

From acclimation to risk: Increasing drought vulnerability of introduced *Pinus strobus* L. across central and Eastern Europe

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ABSTRACT

Climate projections suggest major shifts in tree species distributions, with most conifers expected to lose suitable habitats. In this context, non-native species may offer potential substitutes for native taxa. The introduced *Pinus strobus* exhibits pronounced variability in growth responses across Europe, reflecting varying levels of adaptation to environmental conditions. The aim of this study was to analyze *P. strobus* responses to climatic factors along a latitudinal gradient from the Baltic region to the Balkans. The study was based on data from a large tree-ring network comprising >650 trees from 38 sites, divided into four clusters. Summer precipitation emerges as the dominant factor controlling secondary growth with a pronounced latitudinal gradient that is strongest at the southernmost sites and progressively weaker toward the north. The effect of temperature shifts changed from weakly positive in northern sites to strongly negative in southern ones. The growth trend assessments revealed a significant reduction over the last decades at the southern sites, whereas in the central and northern parts of the network, *P. strobus* basal area increment shows no significant trends. Across the latitudinal gradient, *P. strobus* exhibits reduced resistance and recovery in the Southern cluster, whereas overall resilience does not differ significantly. These findings demonstrate that *P. strobus* possesses considerable climatic plasticity but also increasing sensitivity to high temperatures, particularly at the southern margin of the study network. Consequently, progressive warming and the increasing frequency of waves and droughts will reduce growth potential in southern Europe. Despite generally favorable habitat indicators at the northern sites, temporal trends indicate increasingly negative correlations with summer temperatures, indicating increasing heat sensitivity even there.

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1. Introduction

Forest ecosystems represent one of the largest carbon sinks globally, with an estimated 45% storage of terrestrial carbon (Pan et al., 2011). Tree growth, a key determinant of carbon sequestration in terrestrial ecosystems, is strongly controlled by climate variability, extreme events, and large-scale disturbances. The observed climate changes affect the plants' water management due to shifts in groundwater levels (Cavelan et al., 2022), more frequent droughts (Moravec et al., 2021; Jaagus et al., 2022), rising temperatures, and severe weather events (Dong et al., 2017). The interaction of these factors plays a crucial role in shaping the resilience and functioning of forest ecosystems in terms of both carbon storage and the provision of ecosystem services under changing climatic conditions (Hanewinkel et al., 2013). As climate is the main limiting factor expected to undergo drastic alterations in the near future (IPCC, 2023), such changes may significantly affect tree growth performance, species coexistence, and the capacity of forests to withstand disturbances. Numerous studies indicate that climate change in Europe may drive shifts in potential species' ranges, with warming conditions favoring deciduous species while reducing the prevalence of conifers (Dyderski et al., 2025; Puchalka et al., 2023; Illés and Mórincz, 2022). Consequently, identifying tree species or provenances better adapted to changing climatic conditions and promoting them through adaptive forest management practices will be essential for ensuring the sustainable development and long-term stability of managed forests (Chakraborty et al. 2024). Understanding forest stability under growing environmental pressure requires long-term records of forest responses to climatic and biotic factors, as well as past extremes. Tree rings uniquely capture these responses, revealing growth declines and recovery patterns over time (Babst et al., 2018). Therefore, tree-ring widths or derived parameters (e.g., basal area increment) are commonly used to quantify and to predict species-specific adaptability, vulnerability, or decline across broad spatial scales (e.g., Klesse et al., 2024; Popa et al., 2025).

Tree growth patterns can serve as reliable early warning signals of forest decline (Camarero et al., 2015; Popa et al., 2024a). Given that trees prioritize allocation to stemwood production, thus, a negative growth trend may indicate reduced resource partitioning for defensive compounds, making them vulnerable to pests and pathogens (McDowell et al., 2022). From a complementary perspective, while considering ecological stability, it is necessary to assess the impact of both the stressful conditions in the long term (e.g., increased temperatures) and the effects of short-term events (e.g., droughts, heatwaves). Following Lloret et al. (2011), the ability of trees to regain pre-disturbance growth rates after an extreme event is defined as growth resilience. This index, along with resistance (inverse of growth reduction during the stress event) and recovery (growth increase after the event relative to growth during the event), is a valuable indicator of trees' capacity to cope with climate anomalies (Izmir et al., 2024). Combining analyses of long-term growth trends with short-term responses quantified by resilience indices provides a comprehensive understanding of forest ecosystem responses to changing climatic conditions.

From a wider perspective, tree-ring data also provide a robust proxy for forest productivity and its temporal variability, as radial growth integrates the combined effects of carbon assimilation, resource availability, and environmental constraints over the growing season (Babst et al., 2018). Numerous studies have demonstrated strong relationships between tree-ring width or basal area increment and stand-level productivity, particularly in water-limited environments where growth is coupled with climatic drivers (e.g., Wang et al., 2025; Wei et al., 2025). Furthermore, tree growth responses to climate factors are essential for characterizing species-specific suitability across current or future distribution ranges. However, ongoing climate change is altering the relationship between tree growth and climate, often revealing increasing species vulnerability (Wilmking et al., 2020; Jevšenak et al., 2024). Under this framework, a full understanding of a species' capacity

to thrive under climate change requires up-to-date knowledge of its climatic responses and the temporal stability of these relationships. Such shifts in climate sensitivity over time challenge the calibration of climate reconstruction models (Jevšenak et al., 2024) and reveal critical changes in climatic limitations along elevational and broad spatial gradients (Popa et al., 2024b).

The introduction of forest tree species into environments beyond their natural ranges aligns with the concept of assisted colonisation (Gardner and Bullock, 2025). In Europe, such practices date back >400 years and were initially driven by interest in newly discovered species, their ornamental value, and superior growth properties (Nyssen et al., 2016). It was not until the late 19th century that non-native tree species began to be increasingly considered as alternatives to native species (Herežniak, 1992; Nyssen et al., 2016; Brus et al., 2019). This shift coincided with the Industrial Revolution and a rapidly increasing demand for wood in Western Europe (Kander et al., 2013). Consequently, species selection was primarily determined by growth and yield potential, as well as by similarities of climatic and soil conditions between the introduction sites and the species' native range (Nyssen et al., 2016; Brus et al., 2019). Only recently has the role of non-native tree species in Europe begun to be evaluated from a broader, multi-perspective standpoint. Accelerating environmental changes have highlighted their invasive potential, competitiveness with native tree species, and potential threat to local habitats, as well as on the functional and phylogenetic diversity of ecological communities (Wohlgemuth et al., 2022; Puchalka et al., 2025).

Eastern white pine (*Pinus strobus* L.) is native to North America, where it has been extensively studied (e.g., Bennett, 1994; Marshall, 2009; Sniezko et al., 2011). Within its native range, *P. strobus* occupies the eastern United States, extending north into southeastern Canada and south to Florida (Fig. 1A; Radu, 2008). The species occurs across temperate and subtropical climates, showing broad tolerance to temperature and moisture conditions. It grows in areas with cold to moderately mild winters, ranging from cool continental to humid subtropical climatic conditions, and typically occupies well-drained soils according to the Köppen climate classification. Eastern white pine was introduced to Europe in the early 18th century (ca. 1705) initially as an ornamental tree in parks (Marshall, 2009). Owing to its rapid growth and high-quality timber, it was subsequently planted in forests from the late 18th century onward (Radu, 2008). Extensive research by the Association of Forest Research Institutes of Germany, including collaborations with the International Union of Forest Research Organizations (IUFRO), founded in 1892, further supported its integration into European forestry (Blada and Popescu, 2001). Breeding efforts aimed at improving resistance to white pine blister rust achieved partial success (Radu, 2008), contributing to the species' increasing popularity across Central Europe (Mandak et al., 2013). The study by Munzbergova et al. (2013) clearly indicates that this species employs diverse growth strategies, depending on its developmental stage, to occupy a variety of habitats; hence, it appears that the plasticity of *P. strobus* is the species' key advantage, facilitating its spread across Europe. Among conifers, which generally exhibit conservative resource-use strategies, *P. strobus* is more acquisitive than other introduced conifer species in Central Europe (Augustine and McCulloh, 2024). *Pinus strobus*, as a species with relatively high shade tolerance and long-lived needles (Ninemets and Valladares, 2006), should, according to Walters and Reich (1999) exhibit high tolerance to abiotic stress (with high leaf mass per area). However, its more acquisitive strategy compared to other European conifers is associated with a water-stress response characterized by a negative water balance. This places *P. strobus* among NNTs with high drought sensitivity (Klisz et al. 2022), which may increase its susceptibility to pests (Vacek et al., 2021). Despite its broad distribution, studies on *P. strobus* in Europe remain geographically fragmented and are largely limited to local tree-stands in countries with extensive species presence, such as the Czech Republic (Hadincová et al., 2008; Podrázský et al., 2020), Romania (Radu, 2008), Poland (Klisz et al., 2022;

Wilczyński et al., 2025), Latvia (Jansone et al., 2023), and Estonia (Läänelaid and Helama, 2020). Related studies often address acclimatization only indirectly, for example, by focusing on other aspects, such as white pine blister rust, caused by *Cronartium ribicola*, which severely affects this pine species and contributes to its massive decline (Lu et al., 2005). Taken together, these results provide only a fragmented view of the growth performance and resilience of distinct *P. strobus*-based forests under local conditions. Therefore, systematic assessments across a larger geographic range are needed to evaluate the future performance of *P. strobus* under changing environmental conditions and to assess its potential as a substitute for vulnerable native conifer species in Europe.

To fill this knowledge gap, our study encompasses a broad Central European region spanning a wide climatic gradient, from cold, moist areas in the Baltics, through temperate Central Europe, to warm, dry areas in the Balkans. Because thermal and moisture regimes differ markedly along the studied gradient, we anticipate distinct regional differences in climate sensitivity and resilience of *P. strobus*. Specifically, this study aims to evaluate how non-native *P. strobus* responds to climate change across its current distribution in Europe, particularly given the growing threat that climate change poses to native tree species. We focus on growth patterns and tree responses to temperature and water availability, using a large tree-ring network of >650 trees from 38 *P. strobus*-dominated stands. We hypothesize that:

- H1: Growth of *P. strobus* is primarily limited by water availability during the current growing season, and these limitations are strengthened under increasing drought frequency and severity. The strongest and most persistent drought constraints are expected at the drier southern sites.
- H2: In response to observed increasing drought and heat stress in the drier southern regions, growth trends will decline along the gradient, reflecting increasingly less suitable habitat conditions toward the dry southern margin.
- H3: The capacity of *P. strobus* to recover from growth reductions varies along the spatial gradient. Tree stands at southern sites, which have been more frequently exposed to climatic extremes, are expected to exhibit higher growth resilience as a result of adaptive plasticity. In contrast, northern sites, having experienced fewer recurrent extremes, may show lower resilience and greater vulnerability under recent conditions of increasing water scarcity.

2. Methods

2.1. Site selection

Our study covers a large part of distribution of Eastern white pine in Europe, and spans across Central and Eastern Europe, from the Baltic Sea coast (Estonia, Latvia, Poland) to the Black Sea region (Romania),

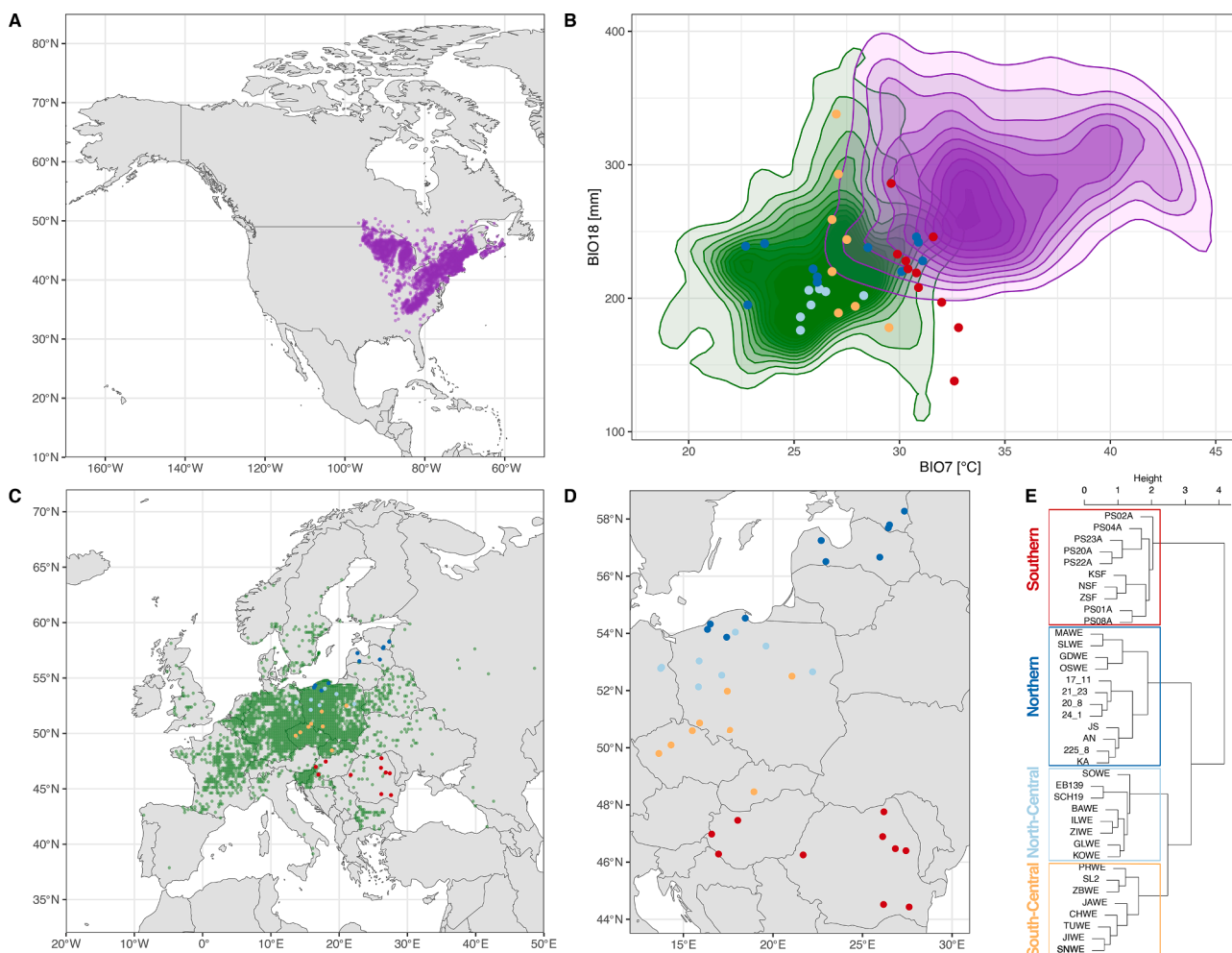


Fig. 1. (A) Natural distribution of *P. strobus* (violet) in North America. (B) Climatic envelope for eastern white pine (*P. strobus*) based on two bioclimatic variables: BIO18 (precipitation of the warmest quarter) and BIO07 (annual temperature range). (C) European distribution of introduced *P. strobus* (green). (D) Location of study sites in Central and Eastern Europe. (E) Dendrogram of hierarchical clustering of study sites (see Section 2.3 for details and Table A1 for site codes; Northern cluster consists of 12 sites, North-Central cluster of 8 sites, South-Central cluster of 8 sites, and Southern cluster of 10 sites). The same color marks the corresponding sites in the D panel and the clusters in the E panel.

and includes sites in Hungary, Slovakia, Germany and the Czech Republic (Fig. 1). The network comprises 38 sites dominated by eastern white pine, with an average age of approximately 97 years (Table A1). Several sites are younger (ranging from 36 to about 60 years). Most sites are located in lowland areas, whereas some are low-elevation mountain sites (up to 556 m a.s.l.), mainly in the Czech Republic, Slovakia, and Romania. The stands occur under a range of site and soil conditions, typical of European coniferous and mixed forests. The dominant soil types in these stands were Podzols, Arenosols, Luvisols, and Cambisols according to WRB classification (IUSS 2022).

Natural regeneration at each site was visually assessed using the following three categories: (1) absent – complete absence of regeneration; (2) spars – presence of one or a few small individuals up to 30 cm in height; and (3) abundant – occurrence of abundant regeneration composed of individuals of varying age and height, reaching up to several meters (Fig. A11).

2.2. Dendrochronological methods

A total of 658 trees from 38 stands were sampled for dendrochronological analyses (Table A1). At each site, we selected 8–30 dominant and apparently healthy trees (median was 16) and extracted one or two increment cores per tree using 5.15 mm Pressler borers. Tree cores were air-dried, glued onto wooden supports, and sanded with progressively finer sandpaper. High-resolution images were obtained using an optical scanner with a minimum resolution of 2400 dpi. Tree-ring widths (TRW) were measured with Coorecorder (Cybis, Sweden), WinDENDRO (Regent Instruments Inc.), or Lintab (Rinntech, Germany) measuring table with the accuracy of 0.01 mm and visually and statistically cross-dated to ensure that each ring was assigned to the correct calendar year (Wigley et al., 1987; Bunn, 2010). To remove non-climatic effects and preserve high-frequency signal, individual tree-ring series were detrended using a fixed 30-year spline with a 0.5 frequency response (Cook, 1985). Autocorrelation was removed by pre-whitening the series, which were then averaged into site-level tree-ring width chronologies (TRWi) using a biweight robust mean. A sensitivity analysis was conducted to assess the robustness of the detrending methods by comparing the climate-growth relationship obtained using different TRWi (15-year spline, 60-year spline, and a negative exponential model as an alternative to the 30-year spline). Results showed similar outputs (data not shown). The quality of TRWi chronologies was assessed using the following statistics (see Table A1 and Supplementary Comment 1): Gleichläufigkeit (GLK; Buras and Wilmking, 2015), first-order autocorrelation (AR1), mean interseries correlation (RBAR), signal-to-noise ratio (SNR), and expressed population signal (EPS) (Table A1). Detrending, chronology building, and quality assessment were conducted with the *dplR* R package (Bunn, 2010).

2.3. Cluster analysis

To identify shared spatial signals in tree-growth patterns, we employed the Ward2 agglomerative clustering algorithm (Murtagh and Legendre, 2014). Clusters were derived using TRWi for 1982–2019, the overlapping period common to all 38 sites. First, we used k-means partitioning to determine the optimal number of clusters, providing a data-driven criterion for cluster selection. We then performed hierarchical clustering using Ward's minimum variance method (Ward, 1963), as implemented in the *cluster* package in R (Maechler et al., 2023), to derive a hierarchical structure that captures the underlying spatial associations among sites.

2.4. Basal area increments and trends assessments

To evaluate growth trends among identified clusters, basal area increment (BAI) was assessed for two thirty-year periods, 1960–1990 and 1991–2022. The two 30-year periods were selected to contrast BAI

trends under different climatic backgrounds, with the split around 1990 motivated by the documented shift in European climate during the 1990s and the stronger warming and drought pressure observed in many parts of Europe thereafter (Sutton and Dong 2012; Dong et al., 2016). Furthermore, a sensitivity analysis was conducted to assess the influence of breakpoint selection on BAI trends. More specifically, BAI trends were assessed in early and late periods with varying ending/starting points (breakpoints – Fig. A4). BAI was calculated from TRW at the individual-tree level (Biondi and Qeadan, 2008), and then averaged by site to obtain annual site-level BAI patterns. BAI trends were examined over the two periods using average values at the cluster level. Trend significance was tested using the Mann-Kendall test at a significance level of $p < 0.05$. The BAI calculation and Mann-Kendall test were implemented using *dplR* (Bunn, 2010) and *trend* (Pohlert, 2020) R packages, respectively.

2.5. Climate-growth analyses

For each site, we extracted monthly precipitation, maximum temperature, mean temperature, and relative humidity data from the E-OBS database v.29.0 at a spatial resolution of 0.1° (Cornes et al., 2018). Using daily mean temperature and relative humidity, we calculated daily vapor pressure deficit (VPD), which was aggregated to the monthly mean. To quantify the influence of water availability, the Standardized Precipitation-Evapotranspiration Index (SPEI) was used. The SPEI was calculated as the difference between monthly precipitation and potential evapotranspiration, using the modified Hargreaves equation (Droogers and Allen, 2002). SPEI values were calculated using the "SPEI" package in R (Beguería et al., 2017). Climate-growth correlations were calculated using the *monthly_response()* function from the *dendroTools* R package (Jevšenak and Levanič, 2018; Jevšenak, 2020). We analyzed individual months as well as aggregated seasonal effects from both the previous and current growing seasons. The previous season spans from July of the year prior to ring formation, while the current season extends to October of the year of ring formation. Climate-growth relationships were evaluated for all seasonal combinations from the previous and current growing seasons, considering individual and aggregated consecutive months (up to 12 months). To account for potential spurious effects arising from long-term trends in climate series, climate series were detrended by fitting a simple linear regression to each series and subtracting the fitted trend component from the original observations (Ols et al., 2023). Climate-growth correlations, using TRWi, were calculated using all available data for individual sites, starting in 1920 and extending to the most recent complete ring. We also tested the effect of varying series length, and the results were consistent (results not shown here). To assess the climate sensitivity of *P. strobus* across study clusters, we averaged the site-level correlation coefficients and calculated the standard deviations to better reflect cluster-level variability. In the main text, we present the mean climate response and its standard deviation across all clusters (Fig. 3), whereas the results for individual sites are shown in Supplementary Figures A5 (precipitation) and A6 (maximum temperature).

Next, to evaluate temporal changes in climate-growth relationships, we applied a moving window approach using 30-year subperiods shifted by one year at a time (Popa et al., 2024b). For each window, we calculated the correlation coefficient between tree growth and climate variables separately. We focused on two-month seasonal combinations, because these generally produced the most significant climate-growth relationships. For each two-month seasonal combination and each 30-year window, we extracted the corresponding correlation coefficients between growth and climate. These coefficients were then used as the response variable in a linear model (Eq. 1), with time as the predictor, to assess whether the strength and direction of climate-growth relationships changed over time.

$$\rho_i(t) = \alpha_i + \beta_i t \quad (1)$$

where:

- $\rho_i(t)$ represents the correlation coefficient for the i th seasonal combination at time t ,
- α_i is the intercept for the i th seasonal combination,
- β_i is the slope, indicating the rate of change of correlation over time for the i th seasonal combination,
- t is the time variable.

To quantify temporal changes in climate–growth relationships, we analysed β coefficients for all two-month seasonal combinations. The sign of β indicates the direction of change over time, with positive values reflecting increasingly positive or less negative relationships (positive climate effects on growth are strengthening, or negative effects are weakening), and negative values indicating increasingly negative or less positive relationships (positive effects are weakening, or negative effects are intensifying). Methodological details are provided in [Popa et al. \(2024b\)](#). To obtain cluster-level trends, β were averaged across sites within each cluster.

2.6. Resilience components

To assess the capacity of *P. strobus* to recover after periods with reduced growth, we first identified the most frequent negative pointer years at each site using the Bias-Adjusted Standardized Growth Change (BSGC) method (Fig. A8). This approach quantifies relative year-to-year changes in growth (TRW) and standardizes them against the variability of the full series, while explicitly correcting for biases that arise during successive growth declines ([Buras et al., 2022](#)). Next, for each identified negative pointer year, we calculated growth-based resilience indices following [Lloret et al. \(2011\)](#): resistance (R_t – growth during the event relative to pre-event growth), recovery (R_c – post-event growth relative to growth during the event), and resilience (R_s – the ability to attain the pre-event growth level). For each identified event, resilience indices were calculated using a 4-year window before and after the negative pointer year associated with growth reduction. Resilience metrics were calculated from raw tree-ring width (TRW), using the *pointRes* R package ([van der Maaten-Theunissen et al., 2015](#)). To assess the potential age/size effect on raw TRW, we compared the resilience indices calculated from raw TRW with those obtained from detrended data (Fig. A13). Differences in the distributions of individual tree resilience indices among the clusters were evaluated using the Kolmogorov-Smirnov test ([Smirnov 1948](#)). To assess the capacity of trees to fully recover, as an indicator of tree growth plasticity, we fitted an exponential model depicting observed (actual) resilience (Eq. 2) and derived the theoretical line of full recovery (Eq. 3) ([Schwarz et al., 2020](#)):

$$R_c = b * R_t^z \quad (2)$$

$$R_c = \frac{1}{R_t} \quad (3)$$

b and z – represent the coefficients of the exponential model adapted from [Schwarz et al. \(2020\)](#). This equation indicates that forest stands with higher growth reductions (lower resistance) recover faster than stands with higher resistance.

The intersection between the fitted and theoretical lines indicates the level of resistance required for trees to achieve full recovery following an extreme event. The actual resilience curve was modeled using the *nls2* R package ([Baty et al., 2015](#)).

3. Results

3.1. Spatial variation in radial growth patterns and cluster structure

The cluster analysis revealed four distinct, spatially coherent groups that clearly reflect the underlying structure and similarity of growth patterns within the dataset (Fig. 1E). These clusters showed a strong spatial correspondence with the geographic distribution of the sampling sites, delineating four distinct regions: Northern (12 sites), North-Central (8 sites), South-Central (8 sites), and Southern (10 sites) clusters. Trees across these clusters formed a relatively homogeneous age group; although younger stands predominated in the Southern cluster, no significant age-related differences were detected among clusters (Fig. A1b). Differences in age structure were also reflected in annual ring widths, with slightly higher growth rates observed in the generally younger Southern clusters (Fig. A1a). A clear latitudinal gradient was evident, with lowland sites dominating in the north and lower-elevation montane sites prevailing in the south (Fig. A1c). Differences between clusters were also associated with climatic conditions, primarily a pronounced temperature gradient (Fig. A1e), while precipitation showed greater variability within the Southern cluster (Fig. A1d). The Southern cluster also exhibited greater variability in quality indicators (Table A1).

3.2. Trends in basal area increment (BAI)

Basal area increment (BAI) increased up to the early 1990s (Fig. 2, Fig. A2, Table A3). Most clusters displayed a similar upward trend, with the exception of the Southern cluster, where growth increase was less pronounced and not statistically significant ($p > 0.5$). From the 1990s onward, a shift towards declining growth is evident, accompanied by a marked increase in interannual BAI variability around the year 2000. For Northern, North-Central, and South-Central clusters, recent trends are statistically insignificant; however, in the Southern cluster, the strongest negative trend in BAI is statistically significant despite the high variability (Fig. 2, Fig. A2). To further test whether stand age influenced this pattern, we subdivided Southern-cluster sites into younger (age < 80) and older categories (age ≥ 80), and in both groups, the negative BAI trends remained consistent (Fig. A3).

Sensitivity analyses varying the breakpoint from 1980 to 2000 (Fig. A4) showed that the positive BAI trends during the early period were generally robust to breakpoint selection. Trend direction remained positive across all tested breakpoints in all four clusters, with particularly stable and consistently significant trends in the North and South-Central clusters. Late-period trends were more sensitive to breakpoint placement. The negative trend in the South remained directionally consistent across all tested breakpoints, although its statistical significance depended on breakpoint choice. In contrast, late-period trends in the North, North-Central and particularly South-Central clusters showed greater variation in magnitude and, in some cases, direction, indicating that these trends should be interpreted more cautiously (Fig. A4).

3.3. Spatial and temporal dynamics in climate-growth relationships

Climate-growth relationships showed pronounced spatial variability across the analyzed clusters, suggesting notable regional disparities in the strength and direction of climate sensitivity (Fig. 3). Overall, growth responses were dominated by climatic conditions during the current growing season, whereas the signals associated with the previous growing season were generally weaker. For both precipitation and maximum temperature, a distinct north-south gradient was evident, with climate-growth relationships progressively strengthening towards the south.

As we move from the Northern to the Southern cluster, positive correlations with precipitation became stronger and persisted over longer periods (Fig. 3). The largest contrasts occur between the Northern and Southern clusters. In the Southern cluster, strong, significant

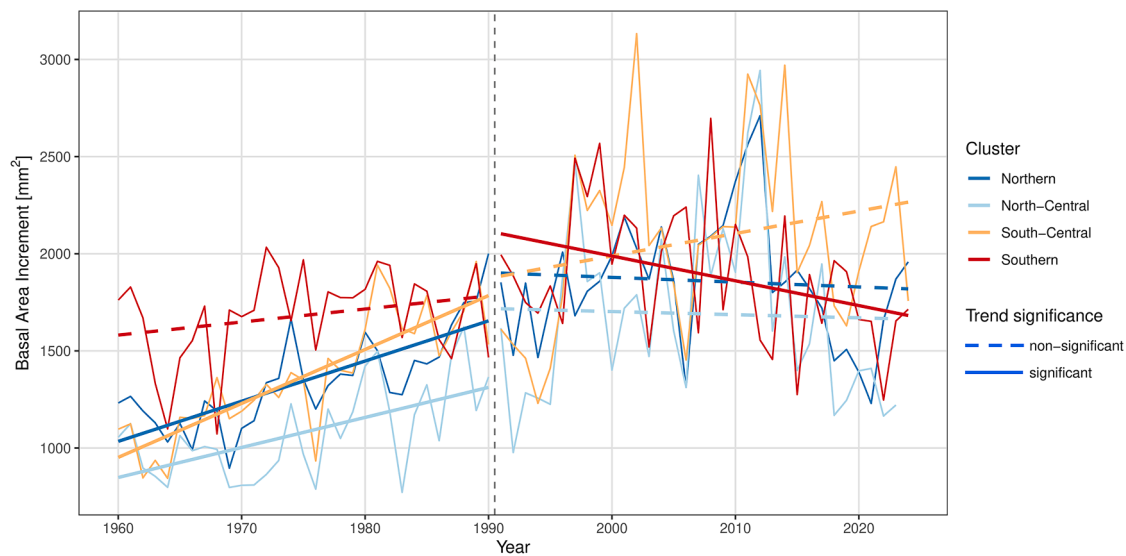


Fig. 2. Temporal dynamics and long-term trends in basal area increment (BAI) across clusters. The breakpoint between periods is set to the early 1990s (vertical dashed line), the start of the accelerated warming across Europe (Dong et al., 2016). The standard deviations at the cluster level are presented in Figure A2. Regression lines represent linear trends before and after the breakpoint, showing shifts in growth direction; dashed lines indicate non-significant trends, while solid lines indicate significant trends. Complete regression statistics are provided in Table A3.

correlations are evident throughout most of the growing season. The two central clusters differed only slightly from each other. Correlations were also consistent among the sites, as reflected by consistently low standard deviations. In contrast, higher variability was observed in the Northern and, especially, the Southern cluster, particularly during the late growing season months of September and October (Fig. 3). Regarding trees' response to drought (SPEI), a similar pattern to the response to precipitation was observed at both plot level (Fig. A8) and at cluster level (Fig. A10).

Maximum temperature was generally negatively associated with *P. strobus* growth, while temperature effects were mostly insignificant in the Northern cluster (Fig. A5). Marked differences in the direction and strength of these correlations were evident, along with significant correlations occurring mainly in the North-Central and Southern clusters. As for precipitation, the highest variability was observed in both marginal clusters (Northern and Southern), whereas sites located in the central clusters exhibited mixed and comparatively weaker temperature signals.

Vapor pressure deficit during the growing season showed a strong negative association with *P. strobus* growth (Fig. A10). In the South-Central cluster, significant negative relationships were observed also with the previous growing season's VPD. Plot-level VPD-growth relationships showed a consistent pattern; only in a few plots no significant relationships with growing season VPD was observed (Fig. A9).

In the Southern cluster, tree age had a significant impact on climate sensitivity intensity (Fig. A7). Overall, younger stands exhibited stronger climate-growth relationships than older stands. In particular, younger stands showed a stronger correlation with precipitation during the current growing season, indicating greater dependence of growth on water availability. Similarly, the correlation with maximum temperature was also stronger in younger stands compared with older ones, and this pattern was evident for both the current and previous growing seasons (Fig. A7).

Temporal trends in climate-growth relationships revealed contrasting and season-specific patterns for precipitation and maximum temperature across the analyzed clusters (Fig. 4). For precipitation, divergence among clusters was the most evident for effects of the previous growing season, whereas for maximum temperature it was stronger for the current growing season. Precipitation effects intensified most strongly in the Southern and North-Central clusters, with the

largest increase in the β coefficients showing the largest positive shifts, particularly for precipitation during autumn of the previous year (September–October) and early summer of the current year (June–July). During the current summer, all clusters showed a significant positive β for precipitation, indicating an increasing dependence of growth on water availability.

For maximum temperature, the largest differences in temporal shifts of climate sensitivity among the clusters were during the current growing season, particularly in spring (February to April) and summer (July to September) (Fig. 4). The Southern cluster showed the largest temporal changes in climate sensitivity. Here, positive β coefficients associated with initially negative correlations indicate a gradual weakening of the adverse effects of high maximum temperatures on growth. On the contrary, the Northern cluster showed mostly negative β coefficients for maximum temperature during the current growing season. These negative trends indicate that the negative influence of high temperatures on growth has intensified over time, resulting in increasing climate sensitivity.

3.4. Disturbance response and recovery of *P. strobus*

The resilience components calculated for the negative pointer years varied among the clusters (Fig. 5A). However, no major differences were observed between resilience indices calculated using raw or detrended TRW (Fig. A13). Recovery showed the strongest inter-cluster differentiation, with the lowest recovery values observed in the Northern cluster. This pattern is consistent with the higher resistance capacity of northern sites, indicating a conservative growth response to extreme events. In contrast, the Southern cluster exhibited both relatively high resistance and substantially higher recovery, reflecting a more dynamic growth response following stress. Despite these differences in individual resilience components, overall resilience values were similar across clusters, and generally close to 1.0, indicating that trees across the entire gradient were, on average, able to fully recover growth following extreme events (Fig. 5A).

The relationship between resistance and recovery was broadly consistent across the study area, as reflected by the overlapping lines of actual resilience (Fig. 5B). Nevertheless, a clear trade-off between resistance and recovery is evident across the entire climatic gradient. Northern sites tend to follow a stability-oriented strategy, characterized

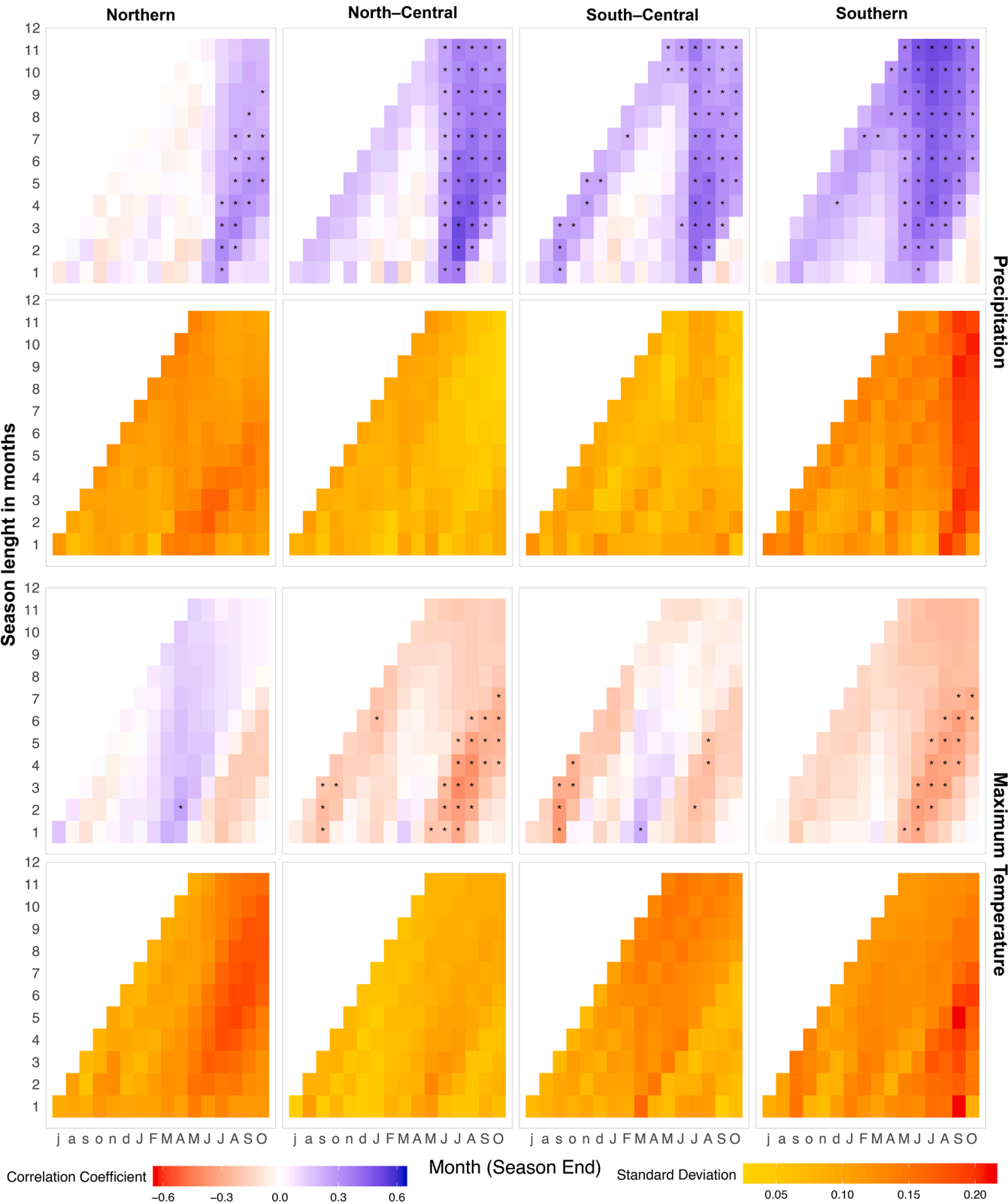


Fig. 3. Mean Pearson correlation coefficients with standard deviations showing relationships between standardized growth indices (TRWi) and climate variables (precipitation and maximum temperature) for the previous and current seasons across the four clusters. An asterisk (*) denotes significance when >50% of sites within a cluster exhibited $p < 0.05$.

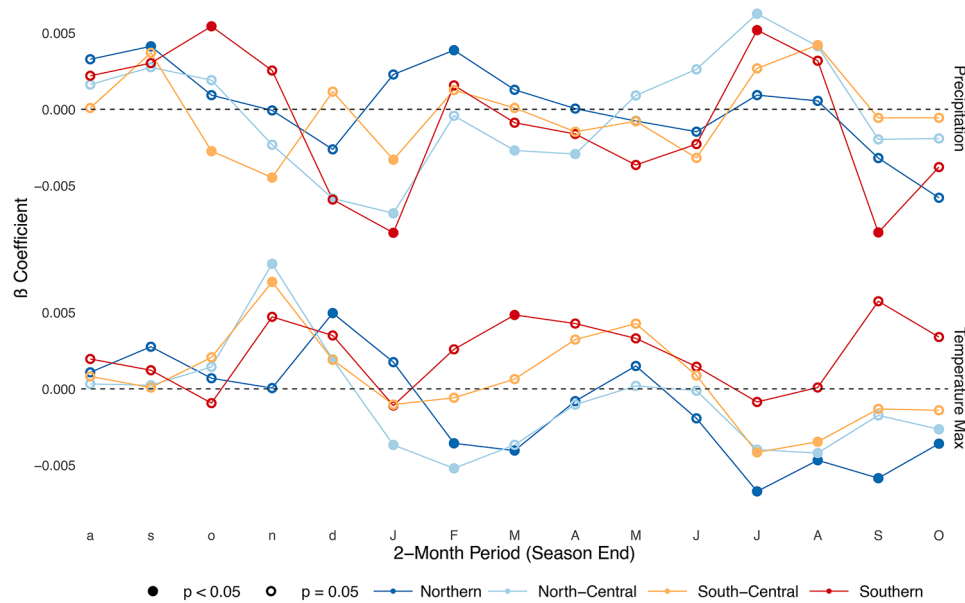


Fig. 4. Temporal shifts in climate sensitivity (mean β coefficients) to precipitation (top) and maximum temperature (bottom) at the cluster level. Positive β indicates strengthening precipitation effects on growth, and for maximum temperature, a weakening of negative temperature effects. Conversely, negative β values indicate decreasing precipitation effects and increasing negative temperature effects on growth. Lowercase letters denote months in the previous year, and uppercase letters denote months in the current year. Closed symbols indicate β coefficients that are significantly ($p < 0.05$) different from zero (t -test), while open symbols indicate non-significant β coefficients.

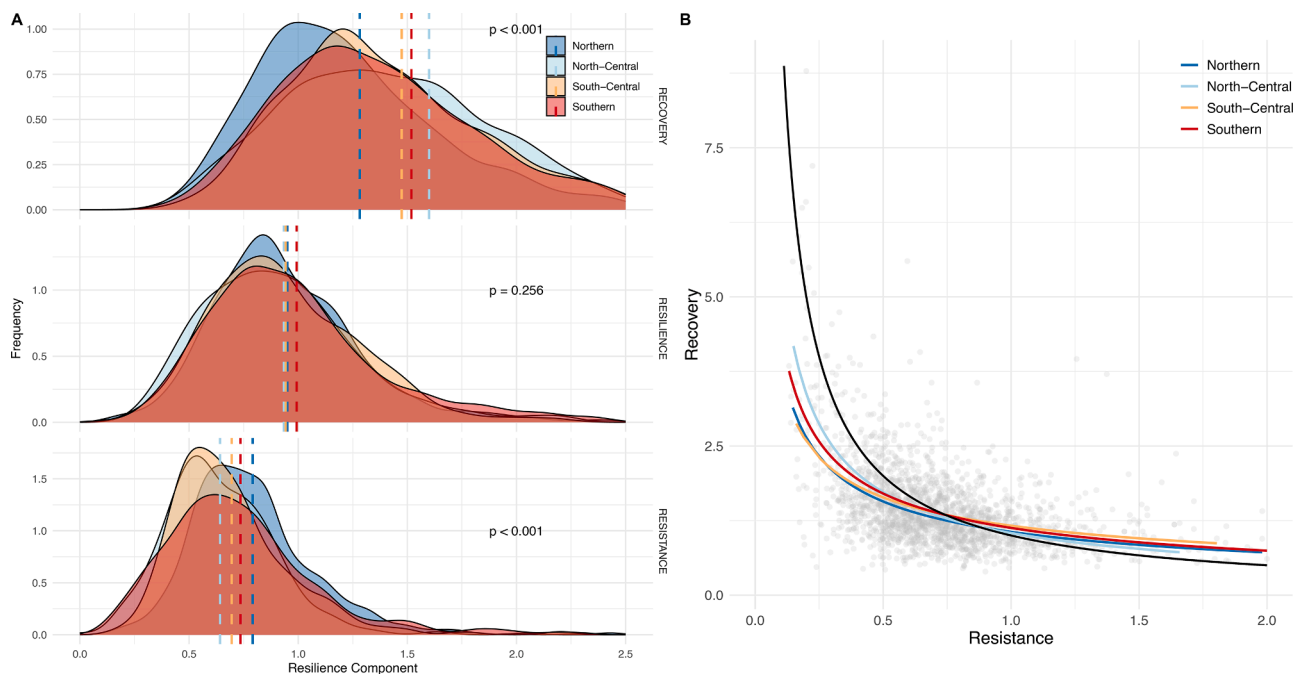


Fig. 5. (A) Density distributions of resilience components (resistance, recovery, and resilience) across the four clusters. The significance of the difference among the distributions of resilience indices at the cluster level according to the Kolmogorov-Smirnov test (Smirnov 1948) is indicated. Vertical dashed lines show the cluster mean. (B) Fitted lines of actual resilience (colored curves) derived from observed resistance and recovery, compared with the theoretical 'line of full resilience' (black line).

by high resistance but low recovery, with lines positioned higher at low recovery values. In contrast, the Southern cluster demonstrates a greater variability, with lower resistance but higher recovery capacity, consistent with adaptation to frequent, short-term stress events such as recurrent droughts. The partial overlap of the lines suggests that *P. strobus* shows a common broadly consistent response strategy across the range, while the intensity of resistance–recovery trade-offs is modulated by local climatic conditions.

4. Discussion

4.1. Interactive effects of water availability and temperature on *P. strobus* growth across the central European climatic gradient

The results support the first hypothesis (H1), showing that radial growth of *P. strobus* is predominantly sensitive to water availability along the latitudinal gradient. Across much of the species' European

range, precipitation rather than temperature is the dominant climatic driver of radial growth (Fig. 3). Although previous regional studies in Central Europe have emphasized the importance of summer precipitation for *P. strobus* growth, a coherent spatial pattern of this climatic driver across its non-native distribution has not been documented (Wilczyński et al., 2025; Mácová, 2008; Klisz et al., 2022).

Comparable spatial differentiation in climate-growth relationships has, however, been observed in provenance studies within the species' native range, where tree-stands originating from different climatic conditions exhibit contrasting sensitivities to temperature and moisture regimes (Chhin et al., 2018). Strong limiting effect of maximum summer temperatures was observed only in Southern and North-Central clusters (Fig. 3) and may be partly driven by warmer winter conditions (Kreyling, 2010). Warmer winters can promote earlier cambial reactivation and earlywood formation, thereby extending the growing season (Máková 2008), but they may also interact with warm and dry summers to exacerbate growth limitations later in the season. Furthermore, an increase in early-season water use can be promoted, leading to earlier depletion of soil moisture and increased vulnerability to summer heat and drought stress (Gonsamo et al., 2019). While high summer temperatures lead to reduced growth in the Southern and North-Central clusters, the opposite effect is observed in the cooler Northern and montane South-Central clusters (Fig. 3), where higher spring temperatures are likely to accelerate the onset of the growing season (Läänelaid and Helama, 2020). Winter warming, well documented in the southern Baltic region (Meier et al., 2022), although it accelerates spring activity of the secondary meristem of introduced species (Klisz et al., 2025), it can also lead to temporal cambium dysfunction as a result of late frost damage (Klisz et al., 2022). Thus, within the Northern cluster, warming at the end of the dormant period, despite its generally auxiliary effect, may also pose a threat to young *P. strobus* trees with a relatively thin insulating bark layer. Given the relatively high genetic diversity of European *P. strobus* stands (Mandak et al., 2013), the interpopulation variation in climate sensitivity observed within the occupied climate zone may result from the phenotypic plasticity of this tree species (Prasad and Leites, 2022; Nadeau, 2014), which in turn gives an advantage over other species in climate change adaptation (Nicotra et al., 2010). Phenotypic plasticity can be adaptive by buffering tree-stands against rapid environmental change, but it may also hinder long-term adaptation (Fox et al., 2019). Therefore, although the pronounced spatiotemporal variability in *P. strobus* responses indicates high plasticity in European tree-stands, this alone does not ensure successful adaptation to climate change.

4.2. Heat limitation and responses of *P. strobus* to climatic stress

Our study revealed intensified negative responses to maximum temperature, particularly in the Southern cluster, indicating emerging heat limitation. This pattern may reflect physiological constraints related to stomatal regulation and carbon assimilation under high temperature and vapor pressure deficit. Relatively isohydric species, such as *Pinus strobus* (Niinemets and Valladares, 2006), tend to maintain stable leaf water potential through early stomatal closure, which can limit transpiration cooling and increase the risk of leaf overheating and photoinhibition under high radiation (Guha et al., 2018; Zweifel et al., 2020). Moreover, experimental evidence from conifers indicates that high temperatures, even under non-limiting water conditions, can induce stem dehydration and reduced nighttime rehydration, suggesting likely incomplete recovery following heat stress events (Salomon et al., 2018). Years with the highest temperatures were associated with a substantial decrease in wood density and tracheid length, indicating disruptions in the process of xylogenesis (Larysch et al., 2022). The stronger negative effects of temperature observed in younger stands (Fig. A7) are consistent with the findings of Tumajer et al. (2025) and of Klisz et al. (2025), who demonstrated that age-related differences significantly modulate the sensitivity of conifers to climatic stressors

near their range limits. Younger trees showed higher vulnerability to temperature extremes, likely due to their limited rooting depth, smaller hydraulic capacity, and greater exposure of the stem base to thermal fluctuations (Tumajer et al., 2025). Since the mid-1990s, Europe has experienced pronounced warming (Dong et al., 2017). This timing coincides with the shift in BAI growth trends observed in our analyses (Fig. 2; A3), thereby supporting the second hypothesis (H2). BAI shows a pronounced decline in the Southern cluster, whereas similar patterns are not evident in the North, North-Central, and South-Central clusters (Fig. 2). This negative trend is not due to age differences but reflects increasingly unsuitable habitat conditions in drier southern regions (Fig. A3). Under high-temperature conditions, *P. strobus* appears to adjust its water-use strategy, although these responses are likely tightly coupled with concurrent changes in water availability. With rising temperatures, stomata tend to close earlier, maintaining a relatively stable water potential but limiting photosynthetic activity. This strategy may ensure relatively high resistance to short-term droughts, but it can simultaneously constrain carbon assimilation during periods of combined heat and water stress. Experimental evidence indicates that extreme heat can directly impair photosynthetic processes and induce photodamage, even under conditions of sufficient water availability, as demonstrated for *P. strobus* in heat wave experiments (Guha et al., 2018). However, the relationship between reduced photosynthetic activity and radial growth is not necessarily direct, as stored carbon reserves may partially buffer growth responses, particularly under longer growing seasons. As an isohydric species, *P. strobus*, may exhibit greater sensitivity to changes in moisture availability than anisohydric NNTs such as *Quercus rubra*, as evidenced by stricter stomatal regulation and a more pronounced reduction in growth (Asbjørnsen et al., 2021). Consequently, a sharp decline in growth in this isohydric species may be followed by a relatively rapid recovery, made possible by a different growth phenology, namely the continuation of growth later in the season (Vose and Swank 1994). The survival of *P. strobus* in warmer regions may be feasible in humid habitats, where soil water uptake compensates for losses associated with inefficient stomatal regulation. Such increased water consumption, although potentially detrimental to ecosystems, may simultaneously reduce thermal stress in *P. strobus*. Similar latitudinal and altitudinal patterns of temperature and precipitation sensitivity have been reported for other European tree species (Martínez del Castillo et al., 2024; Popa et al., 2025). However, the clear separation of four clusters along our latitudinal gradient (Fig. 3) indicates that *P. strobus* responses to climatic factors are strongly structured across latitude. This spatial pattern, together with local adaptation and complex environmental variation across species' range, challenges the prediction of future optimal growth conditions.

To better interpret the regional differences in growth responses, we examined the climatic and edaphic characteristics of the study sites (Table A2). The dataset reveals a clear latitudinal gradient, with *P. strobus* stands in southern regions experiencing higher mean annual temperatures (up to $\sim 12^{\circ}\text{C}$) and generally lower or more variable precipitation compared to northern sites ($\sim 5.5\text{--}7^{\circ}\text{C}$). These conditions are often associated with soils such as Cambisols, Luvisols, and Chernozems, which, depending on texture and structure, may enhance water limitation during the growing season. In contrast, northern sites are characterized by cooler and more humid climates and soils such as Luvisols and Podzols, which tend to support more stable moisture availability. Yet, the spatial distribution of the study area does not fully encompass the entire European range of *P. strobus*, particularly in its eastern part at the most marginal limits. As a result, the analyzed sites represent a substantial but not the entire breadth of its potential distribution. This limitation should be considered when extrapolating the results, as tree stands at distributional margins may be more exposed to extreme climatic conditions. Nevertheless, the analyzed dataset provides a robust basis for identifying general climate-growth relationships within the core part of the species' introduced range.

4.3. Climatic modulation of growth resilience along the spatial distribution of clusters

Differences in the responses to potential drought events among *P. strobus* clusters are evident in the components of growth resilience (Fig. 5). This inter-cluster variation in resilience, resistance, and recovery partially supports our third hypothesis (H3), with the Southern cluster showing low resistance but high recovery, and the Northern cluster exhibiting the opposite pattern. Our results suggest that northern sites follow a stress-tolerant strategy, displaying high resistance coupled with limited recovery. Conversely, the Southern cluster adopts a more flexible strategy, characterized by reduced resistance but enhanced recovery, an adaptive response commonly associated with frequent, short-term stress events such as droughts. Here, this pattern likely reflects the selective pressure imposed by recurrent water shortages, which may have gradually eliminated individuals unable to maintain hydraulic integrity under severe drought (Mantova et al., 2023). Overall, resilience outcomes were broadly similar across clusters, as the resilience indices were close to 1.0 in all cases, indicating full recovery of growth following extreme events, albeit achieved through different resistance-recovery strategies (Fig. 5B). This flexibility in adjusting stress response strategies aimed at enhancing population-level fitness, stabilizing fitness across clusters, and limiting population-level fitness decline under stress, suggest that *P. strobus* exhibits pronounced plasticity in secondary growth processes (Brooker et al., 2022). There is evidence that this species is able to adapt to short-term water deficits by restructuring its xylem, developing intra-annual density fluctuations in early wood (Klisz et al. 2022). The contrasting responses to disturbance events between the Northern and Southern clusters align with the concept of passive and active plastic responses, where the former is associated with resource limitation and the latter with the changes in resource allocation (van Kleunen and Fischer, 2005). Taken together, these results indicate that *P. strobus* maintains overall growth resilience across its range through region-specific resistance recovery trade-offs, consistent with adaptive plasticity in secondary growth (Tao et al., 2024).

Nevertheless, the absence of sites from the marginal tree-stand in the network may contribute to an underestimation of the variability in resilience components. In more limiting environments, where trees grow closer to physiological thresholds, greater deviations in resistance and recovery would be expected (Baranger et al., 2024). Therefore, the relatively stable resilience values observed in this study should be interpreted in the context of the predominantly core distribution of the sampled sites.

4.4. Ecological drivers of growth of *P. strobus* across climatic gradients and under climate change

Our results align with species distribution models (SDMs), which have shown that precipitation in the warmest quarter (BIO18) limits the *P. strobus* range in Europe (Puchałka et al., 2023). However, SDMs describe broad-scale probabilities of species occurrence, whereas the analysed dendrochronological signal reflects the growth responses of established, codominant trees. Accordingly, rather than capturing a species' potential niche, our results identify spatial and climatic gradients in how maximum temperature and precipitation limit the radial growth of *Pinus strobus*. It is important to note that the optimal climatic niche does not equate to optimal growth conditions for mature trees, as it encompasses conditions that enable population persistence (e.g., germination and early development), which can vary across ontogenetic stages (Popa et al., 2025). The observed clustering pattern closely follows the latitudinal gradient and the influence of altitude (Fig. 1D), both of which significantly shape local climatic conditions (Fig. 1B). However, the within-cluster variability in climate-growth responses observed in the South-Central and North-Central clusters suggests that other local site factors, such as altitude, soil depth, texture, nutrient status,

water-holding capacity, stand structure, management history, and provenance, may modulate climate-growth relationships (Magnier et al., 2025; Chhin et al., 2018). The limited influence of maximum temperature in the Northern cluster can be explained by cooler climatic conditions relative to the native range of *P. strobus* (Fig. 1B). Similarly, reduced precipitation sensitivity may be attributed to lower evaporative demand in the cooler southern Baltic Sea region (Meier et al., 2022; Klisz et al., 2025). Despite rising temperatures in the Southern cluster, a reduction in the strength of temperature limitation on radial growth has been observed (Fig. 3), likely because the species operates near its optimal thermal conditions in this region (Fig. 1B). At the same time, the effect of precipitation during the growing season increases, reflecting the patterns observed in its native range (Kilgore and Telewski, 2004). The increasing impact of water availability towards the south can be interpreted as an increased vulnerability to drought in the context of progressive climate warming (Fig. 5). Compared with deciduous species, which have higher water requirements and a less sclerophyllous leaf structure, conifers generally maintain their range, although even more sclerophyllous species may begin to lose theirs (Chabot and Hicks, 1982). Therefore, this phenomenon cannot be explained solely by differences between precipitation and evaporation under elevated temperatures. Gas-exchange regulation mechanisms in conifers likely evolved under cool, temperate climates, making them more effective at lower temperatures but less responsive under the warmer conditions projected for the future (Brodribb and Hill, 1999; Chang et al., 2021). Under a warmer climate, stomatal regulation in pines and other conifers may become less efficient, leading to disturbances in water balance and increased sensitivity to drought (Urban et al., 2017). As a result, many coniferous species, despite their seemingly better ability to mitigate water loss, may respond less effectively to climate warming, while deciduous species display greater flexibility in their responses to changing climatic conditions (Dyderski et al., 2025; Puchałka et al., 2023).

Pinus strobus alters habitat conditions by modifying soil and litter chemistry, primarily through acidification in deciduous and mixed forests (Herr et al., 1999). These changes favor the establishment of its own seedlings, and at the same time hinder the regeneration of native tree species by increasing the competitiveness of *P. strobus*. The fact that abundant natural regeneration occurs at only a few sites (Fig. A11) likely suggests that recruitment depends mainly on local factors such as habitat quality and light conditions resulting from stand structure (Dovčiak et al., 2003; Herr et al., 1999). *P. strobus*'s relatively high shade tolerance may give this species an advantage in establishing a new generation when light conditions become insufficient for native, co-occurring conifer species. However, in the Southern cluster, natural regeneration was entirely absent. It is also important to consider whether the species' expansion may be further constrained by numerous pathogens and pests shared with closely related native *Pinaceae* species (Pötzelsberger et al., 2021). Given its high shade tolerance and long-lived needles, *P. strobus* should potentially exhibit high resistance to biotic stress. Leaf defoliation caused by herbivores should be less restrictive for this species than for the native *P. sylvestris*. *P. strobus* seedlings, when growing under competition from canopy trees and understory plants, are capable of compensatory growth when grazed by herbivores (Puettmann and Saunders, 2001). This strategy contributes to their advantage over seedlings of native species. However, these biotic factors were not explicitly accounted for in the present study and may therefore represent a potential source of unexplained variability in regeneration patterns. These interactions could increase mortality and reduce colonization rates. According to Münzbergová et al. (2013), the plasticity of a species' early life-history strategies depends on habitat conditions and interspecific interactions. In the case of conifer seedlings, the lack of storage reserves and their strong dependence on mycorrhizal associations make them less competitive compared to angiosperm species (Lusk et al., 2003). Hence, the persistence of the climatic niche does not necessarily imply that *P. strobus* will be able to compete effectively with broadleaved species, many of which reach generative reproduction

at a younger age.

5. Outlook and future perspectives

Climate change projections for Europe indicate substantial shifts in the potential distribution of suitable habitats for many tree species (Dyderski et al., 2025). Most SDMs forecast a reduction in climatically suitable habitats for most conifers, with *P. strobus* often identified as a potential exception under certain climate scenarios (Puchałka et al., 2023). Under this framework, there is an increasing need to determine the adaptive capacity of tree species in order to adapt future species composition and forest management strategies to long-term climate trajectories.

From a forest management perspective, *P. strobus*'s response to climate change and resilience may indicate its potential as an adaptive species for future forest ecosystems, particularly in the Northern clusters. However, even in the cooler northern regions, we observed increasing negative effects of rising summer temperatures. Furthermore, the utility of *P. strobus* may be diminished by the ongoing threat of white pine blister rust (*Cronartium ribicola*), which currently poses a greater immediate threat to this species than climate change alone (Duarte et al., 2025). Despite the recognized importance of selecting genotypes resistant to this pathogen, it remains the main biotic factor limiting the use of *P. strobus* in Europe (Bingham and Gremmen, 1971). Beyond its direct silvicultural value, *P. strobus*, despite its non-native status, is phylogenetically and functionally closer to native conifers than to invasive broadleaf species colonizing conifer forests, thereby resulting in lower impacts on these ecosystems. Nevertheless, evidence of the impacts of *P. strobus* on biodiversity and ecosystem functioning in Europe remains limited (Wohlgemuth et al., 2022). Therefore, the cultivation of *P. strobus* in forests should be accompanied by further research on its environmental impacts across a range of habitat conditions to develop rational management approaches that balance the needs of conifer timber production and biodiversity conservation (Wohlgemuth et al., 2022).

In conclusion, our findings show that summer precipitation is the principal climatic factor limiting *P. strobus* growth across its distribution in Europe, underscoring the central role of water availability in governing secondary growth. The strength of this climate-growth relationship follows a clear latitudinal gradient: it is strongest in the southernmost regions, where drought stress is most pronounced, and gradually weakens toward the northern latitudes, where moisture regimes are more favorable. The adverse heat effects were most pronounced in younger stands, which showed a stronger limitation from climate factors. Furthermore, stronger climate limitation in the Southern cluster was accompanied by negative BAI trends and limited regeneration. While *P. strobus*'s productivity in southern Europe is expected to decline, adaptive management interventions, such as careful site selection, reduced stand density, mixed stands with drought-tolerant native species, and active control of natural regeneration, may mitigate the adverse effects of climate change. To better understand the resilience and future performance of *P. strobus*, future studies should include more marginal sites and direct comparisons with coexisting native species. In addition, incorporating a wider range of hydroclimatic and drought-related variables, including vapor pressure deficit (VPD), climatic water balance, soil moisture, and standardized drought indices, would help disentangle the effects of water availability, atmospheric drought, and heat stress on growth. This would provide a more mechanistic basis for assessing the species' vulnerability and adaptive potential under ongoing climate change.

Overall, the pronounced phenotypic plasticity of *P. strobus*, coupled with breeding or selection programs for disease resistance, could lead to an increasing role for this species in future European forests, particularly in more humid and cooler montane regions. Long-term monitoring data and integration of physiological with genetic information will be essential to refine projections and to ensure that management strategies

remain aligned with changing environmental conditions.

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CRediT authorship contribution statement

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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.

Supplementary materials

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Data availability

Data will be made available on request.

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