández, 2004). Soils are thus highly unstructured, poor in nutrients, and with low water holding capacity (Gómez-Sanz & Garcia-Viñas, 2011).

Sampling design

We sampled 90 adult pines (30 individuals per pine species) during the early spring of 2016. We randomly selected dominant or codominant adult pines of different sizes in three stands of about 12.5 ha (10 individuals per pine species and site). We recorded the diameter at breast height (dbh, in centimeters) of each sampled target tree and each neighbor pine within a circular plot of 5-m radius. Target trees ranged in dbh from 33.0 to 69.5 cm, and were at least 20 m from one another, ensuring that neighborhood plots did not overlap. With this information, we calculated the plot basal area in the tree neighborhood and Lorimer's distance-independent competition index (LCI) (Lorimer, 1983) as:

$$\mathrm{LCI}_i = \sum_{j=1}^{n} \mathrm{dbh}_j / \mathrm{dbh}_i,$$

where dbh_i is the diameter at breast height of the target tree i, and dbh_j is the diameter at breast height of the neighboring tree j.

Dendrochronological methods

We used annual tree ring widths to retrospectively observe radial growth in target trees. We extracted two cores at breast height and in opposite directions using a Pressler increment borer (5 mm; Haglöf, Sweden) for each target pine. Wood cores were processed following standard dendrochronological methods (Fritts, 1976). First, we air-dried wood cores and glued them on wooden supports. Second, we polished them using sandpapers of 80, 120, and 600 grit until tree rings were clearly visible. Third, we scanned them at 1200 dpi resolution (Scanjet 300, HP) and measured tree ring widths to the nearest 0.01 mm using ImageJ 1.51k (Schneider et al., 2012). Finally, tree growth series were cross-dated in two steps, first visually using pointer years and then checked with dplR (Bunn et al., 2016). We used mean inter-series correlation (Rbar) and the expressed population signal (EPS) to evaluate the strength of the common growth signal among sampled trees (Wigley et al., 1984). Rbar and EPS were 0.54 (ranged from 0.53 in *P. pinaster* to 0.55 in *P. sylvestris*) and 0.95, respectively, suggesting a strong common signal of growth series.

Tree growth was quantified as basal area increment (BAI, in square centimeters), which reflects whole tree growth better than the one-dimensional growth of tree ring width (Biondi & Qeadan, 2008). BAI was calculated as follows:

$$\mathrm{BAI} = \pi\left(r_t^2 - r_{t-1}^2\right),$$

where r_t and r_{t-1} are the stem radius at the end and at the beginning of a given annual ring, respectively. Our study period was from 1951 to 2015, to ensure a minimum of nine individuals per species and year.

Climatic data

Monthly climatic data (mean temperatures and total precipitation) were obtained using averaged monthly records from the two nearest meteorological stations of the Spanish National Agency for Meteorology (Valladolid and Segovia, both 50 km away from the study area). These climatic series were highly correlated with data from a weather station at the forest site for the period 2001–2015 ($r = 0.99$ and 0.88 for monthly temperature and precipitation, respectively). Monthly water availability was characterized by the Palmer drought severity index (PDSI), which was calculated using the scPDSI package (Zhong et al., 2018). For this, the available soil water capacity of the soil layer was set to 78.5 mm according to previous studies in the area (Gómez-Sanz & Garcia-Viñas, 2011).

Climate–growth correlations

To determine the main climatic factors affecting tree growth, we developed a mean chronology of tree ring width for each species. For this, we first fitted Friedman's super smoother regression to all tree ring width series and then autoregressive models in the resulting values using the dplR package (Bunn et al., 2016). This detrending procedure removes biological trends and first-order autocorrelation producing tree ring width indexes (RWIs) that maximize climatic signal on tree growth (Fritts, 1976). Finally, we calculated Pearson's correlation coefficients between RWI and monthly mean temperature and PDSI (from October of the previous year to September of the current year). We used this period to account for the influence of previous year conditions on the current growing season (Bogino & Bravo, 2008; Madrigal-González et al., 2017), which is critical for the recharge of the soil water fraction that is available for tree growth in Mediterranean environments (Brooks et al., 2010). Based on the correlations between variables (see Appendix S1), we decided to include three climatic variables: mean temperature from December to February (hereafter early season temperature), mean temperature from May to July (hereafter late season temperature), and annual PDSI in further analyses.

Data analyses

To model tree growth for the study species, we fitted generalized additive mixed-effects models following Fajardo and McIntire (2012) and using the gamm4 package (Wood & Scheipl, 2017). We considered as fixed effects tree age as an independent smooth spline for each species (with default package settings), competition (LCI), and the interactions species identity × PDSI × mean early growing season temperature and species identity × PDSI × mean late spring and early summer temperature. The inclusion of these triple interactions allows us to evaluate whether pine species show contrasting responses to the interactive effect of seasonal temperature and water availability. BAI was log-transformed to achieve normality and homoscedasticity. We considered tree identity as a random term to account for nonindependence among observations within the same individual (i.e., repeated measurements) and control for other tree-specific sources of mean growth variation (e.g., variation in soil conditions, microtopography, disturbance, tree health, etc.). We used an autoregressive correlation structure (AR1) to remove the first-order autocorrelation between observations (Pinheiro et al., 2018). Continuous predictor variables were standardized (i.e., the mean was subtracted from each value and divided by the standard deviation) to allow comparisons across model-estimated parameters and test the interactions (Zuur et al., 2009). We checked the collinearity between explanatory variables ($r < 0.6$; Dormann et al., 2013). To identify the best-supported model, we compared the full model with all potential models, and we selected the most parsimonious one using two units of the Akaike information criterion corrected for small samples ($\mathrm{AIC_c}$) as an indicator of parsimony (Burnham & Anderson, 2002). All alternative models were fitted by the maximum likelihood method, whereas the parameters of the selected model were estimated by restricted maximum likelihood (Zuur et al., 2009). The relative importance of fixed effects was evaluated by comparing differences in $\mathrm{AIC_c}$ (i.e., ΔAIC) between the selected model and models without each fixed effect (Zuur et al., 2009).

To evaluate if growth response to seasonal temperature and water availability shifted over the study period (i.e., climate–growth instability), we used the generalized additive mixed model described above with a moving time window. We split the data of the study period (1951–2015) in 1-year lagged windows of 20 years (Battipaglia et al., 2015; i.e., 44 time windows of 20 years with a starting year from 1951 to 1995). All statistical analyses were done in R3.5.3 (R Core Team, 2019) using the packages nlme (Pinheiro et al., 2018) and MuMIn (Barton, 2018).

RESULTS

Characteristics of sampled trees

Sampled trees showed mean dbh and height (±SD) of 50.8 ± 7.8 cm and 13.7 ± 3.9 m, respectively. Mean tree age at 1.3 m was 61 ± 17 years while mean basal area in the tree neighborhood and LCI were $37.6 \pm 29.2\ \mathrm{m^2\ ha^{-1}}$ and 1.85 ± 1.30, respectively. Mean tree growth (BAI) for the period 1951–2015 was $3.3 \pm 2.0\ \mathrm{cm^2}$. *P. sylvestris* showed the greatest mean BAI ($3.8 \pm 2.2\ \mathrm{cm^2}$) followed by *P. pinaster* ($3.5 \pm 2.1\ \mathrm{cm^2}$) and *P. nigra* ($2.6 \pm 1.6\ \mathrm{cm^2}$). *P. nigra* showed the lowest dbh but the highest age, whereas basal area in the tree neighborhood and LCI were not significantly different between species (Appendix S2).

Tree growth temporal patterns and underlying drivers

Pine species showed small differences in growth trend (BAI) over the study period (Figure 1). In general, BAI increased linearly from the beginning of the study period to 1995, especially in *P. sylvestris*. Study species showed decreased growth trends during the last decade, especially *P. sylvestris* and *P. pinaster*. BAI was higher in *P. sylvestris* and *P. pinaster* compared with *P. nigra* for the period 1980–2000. After 2005, pine species showed coupled tree growth trajectories and reduced intraspecific variability (i.e., lower standard error).

The most parsimonious growth model included all fixed effects (i.e., tree size, species identity, LCI, early and late season temperature, and PDSI), and the pairwise interactions early season temperature × PDSI, and late season temperature × PDSI (Appendix S3). However, the most parsimonious model did not include any interaction between species identity and climatic variables. While PDSI and early season temperature had a positive effect on BAI, late season temperature and LCI showed negative effects (Appendix S4). The positive effect of early season temperature on tree growth was more evident with high water availability (i.e., higher PDSI values; Figure 2a). Yet, higher late season temperature only showed positive effects on tree growth in years with high water availability (i.e., high PDSI values, Figure 2b). In fact, high late season temperature strongly reduced tree growth in dry years (i.e., lower PDSI values, Figure 2b). The relative importance of the interaction PDSI × early season temperature was greater than that of PDSI × late season temperature ($\Delta\mathrm{AIC} = 137.4$ and 6.28, respectively). Overall, the positive effect of seasonal temperature on tree growth was modulated by changes in water availability, independently of species identity.

Temporal trends in climate–growth relationships

Climatic trend over the study period shows a decrease in water availability and an increase in early and late season temperature (Figure 3). The effect of water availability and seasonal temperature on tree growth shifted over the study period (Figure 4). Water availability and early season temperature showed positive effects on BAI along time, but the magnitude of the effect increased in the last decades. However, the effect of late season temperature on tree growth shifted from positive to negative (Figure 4).

DISCUSSION

Our results demonstrate the high complexity of climate warming influence on tree growth in drought-prone forests. Early season temperature had a positive effect on tree growth, especially with high water availability (Figure 2). However, late season temperature strongly reduced tree growth in dry years. In the last decades, recent warming and increased frequency of dry years

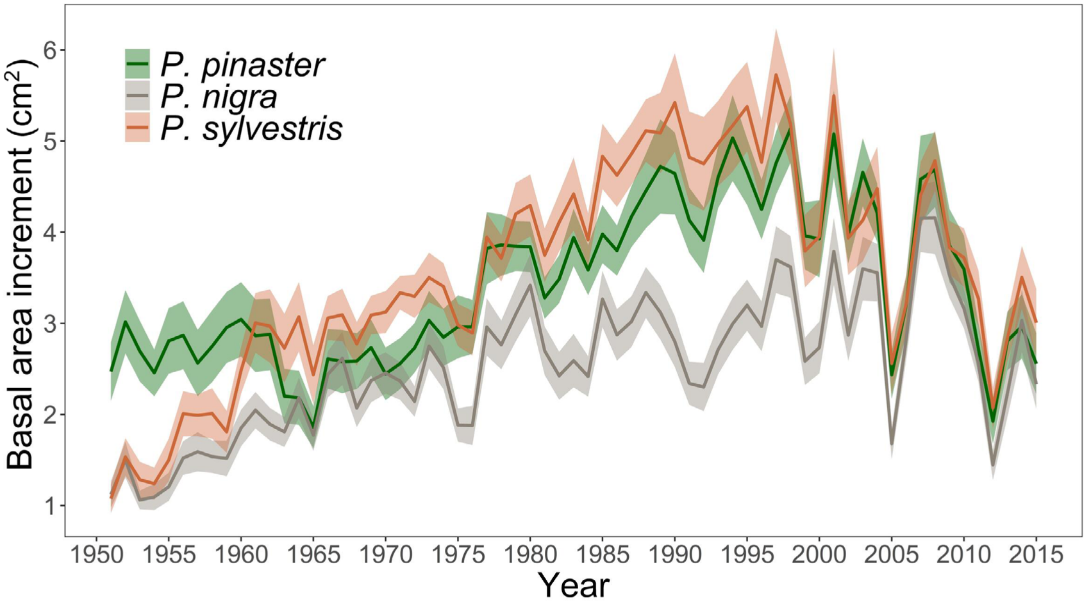

FIGURE 1 Observed basal area increment (mean ± SE) for each pine species (*Pinus pinaster*, *Pinus nigra*, and *Pinus sylvestris*) over the period 1951–2015.

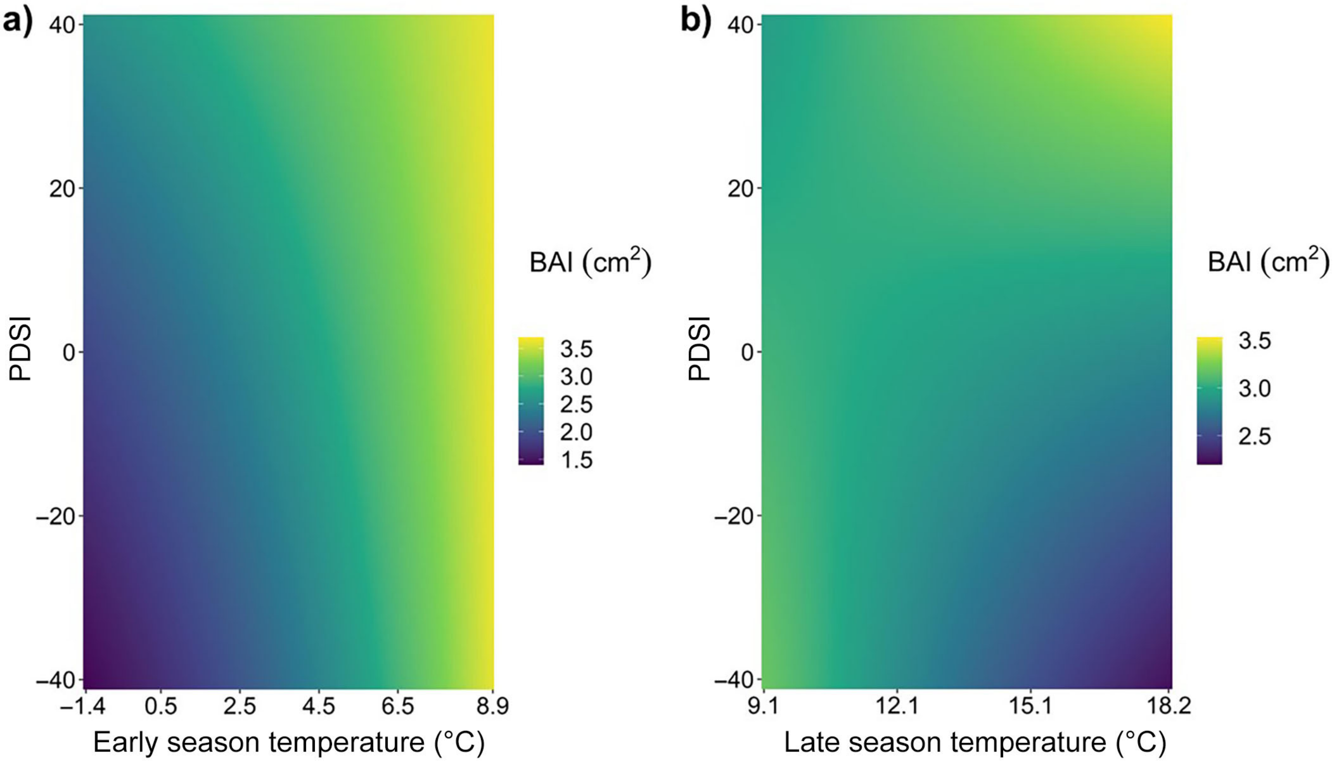

FIGURE 2 Predicted basal area increment (BAI) including the three studied pine species (*Pinus pinaster*, *Pinus nigra*, and *Pinus sylvestris*) in response to the interactive effect of: (a) Palmer drought severity index (PDSI) and mean early season temperature; and (b) PDSI and mean late season temperature.

limited tree growth, probably through increased evaporative demands during the growing season (Figures 1 and 3). Consequently, the interaction between warming and drought could be underlying recent tree growth reduction patterns, despite the positive effect of higher early season temperature on tree growth. Unexpectedly, our results were similar for the three studied pine species despite their contrasting tolerance to water stress. Thus, our

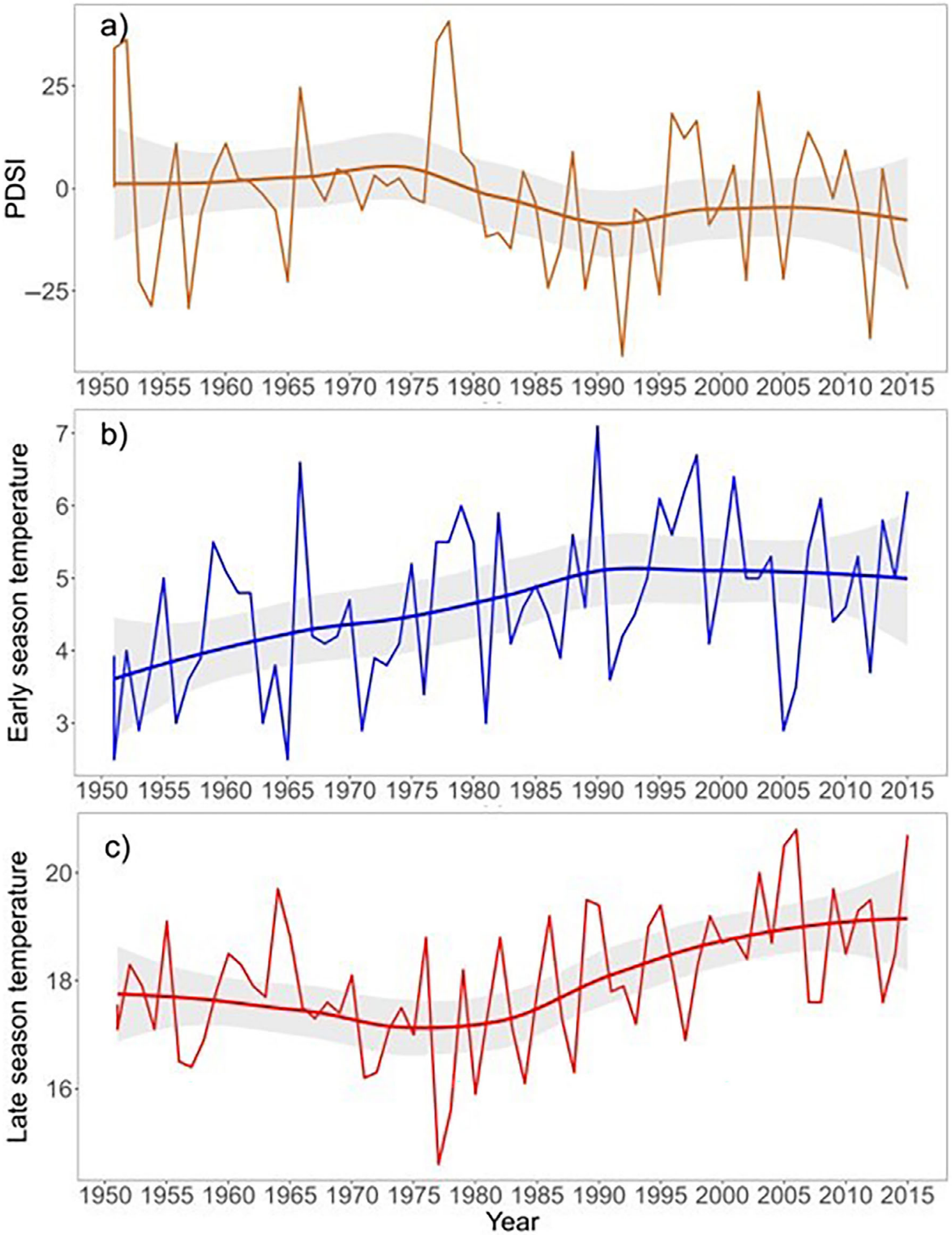

FIGURE 3 Temporal change in annual climatic information from 1951 to 2015 in the study site in central Spain. We included mean (a) Palmer's drought severity index (PDSI), (b) mean early season temperature (in degrees Celcius), and (c) mean late season temperature (in degrees Celcius). We also show a fitted smooth line with confidence intervals to highlight climatic trends over the study period.

results suggest a widespread increase in tree growth vulnerability to drought for temperate and Mediterranean pine species under ongoing climate change.

We found a negative effect of drought on pine growth over the entire study period as expected for drought-prone forest ecosystems (Madrigal-González et al., 2018; Marqués et al., 2016; Sánchez-Salguero et al., 2017). This effect increased in magnitude in recent decades, suggesting a more prominent role of water availability in controlling tree growth. These results agree

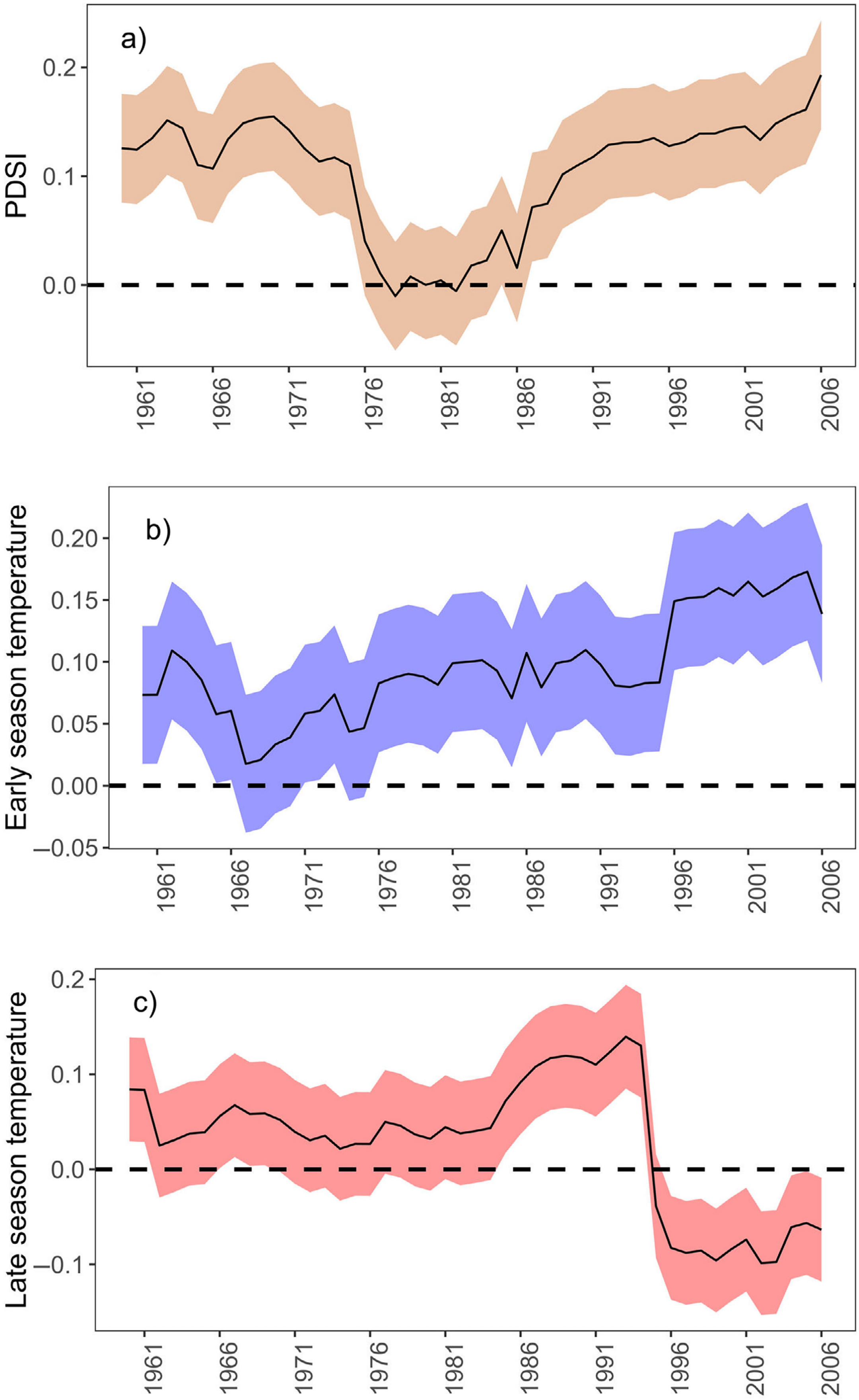

FIGURE 4 Legend on next page.

with strong drought-induced growth reductions reported for different Mediterranean pine species over the last decades (Andivia et al., 2020; Camarero et al., 2018; Herrero & Zamora, 2014; Serra-Maluquer et al., 2018), which have been mainly linked to photosynthetic limitations due to stomatal closure in response to water scarcity (Salazar-Tortosa et al., 2018).

Early season temperatures had a positive effect on tree growth over the study period. Higher early season temperatures enhance forest productivity by promoting earlier growth onset, and thus extending the growing season (Camarero et al., 2010; Madrigal-González et al., 2018; Rossi et al., 2014). Indeed, several studies reported a net positive effect of winter temperatures on pine growth in Mediterranean continental and mountain forests (Andreu et al., 2007; Sánchez-Salguero et al., 2015). However, other studies at the dry edge of pine species distribution show that warming can also reduce tree growth by increasing water stress in late spring (Camarero et al., 2015; Marqués et al., 2018). In this regard, our results showed that increased late season temperatures strongly reduced tree growth in dry years, with limited positive effects as water availability increased.

Our results show that warming effects on tree growth are contingent upon water availability: higher early season temperatures enhanced pine growth, but in dry years they cannot compensate for growth reduction due to water stress. Similar results have been reported for pines and other tree species in different regions under contrasting climate conditions (Mérian et al., 2011; Oberhuber et al., 2008; Yu et al., 2013; Zang et al., 2012). In this regard, Madrigal-González et al. (2018) reported indirect negative effects of warming on pine growth through increased aridity, which agrees with our observations. In Mediterranean continental areas with cold winters, frequent frosts and summer droughts, such as the study area, the effect of temperature on tree growth relies on water availability during the growing season (Marqués et al., 2018). The combination of high late season temperatures and droughts strongly increases vapor pressure deficit and tree transpiration (Dai, 2013), which could lead to indirect negative effects of temperature on pine growth (Ruiz-Benito et al., 2013). Pine growth is especially sensitive to increased transpiration because of its mainly isohydric behavior (McDowell, 2011). Early stomata closure reduces hydraulic failure risks, but it depletes carbohydrate reserves, which might have legacy effects on tree growth (Galiano et al., 2011). In this regard, pine species have shown a strong negative response to extreme climatic events (DeSoto et al., 2020; Gazol, Camarero, Vicente-Serrano, et al., 2018), which might underlie dominance shifts toward angiosperms under ongoing climate change (Ruiz-Benito et al., 2017). The generalized and marked increased growth sensitivity to drought found for the study species may point toward the high vulnerability of pines, regardless of species' drought tolerance. Further studies should compare whether coexisting conifers and angiosperms have similar responses to the combination of water availability and warming conditions.

Interestingly, we found nonstationary relationships indicating that growth response to climate has shifted over the last decades. That is, tree growth has become more constrained by drought as temperature increased. These results agree with a recent global study showing that nonstationarity in growth–climate relationships is more frequent than expected (Wilmking et al., 2020). Dendrochronology relies on stationarity to reconstruct past climate from tree growth series (Wilmking et al., 2017). This growing body of evidence on the prevalence of nonstationary growth sensitivity to climate calls for incorporating new conceptual and analytical approaches to the application of tree ring-based environmental reconstructions to other scientific disciplines (Peltier & Ogle, 2020; Wilmking et al., 2020). For example, the implementation of temporal variability in tree growth–climate sensitivity on land carbon models might improve the estimation of drought impacts on forest productivity and carbon dynamics (Kolus et al., 2019). This is especially true for drought-prone forests, such as those in our study, where warming exacerbates growth sensitivity to drought.

Contrary to our expectations, we did not find species-specific growth responses to annual water availability. Among the study species, *P. sylvestris* is considered the most vulnerable species to drought (Dobbertin, 2005; Eilmann & Rigling, 2012; Galiano et al., 2010; Herrero et al., 2013; Rigling et al., 2013). In addition, the study site is in the dry climatic edge of *P. sylvestris* (Changenet et al., 2021), which might increase species' vulnerability to drought (Matías et al., 2017). Our results agree with other studies that have also reported similar growth responses to drought events between these species when co-occurring (Granda et al., 2018; Herrero & Zamora, 2014; Serra-Maluquer et al., 2018). While we did not find differences in our study species' drought sensitivities, previous work from other regions has indicated substantial differences (Klesse et al., 2020; McCullough et al., 2017),

FIGURE 4 Temporal change in the basal area increment sensitivity to climate (i.e., model slopes ± 95% CI) from the study period 1951 to 2015. We included the effect of (a) Palmer Drought Severity Index (PDSI), (b) mean early season temperature (in degrees Celcius), and (c) mean late season temperature (in degrees Celcius) on tree growth using moving time windows of 1 year and considering a period of 20 years for each model. The year in the *x*-axis indicates the middle year of the 20-year period analyzed at each time step.

pointing to the potential significance of intraspecific variation in shaping species' responses to regional climatic stressors. This high intraspecific variability in pine response to drought can be related to climatic conditions, forest structure, or tree age (Gazol, Camarero, Vicente-Serrano, et al., 2018; Granda et al., 2018; Linares et al., 2010). The existence of local adaptations (Benito Garzón et al., 2011) and microhabitat conditions can also modulate species' response to climate (Loughnan & Gilbert, 2017), which might be especially relevant for *P. sylvestris* in dry sites. We cannot also discard that the lack of species-specific differences in tree growth sensitivity to climate could be due to specific edaphic conditions in the site that might strongly reduce water availability for trees. However, previous research in the study area reported interspecific differences in resilience to drought in saplings of these species (Andivia et al., 2020), which indicates that our results cannot be solely explained by soil conditions.

The fact that pine species with contrasting drought tolerance (Salazar-Tortosa et al., 2018) synchronously reduced their growth rates in response to warming and increased frequency of drought events may foresee critical impacts on forest functioning and ecosystem services supply, such as carbon sequestration (Brodribb et al., 2020; Shestakova et al., 2016). Increased sensitivity of tree growth to water availability and growth decline have been associated with drought-induced tree mortality (Cailleret et al., 2019; Gea-Izquierdo et al., 2019; Keen et al., 2022). Furthermore, an increase in within-population temporal autocorrelation of tree growth has been also identified as evidences of tree vulnerability (Cailleret et al., 2019; Camarero et al., 2015). In our study, growth divergences were evident in the 1990s, but they disappeared during the beginning of the 21st century, particularly in response to the 2005 and 2012 recent droughts (Figure 1). Therefore, our results can be interpreted as early warning signals of forest decay, particularly the negative and generalized growth trends observed since the late 1990s for all species. These results can also suggest that more species do not always represent an insurance against changing environmental conditions or climatic disturbances, such as droughts.

CONCLUSIONS

Our results provide evidence to the generalized expectation that warming effects on tree growth in drought-prone forests rely upon water availability. We found a consistent positive effect of water balance and early season temperature on tree growth, which suggests a beneficial effect of water availability and earlier growth onset on forest productivity. However, in recent decades, the positive effects of higher early season temperatures could be compromised due to increased aridity (i.e., lower water availability and higher late season temperature). Our results were similar to the three studied pine species despite their contrasting tolerance to water stress, suggesting a saturation of the positive effect of climate warming on tree growth and an increase in vulnerability to drought in Mediterranean forests. Negative growth trends, synchronization among species, and climate–growth instability can be interpreted as early warning signals of forest decline, suggesting that projected climatic conditions may negatively impact the carbon sink capacity of these forests.

AUTHOR CONTRIBUTIONS

Enrique Andivia, Paloma Ruiz-Benito, and Jaime Madrigal-González contributed to the conception of the study and collected the data. Paloma Díaz-Martínez measured tree ring widths and analyzed the data with inputs from the rest of the authors. Paloma Díaz-Martínez, Enrique Andivia, and Paloma Ruiz-Benito wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Andivia et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.17105456.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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