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Adaptive responses to thinning: Growth and sensitivity to hydric and thermal stress in four widely planted pine species

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ABSTRACT

In seasonally dry areas, thinning has been proposed as a measure of adaptive forest management to enhance growth and increase drought resistance and resilience. However, long-term growth data on different tree species and site conditions remain scarce for investigating the interactions between thinning and climatic stressors. To fill that research gap, we examined radial growth and its sensitivity to climatic conditions in 19 experimental sites of the four most planted pine species in Spain (*Pinus halepensis, P. pinaster, P. nigra*, and *P. sylvestris*). We also assessed the influence of thinning at varying intensities on growth responsiveness to climate stress. To quantify how climate impacts growth, we used seasonal temperature and water balance anomalies expressed as temperature and drought indices.

Thinning consistently enhanced tree growth for 8–20 years, with the magnitude of this effect modulated by hydric conditions. While drought reduced growth, wetter conditions promoted it—particularly in mesic species such as *P. sylvestris* and *P. nigra*. Importantly, thinning increased trees' sensitivity to climate: thinned stands—especially those of *P. halepensis* and *P. sylvestris*—became more responsive to water availability, exhibiting stronger growth increases during wet years following thinning.

Temperature also played a key role, with high spring and autumn temperature anomalies enhancing growth, comparable in magnitude to favorable hydric conditions. However, in the post-thinning period, spring temperature effects were lower than prior to thinning in species from xeric sites (*P. halepensis* and *P. pinaster*). High summer temperature anomalies negatively affected growth, though more weakly and only in species from xeric

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sites. Thinning, however, aggravated the negative effects of summer temperatures on growth in xeric sites and induced negative effects on growth in mesic sites.

These findings highlight the species-specific interactions between thinning, water availability, and temperature stress, emphasizing the need for tailored, species- and site-specific adaptive management strategies of planted forests in response to climate change.

1. Introduction

Thinning (the selective removal of trees within a stand) is a widely used silvicultural practice aimed at reducing tree-to-tree competition for resources such as light, water, and nutrients. By alleviating competition, thinning typically enhances tree growth, and post-drought resilience of the remaining trees (Moreau et al., 2022; Sohn et al., 2016). At the stand level, thinning can also increase structural and species heterogeneity by creating microclimatic variation that supports diverse habitat preferences (Lettenmaier et al., 2022; Uhl et al., 2024). Additional benefits include improved soil moisture availability (del Campo et al., 2022), increased understory light penetration, and reduced vulnerability to pests and diseases (Li et al., 2020; Prospero and Cleary, 2017). Notably, thinning enhances access to water for residual trees, which has been shown to reduce drought-induced stress and promote both resistance (sustaining growth during drought) and resilience (recovery after drought) (Bréda et al., 1995; Moreno-Gutiérrez et al., 2011; Sohn et al., 2016). As such, thinning is increasingly viewed as a key element of adaptive forest management strategies designed to bolster ecosystem responses to climate change (Manrique-Alba et al., 2020, 2022; Molina et al., 2021; Navarro-Cerrillo et al., 2023).

Despite the recognized benefits of thinning, particularly in mitigating drought impacts, its interplay with other critical climatic drivers of tree growth, such as thermal stress from unusual cold or warm events, remains largely underexplored. Understanding how thinning modulates tree growth responses to temperature anomalies is crucial for effective forest management in a changing climate, especially in regions susceptible to such deviations (Astigarraga et al., 2020). While a few studies have examined thinning effects in relation to temperature (e.g., Lucas-Borja et al., 2021; Navarro-Cerrillo et al., 2023), these have often relied on broad monthly mean temperature data and few sites or species. A more detailed understanding requires examining responses of several sites and species to specific seasonal thermal anomalies, moving beyond generalized temperature metrics to capture the distinct effects of, for example, spring warming versus elevated summer temperatures. This highlights a significant knowledge gap concerning the integrated effects of forest management on tree responses to the combined and temporally varying effects of hydric and thermal stressors, particularly across different tree species and diverse climatic conditions.

Drought-prone pine plantations, which are among the most abundant forest types in the Iberian Peninsula (Vallejo-Bombín, 2023), provide a suitable system for addressing this research gap. While numerous studies have investigated general growth patterns and climatic responses of major pine species such as *Pinus halepensis* (Fernandes et al., 2016; Veuillen et al., 2023), *P. pinaster* (Cachinero-Vivar et al., 2021; Zavala et al., 2024), *P. sylvestris* (Ovenden et al., 2021; Aldea et al., 2023), and *P. nigra* (Linares and Tíscar, 2010; Lucas-Borja et al., 2021), an integrated view of how thinning specifically alters their growth responses to seasonal water availability and temperature anomalies across their bioclimatic ranges and considering plantations is still lacking.

To understand this comprehensively, it is first necessary to consider the ecological and physiological characteristics that distinguish these species within the Mediterranean context. From highest to lowest drought tolerance, *Pinus halepensis* Mill. (Aleppo pine) dominates in low-elevation sites of the western Mediterranean Basin, where it thrives under the characteristic Mediterranean climate of hot, dry summers and mild, wet winters (Fady et al., 2003). In the Iberian Peninsula, it is primarily distributed along the eastern half (Fig. 2), occurring between sea level and 1,400 m a.s.l. in regions characterized by semi-arid to sub-humid conditions (Vallejo-Bombín, 2023). Similarly, *Pinus pinaster* Aiton (Maritime pine) shares a similar distribution across the western Mediterranean, growing at similar elevations. It is particularly well-adapted to sandy, acidic, and nutrient-poor soils (Alía and Martín, 2003). As drought-tolerant species, both *P. halepensis* and *P. pinaster* are characterized by a low rate of stomatal conductance, which reflects a water-saver (isohydric) strategy (Klein et al., 2011; Martínez-Vilalta et al., 2004). These species can assimilate carbon even during mild autumn and winter conditions (Gea-Izquierdo et al., 2019; Sperlich et al., 2019). The carbohydrates stored during this period may support xylogenesis early in the following year if winter temperatures are not restrictive and/or during spring (De Luis et al., 2011). In these species, radial growth is primarily influenced by winter-to-spring conditions (Maseyk et al., 2008). However, a secondary peak in cambial activity can occur in autumn under favorable conditions, though its contribution to annual ring width remains limited compared to that of spring (Camarero et al., 2010, 2021; Pasho et al., 2011a; Olivar et al., 2012).

In contrast to these drought-tolerant species, *Pinus nigra* Arnold (Black pine) and *Pinus sylvestris* L. (Scots pine) are found at higher elevation and show broader native ranges, extending across large parts of Europe, Asia, and North Africa. Their adaptability to diverse climates and soils has made them valuable species for forestry projects worldwide. Within the Iberian Peninsula, they typically inhabit colder and wetter areas at higher elevations (1,200–2,200 m a.s.l.), due to their better frost resistance and lower drought tolerance (Isajev et al., 2004). Radial growth in these species is mainly constrained by winter-spring temperatures and by spring-summer drought (Camarero et al., 2015; Sánchez-Salguero et al., 2015a; Matisons et al., 2019). Compared to the drought-tolerant species, *P. sylvestris* and *P. nigra* exhibit higher hydraulic conductivity (anysohydric behaviour), enabling rapid growth but also making them more sensitive to drought, as they respond quickly to evaporative demand by closing stomata (Domec and Gartner, 2002; Irvine et al., 1998). Recognizing these interspecific differences in hydraulic strategy, carbon assimilation, and growth phenology is key to assessing how thinning might modulate the growth responses to climate of these widely planted pine species under varying climatic pressures.

The main objective of this study is to investigate how thinning interacts with seasonal climatic stressors, specifically hydric and thermal anomalies, to influence tree radial growth in Mediterranean planted pine forests. To this end, we combine dendrochronological data with high-resolution seasonal climate records across a network of experimental sites in eastern Spain, encompassing four ecologically important pine species: *P. halepensis, P. pinaster, P. nigra* and *P. sylvestris*. Building on prior research, we hypothesize that: (1) thinning generally enhances radial growth and improves tree resilience to drought by alleviating hydric stress; (2) warmer temperatures during the shoulders of the growing season (spring and autumn) will promote growth—especially in thinned stands—whereas extreme summer heat will suppress growth, with thinning potentially mitigating this negative effect; and (3) the strength and direction of thinning's influence on tree responses to these seasonal climatic anomalies will vary among species, reflecting differences in their physiological traits and ecological strategies. By examining these interactions, our study aims to generate species-specific insights into how silvicultural interventions can enhance forest adaptation and resilience in the face of increasing climatic variability.

2. Materials and methods

2.1. Study sites and species

Sampled stands correspond to the SilvAdapt.net project (https://silvadapt.com/sitios-demostrativos/), a research network for long-term monitoring of silviculture to improve forest adaptation to climate change in Spanish plantations (Molina et al., 2021). We compiled tree-ring width data from 19 experimental sites, including four widely represented pine species: *P. halepensis, P. pinaster, P. nigra* and *P. sylvestris* (Fig. 1). The sites are located across a wide geographical and altitudinal range (42° 48'−37° 02' N, 3° 34'−0° 51' W; 140−2025 m a.s.l) and cover a significant part of the species' distribution range (Fig. 2, Table 1). The experimental sites extend from mesic conditions in the north to xeric conditions in the southeast. The mean annual temperature varies from 8.0 to 18.2°C, and the mean annual precipitation ranges from 287 to 1632 mm, with the mean annual water balance (precipitation minus potential evapotranspiration) ranging from -990 to +744 mm. Stand ages also vary considerably, which can be inferred from the starting year of monitoring provided in the "time span" column of Table 1."

Except for one site classified as natural forest and two sites where natural regeneration occurred after harvest, the remaining sites are plantations, most of which originated from large-scale afforestation programs implemented in Spain during the 1950s and 1960s in Spain. All these sites are managed, and each site provides data on a single species. The thinning treatments were classified according to the percentage of basal area removed into two intensities: moderate (20-40 % of basal area removed) and heavy (>40 % of basal area removed), adapted from existing classifications (Del Río et al., 2017), to reflect site-specific management practices. In ten out of nineteen sites both thinning intensities were implemented, allowing for a comparison of the two intensities (thinning vs. control or un-thinned plots), in two to three stands per site. The time elapsed since the last thinning varied from 4 to 23 years (Table 2).

2.2. Dendrochronological data

At each site, 10 to 30 healthy, dominant, and mature trees per treatment were selected, resulting in 1,464 samples from 732 undamaged individuals. Two cores per tree were collected at 1.3 m using Pressler increment borers. Relevant silvicultural information was also compiled for each experimental site at the stand level, both before and after thinning took place (Table 2).

The wood cores were processed according to standard dendrochronological methods (Fritts, 2001). They were air-dried, affixed to wooden supports with glue, and sanded until the tree rings became clearly visible. Next, the cores were visually cross-dated and ring widths were measured with a 0.01 mm resolution using a Lintab-TSAP measuring system (Rinntech, Heidelberg, Germany). The quality of the chronologies was assessed by calculating several dendrochronological statistics (Fritts, 2001): tree-ring width (TRW) mean and standard deviation, mean first-order autocorrelation of TRW data (AR1), mean correlation between individual indexed series (Rbar), and the Expressed Population Signal (EPS). A series was considered to be well replicated for EPS $\geq$ 0.85 (Wigley et al., 1984). Chronologies were calculated using the dplR package (Bunn 2008; Bunn et al. 2024). TRW statistics are provided in Table S1 in the Supplementary material.

To assess growth variations between years and treatments, ring-width values were transformed into basal area increments (BAI, cm^2 yr^{-1}), which offers a more biologically relevant measure of growth. BAI was computed annually for each tree-ring width by assuming the stem had a circular cross-section and determining the difference between consecutive yearly basal areas. To minimize the influence of age-related growth trends on basal area increment (BAI), we restricted the analysis to the post-1980 period, when all pine plantations had reached physiological maturity. Additionally, we removed long-term linear trends from each individual core's BAI time series to account for any residual age effects. Given that our data come from even-aged pine plantations, variability in ageing among coexisting trees is minimal, further reducing the likelihood that age dynamics confounded the growth–climate relationships analyzed.

2.3. Climate data

Climate data for the period 1980–2020 were obtained from the 1.1-km^2 Spanish gridded temperature, precipitation and SPEI datasets (Vicente-Serrano et al., 2017). To assess the effects of yearly climate on growth, we analyzed the temperature and water balance anomalies using standardized climate indices: the Standardized Precipitation Evapotranspiration Index (SPEI) and a Standardized Temperature Indices for spring (STI_{spr}), summer (STI_{sum}), and autumn (STI_{aut}). The SPEI was used to characterize hydric conditions during the growing season (Beguería et al., 2014; Vicente-Serrano et al., 2010). This index, which standardizes the climatic water balance (i.e., the difference between cumulative precipitation and reference evapotranspiration), allows for comparisons across time and space. Positive SPEI values indicate wetter-than-normal conditions, while negative values indicate drier-than-normal conditions, or droughts.

The climatic water balance—and, by extension, the SPEI—can be computed for varying time scales, in this case using temporal windows ranging from one month to 18 months. Additionally, the index can be calculated at different times of the year. For this study, we utilized a quasi-weekly dataset with 48 time stamps per year (Vicente-Serrano

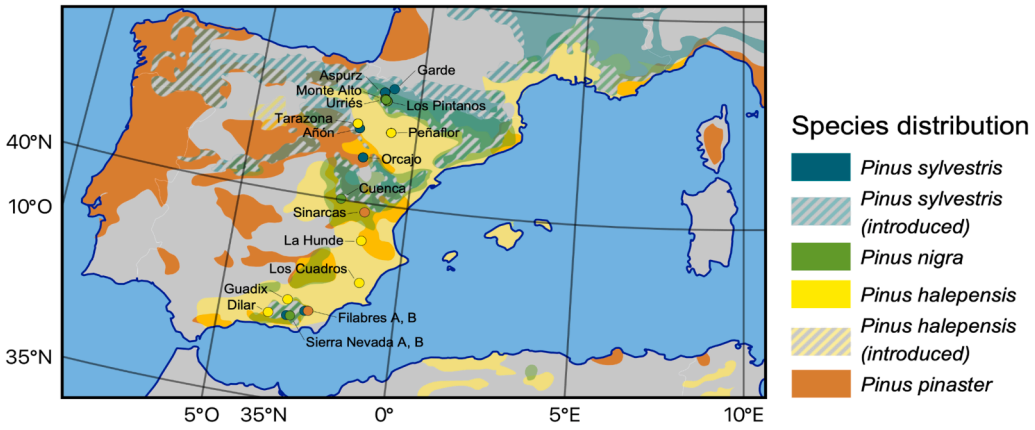


Fig. 1. Regional distribution of the four study pine species and location of the study sites in Spain. Species distribution data sourced from Caudullo et al. (2017); map and figure created by the authors.

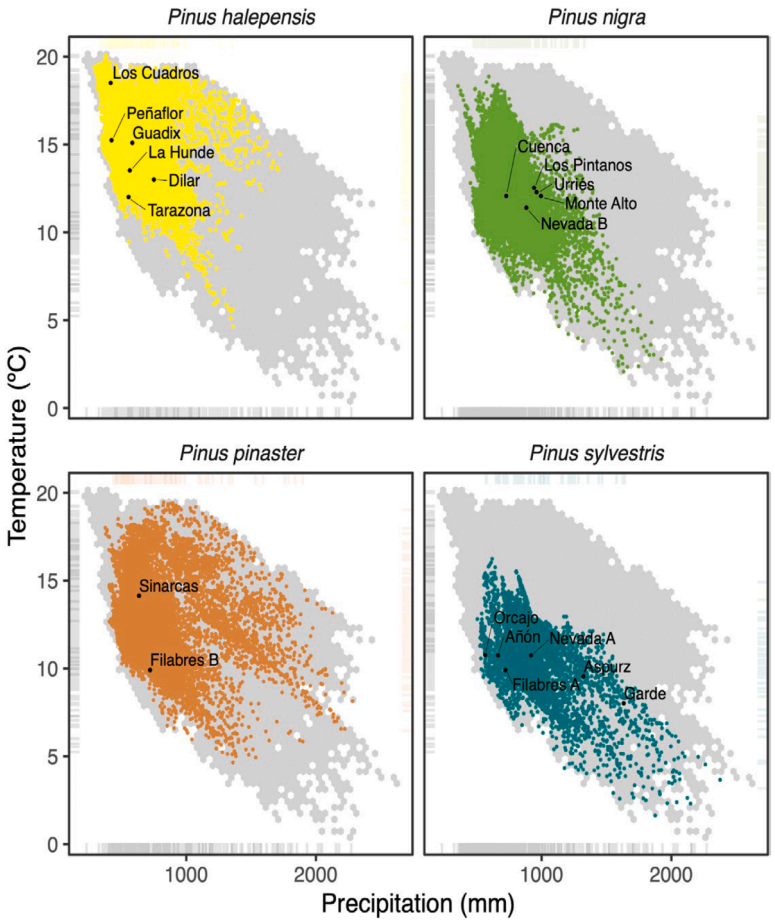


Fig. 2. Annual mean temperature and total precipitation of mainland Spain (grey), climatic distribution of each species (color dots), and climatic conditions of each study site (one point per site). Climate data averages over 1961–2020 from Vicente-Serrano et al. (2017) and Tomas-Burguera et al. (2019).

Table 1
Site descriptions and characteristics of selected plots.

Species	Study site	Latitude N (°)	Longitude W (°)	Aspect	Slope (%)	Elevation (m a.s.l.)	Type of forest	Time span	Thinning year (s)
Pinus halepensis	Tarazona	41° 52’	1° 49’	Flat	5	785	Plantation	1965-2017	1999
	Peñaflor	41° 45’	0° 46’	S	2	282	Plantation	1950-2017	2000
	La Hunde	39° 05’	1° 13’	Flat	5-10	950	Plantation	1960-2018	2008
	Los Cuadros	38° 04’	1° 06’	N-S	15	140	Plantation	1955-2015	2004
	Guadix	37° 25’	3° 04’	N-S	5-10	1115	Plantation	1994-2020	2005
	Dílar	37° 02’	3° 34’	W	5	1260	Plantation	1960-2020	2011
Pinus pinaster	Sinarcas	39° 46’	1° 14’	Flat	5-10	870	Plantation	1979-2021	2005
	Filabres B	37° 13’	2° 33’	N	20-30	1600	Plantation	1976-2016	2008
Pinus nigra	Monte Alto	42° 33’	1° 06’	W	20	705	Plantation	1975-2018	2003
	Urriés	42° 31’	1° 04’	NW	25	705	Plantation	1975-2018	2006
	Los Pintanos	42° 30’	1° 01’	W	12	907	Plantation	1975-2018	2000
	Cuenca	40° 01’	1° 59’	Flat	3-5	1250	Natural forest	1836-2012	1997
	Nevada B	37°02’	3° 02’	S-SW	4	1800	Plantation	1987-2020	2009
Pinus sylvestris	Aspurz	42° 42’	1° 08’	N	7	625	Natural regeneration after harvest	1985-2013	1999, 2009
	Garde	42° 48’	0° 51’	NE	40	1335	Natural regeneration after harvest	1985-2013	1999
	Nevada A	37° 03’	3° 03’	S-SW	4	2025	Plantation	1977-2020	2010
	Filabres A	37° 13’	2° 33’	N	20-30	1600	Plantation	1979–2018	2009
	Orcajo	41° 04’	1° 31’	NW	15	1200	Plantation	1933-2021	2001
	Añón	41° 45’	1 ° 45’	SE	20	1200	Plantation	1940-2021	1998

et al., 2017), yielding a total of 48 × 18 = 864 possible SPEI indices. To identify the optimal combination of time scale and time of year for characterizing hydric stress at each experimental site, we fitted a simplified version of the model described in section 2.4, with a linear relation between log(BAI) and the SPEI, while accounting for random variability across individuals and autocorrelation through a first-order

Table 2
Silvicultural characteristics according to thinning intensity (% of basal area removed). Variables and abbreviations: D, stem density (stems ha^{-1}); diameter at breast height (Dbh, in cm); and basal area (G, in m^2 ha^{-1}). Values are means. The last column showed the number of sampled trees and cores.

Species	Study site	D before thinning	Dbh before thinning	G before thinning	Thinning intensity	D after thinning	Dbh after thinning	G after thinning	**No. sampled trees (No. measured cores)**
Pinus halepensis	Tarazona	2000	13.6	31.0	T60/T40	1050/975	14.5/14.6	21.3/15.5	45 (90)
	Peñaflor	973	15	16.3	T30	622	14	13.2	24 (48)
	La Hunde	1489	16.9	40	T40/T70/T90	744/478/178	17.7/17.5	27.2/18.2	45 (90)
	Los Cuadros	1400	14.1	24.6	T20/T35	770/550	14.1/14.9	12.8/10.0	45 (78)
	Guadix	1444	7.9	7.79	T48/T60/T75	681/513/325	9.1/10.1/10.1	4.71/4.12/2.60	128 (256)
	Dílar	628	24.04	28.50	T30/T50	439/314	25.18/26.80	21.86/17.72	45 (90)
Pinus pinaster	Sinarcas	580	22.6	22.2	T30	180	30	12.8	18 (36)
	Filabres B	1600	19.6	48.3	T30/T60	1120/640	23.3/27.4	47.8/37.7	23 (45)
Pinus nigra	Monte Alto	1800	15.3	34.5	T40	580	21	20.5	20 (40)
	Urriés	1900	15.9	42	T50	450	26.5	23.1	20 (40)
	Los Pintanos	2741	15.3	54.8	T40	980	20.5	34.5	20 (40)
	Cuenca	532	16.7	40.3	T30	379	17.7	34.1	(41) 82
	Nevada B	1240	16.50	26.51	T50/T70	620/372	18.63/18.75	16.90/10.27	45 (90)
Pinus sylvestris	Aspurz	3517	12.7	42.3	T30	2200	13.1	29.0	72 (144)
	Garde	3555	13.3	49.0	T30	1478	16.7	32.7	72 (144)
	Filabres A	910	17.9	20.4	T30/T60	637/364	18.3/18.6	16.8/9.9	45 (90)
	Nevada A	1160	21.97	43.9	T50/T70	580/348	21.3/18.17	20.66/9.09	45 (90)
	Orcajo	1150	25.6	59.5	T50	600	31.8	45.4	30 (60)
	Añón	1250	27	83	T50	550	30.7	39	30 (60)

random walk. For each fitted model, we computed the Pearson's R correlation between the predicted and observed values, as a simple measure of goodness of fit.The SPEI combination of week and scale yielding the highest correlation was selected for further analysis. This methodology is illustrated in Supplementary Figure S12 for two of the study sites.

To characterize the thermal drivers of growth we used a Standardized Temperature Index (STI), where positive values indicate warmer-than-normal conditions and negative values represent colder-than-normal. The effects of thermal stress were expected to vary across the growing season, so we computed seasonal indices to represent thermal conditions during spring (STI_{spr}), summer (STI_{sum}), and autumn (STI_{aut}). As with the SPEI, we used correlation analysis to determine the most relevant time scales of the seasonal STI indices for each site.

The complete dataset, including dendrochronological and climate indices, can be found at https://doi.org/10.20350/digitalCSIC/17165 (Manrique-Alba et al., 2025).

2.4. Statistical analysis: Bayesian hierarchical modeling framework

In this section, we describe the Bayesian hierarchical modeling (BHM) framework used to analyze the effects of thinning and seasonal climatic anomalies on basal area increment (BAI), capturing both fixed and random effects while formally testing the hypothesis introduced earlier. BHMs are statistical models that incorporate multiple levels of uncertainty and structure by using Bayesian inference, and are particularly suited to analyzing complex data with nested or grouped structures (Gelman et al., 2004). They present several advantages over other approaches to hierarchical (or mixed-effects) analysis, such as more flexibility in model specification; more robust parameter estimation and prediction resulting from a natural incorporation of partial pooling; improved uncertainty estimation with full probability distributions for the model parameters rather than point estimates; better model interpretability.

Given the distributional characteristics of BAI (a strictly positive and skewed variable), we assumed a Gamma likelihood with a logarithmic link function. The fixed effects in the model included species (four nominal classes), thinning (three levels: control plus two thinning levels), SPEI, STI_{spr}, STI_{sum} and STI_{aut} (continuous variables representing annual climatic conditions at each site), and the interactions between them. Since the effect of thinning is known to fade out with time, we included an exponential decay term by the interaction between the treatment and the time since the thinning took place.

To account for the nested data structure, with individuals measured repeatedly over years and grouped within larger units, we incorporated a mixed-effects framework. Specifically, we modelled the individual as a random effect on the intercept, and, since the sites were sampled with two cores per individual, we also included a nested random effect within individuals to account for within-tree sampling variability. Additionally, recognizing the temporal nature of the data, we included a random walk component to capture autocorrelation in the data, allowing for potential dependence of each year's BAI on previous-year BAI values. Non-informative priors were used for both fixed-effect parameters and hyperparameters to ensure minimal prior influence on model estimates.

The mathematical formulation of this model can be structured as follows. Let y_{ijn} represent the BAI for individual (tree) i and core j at time t. The model assumes a Gamma distribution for y_{ijt}:

$$y_{ijt} \sim Gamma\left(\mu_{ijt,\tau}\right)1 \tag{1}$$

with expectation and variance given by:

$$E\left(y_{ijt}\right) = \mu_{ijt};\ var\left(y_{ijt}\right) = \mu_{ijt} \Big/ \tau. \tag{2}$$

where μ_{ijn} is the mean of the Gamma distribution, and τ is the shape parameter. The mean μ_{ijn} is linked to the linear predictor η_{ijn} via a logarithmic link:

$$log\left(\mu_{ijt}\right) = \eta_{ijt} \tag{3}$$

The linear predictor η_{ijn} includes fixed effects and random effects. The model structure is therefore:

$$\eta_{Core[i],\ Individual[j],\ Species[k],\ Thinning[l],\ Time[t]} = \beta_k + \beta_l + Time^{\beta_{t,k}} + \ldots\ldots + \beta_{SPEI,kl}\ SPEI_t + \beta_{STIspr,kl}\ STIspr_t + \beta_{STIsum,kl}\ STIsum_t + \beta_{STIaut,kl}\ STIaut_t + \ldots\ldots + RW_{kt} + u_j + v_{ij}\ . \quad (4)$$

The fixed effects, thus, include:

- β_k: fixed effect for species k (categorical variable with 4 classes);
- β_l: fixed effect for thinning level l (categorical variable with 3 levels);
- β_t: exponential decay, in interaction with species;
- $\beta_{SPEI,kl}$, $\beta_{STIspr,kl}$, $\beta_{STIsum,kl}$, $\beta_{STIaut,kl}$: fixed effects for SPEI, STI_{spr}, STI_{sum} and STI_{aut} (continuous variables), in interaction with species and treatment.

With random effects:

- $u_j \sim (N(0,\ \sigma_u^2))$: random intercept for individual j;
- $v_{ij} \sim (N(0,\ \sigma_v^2))$: random intercept for core i within individual j.

And first-order random walk components:

- RW_{kt} : species-specific random walk to account for temporal autocorrelation in growth across years:

$RW_{kt} \sim N(\eta_{k,t-1},\ \sigma_{BAI}^2)$, for all $t > 1$.

Non-informative priors were assigned to the model parameters and hyperparameters, such as:

$\beta_j,\ \beta_k,\ \beta_t,\ \beta_{SPEI},\ \beta_{STIspr},\ \beta_{STIsum},\ \beta_{STIaut} \sim N(0,\ 31.62)$, $\theta^2,\ \sigma_u^2,\ \sigma_v^2,\ \sigma_{BAI}^2 \sim LogGamma(0,\ 0.00005)$, and β_t was restricted to have a negative value to represent an exponential decay.

After model fitting using the R-INLA package (Rue et al., 2009; 2017), we focused on the posterior distributions of the model coefficients to interpret the effects of the covariates (species, treatment, climate), their interactions, and the random effects. This approach enabled us to evaluate uncertainties around the parameter estimates and gain insight into the relationships between variables.

We examined the marginal posterior distributions of the model parameters to obtain estimates and credible intervals (range of possible values of the parameter with a given probability, here set at 95 %) to evaluate the magnitude and direction of the fixed effects and interactions. For the random effects, the posterior distributions of the random intercepts for sites and individuals were examined to assess the variability among individuals and groups. We also focused on the posterior distribution of the temporal random walk components to understand the degree of autocorrelation in the data and its variation across treatments.

To further explore the interactions between species, thinning, and climate, we derived joint posterior distributions by generating a large number of simulated draws using a Gaussian approach under INLA. These simulations allowed us to derive interaction terms that were not explicitly included in the fixed effects. For example, this approach enabled evaluating how the effect of SPEI varied across tree species and under different treatments.

2.5. Growth simulations

After gaining a clear understanding of the posterior distributions and interactions, we used the model to simulate growth (BAI) trajectories for each species under different treatment and climate scenarios. These simulations considered both fixed (e.g., species-specific treatment and climate effects) and autocorrelation effects (temporal autocorrelation and thinning effect decay), but excluded random effects (individual and core-level variability). These projections provide species-specific growth scenarios under different experimental and environmental conditions, allowing us to explore how BAI changes over time and across various external factors, and the time persistence of the treatment effects, while discarding variability at the individual and core levels. This analysis also offers forecasting insights into potential future outcomes under different management and climatic scenarios.

We assessed the relevance of each predictor by examining the posterior distributions of their coefficients, focusing on properties such as the width of credible intervals and the density around non-zero values. Instead of traditional significance tests, this approach allowed us to quantify the evidence supporting each parameter's contribution. To compare alternative model configurations—ranging from simple additive models to those incorporating complex variable interactions—we calculated the Watanabe-Akaike Information Criterion (WAIC), with lower WAIC values indicating a better balance between model fit and complexity.

Model validation was crucial for assessing predictive performance of the model. We simulated BAI series using the fitted model and compared these simulations with the observed data. Additionally, we performed cross-validation by computing Conditional Predictive Ordinates (CPO) were calculated for each species, treatment, and site to ensure robust model performance across diverse experimental conditions. CPOs are a measure used in Bayesian analysis to evaluate a model's predictive performance using an out-of-bag, or leave-one-out, approach. For each observation, the CPO represents the probability density of that observation given a model fitted without it. High CPO values (close to one) indicate that the model successfully predicts the left-out data point, while low values (close to zero) suggest poor predictive performance, flagging potential issues such as model misspecification or the presence of outliers. Finally, q-q plots of predicted versus observed BAI values were examined to evaluate the models' accuracy across the entire range of observed measurements.

3. Results

3.1. Growth series

The BAI series for each study site are presented in Fig. 3, encompassing both control and thinned plots. At this stage, we rely on a visual, exploratory analysis aimed at identifying potential patterns in the data that will be formally tested in the subsequent modeling stages.

As expected, visual inspection reveals pronounced differences in BAI between control and thinned plots following thinning treatments, a pattern that appears consistent across all four species. Thinned plots generally showed enhanced growth compared to control plots after treatment application. Differences between moderate and heavy thinning treatments are also discernible. Estimated increases in BAI under moderate thinning vary, with *P. sylvestris* and *P. nigra* showing moderate gains (50–53 %), while *P. halepensis* and *P. pinaster* exhibit larger increases (107–132 %). Under heavy thinning, BAI increases are approximately 71–75 % for *P. sylvestris* and *P. nigra*, with *P. halepensis* and *P. pinaster* showing even higher relative gains (160–200 %). Across species, mesic *P. sylvestris* and *P. nigra* show higher average growth rates (5.6 ± 3.57 and 7.9 ± 5.3 $cm^2\ yr^{-1}$, respectively) than the xeric *P. halepensis* and *P. pinaster* (4.3 ± 4.2 and 3.4 ± 3.2 $cm^2\ yr^{-1}$).

Some additional trends emerge when considering the time elapsed since thinning. A gradual convergence of BAI values between thinned and control plots seems to occur over time, suggesting a possible diminishing treatment effect. When general hydric conditions (SPEI) are taken into account, low BAI values tend to coincide with dry years, while wet years appear associated with increased growth. Notably, the range of BAI variation between dry and wet years seems to widen following thinning, relative to the more constrained variation observed in untreated plots. A similar, though less consistent, pattern may also be observed in relation to seasonal thermal anomalies—such as unusually

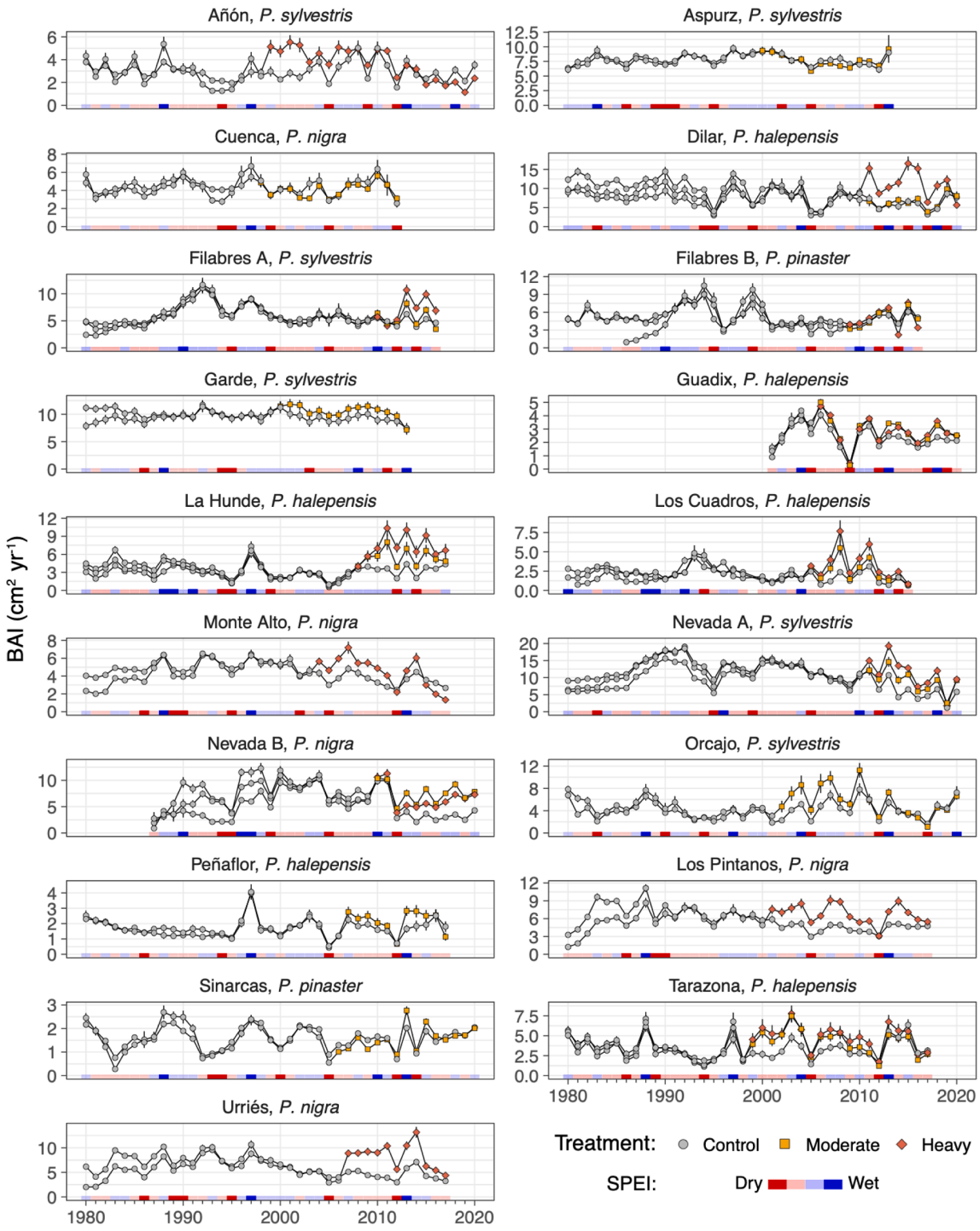


Fig. 3. Mean values and standard errors of basal area increment (BAI) for P. halepensis, P. nigra, P. pinaster, and P. sylvestris plantations across the nineteen study sites presented for control plots (black points) and thinned plots subjected to varying treatment intensities: moderate (circles) and heavy (squares). Different fill colours in the thinned plots differentiate between treatments: control (grey), moderate (orange) and heavy (red) thinning. Vertical rectangles at the bottom of the plots represent a gradient from dry to wet years, with red rectangles indicating dry years (SPEI < -1.28) and blue rectangles indicating wet years (SPEI > 1.28). Notice the site-specific y-axes.

cold or warm years—with species-specific differences apparent (Supplementary Figures S1 to S3).

These observations served as a hypothesis-generating step in our workflow. In the following sections, we use a formal statistical analysis to test and quantify these visually identified trends.

3.2. Tree growth dynamics inferred from statistical modelling

Selection of optimal seasonal windows for climate–growth modelling

As part of the modeling process, an essential preliminary step involved identifying the optimal seasonal window, defined by both the timing (week of the year) and duration (timescale), for each climatic index used to explain BAI. This step ensures that the seasonal indicators (e.g., SPEI, temperature anomalies) reflect the most relevant climate conditions affecting tree growth. To do so, we systematically evaluated all possible week–timescale combinations and selected the one that maximized the explanatory power of each index, based on its marginal effect on BAI in a simplified model (see Methods).

Fig. 4 summarizes the results of this selection process across all sites and species, while numeric results are presented in Supplementary Table S2. In the figure, horizontal lines indicate the duration of the temporal windows that produced the best predictive models of BAI, with final dots marking the optimal week. Among the climatic variables, SPEI generally required longer timescales—ranging from 6 to 15 months, with a median of 11 months—indicating that cumulative water availability over extended periods is particularly relevant for radial growth. While some variation in selected time windows was observed across sites, differences among species were less pronounced, suggesting that local site conditions may be more influential than species identity in shaping climate sensitivity at this stage.

In contrast, the thermal indices operated on much shorter time scales. The median durations were one month for STI_{spr} and STI_{aut}, and two months for STI_{sum}. Optimal weeks varied considerably across sites, ranging from week 6 (February) to week 21 (May) for the spring index, from week 19 (April) to week 42 (October) for the summer index, and from week 32 (August) to week 47 (November) for the autumn index. Similar to SPEI, no apparent species-specific differences were observed.

Weak but significant correlation was found between SPEI optimum week and longitude, latitude and elevation (r = 0.47, 0.53, -0.62, respectively), and between scale and longitude and latitude (0.53, 0.54), as shown in Supplementary Figures S4 and S5. For the thermal indices, significant correlations were found between the optimum STI_{spr} week and the annual precipitation (r = 0.46); between STI_{sum} week and elevation (r = -0.63); and between STI_{aut} week and elevation (r = -0.60).

Model coefficients across species: thinning and climatic effects

Having identified the optimal climate indices for each site, we fitted a full hierarchical model including fixed effects, interactions, and random components to evaluate how thinning and seasonal climate anomalies influence tree growth. Fig. 5a shows the posterior distributions of model coefficients, with 95 % credible intervals excluding zero indicating strong effects. Pairwise comparisons between species and treatments (Figure S6) highlight significant contrasts where credible intervals do not overlap zero.

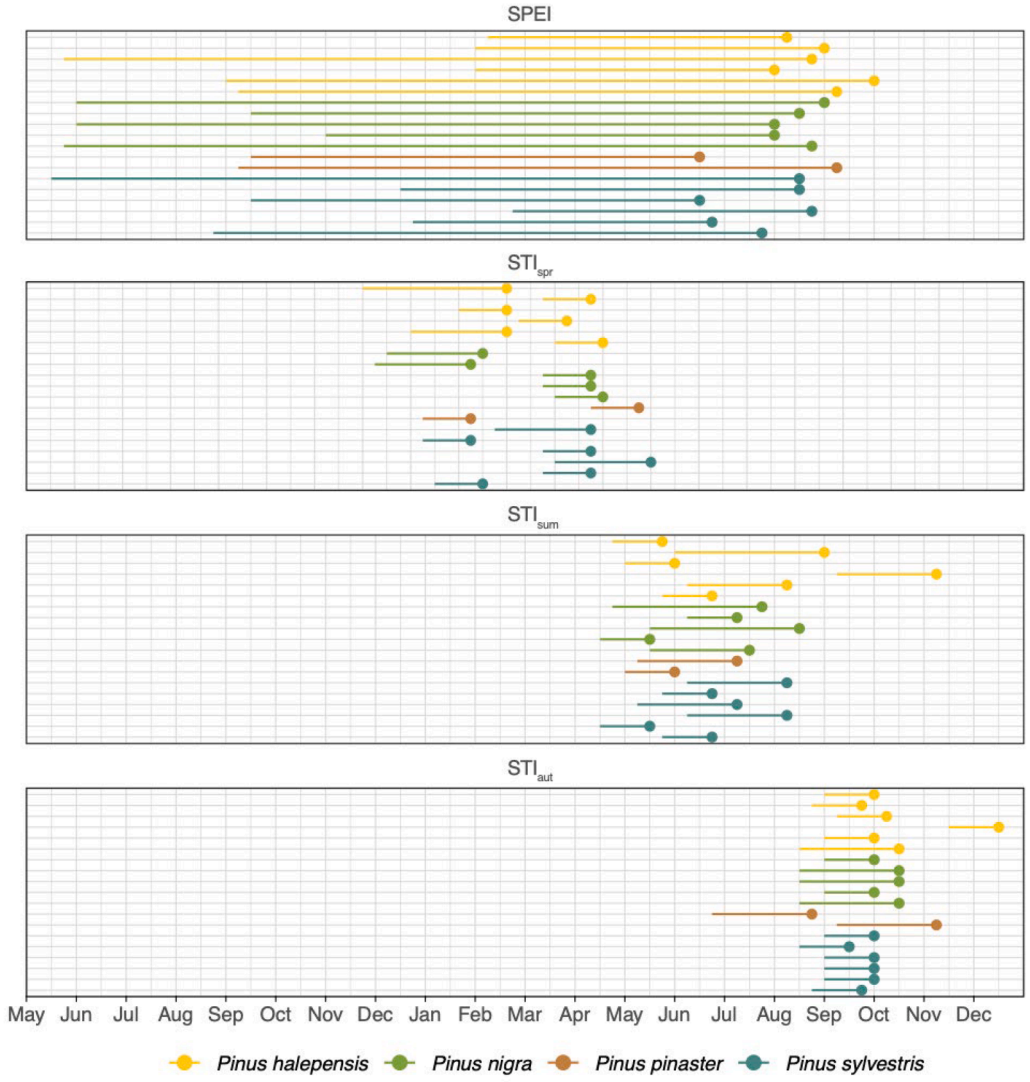


Fig. 4. Optimal seasonal windows of the SPEI, STI_{spr}, STI_{sum} and STI_{aut} at the different study sites, classified by species.

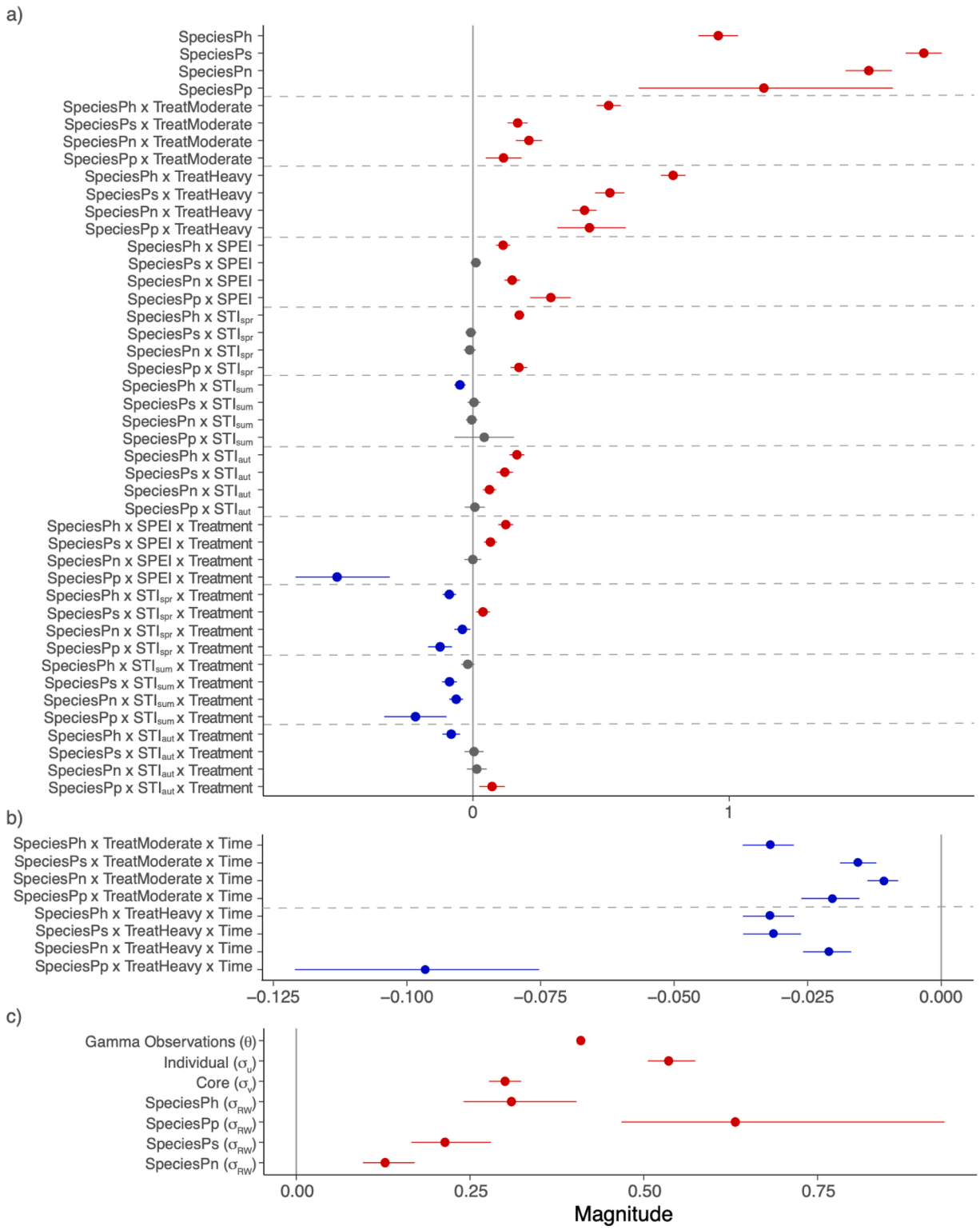


Fig. 5. Model coefficients and 95 % credible intervals of (a, b) the model parameters (fixed effects, in the log scale); and (c) hyper-parameters. Red points are positive and credible, blue points are negative and credible, and grey points are not credible (the credible interval contains zero). Species' abbreviations: Ph, P. halepensis; Ps, P. sylvestris; Pn, P. nigra; and Pp, P. pinaster.

Mean growth coefficients were positive and significant for all species, with two distinct growth groups: *P. halepensis* and *P. pinaster* (not significantly different from each other), and *P. nigra* and *P. sylvestris*, the latter showing the highest growth.

Thinning effects were clearly positive for all species and stronger under heavy thinning. Pairwise comparisons confirmed significantly higher growth in heavily thinned plots, especially for *P. halepensis*. Fig. 6 illustrates these effects, with distinct separation between thinning intensities for most species, except *P. pinaster*, where overlapping densities suggest a weaker or less certain response.

Regarding climate effects, SPEI coefficients were positive and significant for all species except *P. sylvestris*, indicating enhanced growth

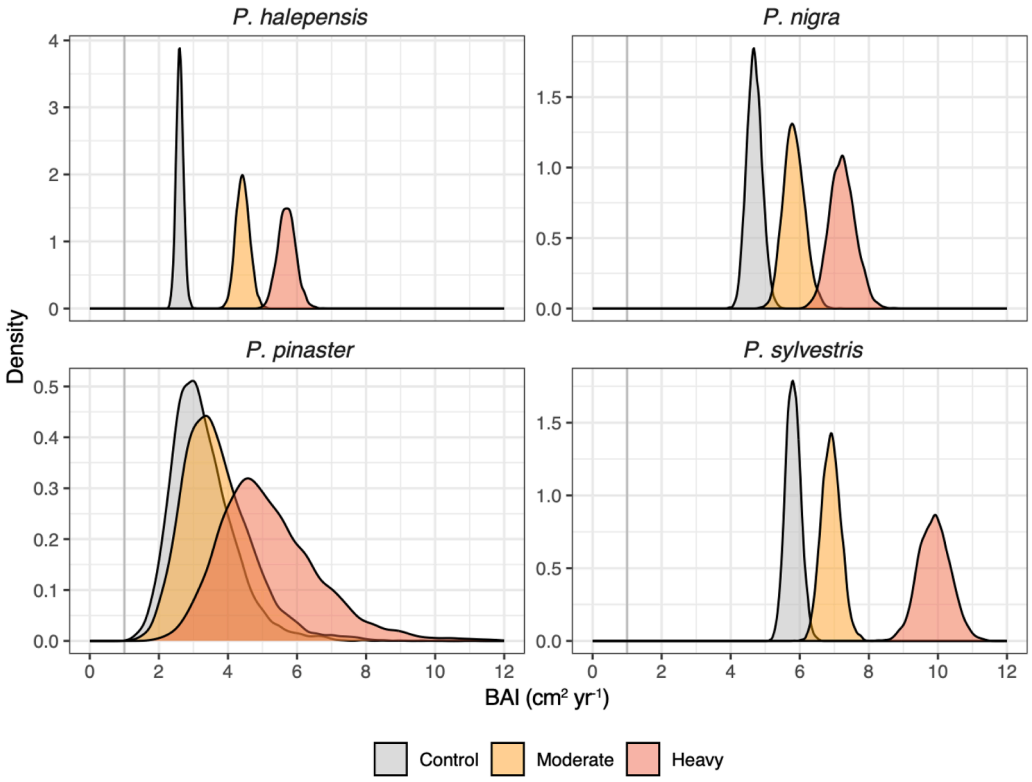


Fig. 6. Joint posterior densities of species and thinning effects on growth, in the scale of the variable, for control (Species*), moderate (Species* + TreatModerate) and heavy (Species* + TreatHeavy) thinning treatments.

under wetter conditions. The response of *P. sylvestris* differed notably from other species, with additional differences observed between *P. nigra* and *P. pinaster*.

Spring temperature (STIspr) had a positive effect on growth for *P. halepensis* and *P. pinaster*, while no clear effect was found for *P. nigra* and *P. sylvestris*. Summer temperature (STIsum) only affected *P. halepensis* negatively, suggesting sensitivity to summer heat. In contrast, autumn temperature (STIaut) positively influenced growth for all species except *P. pinaster*, with *P. halepensis* showing the strongest response.

Overall, SPEI, STIspr, and STIaut coefficients had similar magnitudes, highlighting the combined role of water availability and temperature in shaping growth responses. Species from xeric environments (*P. halepensis, P. pinaster*) generally showed stronger responses to temperature, while mesic species (*P. nigra, P. sylvestris*) were more sensitive to water availability.

Model coefficients: high-order interactions

Beyond first-order effects and two-way interactions, our HBM analysis provides insights into three-way interactions between species, thinning, and climate drivers. These are visualized in Fig. 5 (combining thinning levels due to overlapping posteriors) and Fig. 7 (joint posterior densities of thinning and climate effects per species). Values in the latter figure are expressed as multiplicative effects on the species-level baseline; a value of one indicates no interaction. Pairwise differences are provided in Figure S6.

For the Species × Treatment × SPEI interaction, thinning amplified the positive effect of SPEI in *P. halepensis* and *P. sylvestris*, particularly in the former. In *P. nigra*, the SPEI effect remained unchanged after thinning. In *P. pinaster*, the SPEI effect appeared to reverse, though with high uncertainty

Thinning × STIspr interactions were significant in all species. In *P. halepensis* and *P. pinaster*, thinning reduced sensitivity to spring warming. In contrast, *P. nigra* and *P. sylvestris* showed enhanced sensitivity, but with opposite outcomes: *P. sylvestris* responded positively to warmer springs post-thinning, while *P. nigra* showed a negative response.

For STIsum, thinning consistently increased sensitivity to summer warming across all species. In *P. halepensis*, the pre-existing negative effect was intensified. In *P. pinaster, P. nigra*, and *P. sylvestris*, a new negative response to warmer summers emerged following thinning.

STIaut interactions varied. In *P. halepensis*, thinning strengthened the existing positive effect of warmer autumns. In *P. pinaster*, a positive effect appeared post-thinning. For *P. nigra* and *P. sylvestris*, the positive effect persisted but did not change notably.

Temporal decline of thinning effects

The model coefficients for time since treatment (Species × Treatment × Time, Fig. 5b) were negative, as expected, with credible intervals excluding zero for all species and thinning intensities—indicating a consistent decline in the thinning effect over time. *P. halepensis* showed the fastest decay, except for *P. pinaster* under heavy thinning, where large uncertainty (due to a single site) limited inference. In all species except *P. nigra*, heavy thinning led to faster decay than moderate thinning, as reflected in lower coefficient values.

Model coefficients: hyperparameters

Fig. 5c presents the model's hyperparameters (expressed as standard deviations, i.e., sigmas). Variance components for individual-level (σ_u) and core-level (σ_v) effects were comparable to the residual error (θ), suggesting similar contributions to total variability. Supplementary Figures S7 and S8 show these random effects grouped by site. While core-level effects were broadly distributed—indicating sampling variability or measurement error—individual-level effects clustered by site, pointing to local environmental or genetic influences.

Year-to-year growth variability (σ_RW) differed across species: *P. nigra* and *P. sylvestris* had the lowest values, reflecting more stable growth, while *P. pinaster* showed the highest interannual variability, suggesting greater responsiveness to annual fluctuations.

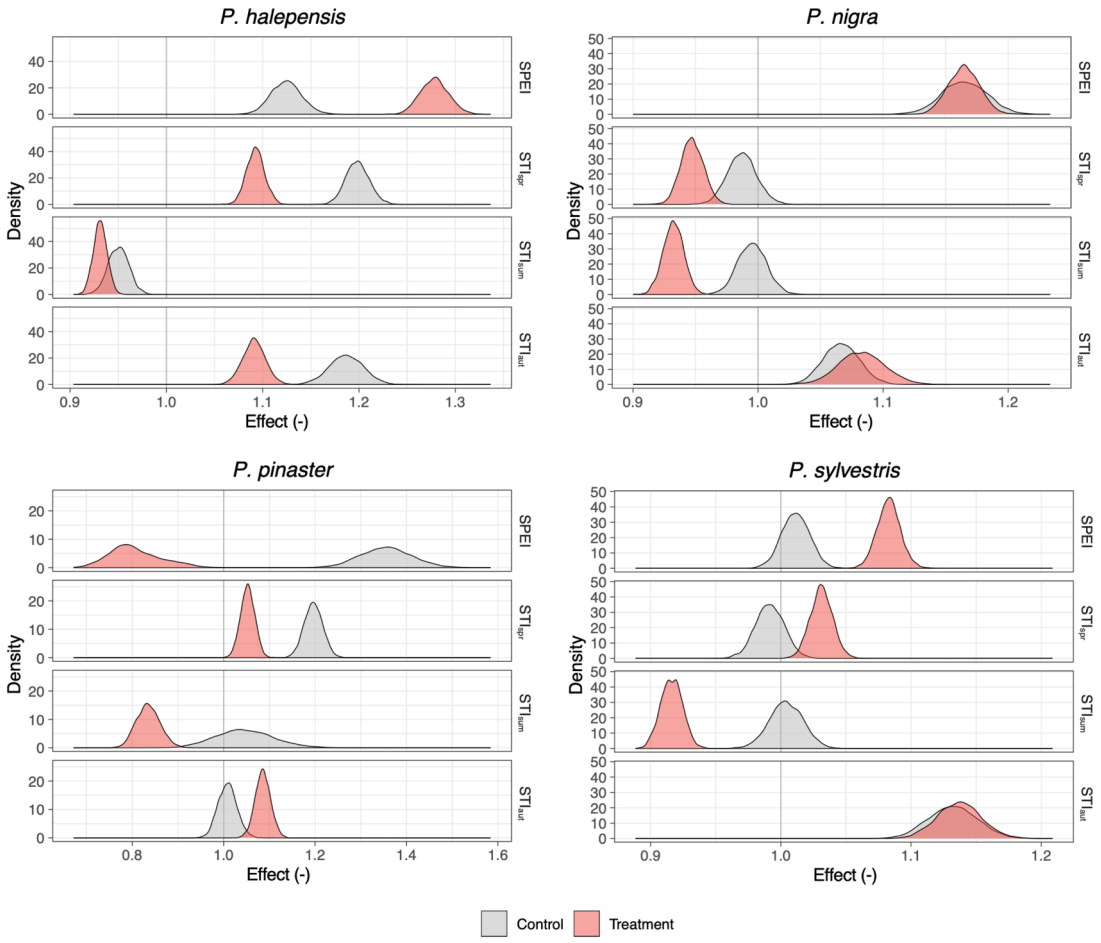


Fig. 7. Joint posterior densities of climate effects (SPEI: hydric stress index; STI_{spr}: spring temperature index; STI_{sum}: summer temperature index; and STI_{aut}, autumn temperature index) on growth for control and thinning treatments in the scale of the variable (multiplicative effect). Values in the x-axis represent a multiplicative effect, where a value of 1 indicates no impact, values greater than 1 signify a positive effect (growth enhancement), and values less than 1 indicate a negative effect (growth reduction).

3.3. Model validation

Supplementary Figure S9 shows CPO values for all combinations of species and treatment levels. CPO values tended to be higher for *P. halepensis*, indicating that the model better predicts the data for this species. Conversely, *P. nigra* and *P. sylvestris* exhibited lower CPO values. Regarding treatments, the un-thinned (control) plots had the highest CPO values, followed by moderately thinned and then heavily thinned plots, implying that the model predictive capacity diminishes with increasing thinning intensity.

Supplementary Figure S10 provides a quantile-quantile plot of predicted vs. observed values. It shows a good fit overall, with a tendency to under-predict extremely high BAI values. A simulation of the observed time series using the fitted model (Figure S11), however, shows good similarity with the observed time series shown above (Fig. 3).

3.4. Simulating growth trajectories

Fig. 8 shows simulated growth trajectories under neutral climatic conditions for each species and thinning intensity. As expected, thinning led to a marked initial increase in BAI. The strongest response was observed in *P. halepensis*, with BAI increasing by 25 % (moderate) and 42 % (heavy) in the first year post-thinning. In contrast, *P. nigra* and *P. pinaster* showed the smallest gains under heavy thinning (19 % and 18 %, respectively).

Across all species, the thinning effect declined over time. *P. nigra* showed the most prolonged response, with effects persisting up to 20 years. *P. halepensis* had a similar duration (18–20 years), followed by *P. sylvestris* (13–18 years). *P. pinaster* exhibited the shortest persistence—about 8 years under moderate thinning—but with wide uncertainty (0–20 years). Simulations for heavy thinning in *P. pinaster* were not included due to data from only one site.

4. Discussion

4.1. Thinning effect on growth varies across species

As expected, thinning enhanced radial growth of the four pine species (Moreau et al., 2022; Sohn et al., 2016). Despite the wide distribution ranges and diverse environmental gradients occupied by the species studied, thinning consistently demonstrated positive effects across all cases. Specifically, the positive impact of thinning on growth is well-supported for the studied pine species by previous research. For *P. halepensis* studies such as del Campo et al. (2014), González-Zamora et al. (2023), Manrique-Alba et al. (2020, 2022), Veuillen et al. (2023), Sarris et al. (2011) provide strong support. Similarly, for *P. nigra*, evidence comes from Esteban et al. (2012), Linares and Tíscar (2010), Lucas-Borja et al. (2021), Martín-Benito et al. (2010). For *P. sylvestris*, the benefits are supported by Aldea et al. (2023), Giuggiola et al. 2013, Navarro-Cerrillo et al. (2019), and Ovenden et al. (2021). Lastly, for *P. pinaster*, studies by Cachinero-Vivar et al. (2021), Ferriz et al. (2021), and Zavala et al. (2024) confirm the enhancing effects of thinning.

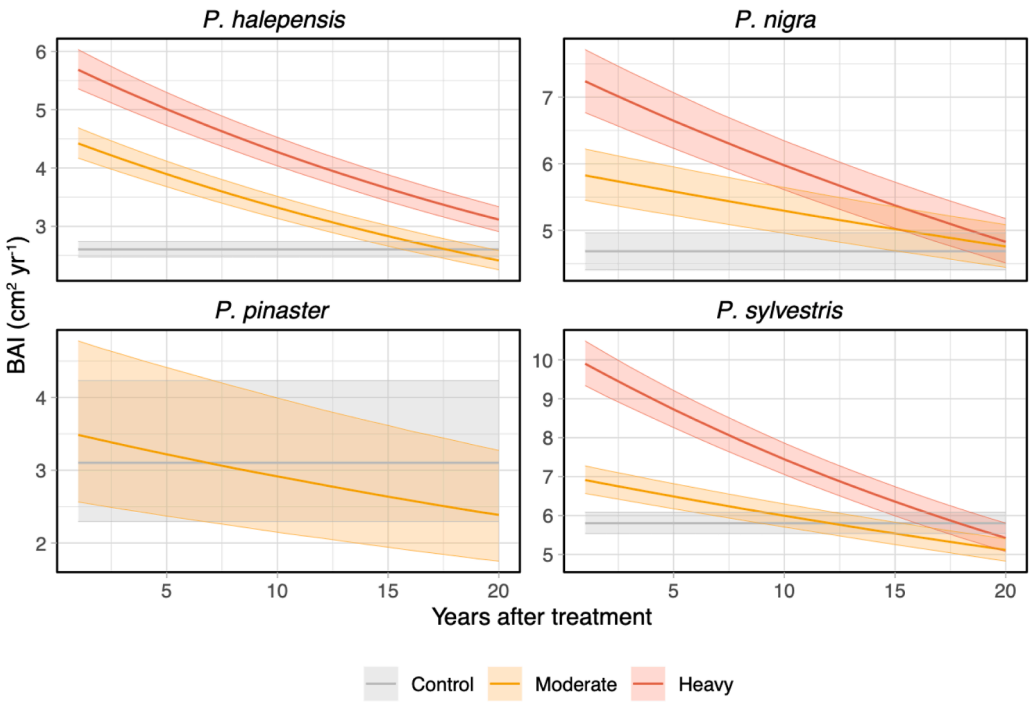


Fig. 8. Simulated post-thinning growth (BAI, in $cm^2\ yr^{-1}$) trajectories for control, moderate, and heavy thinning treatments for each species over a 20-year period following thinning, considering neutral climate conditions (SPEI, STI_{spr}, STI_{sum}, and $STI_{aut} = 0$). The shaded areas represent 95 % confidence intervals.

Physiologically, this is justified because thinning adjusts functional traits involved in leaf and wood economics, i.e. leaf mass area or wood density, and hydraulic traits, i.e. Huber value and water potential, thereby enhancing radial growth and transpiration (Cachinero-Vivar et al., 2024).

However, two groups of species can be distinguished based on their dominance in xeric lowlands (the drought-tolerant *P. halepensis* and *P. pinaster*) or in wet-cool mesic sites at higher elevation (the drought-sensitive *P. nigra* and *P. sylvestris*). Our results do in fact show some differences between these two groups, in agreement with Gazol et al. (2022): after thinning, *P. halepensis* presented the highest growth increase, followed by *P. pinaster*, while the lowest growth increase corresponded to *P. sylvestris* and *P. nigra*. It is worth noting, however, that the response for *P. pinaster*, while positive, exhibited greater variability and more overlap in the posterior distributions of growth between control and thinned treatments compared to other species, suggesting a less consistently clear-cut thinning benefit in our dataset. This higher uncertainty for *P. pinaster* may, in part, be related to the smaller sample size available for this species in our study. The lowest growth increase corresponded to *P. sylvestris* and *P. nigra*, supporting the idea that thinning effects were more noticeable in warmer and drier sites, where drought stress is the main factor constraining growth (Manrique-Alba et al., 2022).

The more pronounced post-thinning growth increase in *P. halepensis* and *P. pinaster* on xeric sites could be attributed not only to the greater alleviation of pre-existing stress but also to inherent physiological adaptations. These species, having evolved in resource-scarce and disturbance-prone (e.g. wildfire) environments, may possess traits such as higher root-to-shoot and root-to-leaf ratios for efficient water uptake (Bao et al., 2014; Lemaire et al., 2021) or more conservative water-use strategies (Klein et al., 2011; Martínez-Vilalta et al., 2004) that become highly advantageous when competition is suddenly reduced and resources are readily available. Thinning might allow them to shift from a survival-focused 'conservative' mode to an opportunistic mode, more effectively capitalizing on the increased availability of soil water and nutrients. For instance, an enhanced capacity for photosynthetic upregulation when water is not limiting, or a more flexible carbon allocation strategy and growth phenology, could contribute to this stronger response. In contrast, mesic species (*P. nigra, P. sylvestris*), typically experiencing less intense chronic water stress, might already operate closer to their physiological optimum for growth in unthinned stands, particularly concerning water resource utilization. While they benefit from reduced competition for light and nutrients, the marginal gain from increased water availability might be less impactful on their overall growth stimulation compared to xeric species. Evolutionarily, the distinct responses may reflect divergent life-history strategies, associated with regulatory mechanisms, such as epigenomic used as a proxy for stress memory (Lämke and Bäurle, 2017). Species from xeric environments have likely faced strong selective pressures for traits that maximize resource capture and growth during infrequent pulses of resource availability (e.g., after rainfall events or after wildfires). Thinning could partially mimic such a pulse, triggering a robust growth response. Mesic species, adapted to more consistently favorable conditions, may have evolved strategies favoring sustained, more stable growth and competitive ability in denser stands, rather than rapid bursts in response to sudden resource influxes.

4.2. *Thinning modulates tree growth response to hydric conditions*

The ecophysiological responses of pine species to hydric conditions have been extensively studied (Klein et al., 2011; Martínez-Vilalta et al., 2004), revealing the mechanisms explaining growth reduction due to reduced water availability. As isohydric species, pines regulate their stomata to maintain relatively constant water potential (Resco de Dios, 2021), thereby minimising water loss and keeping high turgor levels in the cambium and derived xylem cells. In this context, our results revealed that growth in *P. pinaster, P. halepensis*, and *P. nigra* was more sensitive to interannual hydric variability, while *P. sylvestris* showed the weakest response to these fluctuations. These results align with previous drought-response classifications of pine species based on their growth patterns (Camarero et al., 2015; Pasho et al., 2011b). Furthermore, other studies also found that *P. sylvestris* displays the weakest relationship with SPEI at the tree and stand levels (Gazol et al., 2022; González-Zamora et al., 2023).

From a management perspective, reducing tree competition through thinning is an effective strategy to mitigate the effects of drought on climate-stressed forests (Aldea et al., 2017; Moreau et al., 2022; Navarro-Cerrillo et al., 2023; Sohn et al., 2016). However, differences between species appear. In particular, the effect of hydric stress on growth after thinning on growth was more pronounced in *P. halepensis* and *P. sylvestris,* two species occupying opposite locations along the xericity gradient. This could indicate a more plastic response of growth to climatic conditions (Manrique-Alba et al., 2020; 2022; Navarro-Cerrillo et al., 2023), i.e., the ability to grow more and take advantage of favourable wet conditions (positive SPEI values). Pine species plasticity implies a rapid response to changes in the environment, which can contribute to the persistence of populations, at least in the short term (Benito Garzón and Vizcaíno-Palomar, 2021). These findings are consistent with those of previous studies, which showed that the plasticity in pines is related to the adaptation of their cambial activity and growth rate in response to climate variability (Camarero et al., 2010; Prislan et al., 2016). The observation that thinning enhanced the growth plasticity in response to hydric conditions for *P. halepensis* and *P. sylvestris* is particularly noteworthy. For *P. halepensis*, its well-documented 'water-saver' strategy and resilience to xylem cavitation (Borghetti et al., 1998; Klein et al., 2011) may be further leveraged in thinned stands. The increased soil water availability post-thinning could reduce the frequency and severity of hydraulic stress, allowing for periods of higher stomatal conductance and photosynthetic activity during favorable moisture conditions without the immediate risk of reaching critical water potential values. This could translate to a greater ability to capitalize on wet periods and lead to higher growth rates. For *P. sylvestris*, a species from more mesic origins with a 'riskier' hydraulic strategy involving higher stomatal conductance (Domec and Gartner, 2002), thinning might fundamentally alter the risk-benefit balance. By substantially increasing the soil water reservoir per tree, thinning could mitigate the danger associated with its high conductivity, allowing it to maintain open stomata and high assimilation rates for longer periods when water is available. This could explain its increased responsiveness to positive SPEI values post-thinning, effectively enabling it to more fully express its growth potential under non-limiting water conditions.

Pinus nigra exhibits eco-physiological characteristics intermediate between *P. halepensis* and *P. sylvestris* (Martínez-Vilalta et al., 2004). In our study, thinning did not significantly modify the relationship between water availability and growth (BAI) for *P. nigra* compared to control plots. This could indicate either a lower plasticity in the species' growth response, or that under current site conditions, *P. nigra* is less limited by hydric variability, and therefore less responsive to thinning in this regard. However, an alternative explanation may lie in the location of our study sites, which are situated within the core climatic range of *P. nigra* in the Iberian Peninsula and do not represent the more xeric locations of its distribution. As such, water stress may not have been the primary limiting factor for growth in these stands, potentially reducing the scope for thinning to modulate hydric sensitivity. This interpretation is supported by the climatic positioning of the study sites relative to the species' broader distribution (Fig. 2).

For *P. pinaster*, the counterintuitive reversal of the SPEI effect observed post-thinning (suggesting increased growth under drier conditions) is most likely driven by statistical uncertainty. This interpretation is supported by the wide credible intervals of the corresponding model parameters and the limited sample size available for this species, which was represented at only two sites. As such, this result should be interpreted with caution, as it may not reflect a robust biological response. Further investigation with larger and more representative datasets is needed before drawing firm conclusions.

4.3. Thinning modifies species-specific growth responses to temperature

A review of the literature reveals a relative scarcity of studies investigating the influence of temperature anomalies on tree growth in thinned pine stands. To our knowledge, only a few studies (e.g., Lucas-Borja et al., 2021; Navarro-Cerrillo et al., 2023) have examined how forest management affects the growth response to temperature in both managed and unmanaged plots of *P. nigra, P. sylvestris*, and *P. halepensis*. However, these studies primarily relied on monthly mean temperature, which may obscure the finer-scale dynamics of climate–-growth relationships. In contrast, our study introduces a novel approach by using seasonal thermal indices derived from weekly temperature anomalies relative to long-term site-specific norms. This method allows for greater temporal precision in identifying the periods during which thermal stress exerts the strongest influence on growth. Additionally, the use of standardized indices facilitates consistent comparisons across sites, management treatments, and climatic drivers, but restricts mechanistic explanations which require more physical measures of climate stress (e.g., soil water potential, vapor pressure deficit, leaf and meristem temperature, etc.).

Our results show a significant and positive effect of the STI_{spr} and STI_{aut} indices, implying that positive anomalies (warmer spring and autumn) enhance growth, while the STI_{sum} index exhibited a negative influence, indicating that warmer summers reduce growth. These findings align with evidence that some Mediterranean pines exhibit bimodal xylogenesis (xylem production in spring-early summer and autumn) under mild and wet conditions (Camarero et al., 2010; Vieira et al., 2014, 2020). This facultative growth pattern, observed in species like *P. halepensis* and *P. pinaster* in coastal regions with bimodal precipitation, may confer an advantage over species from more continental environments, such as *P. nigra* and *P. sylvestris*, which typically show unimodal growth linked to winter–spring precipitation (Castagneri et al., 2018; Campelo et al., 2021; Rossi et al., 2006). During summer, high temperatures and vapor pressure deficit reduce growth by increasing evaporative demand, limiting photosynthesis and reducing the turgor of cambium cells (Grossiord et al., 2020; McDowell et al., 2020).

Per species, STI_{spr} had a stronger positive effect on *P. halepensis* and *P. pinaster*. These results are in agreement with those obtained by Navarro-Cerrillo et al. (2023) for *P. halepensis*, while for *P. pinaster* the results obtained by Gea-Izquierdo et al. (2019) differ from the findings presented here. Comparison of the findings with those of other studies confirms the positive effect of STI_{spr} on growth for *P. nigra* (Gazol et al., 2022; Navarro-Cerrillo et al., 2023) and *P. sylvestris* (Candel-Pérez et al., 2012; Gazol et al., 2022; Martínez del Martínez del Castillo et al., 2024). Regarding STI_{sum}, the negative effect on growth was only significant for *P. halepensis*, while previous studies reported a negative effect for all study species: *P. halepensis* (Camarero et al., 2010; Calev et al., 2016; De Luis et al., 2011), *P. pinaster* (Ferriz et al., 2021; Gea-Izquierdo et al., 2019), *P. nigra* (Lucas-Borja et al., 2021; Navarro-Cerrillo et al., 2023; Sánchez-Salguero et al., 2013) and *P. sylvestris* (Gómez-Aparicio et al., 2011). One likely explanation lies in the geographic location of our study sites relative to each species' full climatic range in the Iberian Peninsula (Fig. 2), where only for *P. halepensis* some sites are located near the species' upper thermal limit of its regional distribution. For STI_{aut}, it had a positive significant effect on growth for all species except *P. pinaster*, and these results match those observed in earlier studies for all species (Gea-Izquierdo et al., 2019; Lucas-Borja et al., 2021; Navarro-Cerrillo et al., 2023). Conversely, the positive impact of rising temperatures during the previous winter on growth has also been documented for various pine species in Mediterranean continental forests (Andreu et al., 2007; Peñuelas and Filella 2001; Sánchez-Salguero et al., 2015b).

Following thinning, we observed an attenuation of the positive effect of spring temperature anomalies (STIspr) on growth, particularly for the xeric *P. halepensis* and *P. pinaster* sites. This pattern should be understood in the context of their overall growth strategy, which relies heavily on early-season growth. These species are adapted to exploit winter-spring soil moisture reserves under mild temperatures before the onset of prolonged summer drought. In high-competition environments (control

plots), favorable spring temperatures are critical, as they enable early resource acquisition and significantly influence annual growth—leading to a strong positive response to STIspr. After thinning, however, reduced competition for water relaxes this dependence on early spring conditions. With improved soil moisture availability extending further into the growing season, trees are less constrained to capitalize solely on the early-season window. As a result, while warm spring conditions remain beneficial, their marginal effect on total growth becomes less pronounced. In contrast, on mesic *P. sylvestris* sites, thinning enhanced the positive effect of STIspr on growth. This is consistent with previous findings showing that warmer spring temperatures promote *P. sylvestris* growth in heavily thinned stands (Navarro-Cerrillo et al., 2023), likely due to thinning-induced improvements in microclimatic and soil moisture conditions (Margalef-Marrasé et al., 2022).

With regard to summer temperature anomalies (STIsum), thinning had a marked effect in increasing growth sensitivity, particularly for species from mesic sites where summer drought is typically less severe. Notably, these species—*P. nigra* and *P. sylvestris*—showed no significant response to summer temperatures under unthinned conditions. The emergence of this sensitivity following thinning represents a novel and important finding for adaptive forest management. Physiologically, these mesic-adapted species evolved under cooler, more humid conditions and may lack the traits needed to cope with the hotter, drier microclimates created by canopy opening in summer. For instance, they may have less efficient stomatal regulation under high vapor pressure deficit, lower heat tolerance in their foliage, or a reduced capacity for transpirational cooling compared to xeric species. As a result, they may respond to elevated summer temperatures with more frequent or prolonged stomatal closure, limiting carbon assimilation, or may even experience direct thermal damage to photosynthetic machinery if leaf temperatures become excessive. By exposing these species to conditions more typical of drier environments, thinning may inadvertently push them beyond their physiological comfort zones, reducing growth under summer heat stress. This interpretation aligns with previous findings by Lempereur et al. (2015), who highlighted the strong negative impact of high summer temperatures on growth, and is further supported by the results of Lucas-Borja et al. (2021), who reported a stronger temperature response in *P. nigra* during June and July in managed stands.

Thinning appeared to weaken the effect of autumn temperature anomalies (STIaut) on growth in *P. halepensis*. This pattern can be interpreted similarly to the STIspr response, in terms of diminishing marginal effects. Under unthinned, water-limited conditions, warm autumn temperatures can play a crucial role in extending the growing season, allowing *P. halepensis* to increase its annual carbon gain during a critical late-season window. However, post-thinning, the improvement in water availability reduces this reliance on favorable autumn conditions. With less restrictive resource limitations extending later into the year, the relative importance of autumn warmth for driving growth declines. As a result, while warm autumns remain advantageous, their marginal contribution to total annual growth is less pronounced. In contrast, *P. pinaster* exhibited a strengthening STIaut effect following thinning, suggesting a more plastic response to climatic variability. This aligns with previous research showing that *P. pinaster* can rapidly adjust its growth dynamics to benefit from favorable conditions (Sánchez-Salguero et al., 2018). No significant STIaut effect was observed in the species from mesic sites, which rely predominantly on their main spring growth period. This is despite some earlier studies reporting a positive influence of autumn temperature on *P. nigra* growth following thinning (Navarro-Cerrillo et al., 2023), indicating that such responses may be highly site- and context-dependent.

In addition to species-specific water-use strategies, differences in canopy architecture may also influence how thinning alters tree responses to temperature. It is well established that canopy opening increases wind exposure, solar radiation, and near-surface temperatures, often leading to warmer and drier microclimatic conditions (Anderegg et al., 2013; Russell et al., 2018). These microclimatic changes may interact differently with the structural traits of species from xeric and mesic sites. In xeric sites, for example, increased post-thinning temperatures may exacerbate soil moisture loss (Doblas-Miranda et al., 2015), potentially extending periods of cambial quiescence and reducing radial growth (Lempereur et al., 2015). In contrast, for both mesic and xeric sites, warming may also promote growth by extending the growing season and stimulating cambial activity (Balducci et al., 2016; Jiménez et al., 2019), though the balance of these effects likely varies by site and species. These complex responses underscore the need to consider structural traits, such as crown or root architecture, alongside physiological strategies when evaluating species-specific sensitivity to thinning and climate. Future research should further explore how thinning interacts with drought and thermal extremes to influence key functional traits underlying tree growth and vigor, including hydraulic conductivity, vulnerability to xylem cavitation, and non-structural carbohydrate concentrations (e.g., Cachinero-Vivar et al., 2024).

4.4. Thinning legacy effects are modulated by species traits

While the positive impact of thinning on tree growth is well established, uncertainties remain regarding the duration and species-specific nature of its legacy effects. Our results show that the growth enhancement following thinning declines progressively over time across all experimental sites. Unlike many previous studies, we explicitly modeled this decline as an exponential decay process, providing a more nuanced understanding of how thinning effects diminish post-treatment.

Importantly, we found clear differences among species. The species from mesic sites such as *P. nigra* and *P. sylvestris* exhibited the lowest decay rates, indicating longer-lasting responses to thinning. In contrast, the species from xeric sites showed more rapid decay of the thinning effect. This was particularly the case of *P. pinaster*, although this estimate carried a large credible interval, reflecting substantial uncertainty likely tied to smaller sample size. These patterns must be interpreted alongside our earlier findings, which showed that mesic species had generally higher growth rates, while xeric species displayed stronger initial responses to thinning.

These contrasting trajectories likely reflect differences in ecological strategy and stand dynamics. Mesic species may maintain lower competition levels for longer periods due to slower canopy closure, possibly linked to differences in structural traits (crown architecture, root structure) as well as physiological differences such as conservative resource-use strategies and greater shade tolerance. Such traits could allow them to sustain the benefits of thinning over longer timescales, gradually translating released resources into structural growth.

By contrast, the faster decay observed in species from xeric sites may be attributed to its pioneer-like, acquisitive growth strategy. Despite occurring in resource-limited environments, these species are known for its rapid post-disturbance recovery and aggressive crown and root expansion. In thinned stands, this can lead to a swift reoccupation of growing space and a faster return to competitive conditions, shortening the duration of thinning benefits. This strategy, while adaptive for exploiting short-term resource pulses or post-fire environments, may reduce the long-term effectiveness of a single thinning intervention.

Our findings are consistent with previous long-term studies showing thinning effects persisting for up to 20 years in *P. halepensis* (Manrique-Alba et al., 2020), 18 years in *Pinus contorta* (Prescott et al., 2019), and 15 years in *P. pinaster* and *P. sylvestris* (Navarro-Cerrillo et al., 2016). Interestingly, our results suggest that *P. nigra* may exhibit even longer-lasting responses than previously reported (13–14 years; Manrique-Alba et al., 2021) which concurs with its long lifespan (800-1200 years). As emphasized by Navarro-Cerrillo et al. (2023), thinning interventions can be considered effective if their impacts persist for at least a decade—an important benchmark that most of our observed legacy effects surpass.

5. Conclusions

Our study highlights the significant influence of climatic factors on pine growth, with wetter conditions generally promoting growth and drought causing a stronger negative effect, particularly in species from mesic environments. Temperature anomalies during spring and autumn also positively affect growth, whereas elevated summer temperatures tend to reduce growth, especially in xeric species. Thinning consistently enhances growth across all studied species, with effects lasting up to 20 years, and modifies species' sensitivity to climate stressors by amplifying the effects of hydric anomalies and intensifying the negative impacts of summer heat. Additionally, thinning weakens the positive influence of spring temperatures in xeric species while enhances it in mesic species. These findings emphasize the importance of accounting for species-specific responses to both climate variability and forest management when designing adaptive strategies under changing environmental conditions.

CRediT authorship contribution statement

Àngela Manrique-Alba: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Santiago Beguería:** Writing – original draft, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **J. Julio Camarero:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Antonio J. Molina:** Investigation, Data curation. **Gonzalo G. Barberá:** Investigation. **Juan A. Blanco:** Investigation. **Antonio M. Cachinero-Vivar:** Investigation. **Víctor M. Castillo:** Investigation. **Antonio D. del Campo:** Investigation. **Álvaro Hernández:** Investigation. **J. Bosco Imbert:** Investigation. **María N. Jiménez:** Investigation. **Yueh-Hisn Lo:** Investigation. **Manuel E. Lucas-Borja:** Investigation. **Gerardo Moreno:** Investigation. **Francisco B. Navarro:** Investigation. **Rafael M. Navarro-Cerrillo:** Investigation. **M^{a} Ángeles Ripoll:** Investigation. **Ángela Sánchez-Miranda:** Investigation.

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110777.

Data availability

The data that support the findings of this study are openly available in DIGITAL.CSIC at https://doi.org/10.20350/digitalCSIC/17165.

References

Aldea, J., Bravo, F., Bravo-Oviedo, A., Ruiz-Peinado, R., Rodríguez, F., del Río, M., 2017. Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands. Agric. For. Meteorol. 237, 371–383.

Aldea, J., del Río, M., Cattaneo, N., Riofrío, J., Ordóñez, C., Uzquiano, S., Bravo, F., 2023. Short-term effect of thinning on inter-and intra-annual radial increment in Mediterranean scots pine-oak mixed forests. For. Ecol. Manage 549, 121462.

Alía, R., Martín, S., 2003. EUFORGEN Technical Guidelines for genetic conservation and use for Maritime pine (*Pinus pinaster*). Int. Plant Genet. Resour. Inst. Rome Italy, 6 pages.

Anderegg, W.R., Kane, J.M., Anderegg, L.D., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nat. Clim. Change 3, 30–36.

Andreu, L., Gutiérrez, E., Macias, M., Ribas, M., Bosch, O., Camarero, J.J., 2007. Climate increases regional tree growth variability in Iberian pine forests. Glob. Change Biol. 13, 1–12.

Astigarraga, J., Andivia, E., Zavala, M.A., Gazol, A., Cruz-Alonso, V., Vicente-Serrano, S. M., et al., 2020. Evidence of non-stationary relationships between climate and forest responses: increased sensitivity to climate change in Iberian forests. Glob. Change Biol. 26, 5063–5076. https://doi.org/10.1111/gcb.15198.

Balducci, L., Cuny, H.E., Rathgeber, C.B., Deslauriers, A., Giovannelli, A., Rossi, S., 2016. Compensatory mechanisms mitigate the effect of warming and drought on wood formation. Plant Cell Environ. 39, 1338–1352.

Bao, Y., Aggarwal, P., RobbinsNE, I.I., Sturrock, C.J., Thompson, M.C., Tan, H.Q., Tham, C., Duan, L., Rodriguez, P.L., Vernoux, T., et al., 2014. Plant roots use a patterning mechanism to position lateral root branches toward available water. Proc. Natl. Acad. Sci. USA 111, 9319–9324.

Beguería, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. Int. J. Clim. 34, 3001–3023.

Benito Garzón, M., Vizcaíno-Palomar, N., 2021. Biogeographical patterns of local adaptation and plasticity of mediterranean pines and their implications under climate change. In: Ne'eman, G., Osem, Y. (Eds.), Pines and Their Mixed Forest Ecosystems in the Mediterranean Basin. Managing Forest Ecosystems, Pines and Their Mixed Forest Ecosystems in the Mediterranean Basin. Managing Forest Ecosystems, 38. Springer, Cham.

Borghetti, M., et al., 1998. Impact of long-term drought on xylem embolism and growth in *Pinus halepensis* Mill. Trees Struct. Funct. 12, 187–195.

Bréda, N., Granier, A., Aussenac, G., 1995. Effects of thinning on soil and tree water relations. Transpiration and growth in an oak forest (*Quercus petraea* (Matt.)). Tree Physiol. 15, 295–306.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002.

Bunn, A.G., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2024. dplR: dendrochronology program library in R. R Package Version 1.7.7. htt ps://CRAN.R-project.org/package=dplR.Cachinero-Vivar.

Cachinero-Vivar, A.M., Navarro-Cerrillo, R.M., Cabrera-Puerto, R.J., Pérez-Priego, O., 2024. Impact of thinning on leaf economics, plant hydraulics, and growth dynamics. For. Ecol. Manage 562, 121914.

Cachinero-Vivar, A.M., Palacios-Rodríguez, G., Lara-Gómez, M.A., Navarro-Cerrillo, R. M., 2021. Thinning effect of C sequestration along an elevation gradient of Mediterranean Pinus spp. plantations. Forests 12 (11), 1583.

Calev, A., Zoref, C., Tzukerman, M., Moshe, Y., Zangy, E., Osem, Y., 2016. High-intensity thinning treatments in mature *Pinus halepensis* plantations experiencing prolonged drought. Eur. J. For. Res. 135, 551–563.

Camarero, J.J., Olano, J.M., Parras, A., 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New. Phytol. 185, 471–480.

Camarero, J.J., Gazol, A., Tardif, J.C., Conciatori, F., 2015. Attributing forest responses to global-change drivers: limited evidence of a CO_2-fertilization effect in Iberian pine growth. J. Biogeogr. 42 (11), 2220–2233.

Camarero, J.J., Gazol, A., Sánchez-Salguero, R., 2021. Effects of global change on tree growth and vigor of Mediterranean pines. In: Ne'eman, G., Osem, Y. (Eds.), Effects of global change on tree growth and vigor of Mediterranean pines. Pines and Their Mixed Forest Ecosystems in the Mediterranean Basin. Managing Forest Ecosystems 38.

Campelo, F., Ribas, M., Gutiérrez, E., 2021. Plastic bimodal growth in a Mediterranean mixed-forest of *Quercus ilex* and *Pinus halepensis*. Dendrochronologia 67, 125836.

Candel-Pérez, D., Linares, J.C., Viñegla, B., Lucas-Borja, M.E., 2012. Assessing climate–growth relationships under contrasting stands of co-occurring Iberian pines along an altitudinal gradient. For. Ecol. Manage 274, 48–57.

Castagneri, D., Battipaglia, G., von Arx, G., Pacheco, A., Carrer, M., 2018. Tree-ring anatomy and carbon isotope ratio show both direct and legacy effects of climate on bimodal xylem formation in *Pinus pinea*. Tree Physiol. 38, 1098–1109.

Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. Data Brief 12, 662–666. https://doi.org/10.1016/j.dib.2017.05.007.

del Campo, A.D., Fernandes, T.J., Molina, A.J., 2014. Hydrology-oriented (adaptive) silviculture in a semiarid pine plantation: how much can be modified the water cycle through forest management? Eur. J. For. Res. 133, 879–894.

del Campo, A.D., Otsuki, K., Serengil, Y., Blanco, J.A., Yousefpour, R., Wei, X., 2022. A global synthesis on the effects of thinning on hydrological processes: Implications for forest management. For. Ecol. Manag. 519, 120324.

Del Río, M., Oviedo, J.A.B., Pretzsch, H., Löf, M., Ruiz-Peinado, R., 2017. A review of thinning effects on Scots pine stands: From growth and yield to new challenges under global change. For. Syst. 26 (2), 9.

De Luis, M., Novak, K., Raventós, J., Gričar, J., Prislan, P., Čufar, K., 2011. Climate factors promoting intra-annual density fluctuations in Aleppo pine (Pinus halepensis) from semiarid sites. Dendrochronologia 29 (3), 163–169.

Doblas-Miranda, E., Martínez-Vilalta, J., Lloret, F., Álvarez, A., Ávila, A., Bonet, F.J., Brotons, L., Castro, J., Curiel Yuste, J., Díaz, M., et al., 2015. Reassessing global

change research priorities in Mediterranean terrestrial ecosystems: How far have we come and where do we go from here? Glob. Ecol. Biogeogr. 24, 25–43.
Domec, J.C., Gartner, B.L., 2002. Age-and position-related changes in hydraulic versus mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. Tree Physiol. 22 (2-3), 91–104.
Esteban, L.G., Martín, J.A., de Palacios, P., Fernández, F.G., 2012. Influence of region of provenance and climate factors on wood anatomical traits of *Pinus nigra* Arn. subsp. *salzmannii*. Eur. J. For. Res. 131, 633–645.
Fady, B., Semerci, H., Vendramin, G.G., 2003. EUFORGEN Technical Guidelines for genetic conservation and use for Aleppo pine (*Pinus halepensis*) and Brutia pine (*Pinus brutia*). Int. Plant Genet. Resour. Inst. Rome Italy, 6 pages.
Fernandes, T.J., Del Campo, A.D., Herrera, R., Molina, A.J., 2016. Simultaneous assessment, through sap flow and stable isotopes, of water use efficiency (WUE) in thinned pines shows improvement in growth, tree-climate sensitivity and WUE, but not in WUEi. For. Ecol. Manag 361, 298–308.
Ferriz, M., Martin-Benito, D., Cañellas, I., Gea-izquierdo, G., 2021. Sensitivity to water stress drives differential decline and mortality dynamics of three co-occurring conifers with different drought tolerance. For. Ecol. Manag 486, 118964.
Fritts, H.C., 2001. Tree Rings and Climate. Blackburn, USA.
Gazol, A., Oliva, J., Valeriano, C., Colangelo, M., Camarero, J.J., 2022. Mixed pine forests in a hotter and drier world: the great resilience to drought of aleppo pine benefits it over other coexisting pine species. Front. For. Glob. Change 5, 899425.
Gea-Izquierdo, G., Férriz, M., García-Garrido, S., Aguín, O., Elvira-Recuenco, M., Hernandez-Escribano, L., Raposo, R., 2019. Synergistic abiotic and biotic stressors explain widespread decline of *Pinus pinaster* in a mixed forest. Sci. Total Environ. 685, 963–975.
Gelman, Andrew, Carlin, John B., Stern, Hal S., Rubin, Donald B, 2004. Bayesian Data Analysis (second ed.). CRC Press, Boca Raton, Florida, pp. 4–5. ISBN 1-58488-388-X.
Giuggiola, A., Bugmann, H., Zingg, A., Dobbertin, M., Rigling, A., 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. For. Ecol. Manag 310, 827–835.
Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Glob. Change Biol. 17, 2400–2414.
González-Zamora, Á., Almendra-Martín, L., de Luis, M., Gaona, J., Martínez-Fernández, J., 2023. How are pine species responding to soil drought and climate change in the iberian peninsula? Forests. 14 (8), 1530.
Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. New Phytol. 226 (6), 1550–1566.
Irvine, J., Perks, M.P., Magnani, F., Grace, J., 1998. The response of *Pinus sylvestris* to drought: Stomatal control of transpiration and hydraulic conductance. Tree Physiol. 18, 393–402.
Isajev, V., Fady, B., Semerci, H., Andonovski, V., 2004. EUFORGEN Technical Guidelines for genetic conservation and use for European black pine (*Pinus nigra*). International Plant Genetic Resources Institute, Rome (Italy), p. 6.
Jiménez, M.N., Navarro, F.B., Sánchez-Miranda, A., Ripoll, M.A., 2019. Using stem diameter variations to detect and quantify growth and relationships with climatic variables on a gradient of thinned Aleppo pines. For. Ecol. Manag. 442, 53–62.
Klein, T., Cohen, S., Yakir, D., 2011. Hydraulic adjustments underlying drought resistance of *Pinus halepensis*. Tree Physiol. 31 (6), 637–648.
Lämke, J., Bäurle, I., 2017. Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. Genome Biol. 18, 124.
Lemaire, C., Blackman, C.J., Cochard, H., Menezes-Silva, P.E., Torres-Ruiz, J.M., Herbette, S., 2021. Acclimation of hydraulic and morphological traits to water deficit delays hydraulic failure during simulated drought in poplar. Tree Physiol. 41 (11), 2008–2021.
Lempereur, M., Martin-StPaul, N.K., Damesin, C., Joffre, R., Ourcival, J.M., Rocheteau, A., Rambal, S., 2015. Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: implications for assessing forest productivity under climate change. New Phytol. 207 (3), 579–590.
Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J., Hagge, J., 2022. Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. Oecologia 198 (3), 825–834.
Li, X., Li, Y., Zhang, J., Peng, S., Chen, Y., Cao, Y., 2020. The Effects of Forest Thinning on Understory Diversity in China: a Meta-Analysis, 31. Land Degradation & Development, pp. 1225–1240.
Linares, J.C., Tíscar, P.A., 2010. Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. Tree Physiol. 30, 795–806.
Lucas-Borja, M.E., Andivia, E., Candel-Pérez, D., Linares, J.C., Camarero, J.J., 2021. Long term forest management drives drought resilience in Mediterranean black pine forest. Trees 35, 1651–1662.
Manrique-Alba, À., Beguería, S., Molina, A.J., González-Sanchis, M., Tomàs-Burguera, M., Del Campo, A.D., Camarero, J.J., 2020. Long-term thinning effects on tree growth, drought response and water use efficiency at two Aleppo pine plantations in Spain. Sci. Total Environ. 728, 138536.
Manrique-Alba, À., Beguería, S., Tomàs-Burguera, M., Camarero, J.J., 2021. Increased post-drought growth after thinning in *Pinus nigra* plantations. Forests. 12 (8), 985.
Manrique-Alba, À., Beguería, S., Camarero, J.J., 2022. Long-term effects of forest management on post-drought growth resilience: An analytical framework. Sci.Total Env. 810, 152374.
Manrique-Alba, À., Molina, A.J., Beguería, S., Camarero, J.J., Barberá, G.G., Blanco, J.A., Sánchez-Miranda, Á., 2025. Basal area increment and climate data from long-term silviculture monitoring sites in Spain (SilvAdapt.net) [Data set]. http://doi.org/10.20350/DIGITALCSIC/17165.
Margalef-Marrasé, J., Bagaria, G., Lloret, F., 2022. Canopy self-replacement in Pinus sylvestris rear-edge populations following drought-induced die-off and mortality. For. Ecol. Manage 521, 120427.
Martín-Benito, D., Del Río, M., Heinrich, I., Helle, G., Cañellas, I., 2010. Response of climate growth relationships and water use efficiency to thinning in a Pinus nigra afforestation. For. Ecol. Manag. 259, 967–975.
Martínez del Castillo, E., Torbenson, M.C., Reinig, F., Tejedor, E., de Luis, M., Esper, J., 2024. Contrasting Future Growth of Norway Spruce and Scots Pine Forests Under Warming Climate. Glob. Change Biol. 30 (11), e17580.
Martínez-Vilalta, J., Sala, A., Piñol, J., 2004. The hydraulic architecture of Pinaceae–a review. Plant Ecol. 171, 3–13.
Maseyk, K.S., Lin, T., Rotenberg, E., Grünzweig, J.M., Schwartz, A., Yakir, D., 2008. Physiology – phenology interactions in a productive semi-arid pine forest. New. Phytol. 178, 603–616.
Matisons, R., Jansone, D., Elferts, D., Adamovičs, A., Schneck, V., Jansons, A., 2019. Plasticity of response of ring-width of Scots pine provenances to weather extremes in Latvia. Dendrochronologia 54, 1–10.
McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368 (6494), eaaz9463.
Molina, A.J., Navarro-Cerrillo, R.M., Pérez-Romero, J., Alejano, R., Bellot, J.F., Blanco, J. A., Camarero, J.J., Carrara, A., Castillo, V.M., Cervera, T., Barberá, G.G., González-Sanchis, M., Á, Hernández, Imbert, J.B., Jiménez, M.N., Llorens, P., Lucas-Borja, M. E., Moreno, G., MM-dl, Heras, Navarro, F.B., Palacios, G., Palero, N., Ripoll, M.A., Regües, D., Ruiz-Gómez, F.J., Vilagrosa, A., del Campo, A.D., 2021. SilvAdapt.Net: a site-based network of adaptive forest management related to climate change in Spain. Forests. 12 (12), 1807.
Moreau, G., Chagnon, C., Achim, A., Caspersen, J., D'Orangeville, L., Sánchez-Pinillos, M., Thiffault, N., 2022. Opportunities and limitations of thinning to increase resistance and resilience of trees and forests to global change. Forestry 95 (5), 595–615.
Moreno-Gutiérrez, C., Barberá, G.G., Nicolás, E., de Luis, M., Castillo, V.M., Martínez-Fernández, F., Querejeta, J.I., 2011. Leaf δ18O of remaining trees is affected by thinning intensity in a semiarid pine forest. Plant Cell Environ. 34, 1009–1019.
Navarro-Cerrillo, R.M., Sánchez-Salguero, R., Herrera, R., Ceacero Ruiz, C., Moreno-Rojas, J., Delgado Manzanedo, R., López-Quintanilla, J., 2016. Contrasting growth and water use efficiency after thinning in mixed Abies pinsapo–*Pinus pinaster*–*Pinus sylvestris* forests. J. For. Sci 62, 53–64.
Navarro-Cerrillo, R.M., Sánchez-Salguero, R., Rodriguez, C., Lazo, J.D., Moreno-Rojas, J. M., Palacios-Rodriguez, G., Camarero, J.J., 2019. Is thinning an alternative when trees could die in response to drought? The case of planted *Pinus nigra* and *P. Sylvestris* stands in southern Spain. For. Ecol. Manage 433, 313–324.
Navarro-Cerrillo, R.M., Cachinero-Vivar, A.M., Pérez-Priego, Ó., Cantón, R.A., Begueria, S., Camarero, J.J., 2023. Developing alternatives to adaptive silviculture: Thinning and tree growth resistance to drought in a Pinus species on an elevated gradient in Southern Spain. For. Ecol. Manage 537, 120936.
Olivar, J., Bogino, S., Spiecker, H., Bravo, F., 2012. Climate impact on growth dynamic and intra-annual density fluctuations in Aleppo Pine (*Pinus halepensis*) trees of different crown classes. Dendrochronologia 30, 35–47.
Ovenden, T.S., Perks, M.P., Clarke, T.-K., Mencuccini, M., Jump, A.S., 2021. Life after recovery: increased resolution of forest resilience assessment sheds new light on post-drought compensatory growth and recovery dynamics. J. Ecol 1–14. XXX.
Pasho, E., Camarero, J.J., de Luis, M., Vicente–Serrano, S.M, 2011. Spatial variability in large–scale and regional atmospheric drivers of *Pinus halepensis* growth in eastern Spain. Agr. For. Meteorol. 151, 1106–1119.
Pasho, E., Camarero, J.J., de Luis, M., Vicente-Serrano, S.M., 2011b. Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. Agric. For. Meteorol. 151, 1800–1811.
Peñuelas, J., Filella, I., 2001. Responses to a warming world. Science 294 (5543), 793–795.
Prescott, C., deMontigny, L., Harper, G., 2019. Eighteen-year growth responses to thinning and fertilisation of a height-repressed lodgepole pine stand in interior British Columbia. For. Chron. 95, 207–221.
Prislan, P., Gričar, J., de Luis, M., Novak, K., del Castillo, E.M., Schmitt, U., Koch, G., Štrus, J., Mrak, P., Žnidarič, M.T., et al., 2016. Annual Cambial Rhythm in *Pinus halepensis* and *Pinus sylvestris* as Indicator for Climate Adaptation. Front. Plant Sci. 7, 1923.
Prospero, S., Cleary, M., 2017. Effects of host variability on the spread of invasive forest diseases. Forests. 8, 80.
Resco de Dios, V., 2021. What Is a Mediterranean Pine? Physiological Trade-Offs Under Stress and Perturbation. In: Ne'eman, G., Osem, Y. (Eds.), Pines and Their Mixed Forest Ecosystems in the Mediterranean Basin. Managing Forest Ecosystems, Pines and Their Mixed Forest Ecosystems in the Mediterranean Basin. Managing Forest Ecosystems, 38. Springer, Cham.
Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., et al., 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New. Phytol. 170, 301–310.
Rue, H., Martino, S., Chopin, N., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. J. R. Stat. Soc. B: Stat. Methodol. 71, 319–392.
Rue, H., Riebler, A., Sørbye, S.H., Illian, J.B., Simpson, D.P., Lindgren, F.K., 2017. Bayesian computing with INLA: a review. Annu. Rev. Stat. Appl. 4, 395–421.
Russell, E.S., Liu, H., Thistle, H., Strom, B., Greer, M., Lamb, B., 2018. Effects of thinning a forest stand on sub-canopy turbulence. Agric. For. Meteorolo 248, 295–305.
Sánchez-Salguero, R., Camarero, J.J., Dobbertin, M., Fernández-Cancio, Á., Vilà-Cabrera, A., Manzanedo, R.D., Navarro-Cerrillo, R.M., 2013. Contrasting

vulnerability and resilience to drought-induced decline of densely planted vs. Natural rear-edge Pinus nigra forests. For. Ecol. Manage 310, 956–967.
Sánchez-Salguero, R., Camarero, J.J., Hevia, A., Madrigal-González, J., Linares, J.C., Ballesteros-Canovas, J.A., Sánchez-Miranda, A., Alfaro-Sánchez, R., Sangüesa-Barreda, S., Galván, J.D., Gutiérrez, E., Génova, M., Rigling, A., 2015a. What drives growth of Scots pine in continental Mediterranean climates: Drought, low temperatures or both? Agric. For. Meteorol. 206, 151–162.
Sánchez-Salguero, R., Linares, J.C., Camarero, J.J., Madrigal-González, J., Hevia, A., Sánchez-Miranda, A., Ballesteros-Cánovas, J.A., Sánchez, R.A., García-Cervigón, A.I., Bigler, C., et al., 2015b. Disentangling the effects of competition and climate on individual tree growth: A retrospective and dynamic approach in Scots pine. For. Ecol. Manage 358, 12–25.
Sánchez-Salguero, R., Camarero, J.J., Rozas, V., Génova, M., Olano, J.M., Arzac, A., Gazol, A., Caminero, L., Tejedor, E., de Luis, M., Linares, J.C., 2018. Resist, recover or both? Growth plasticity in response to drought is geographically structured and linked to intra-specific variability in *Pinus pinaster*. J. Biogeogr. 45, 1126–1139.
Sarris, D., Christodoulakis, D., Körner, C., 2011. Impact of recent climatic change on growth of low elevation eastern Mediterranean forest trees. Clim. Change 106, 203–223.
Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: A meta-analysis. For. Ecol. Manage 380, 261–273.
Sperlich, D., Chang, C.T., Peñuelas, J., Sabaté, S., 2019. Responses of photosynthesis and component processes to drought and temperature stress: are Mediterranean trees fit for climate change? Tree Physiol. 39, 1783–1805.
Tomas-Burguera, M., Vicente-Serrano, S.M., Beguería, S., Reig, F., Latorre, B., 2019. Reference crop evapotranspiration database in Spain (1961–2014). Earth Syst. Sci. Data 11, 1917–1930.
Uhl, B., Schall, P., Bässler, C., 2024. Achieving structural heterogeneity and high multi-taxon biodiversity in managed forest ecosystems: a European review. Biodivers. Conserv. 1–32.
Vallejo-Bombín, R., 2023. Tercer Inventario Forestal Nacional. Ministerio de Agricultura, Alimentación y Medio Ambiente. (Esp./Spain).
Veuillen, L., Prévosto, B., Alfaro-Sánchez, R., Badeau, V., Battipaglia, G., Beguería, S., Cailleret, M., 2023. Pre-and Post-Drought Conditions Drive Resilience of *Pinus halepensis* Across its Distribution Range, 339. Agricultural and Forest Meteorology, 109577.
Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim 23, 1696–1718.
Vicente-Serrano, S.M., Tomàs-Burguera, M., Beguería, S., Reig, F., Latorre, B., Peña-Gallardo, M., González-Hidalgo, J.C., 2017. A high resolution dataset of drought indices for Spain. Data 2 (3), 22.
Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2014. Xylogenesis of *Pinus pinaster* under a Mediterranean climate. Ann. For. Sci 71, 71–80. https://doi.org/10.1007/s13595-013-0341-5.
Vieira, J., Carvalho, A., Campelo, F., 2020. Tree growth under climate change: evidence from xylogenesis timings and kinetics. Front. Plant Sci. 11, 90.
Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol 23, 201–213.
Zavala, M.A., Angulo, Ó., de la Parra, R.B., Moreno-Fernández, D., Madrigal-González, J., 2024. Scaling up tree growth to assess forest resilience under increasing aridity: the case of Iberian dry-edge pine forests. Landsc. Ecol. 39 (1), 1–22.