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Contrasting Future Growth of Norway Spruce and Scots Pine Forests Under Warming Climate

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ABSTRACT

Forests are essential to climate change mitigation through carbon sequestration, transpiration, and turnover. However, the quantification of climate change impacts on forest growth is uncertain and even contradictory in some regions, which is the result of spatially constrained studies. Here, we use an unprecedented network of 1.5 million tree growth records from 493 *Picea abies* and *Pinus sylvestris* stands across Europe to predict species-specific tree growth variability from 1950 to 2016 ($R^2 > 0.82$) and develop 21st-century gridded projections considering different climate change scenarios. The approach demonstrates overall positive effects of warming temperatures leading to 25% projected conifer growth increases under the SPP370 scenario, but these additional carbon gains are spatially inhomogeneous and associated with geographic climate gradients. Maximum gains are projected for pines in Scandinavia, where growth trajectories indicate 50% increases by 2071–2100. Smaller but significant growth reductions are projected in Mediterranean Europe, where conifer growth shrinks by 25% in response to warmer temperatures. Our results reveal potential mitigating effects via forest carbon sequestration increases in response to global warming and stress the importance of effective forest management.

1 | Introduction

The productivity of the forest ecosystems is strongly determined and influenced by regional climate conditions (Ammer 2019). Given the rapid pace of climate change (IPCC 2021), significant alterations in forest growth dynamics and subsequent carbon sequestration capacities are anticipated. European forests currently absorb 7%–12% of the continent's carbon emissions (Janssens et al. 2003), numbers which have been increasing since the 1990s, reaching a total living biomass of nearly 110 gigatons as of 2020 (FAO 2020). Vegetation model ensembles project increases in terrestrial carbon sink capacity (Arora et al. 2020), but the role of forests as carbon reservoirs is being challenged by rapid warming and disturbances, including insect outbreaks, soil erosion, forest fires, and tree mortality (Forzieri et al. 2021; Hartmann et al. 2022; McDowell et al. 2020; Patacca et al. 2023). A comprehensive understanding and quantification of growth dynamics and trends is crucial to assess the impact of changing climate on forest sequestration and necessary adaptation strategies. This resolution is further complicated by the wide range of anticipated climate change scenarios projecting varying risks on forest growth dynamics and changes of ecological, economic, and societal forest services.

Within forest ecosystems in Europe, Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) represent

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two key conifer species and cover around 30 and 28 million hectares, respectively (Caudullo, Tinner, and de Rigo 2016; Houston Durrant, de Rigo, and Caudullo 2016), representing the main habitat for numerous species and contributing significantly to the continent's ecological biodiversity. Moreover, both species hold considerable economic significance for the European forestry industry, including timber production, pulp and paper manufacturing, and renewable energy sources (FAO 2020). Despite their high ecological plasticity and resilience (Bose et al. 2020; Martínez del Castillo et al. 2018), these conifers face future challenges with increased risks of droughts (Bottero et al. 2021; Lévesque et al. 2013), especially in pure and even-aged forests (Castagneri et al. 2022). Prolonged periods of drought, heatwaves, and increased vulnerability to pests have accelerated forest decline, particularly in areas with poor site conditions. *Picea abies*, generally less drought-tolerant, has experienced extensive dieback during the last years, especially in lowland regions, while *Pinus sylvestris*, though more resilient, has also suffered in regions facing severe water deficits (Hlásny et al. 2021; Seidl et al. 2017). The current state of these forests is precarious, with many stands showing reduced vitality, increased mortality, and slower regeneration, highlighting the vulnerability of these species to ongoing climate change (Hlásny et al. 2021; Senf et al. 2020). Conversely, beneficial changes may arise from changes in mean temperatures, leading to longer growing seasons, enhanced photosynthesis rates, and accelerated nutrient cycling (Keenan 2015; Morin et al. 2018).

The historical impact of climate variability is preserved in tree-ring width records. Annual tree growth is determined by complex ecological interactions influenced by numerous factors, including inter- and intra-annual variation in climate, endogenous and exogenous disturbances, and size-related growth trends (Cook 1987; Fritts 1972). Furthermore, secondary growth variability is often linked to general tree health and performance, reflecting the phenotypic plasticity of trees to adapt to specific conditions crucial to overcome environmental changes throughout their lifespan (Housset et al. 2018). Respectively, annually resolved tree-ring records are essential to assess growth changes over decades to millennia (Esper et al. 2018), outperforming other sources of forest growth records, such as national forest inventories (Evans et al. 2022), both temporally and in resolution. Relative estimations of annual biomass production or carbon uptake based on tree rings are often used for comparisons against other methods, such as remote sensing, vegetation models, or eddy covariance (Babst et al. 2014). Integrating temporal measurements of secondary tree growth from tree-ring data is indispensable for characterizing ecological complexity and resolving some uncertainties regarding the effects of climate change on forest carbon dynamics (Domke et al. 2020; Zald et al. 2016).

Recently, multiple statistical modeling techniques based on tree-ring records have been developed and used in forest ecology for retrospective analyses, evaluating tree growth, and identifying the drivers of growth variability (Bosela et al. 2023; Heilman et al. 2022; Jiang et al. 2024; Klesse et al. 2020). Growth models are applicable across different temporal scales, extending both into the past and the future (Sheng, Liu, and Dong 2023; Wang, Taylor, and D'Orangeville 2023), often employing space-for-time substitution approaches (Klesse et al. 2020). Despite their versatility, these models predominantly operate at an individual spatial scale, typically focusing on forest stands. Conversely, spatial projections of radial tree growth variability remain scarce, particularly at large inter-regional to continental scales, incorporating species distribution ranges (e.g., Bodesheim et al. 2022; Jevšenak et al. 2024; Martínez del Castillo et al. 2022). By using the data-driven nonlinear regression approaches within generalized linear mixed-effects models, tree-ring variability can be linked to inferred relationships between climatic conditions and site-level characteristics. Once size-related trends and endogenous disturbances have been taken into account, spatial estimates can be computed throughout the environmental space covered by the tree-ring data, being comparable to other spatial forest dynamic datasets as derived by remotely sensed observations or mechanistic model estimates (Babst et al. 2021).

Here, we model spatiotemporal growth dynamics of *Picea abies* and *Pinus sylvestris* forests across European ecological ranges considering current and projected future climate. Compiling a large dataset of 493 tree-ring chronologies from both species in total enables us to reproduce species-specific growth estimates and evaluate spatial patterns of temporal trends. The verified growth models are applied to varying scenarios of the Coupled Model Intercomparison Project Phase 6 (CMIP6) to forecast future changes in conifer growth performance until the end of the 21st century.

2 | Methods

2.1 | Tree-Ring Database

Our data originate from an extensive tree-ring dataset focused on the species *Picea abies* and *Pinus sylvestris*, compiled from the available records in the International Tree-Ring Database (ITRDB) of the species in Europe and 117 additional sites. In total, the network comprises 493 chronologies comprised of more than 15.000 trees, spread over the geographical distribution of the species (Figure 1). The network covers the climate niches and the elevation ranges of the species (i.e., from 1 to 2300 m asl in *Picea abies* and to 1990 m asl in *Pinus sylvestris*), across latitudes ranging from 41.5° to 68° N for *Picea abies* (PCAB) and from 40° to 69.8° N in case of *Pinus sylvestris* (PISY).

Tree-ring widths were converted into annual Basal Area Increment (BAI), in cm^2 $year^{-1}$, which is commonly used for tree-growth modeling (Bosela et al. 2023; Camarero et al. 2015; Di Cosmo et al. 2020; Heilman et al. 2022; Pretzsch et al. 2021; Wang, Taylor, and D'Orangeville 2023). The rate of BAI increase in mature stages tend to stabilize, as long as the trees are not close to the biological senescence (Weiner and Thomas 2001) and have reached their maximum height (Biondi and Qeadan 2008). The BAI series of each tree was obtained by the *bai.out* function of the *dplR* R package (Bunn 2008) from the bark to the pith following the formula (Equation 1):

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

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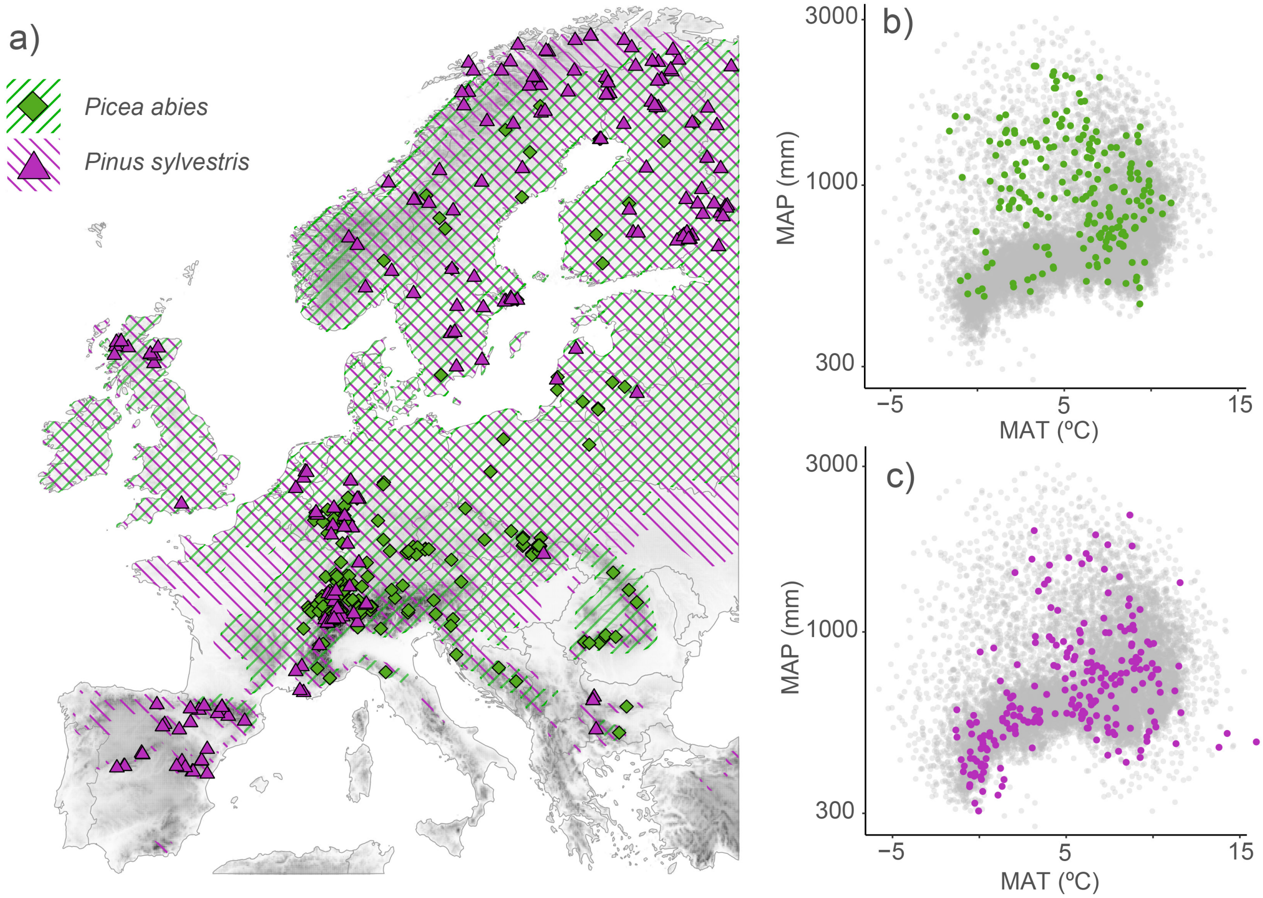

FIGURE 1 | European distribution of *Picea abies* and *Pinus sylvestris* forests and location of tree-ring chronologies (a). Climatic space coverage of the sites, shown in color compared with the shared species distribution shown in grey, considering the mean annual temperate (MAT) and the mean annual precipitation sum (MAP) (b). Elevation coverage of studied sites (c). Distribution maps were obtained from the European Forest Genetic Resources Programme EUFORGEN (www.euforgen.org). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

where $r_{t,y}$ and $r_{t,y-1}$ are the stem radius corresponding to the tree *t* for years *y* and *y-1*, respectively. In order to construct a representative BAI series for each study site, we averaged the BAI values at a yearly resolution for all samples.

2.2 | Gridded Variables

We considered a set of predictive variables known to impact tree growth variability for the target species (Cienciala et al. 2018; Lévesque et al. 2013; Treml et al. 2022; Tumajer et al. 2017). These variables were required to be site-specific, with spatial resolution at a detailed scale across Europe and projections extending into the future. High spatial resolution (i.e., 0.5°) temperature and precipitation time series from CHELSAcruts (Karger et al. 2017; Karger and Zimmermann 2018) were downloaded at a monthly scale and used to calculate seasonal climate aggregations for every year in the period 1950–2016. The starting year of the period is defined based on the quality of climate data; as CHELSAcruts uses the temporal signal from CRU TS 4.01 dataset (Harris et al. 2014), its quality is influenced by this dataset as well. Problems arose in years before 1950, when weather station density was low. De Martonne Aridity Index (DMI, De Martonne 1926) was calculated to categorize the mean water availability of each site, following the formula (Equation 2):

$$\mathrm{DMI} = \frac{P}{10 + T} \tag{2}$$

where P is the annual mean precipitation (in mm) and T (in°C) the annual mean air temperature. The climate types defined by DMI vary from arid (values from 0 to 10), semi-arid (10–20), Mediterranean (20–24), semi-humid (24–28), humid (28–35), very humid (35–55) to extremely humid (>55). Soil property information was extracted from the European Soil Database. Quantitative information about soil depth available for roots (measured in cm^2) and water content availability (measured in mm) were considered for the analysis (STU_EU_DEPTH_ROOTS and STU_EU_T_TAWC layers, respectively (Panagos et al. 2022)).

Future climate projections were obtained from the Coupled Model Intercomparison Project 6 (CMIP6) of the World Climate Research Programme, which comprises scenario runs for the 21st century (Karger et al. 2017). The Shared Socioeconomic Pathways (SSP) scenarios used are downscaled from five Global Climate Models, based on a preselection given by the Intersectoral Impact Model Intercomparison Project (specifications in CHELSA V2.1, Karger et al. 2017). Three contrasted SSP scenarios representing different socio-economic developments and different pathways of atmospheric greenhouse gas

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concentrations were considered to estimate the future growth performance of the species. The optimistic SSP126 (so-called *Sustainability*) aligns with temperature increases of 2°C, reflecting a scenario where stringent climate protection measures are implemented, contrasting with SSP585 (*Fossil-Fueled Development*) where increases up to 5°C are very likely to occur by the end of the century (IPCC 2021). Scenario SSP370 (*Regional Rivalry*) was chosen as an intermediate and likely pathway to illustrate the growth projections (data specifications in Karger et al. 2021).

2.3 | Predictive Growth Model

Generalized linear mixed-effects models (GLMM) were used to estimate the joint effects of climate, soil, latitude, and altitude on tree growth. The complexity of the selected model is given by the statistical properties of the target variable and the predictors. GLMMs are particularly useful, as they combine the properties of linear mixed models and generalized linear models, allowing the inclusion of random effects and the analysis of non-normal data (Harrison et al. 2018). Furthermore, mixed models are well suited for long-term studies influenced both by factors that can be assumed to be similar for many sites (e.g., the effect of climate or soil properties) and by characteristics that substantially vary from site to site (i.e., forest populations). These models explicitly account for nested data structures, such as repeated measurements from individuals within and across units of time (in this case, individual tree measurements) (Zuur et al. 2009).

To effectively model non-Gaussian distributed time series data, such as tree growth represented by the Basal Area Increment (BAI), and considering the interdependence of observations, the complexity of modeling choices increases in order to ensure the robustness of the selected model. A transformation of the response variable is required to ensure the independence and equal variance of errors (homoscedasticity), making the variance around the fitted mean of each group homogenous (Harrison et al. 2018; Zuur, Ieno, and Elphick 2010). In this case, BAI values are normalized by a logarithmic transformation. All explanatory variables also require standardization, which considers the distribution of our data by transforming the linear predictor within the model (Harrison et al. 2018) using either a logarithmic transformation or a standardization function (data transformation around the mean and scaled by its standard deviation). A compensated weight of each variable, avoiding effects related to the range of variables, is therefore guaranteed.

First, a full model for each species was fitted to predict the annual BAI of a tree j in year t in a site i as a function of mean and seasonal climate, soil characteristics, latitude, and altitude, assuming a gamma distribution of the response variable (Equation 3).

$$\begin{aligned}\mathrm{BAI}_{i,t,j} = \; & \beta_0 + \beta_n\big(\beta_1 \mathit{log}(\mathrm{DMI}_i) + \beta_2 f(\mathrm{LAT}_i) + \\ & \beta_3 f(\mathrm{ALT}_i) + \beta_4 f(\mathrm{SoilD}_i) + \beta_5 f(\mathrm{SoilW}_i) + \\ & \beta_6 f(\mathrm{Tmax}_{i,t}) + \beta_7 \log\left(PP_{i,t}\right)\big)^2 + \left(BA_{t-1} \mid Code_j\right)\end{aligned} \tag{3}$$

where β represents the coefficients associated with the intercept (β_0), *log* refers to a logarithmic link function, and f to a standardization function applied to the variables. The initial set of independent variables were DMI, LAT (latitude), ALT (altitude), Tmax (seasonal maximum temperatures), and PP (seasonal precipitation sums). As the influence of climate on tree growth is known to fluctuate across environmental gradients (Fritts 1972), we incorporated interactions between seasonal climate variables and the other independent variables. The basal area of the tree in the previous year of each tree-ring formation (BA) and tree identity (Code) were included as crossed random-effect variables to account for the variance associated with tree age and avoid the influence of particularities of each individual tree. A total number of 2,241,365 and 805,043 individual tree-ring measurements from the period 1950–2016 were used to build the PCAB and PISY models, respectively.

The primary aim of our statistical modeling is prediction rather than inference. Thus, the predictive performance of the selected model is prioritized over its possible interpretability. However, high collinearity among predictor variables can cause overfitting and problems in their interpretation, as different predictors can explain some of the same variance in the response variable, and their effects cannot be estimated independently (Montesinos López, Montesinos López, and Crossa 2022). We reduced collinearity using a reiterative two-steps procedure in which non-significant and high-intercorrelated independent variables were excluded as a trade-off between goodness of fit and parsimony. The first step is a backward deletion from a full model including all available variables and interactions between them, based on the variance inflation factor (VIF) and the p-value. All non-significant ($p < 0.05$) variables from the full model were excluded. Afterwards, the covariate with the highest VIF was sequentially dropped until all VIFs were smaller than five (threshold based on Menard 2001). The second step is a multi-model inference method based on Akaike Information Criterion (AIC) scores, where multiple models were built with all possible variable combinations. The model showing the lowest AIC value and largest Akaike weight (relative probability of each model being the best one given the experimental data and the collection of models considered) was selected as the definitive model. In the end, the PCAB model contained 12 independent variables and 20 interactions, and the PISY model, 9, and 12 respectively (Table S1). For quantifying the model's fit and performance (i.e., the ability to reproduce the growth variability), fitted BAI values and residuals of the models were evaluated (Figures S1 and S2).

2.4 | Model Application

The GLMMs were used to assess tree growth variations across the species' distribution. Growth values were computed individually for each grid cell, representing a theoretical tree with a fixed basal area of 2100 cm^2 (approximately 51 cm DBH) for PCAB and 690 cm^2 (approximately 30 cm DBH) for PISY—reflecting the mean size of trees within the model. Annual Basal Area Increment (BAI) values spanning the period 1950–2016 were calculated and subsequently averaged over two 30-year intervals (1955–1985 and 1986–2016) to facilitate the comparison of mean growth rates across Europe.

Future growth estimates were generated by applying the models to the new climate conditions projected for the three selected

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SSP scenarios. Applicability domains were calculated for each scenario, and areas that exceed seasonal climate conditions outside the range used in each of the models were excluded (Norinder, Rybacka, and Andersson 2016; Table S2). Certain independent variables, including latitude, altitude, soil properties, and DMI, were assumed to remain constant over time. Although DMI is expected to change under future scenarios due to projected shifts in precipitation and temperature, we chose to keep it constant as a reference point to the initial water availability conditions of each site. Projections were assessed for three future periods (2011–2040, 2041–2070, and 2071–2100) and contrasted with the 1986–2016 growth means. Finally, we examined the relative growth change for both species, spatially analyzing their future performance over the shared species distribution, where BAI variations below −5% and above 5% are considered changes, while changes between −5% and 5% are deemed and displayed neutral. This comprehensive approach allows us to gain insights into tree growth's spatial and temporal dynamics in response to projected climate scenarios. All data processing and statistical analyses were performed in R v4.2.2 (R Core Team 2020) using the packages dplR v.1.7.4 (Bunn 2008), lme4 v.1.1–32 (Bates et al. 2014), MuMIn v.1.47.5 (Bartoń 2023), and maps v3.4.1 (Becker and Wilks 1993).

3 | Results

3.1 | Growth Models' Performance and Limitations

The individual models developed for the species explained a similar variance, even containing different variables and number of variables, and demonstrated a good agreement with the observed growth values ($R^2 = 0.828$ for PCAB and $R^2 = 0.832$ for PISY; Figure S1). The distribution of the model residuals was exanimated versus fitted values for the entire model (Figure S2), as well as versus all explanatory variables to look for patterns of possible bias of the model prediction across gradients (graphs not shown). The residuals were evenly scattered around the horizontal axis, indicating an overall constant variance across all levels of the fitted values (i.e., homoscedasticity) and randomly distributed around the $y = 0$ line. No systematic pattern was detected between residuals and main explanatory variables.

Complex models have some inherent challenges, such as collinearity among predictor variables and balance between model fit and performance, that need careful consideration to yield robust insights into tree growth dynamics. While these models offer promising possibilities for modeling tree growth (i.e., handling complex non-Gaussian distributed, data nested structures and repeated measurements, Harrison et al. 2018; Zuur et al. 2009), addressing biases and uncertainties in future projections is key for refining their accuracy and reliability. Future research should prioritize incorporating important factors playing a role in tree growth, such as changes in CO_2 concentration, competition, forest structure, mortality, or natural regeneration, which can enhance the growth model performance (Sheng, Liu, and Dong 2023). Moreover, integrating independent gridded observations from remotely sensed data, such as satellite imagery and LiDAR (light detection and ranging), holds promise for enhancing tree growth modeling across large regions (Coops et al. 2021).

3.2 | Spatial Patterns of Conifer Forest Growth

Comparison of the applied dendrochronological network against the species' complete distribution in Europe reveals an adequate spatial coverage for model application (Figure 1a). Although the mean climatic conditions within the range of the two species slightly surpass the mean conditions of the sampled sites (Figure 1b,c), the interannual variability of climate ensures coverage across the full climatic range. Therefore, the model can be applied to all combinations of average climatic conditions in all locations where the range of applicability is not exceeded (Table S2).

The spatial patterns of tree growth for *Picea abies* and *Pinus sylvestris* derived from the fitted models over the period 1986–2016 outline species-dependent growth variations across their European distribution (Figure 2). The size of the standard tree (see methods) varies between the two species, with the *Picea abies* being three times larger than the *Pinus sylvestris* standard tree, a result of the different average sizes of trees included in the analysis. This difference only influences the magnitude of the estimated growth, with no effect on the spatial patterns or temporal changes in growth, thus enabling direct comparison of the species across space and time. The mean expected growth for a *Picea abies* tree with a Basal Area Increment (BAI) of 2100 cm^2 is $11.5 \pm 2.3\,cm^2$, while for a *Pinus sylvestris* tree with a BAI of 690 cm^2 is $5.1 \pm 1.2\,cm^2$. These magnitudes are in line with the mean growth of all BAI chronologies (Figure S3), despite the high variance of growth across sites.

For *Picea abies*, the highest growth values are observed along the western coastal regions of the British Isles and Scandinavia, as well as in lowlands areas of Western Europe and the northern Balkans (Figure 2a). Lower growth is recorded at the northernmost extent of the species distribution in Scandinavia and the Kola Peninsula. The overall *Picea abies* growth distribution pattern follows a distinct west-to-east gradient in three sub-regions (British Isles, Scandinavia, and continental Central Europe); in contrast to the clear south-to-north gradient revealed for *Pinus sylvestris* mean growth (Figure 2b). The highest annual pine growth is recorded at the southern extent of the species' distribution, gradually decreasing towards northern locations, and reaches a minimum in the Scandinavian Mountains.

Across Europe, growth of both species in the most recent 30-year period (1986–2016) only exhibits slight variations compared to the mean growth observed in the preceding period (1950–1985), with values of $10.9 \pm 2.1\,cm^2$ for a standard *Picea abies* tree and $5.0 \pm 1.3\,cm^2$ for the standard *Pinus sylvestris* tree during the earlier period. However, on the spatial scale, regional differences within the species distributions can be observed (Figure 3). A general increase in growth performance is detected across most of *Picea abies* distribution area, apart from the southern distribution of the species (e.g., Pyrenees, French Alps, Carpathians, and Rhodope Mountains) and in a region spanning Poland. The mean increase over time is 5.7% ± 3%, ranging from 6.7% ± 3.1% in cold areas (mean annual

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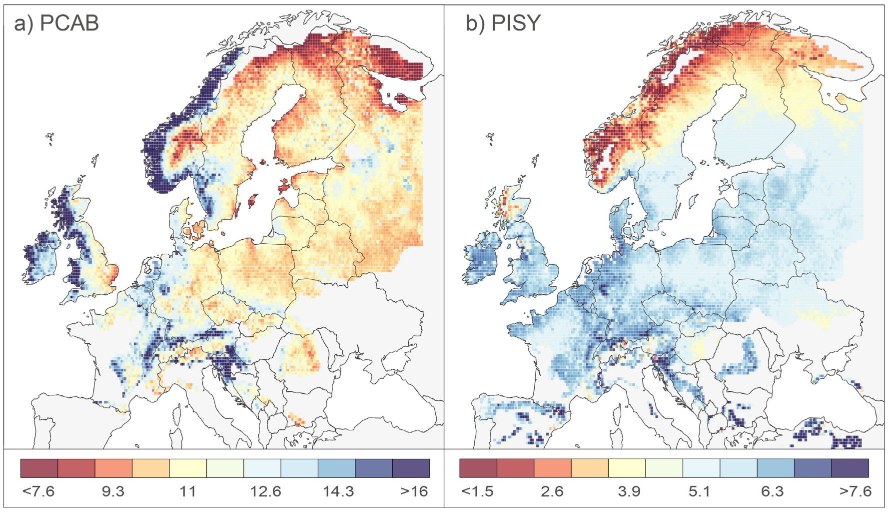

FIGURE 2 | Spatial patterns of tree growth for *Picea abies* (a) and *Pinus sylvestris* (b) over their distribution in Europe. Growth is expressed as mean Basal Area Increment (in cm^2) from 1986 to 2016, estimated for a standard tree with a fixed basal area of 2100 cm^2 for *Picea abies* and 690 cm^2 for *Pinus sylvestris*. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

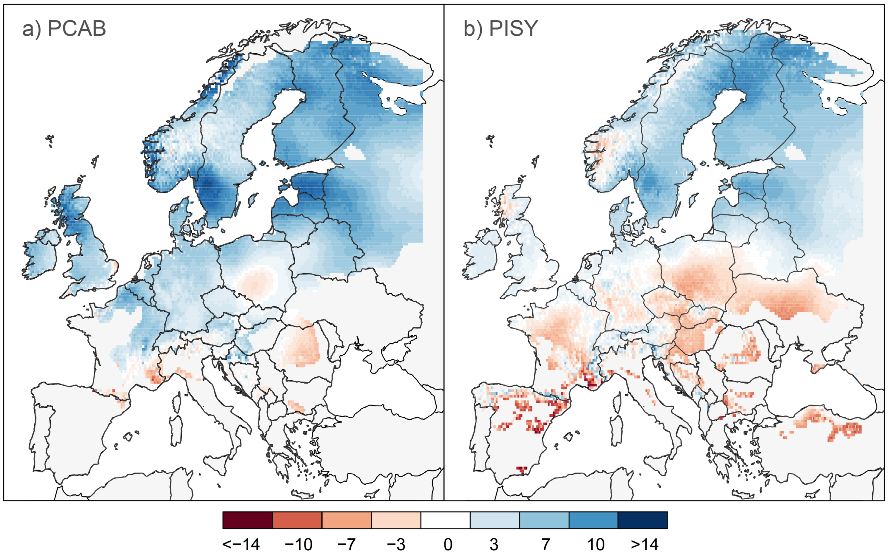

FIGURE 3 | Relative changes of Basal Area Increment (in %) of *Picea abies* (a) and *Pinus sylvestris* (b) between 30-year period from 1955–1985 to 1986–2016. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

temperatures below 5°C) to 4.9% ± 3.9% in warmer areas (mean annual temperatures above 5°C). The most substantial increases are recorded in southern Sweden and in the Baltic region, where tree growth is ~14% higher on average during the latter period. A gradual shift in *Pinus sylvestris* growth spatial patterns is present, characterized by decreases of up to 10% in southern Europe and increases towards northern latitudes, but notably altered across altitude (Figure 3b). During the most recent period, tree growth is enhanced in high-elevation locations across southern and Central Europe, particularly in regions such as the Pyrenees and Alps. The mean growth increase in cold areas is 5.7% ± 2% change, differing from 0.1% ± 4.3% change recorded in warm areas, where the change is more variable. Overall, *Pinus sylvestris* exhibits growth increases in areas characterized by lower average growth (Figure 2b) and experiences decreases in zones with above-average growth, except in major mountain ranges and high latitudes (> 55°), where this trend is not observed.

3.3 | Projected Growth Assessment of Future Forests

Our results for the climate change scenarios SSP126, SSP370, and SSP585 outline highly diverse growth projections across Europe. The SSP370 scenario predicted increases in mean maximum temperatures of 1.2°C ± 0.3°C, 2.3°C ± 0.5°C, and 3.5°C ± 0.6°C for the periods 2011–2040, 2041–2070, and 2071–2100, respectively, compared to the period 1985–2016. Mean annual precipitation is expected to increase moderately for the three future periods (2011–2040: 32 ± 24 mm^2, 2041–2070: 33 ± 52 mm^2, and 2071–2100: 22 ± 45 mm^2), although the changes vary considerably across the species' distribution, with decreases in precipitation to expected for some regions (Tebaldi et al. 2021). *Picea abies* is projected to experience a general growth increase up to 10% in the near future (Figure 4a), which increases to 15% towards the end of the century (Figure 4c). While the magnitude

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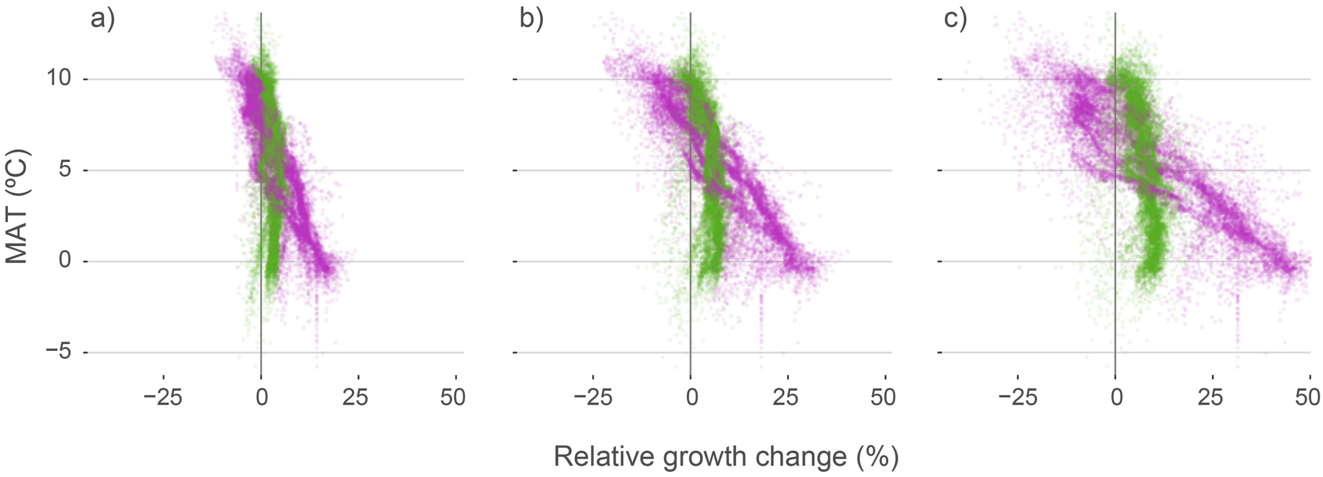

FIGURE 4 | Projected growth changes of *Picea abies* (green) and *Pinus sylvestris* (purple) growth along Mean Annual Temperature (MAT) gradients under SSP3-7.0 climate change scenario. Changes are expressed as relative differences of Basal Area Increment (in %) for the periods 2011–2040 (a), 2041–2070 (b), and 2071–2100 (c) relative to the 1986–2016 mean.

of this positive change is relatively low, it is homogenous across the species' range, with exceptions observed in a limited number of locations in the southern distribution (Figure S5). These regional patterns are largely consistent across different scenarios. The overall growth change is expected to reach 10% by the end of the century under SSP126 (Figure S4). For SSP585, the projected changes show greater differences between the southern and northern regions.

The projected BAI changes for *Pinus sylvestris* display greater differences across the climatic gradient, being positive in colder areas and negative in warmer regions (Figure 4). These contrasting growth changes are projected to intensify with time under the SSP370 scenario, as well as under even warmer conditions (SSP585; Figure S6). In contrast to the projections for *Picea abies*, the range of forecasted growth is wider for *Pinus sylvestris* in any given climatic condition. For instance, at locations with a mean annual temperature of 5°C, the estimated BAI changes range from 6.4% to 10.4% for *Picea abies*, but from 2.8% to 16.3% for *Pinus sylvestris* (1st quartile–3rd quartile), under the SSP370 scenario for the period 2071–2100 (Figure 4c).

Growth projection changes across the species-shared distribution indicate the highly variable spatial response of each species. During 2011–2040, the most substantial changes are projected to occur in northern latitudes, where widespread increases across the Scandinavian Peninsula are observed (Figure 5a). While *Pinus sylvestris* displays the most notable increase during this first period, *Picea abies* growth excels from 2041 until the end of the century. Overall, the projected climate conditions for the area above 55° latitude prove particularly beneficial for both species (Figure 5c). Changes in Central Europe climate during 2011–2040, result in growth changes between −5% and 5% with no significant outliers. For the 1971–2100 period, however, mixed patterns of positive and neutral growth changes for *Picea abies*, combined with neutral and negative growth trends for *Pinus sylvestris*, are forecasted. Accordingly, only small areas over Europe located at the southern edge are projected to be worse for both conifer species in terms of tree growth, even considering different future scenarios (Figures S7 and S8).

4 | Discussion

The dataset analyzed comprises a broad geographical distribution of *Picea abies* and *Pinus sylvestris*, including both core and marginal populations. Despite certain spatial gaps, such as the absence of data from eastern Central Europe for *Pinus sylvestris* and the British Isles for *Picea abies*, the dendrochronological network remains sufficiently diverse and well distributed to capture the range of climatic gradients of the species (Figure S9). The time-for-space substitution (reverse approach of space-for-time, Costa et al. 2021) is applied; as multiple observations (i.e., sites) over time intervals (i.e., tree-rings) are used for space replicates (i.e., distribution of the species), as long as certain conditions are met (i.e., range of climate variability, Table S2). The sufficient climate coverage of the study sites allows spatial upscaling through modeling, and provides a unique perspective on the spatial dynamics of tree growth. Nonetheless, adding information from these regions would be advisable for future studies analyzing spatial patterns of forests at European scales.

The predictive variables used for modeling are highly relevant for capturing the year-to-year tree growth variability for these species (Lévesque et al. 2013; Treml et al. 2022; Tumajer et al. 2017) and are primarily linked to seasonal climate fluctuations. Additionally, the models integrate site-specific factors such as soil properties, average moisture conditions, elevation, and latitude, which can influence climate-growth relationships of the species (Diers, Weigel, and Leuschner 2023; Morin et al. 2018; Ponocná et al. 2016; St. George 2014). There are other highly relevant factors for understanding tree growth spatial and temporal behavior, such as competition (Castagneri et al. 2022), genetics (Moran et al. 2017), or disturbances (Vacek, Vacek, and Cukor 2023). However, integrating these variables into the models at continental scales is not feasible due to the lack of spatially explicit information. Even when such relevant data is

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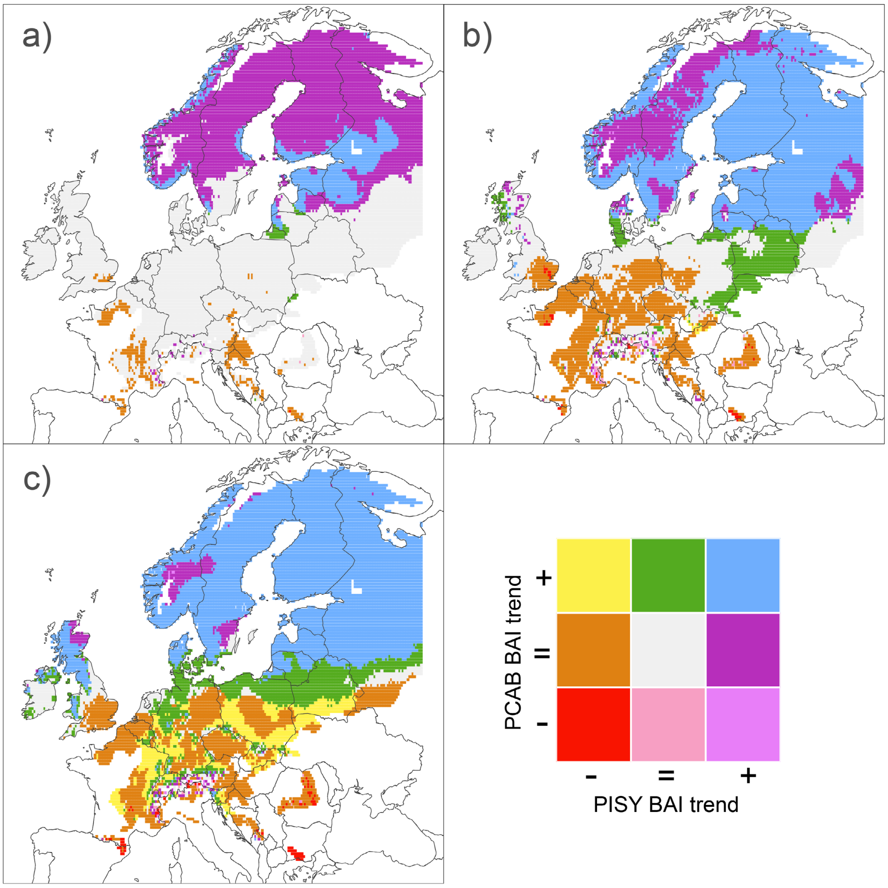

FIGURE 5 | Combined growth trends projections at shared *Picea abies* and *Pinus sylvestris* distribution across Europe. Colors represent combinations of Basal Area Increment (BAI) trends (positive +, neutral =, negative −; see Methods) over the periods 2011–2040 (a), 2041–2070 (b), and 2071–2100 (c) relative to the 1986–2016 mean. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

available spatially, as the soil characteristics (i.e., European Soil Data Centre Panagos et al. 2022), there are still limitations in its use related to resolution or the lack of harmonization across the entire dataset.

Tree-ring-based growth models provide valuable insights into future forest growth dynamics, but the interpretability of their results is limited in different ways (Babst et al. 2018; Bosela et al. 2023). These models likewise weigh the influence of past and future climate conditions, potentially overlooking changes in climate sensitivities over time. The multiple causes and situations that alter climate-growth relationships in trees are diverse, such as ontogenetic dynamics (Carrer 2011), divergence (D'Arrigo et al. 2008), non-stationary responses (Stolz et al. 2021), or dynamic sensitivities (Peltier and Ogle 2020), have not been included in this type of growth models. Additionally, the aggregation of annually resolved tree-ring and climate data into longer periods hides the shorter-term growth responses to harmful extreme climatic events (such as droughts or late-frosts). The impacts of such events can be significant and have medium to long-term consequences, influencing growth trends and even changing the climate sensitivity of trees (Anderegg et al. 2020; Martínez del Castillo et al. 2024; Peltier and Ogle 2020), but are not explicitly included in the modeling as the climate variables are aggregated on a seasonal basis. On the other hand, future extreme climate impacts are equally not addressed, as the models are applied to average climate conditions corresponding to 30-year aggregations. Important future forest challenges related to short-term climate disturbances or increased mortality are not included in this analysis, so extrapolation of future tree growth and carbon storage in these forests is not direct, only an approximation. In addition, the complex interaction of the various biotic and abiotic factors that drive forest productivity, such as forest fires, insect outbreaks, forest management actions, and other disturbances, may have counteracting effects on the overall carbon sequestration capacity. These limitations should be considered, although the main objective of the analysis is to describe the general trends and patterns of tree growth spatially, and project them over decadal aggregates of future climatic conditions.

The mean growth of the species differs significantly across their shared distribution over Europe. Spatial patterns of growth for *Picea abies* were influenced by water availability, with average growth displaying a distinct West–East gradient across Europe, mirroring the patterns of mean annual precipitation (Buontempo et al. 2022). This pattern becomes evident in the British Isles and the Scandinavian coast, where the predicted growth follows a similar regional distribution as the total amount of precipitation. Notably, for this species, both inter-annual growth variability and average growth are strongly associated with changes in precipitation, becoming more evident in low-elevation areas (D'Andrea et al. 2023). In contrast, spatial growth patterns of *Pinus sylvestris* follow a clear north–south gradient, correlating closely with mean annual temperature across Europe. Northern

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pine populations can benefit from warmer climates, extending the growing season into longer periods with an increased photosynthesis activity and water-use efficiency, as long as moisture is not a constrain (Assefa et al. 2024). In cold regions, the wood formation activity of conifers is constrained at both the beginning and the end of the season, limiting the growing period to 2–3 months (Jyske et al. 2014). Progressively, the duration of cell production is longer in warmer areas, where *Pinus sylvestris* trees can be active for more than 5 months (Martínez del Castillo et al. 2016), allowing potentially the formation of wider rings. Warmer winters in certain regions can produce a shift from snowfall to rainfall that might have a bouncing effect on tree growth, given the increased risk of root damage (Weigel et al. 2021).

The growth dynamics of European forests have undergone significant changes in recent decades due to increases in mean temperatures and changes in precipitation (e.g., Diers et al. 2024; Treml et al. 2022; Vacek, Vacek, and Cukor 2023), together with increases in air quality and atmospheric CO_2 concentrations (Pretzsch et al. 2023; Seidl et al. 2017). Moreover, the carbon fertilization effect is emphasized when combined with nitrogen deposition (Cienciala et al. 2018; Etzold et al. 2020), which has progressively increased eutrophication, especially in Central and Northern Europe (Holland et al. 2005). Our results highlight these changes and suggest that mean tree growth of the two species will likely increase under warming conditions, in colder regions, peaking up to a 50% increase in the case of *Pinus sylvestris* under the SSP370 scenario (Figure 4).

In temperature-limited boreal and mountain forests, the warming benefits are numerous and include an extension of the growing season, an improved tree growth and vigor, and expansion of the forests' extension towards tree-line limits (Bastien-Olvera et al. 2023; Takolander et al. 2019; van der Maaten et al. 2017; Vitasse et al. 2021; Wang, Taylor, and D'Orangeville 2023). Our findings similarly reveal a general increase in tree secondary growth over the past 60 years, alongside localized decreases (Figure 3), trends that align with the ones projected for future scenarios. The area in which tree growth is limited by temperature globally shrank between 1930 and 1960 and even further between 1960 and 1990 (Babst et al. 2019), which agrees with the general fading of temperature limitations and subsequent enhanced tree growth (Cienciala et al. 2018). Subsequently, the probability that precipitation exceeded temperature as the main driver of tree growth has increased throughout the boreal zone during the last decades (Babst et al. 2019). Our results suggest that the potential negative impact of warming summers on growth could be compensated by the positive effect of longer growing seasons at cold sites, resulting in increasing growth trends.

However, the beneficial compensation could be mitigated by increasing drought exposure, particularly in regions where water stress is already prevalent (Díaz-Martínez et al. 2023). The overall growth decrease observed in locations with mean annual temperatures exceeding 8°C aligns with projections indicating decreases in growth and survival due to increasing heat stress and water deficit in many parts of its distribution range (Allen, Breshears, and McDowell 2015; Bauwe et al. 2016; Buras and Menzel 2019; Camarero et al. 2015). In recent years, coniferous forests have experienced a pronounced decline in growth, primarily attributed to increasing temperatures, and exacerbated drought conditions (D'Andrea et al. 2023; Sidor et al. 2015; Treml et al. 2022). Increases in temperature at warmer sites could further challenge the photosynthesis, transpiration, and overall physiological performance of trees in the future (Leuschner 2020).

Over the past 30 years, *Picea abies* displayed an overall increasing growth across the distribution range, consistent with findings from other regional studies (Cienciala et al. 2018; Pretzsch et al. 2020; Tumajer et al. 2017). This trend aligns with projections suggesting future growth increases, particularly in mountainous and cold-limited regions (Ponocná et al. 2016; van der Maaten et al. 2017). While rising temperatures are a key factor influencing radial growth, their benefits are predominantly observed in colder environments. Studies have shown that beyond a certain threshold, typically around 13°C, the stimulating effect of temperature on *Picea abies* growth diminishes, shifting towards a limiting effect due to increased water stress (Deslauriers et al. 2003; Sidor et al. 2015). This is consistent with our findings of reduced growth at the warmer edge of the species' distribution in recent decades. Additionally, the species' high sensitivity to drought (Treml et al. 2022) further underscores the importance of precipitation patterns and totals for this species, particularly in low-altitude regions (D'Andrea et al. 2023). Assuming that the physiological thresholds shaping the response of tree growth to climatic conditions are temporally stable in the absence of significant disturbances (Tumajer et al. 2017), our results support the good performance of this species in response to changes in average climate.

Pinus sylvestris exhibited growth increases primarily in colder areas at high latitudes or in mountainous regions, which is highly consistent with future projections. Growth conditions have markedly improved over the last century at the species' northern distribution limit (Vacek, Vacek, and Cukor 2023) and in other locations such as northern Germany (Diers et al. 2024). The future growth increases projected under additional warming beyond 4°C (SSP585) indicate that pines will not reach a temperature threshold above which warming will be detrimental in such cold areas, especially when combined with precipitation increases (D'Orangeville et al., 2018).

Species comparison reveals differing levels of susceptibility between Europe's primary coniferous forests under varying climate change scenarios, with *Pinus sylvestris* exhibiting higher sensitivity and greater response to climate warming than *Picea abies*. Only small areas in the south are projected to experience notable declines in both species, while widespread increases are expected at colder locations. These regions have dense conifer covers dominated by the studied species, indicating potential enhancements in carbon sequestration capacity throughout the 21st century. Nonetheless, there are possible negative consequences of rapid growth increases, including amplified risks of disturbances such as fires and pest outbreaks and alterations in competition dynamics (Seidl et al. 2017). Altered forest growth dynamics must, therefore, be accompanied by adapted management practices (Sommerfeld et al. 2018) including mitigating thinning and assisted migration techniques (Koralewski et al. 2015). The anticipated changes in forest productivity, carbon sequestration capacity, and the anticipated spatial

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differences underscore the need for region-specific management approaches to cultivate climate-resilient forests and safeguard diverse European forest services.

Author Contributions

Edurne Martinez del Castillo: conceptualization, data curation, formal analysis, investigation, methodology, resources, validation, visualization, writing – original draft, writing – review and editing. **Max C. A. Torbenson:** investigation, methodology, validation, visualization, writing – review and editing. **Frederick Reinig:** investigation, validation, visualization, writing – review and editing. **Ernesto Tejedor:** data curation, resources, validation, writing – review and editing. **Martín de Luis:** conceptualization, methodology, supervision, validation, writing – review and editing. **Jan Esper:** funding acquisition, investigation, resources, supervision, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The required data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.13935098. The additional data is available on request from the corresponding author.

References

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. "On Underestimation of Global Vulnerability to Tree Mortality and Forest Die-Off From Hotter Drought in the Anthropocene." *Ecosphere* 6: 1–55. https://doi.org/10.1890/ES15-00203.1.

Ammer, C. 2019. "Diversity and Forest Productivity in a Changing Climate." *New Phytologist* 221: 50–66. https://doi.org/10.1111/nph.15263.

Anderegg, W. R. L., A. T. Trugman, G. Badgley, A. G. Konings, and J. Shaw. 2020. "Divergent Forest Sensitivity to Repeated Extreme Droughts." *Nature Climate Change* 10: 1091–1095. https://doi.org/10.1038/s41558-020-00919-1.

Arora, V. K., A. Katavouta, R. G. Williams, et al. 2020. "Carbon-Concentration and Carbon-Climate Feedbacks in CMIP6 Models and Their Comparison to CMIP5 Models." *Biogeosciences* 17: 4173–4222. https://doi.org/10.5194/bg-17-4173-2020.

Assefa, S., M. Ventura, F. Bravo, et al. 2024. "Pure and Mixed Scots Pine Forests Showed Divergent Responses to Climate Variation and Increased Intrinsic Water Use Efficiency Across a European - Wide Climate Gradient." *European Journal of Forest Research*. https://doi.org/10.1007/s10342-024-01731-8.

Babst, F., M. R. Alexander, P. Szejner, et al. 2014. "A Tree-Ring Perspective on the Terrestrial Carbon Cycle." *Oecologia* 176: 307–322. https://doi.org/10.1007/s00442-014-3031-6.

Babst, F., P. Bodesheim, N. Charney, et al. 2018. "When Tree Rings Go Global: Challenges and Opportunities for Retro- and Prospective Insight." *Quaternary Science Reviews* 197: 1–20. https://doi.org/10.1016/j.quascirev.2018.07.009.

Babst, F., O. Bouriaud, B. Poulter, V. Trouet, M. P. Girardin, and D. C. Frank. 2019. "Twentieth Century Redistribution in Climatic Drivers of Global Tree Growth." *Science Advances* 5: eaat4313. https://doi.org/10.1126/sciadv.aat4313.

Babst, F., A. D. Friend, M. Karamihalaki, et al. 2021. "Modeling Ambitions Outpace Observations of Forest Carbon Allocation." *Trends in Plant Science* 26: 210–219. https://doi.org/10.1016/j.tplants.2020.10.002.

Bartoń, K. 2023. "MuMIn: Multimodal Inference." R Packag. ver. 1.47.5.

Bastien-Olvera, B. A., M. N. Conte, X. Dong, et al. 2023. "Unequal Climate Impacts on Global Values of Natural Capital." *Nature* 625: 722–727. https://doi.org/10.1038/s41586-023-06769-z.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. "lme4: Linear Mixed-Effects Models Using Eigen and S4." *Journal of Statistical Software* 67: 1–48.

Bauwe, A., G. Jurasinski, T. Scharnweber, C. Schröder, and B. Lennartz. 2016. "Impact of Climate Change on Tree-Ring Growth of Scots Pine, Common Beech and Pedunculate Oak in Northeastern Germany." *iForest* 9: 1–11. https://doi.org/10.3832/ifor1421-008.

Becker, R. A., and R. A. Wilks. 1993. "Maps in S." AT&T Bell Laboratories Statistics Research Report [93.2].

Biondi, F., and F. Qeadan. 2008. "A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend From Expected Basal Area Increment." *Tree-Ring Research* 64: 81–96. https://doi.org/10.3959/2008-6.1.

Bodesheim, P., F. Babst, D. C. Frank, et al. 2022. "Predicting Spatiotemporal Variability in Radial Tree Growth at the Continental Scale With Machine Learning." *Environmental Data Science* 1: 1–35. https://doi.org/10.1017/eds.2022.8.

Bose, A. K., A. Gessler, A. Bolte, et al. 2020. "Growth and Resilience Responses of Scots Pine to Extreme Droughts Across Europe Depend on Predrought Growth Conditions." *Global Change Biology* 26: 4521–4537. https://doi.org/10.1111/gcb.15153.

Bosela, M., Á. Rubio-Cuadrado, P. Marcis, et al. 2023. "Empirical and Process-Based Models Predict Enhanced Beech Growth in European Mountains Under Climate Change Scenarios: A Multimodel Approach." *Science of the Total Environment* 888: 164123. https://doi.org/10.1016/j.scitotenv.2023.164123.

Bottero, A., D. I. Forrester, M. Cailleret, et al. 2021. "Growth Resistance and Resilience of Mixed Silver Fir and Norway Spruce Forests in Central Europe: Contrasting Responses to Mild and Severe Droughts." *Global Change Biology* 27: 4403–4419. https://doi.org/10.1111/gcb.15737.

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.

Buontempo, C., S. N. Burgess, D. Dee, et al. 2022. "The Copernicus Climate Change Service Climate Science in Action." *Bulletin of the American Meteorological Society* 103: E2669–E2687. https://doi.org/10.1175/BAMS-D-21-0315.1.

Buras, A., and A. Menzel. 2019. "Projecting Tree Species Composition Changes of European Forests for 2061–2090 Under RCP 4.5 and RCP 8.5 Scenarios." *Frontiers in Plant Science* 9: 1–13. https://doi.org/10.3389/fpls.2018.01986.

Camarero, J. J., A. Gazol, G. Sangüesa-Barreda, J. Oliva, and S. M. Vicente-serrano. 2015. "To Die or Not to Die: Early Warnings of Tree Dieback in Response to a Severe Drought." *Journal of Ecology* 103: 44–57. https://doi.org/10.1111/1365-2745.12295.

Carrer, M. 2011. "Individualistic and Time-Varying Tree-Ring Growth to Climate Sensitivity." *PLoS One* 6: e22813. https://doi.org/10.1371/journal.pone.0022813.

Castagneri, D., G. Vacchiano, A. Hacket-Pain, R. J. DeRose, T. Klein, and A. Bottero. 2022. "Meta-Analysis Reveals Different Competition Effects

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on Tree Growth Resistance and Resilience to Drought." *Ecosystems* 25: 30–43. https://doi.org/10.1007/s10021-021-00638-4.

Caudullo, G., W. Tinner, and D. de Rigo. 2016. "*Picea abies* in Europe: distribution, habitat, usage and threats." In *European Atlas of Forest Tree Species*, 114–116. Luxemburg: European Commission.

Cienciala, E., J. Altman, J. Doležal, et al. 2018. "Increased Spruce Tree Growth in Central Europe Since 1960s." *Science of the Total Environment* 619–620: 1637–1647. https://doi.org/10.1016/j.scitotenv.2017.10.138.

Cook, E. R. 1987. "The Decomposition of Tree-Ring Series for Environmental Studies." *Tree-Ring Bulletin* 47: 37–59.

Coops, N. C., P. Tompalski, T. R. H. Goodbody, et al. 2021. "Modelling Lidar-Derived Estimates of Forest Attributes Over Space and Time: A Review of Approaches and Future Trends." *Remote Sensing of Environment* 260: 112477. https://doi.org/10.1016/j.rse.2021.112477.

Costa, A., S. Salvidio, J. Penner, and M. Basile. 2021. "Time-For-Space Substitution in N-Mixture Models for Estimating Population Trends: A Simulation-Based Evaluation." *Scientific Reports* 11: 1–10. https://doi.org/10.1038/s41598-021-84010-5.

D'Andrea, G., V. Šimůnek, O. Pericolo, et al. 2023. "Growth Response of Norway Spruce (*Picea abies* [L.] Karst.) in Central Bohemia (Czech Republic) to Climate Change." *Forests* 14: 1215. https://doi.org/10.3390/f14061215.

D'Arrigo, R., R. Wilson, B. Liepert, and P. Cherubini. 2008. "On the "Divergence Problem" in Northern Forests: A Review of the Tree-Ring Evidence and Possible Causes." *Global and Planetary Change* 60: 289–305. https://doi.org/10.1016/j.gloplacha.2007.03.004.

De Martonne, E. 1926. "Une nouvelle fonction climatologique: L'indice d'aridité." *La Meteorol* 35: 449–458.

Deslauriers, A., H. Morin, C. Urbinati, and M. Carrer. 2003. "Daily Weather Response of Balsam Fir (*Abies balsamea* (L.) Mill.) Stem Radius Increment From Dendrometer Analysis in the Boreal Forests of Quebec (Canada)." *Trees* 17: 477–484. https://doi.org/10.1007/s00468-003-0260-4.

Di Cosmo, L., D. G. Giuliani, M. M. D. Dickson, M. Maria, and G. Gasparini. 2020. "An Individual-Tree Linear Mixed-Effects Model for Predicting the Basal Area Increment of Major Forest Species in Southern Europe." *Forestry Systems* 29: e019.

Díaz-Martínez, P., P. Ruiz-Benito, J. Madrigal-González, A. Gazol, and E. Andivia. 2023. "Positive Effects of Warming Do Not Compensate Growth Reduction due to Increased Aridity in Mediterranean Mixed Forests." *Ecosphere* 14: 1–14. https://doi.org/10.1002/ecs2.4380.

Diers, M., C. Leuschner, C. Dulamsuren, T. C. Schulz, and R. Weigel. 2024. "Increasing Winter Temperatures Stimulate Scots Pine Growth in the North German Lowlands Despite Stationary Sensitivity to Summer Drought." *Ecosystems* 27: 428–442. https://doi.org/10.1007/s10021-023-00897-3.

Diers, M., R. Weigel, and C. Leuschner. 2023. "Both Climate Sensitivity and Growth Trend of European Beech Decrease in the North German Lowlands, While Scots Pine Still Thrives, Despite Growing Sensitivity." *Trees* 37: 523–543. https://doi.org/10.1007/s00468-022-02369-y.

Domke, G. M., S. N. Oswalt, B. F. Walters, and R. S. Morin. 2020. "Tree planting has the potential to increase carbon sequestration capacity of forests in the United States." *Proceedings of the National Academy of Sciences of the USA* 1: 24649–24651. https://doi.org/10.1073/pnas.2010840117.

Esper, J., S. S. George, K. Anchukaitis, et al. 2018. "Large-Scale, Millennial-Length Temperature Reconstructions From Tree-Rings." *Dendrochronologia* 50: 81–90. https://doi.org/10.1016/j.dendro.2018.06.001.

Etzold, S., M. Ferretti, G. J. Reinds, et al. 2020. "Nitrogen Deposition Is the Most Important Environmental Driver of Growth of Pure, Even-Aged and Managed European Forests." *Forest Ecology and Management* 458: 117762. https://doi.org/10.1016/j.foreco.2019.117762.

Evans, M. E. K., R. Justin Derose, S. Klesse, et al. 2022. "Adding Tree Rings to North America's National Forest Inventories: An Essential Tool to Guide Drawdown of Atmospheric CO_2." *Bioscience* 72: 233–246. https://doi.org/10.1093/biosci/biab119.

FAO. 2020. "Global Forest Assessment Resources 2020 Main Report." Rome. https://doi.org/10.4324/9781315184487-1.

Forzieri, G., M. Girardello, G. Ceccherini, et al. 2021. "Emergent Vulnerability to Climate-Driven Disturbances in European Forests." *Nature Communications* 12: 1–12. https://doi.org/10.1038/s41467-021-21399-7.

Fritts, H. C. 1972. "Tree Rings and Climate." *Scientific American* 226: 92–100. https://doi.org/10.1038/scientificamerican0572-92.

Harris, I., P. D. Jones, T. J. Osborn, and D. H. Lister. 2014. "Updated High-Resolution Grids of Monthly Climatic Observations - The CRU TS3.10 Dataset." *International Journal of Climatology* 34: 623–642. https://doi.org/10.1002/joc.3711.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, et al. 2018. "A Brief Introduction to Mixed Effects Modelling and Multi-Model Inference in Ecology." *PeerJ* 2018: 1–32. https://doi.org/10.7717/peerj.4794.

Hartmann, H., A. Bastos, A. J. Das, et al. 2022. "Climate Change Risks to Global Forest Health: Emergence of Unexpected Events of Elevated Tree Mortality Worldwide." *Annual Review of Plant Biology* 73: 673–702. https://doi.org/10.1146/annurev-arplant-102820-012804.

Heilman, K. A., M. C. Dietze, A. A. Arizpe, et al. 2022. "Ecological Forecasting of Tree Growth: Regional Fusion of Tree-Ring and Forest Inventory Data to Quantify Drivers and Characterize Uncertainty." *Global Change Biology* 28: 1–19. https://doi.org/10.1111/gcb.16038.

Hlásny, T., S. Zimová, K. Merganičová, P. Štěpánek, R. Modlinger, and M. Turčáni. 2021. "Devastating Outbreak of Bark Beetles in The Czech Republic: Drivers, Impacts, and Management Implications." *Forest Ecology and Management* 490: 119075. https://doi.org/10.1016/j.foreco.2021.119075.

Holland, E. A., B. H. Braswell, J. Sulzman, and J. F. Lamarque. 2005. "Nitrogen Deposition Onto the United States and Western Europe: Synthesis of Observations and Models." *Ecological Applications* 15: 38–57. https://doi.org/10.1890/03-5162.

Housset, J. M., S. Nadeau, N. Isabel, et al. 2018. "Tree Rings Provide a New Class of Phenotypes for Genetic Associations That Foster Insights Into Adaptation of Conifers to Climate Change." *New Phytologist* 218: 630–645. https://doi.org/10.1111/nph.14968.

Houston Durrant, T., D. de Rigo, and G. Caudullo. 2016. "*Pinus sylvestris* In Europe: Distribution, Habitat, Usage and Threats." In *European Atlas of Forest Tree Species*, edited by J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, and A. Mauri, E016b94. Luxembourg: European Union.

IPCC. 2021. "Climate Change 2021: The Physical Science Basis." In *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. United Kingdom: Cambridge University Press.

Janssens, I. A., A. Freibauer, P. Ciais, et al. 2003. "Europe's Terrestrial Biosphere absorbs 7 to 12% of European Anthropogenic CO_2 Emissions." *Science* 300: 1538–1542.

Jevšenak, J., M. Klisz, J. Mašek, et al. 2024. "Incorporating High-Resolution Climate, Remote Sensing and Topographic Data to Map Annual Forest Growth in Central and Eastern Europe." *Science of the Total Environment* 913: 169692. https://doi.org/10.1016/j.scitotenv.2023.169692.

Jiang, Y., W. Marchand, M. Rydval, et al. 2024. "Drought Resistance of Major Tree Species in The Czech Republic." *Agricultural and Forest Meteorology* 348: 109933. https://doi.org/10.1016/j.agrformet.2024.109933.

13652486, 2024, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17580 by Universidad De Zaragoza, Wiley Online Library on [16/12/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Jyske, T., H. Mäkinen, T. Kalliokoski, and P. Nöjd. 2014. "Intra-Annual Tracheid Production of Norway Spruce and Scots Pine Across a Latitudinal Gradient in Finland." *Agricultural and Forest Meteorology* 194: 241–254. https://doi.org/10.1016/j.agrformet.2014.04.015.

Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the earth's Land Surface Areas." *Scientific Data* 4: 1–20. https://doi.org/10.1038/sdata.2017.122.

Karger, D. N., O. Conrad, J. Böhner, et al. 2021. "Climatologies at High Resolution for the earth's Land Surface Areas." EnviDat. https://doi.org/10.16904/envidat.228.

Karger, D. N., and N. E. Zimmermann. 2018. "CHELSAcruts - High Resolution Temperature and Precipitation Timeseries for the 20th Century and Beyond." EnviDat. https://doi.org/10.16904/envidat.159.

Keenan, R. J. 2015. "Climate Change Impacts and Adaptation in Forest Management: A Review." *Annals of Forest Science* 72: 145–167. https://doi.org/10.1007/s13595-014-0446-5.

Klesse, S., R. J. DeRose, F. Babst, et al. 2020. "Continental-Scale Tree-Ring-Based Projection of Douglas-Fir Growth: Testing the Limits of Space-For-Time Substitution." *Global Change Biology* 26: 5146–5163. https://doi.org/10.1111/gcb.15170.

Koralewski, T. E., H. H. Wang, W. E. Grant, and T. D. Byram. 2015. "Plants on the Move: Assisted Migration of Forest Trees in the Face of Climate Change." *Forest Ecology and Management* 344: 30–37. https://doi.org/10.1016/j.foreco.2015.02.014.

Leuschner, C. 2020. "Drought Response of European Beech (*Fagus sylvatica* L.)–A Review." *Perspectives in Plant Ecology, Evolution and Systematics* 47: 125576. https://doi.org/10.1016/j.ppees.2020.125576.

Lévesque, M., M. Saurer, R. Siegwolf, et al. 2013. "Drought Response of Five Conifer Species Under Contrasting Water Availability Suggests High Vulnerability of Norway Spruce and European Larch." *Global Change Biology* 19: 3184–3199. https://doi.org/10.1111/gcb.12268.

Martínez del Castillo, E., L. A. Longares, J. Gričar, et al. 2016. "Living on the Edge: Contrasted Wood-Formation Dynamics in Fagus Sylvatica and *Pinus sylvestris* Under Mediterranean Conditions." *Frontiers in Plant Science* 7: 370. https://doi.org/10.3389/fpls.2016.00370.

Martínez del Castillo, E., P. Prislan, J. Gričar, et al. 2018. "Challenges for Growth of Beech and Co-Occurring Conifers in a Changing Climate Context." *Dendrochronologia* 52: 1–10. https://doi.org/10.1016/J.DENDRO.2018.09.001.

Martínez del Castillo, E., M. C. A. Torbenson, F. Reinig, et al. 2024. "Diverging Growth Trends and Climate Sensitivities of Individual Pine Trees After the 1976 Extreme Drought." *Science of the Total Environment* 946: 174370. https://doi.org/10.1016/j.scitotenv.2024.174370.

Martínez del Castillo, E., C. S. Zang, A. Buras, et al. 2022. "Climate-Change-Driven Growth Decline of European Beech Forests." *Communications Biology* 5: 1–9. https://doi.org/10.1038/s42003-022-03107-3.

McDowell, N. G., C. D. Allen, K. Anderson-Teixeira, et al. 2020. "Pervasive Shifts in Forest Dynamics in a Changing World." *Science* 368: eaaz9463. https://doi.org/10.1126/science.aaz9463.

Menard, S. 2001. *Applied Logistic Regression Analysis*. 2nd ed. London: Sage Publications.

Montesinos López, O. A., A. Montesinos López, and J. Crossa. 2022. *Multivariate Statistical Machine Learning Methods for Genomic Prediction*. Cham: Springer. https://doi.org/10.1007/978-3-030-89010-0.

Moran, E., J. Lauder, C. Musser, A. Stathos, and M. Shu. 2017. "The Genetics of Drought Tolerance in Conifers." *New Phytologist* 216: 1034–1048. https://doi.org/10.1111/nph.14774.

Morin, X., L. Fahse, H. Jactel, M. Scherer-Lorenzen, R. García-Valdés, and H. Bugmann. 2018. "Long-Term Response of Forest Productivity to Climate Change Is Mostly Driven by Change in Tree Species Composition." *Scientific Reports* 8: 1–12. https://doi.org/10.1038/s41598-018-23763-y.

Norinder, U., A. Rybacka, and P. L. Andersson. 2016. "Conformal Prediction to Define Applicability Domain - A Case Study on Predicting ER and AR Binding." *SAR and QSAR in Environmental Research* 27: 303–316. https://doi.org/10.1080/1062936X.2016.1172665.

Panagos, P., M. Van Liedekerke, P. Borrelli, et al. 2022. "European Soil Data Centre 2.0: Soil Data and Knowledge in Support of the EU Policies." *European Journal of Soil Science* 73: 1–18. https://doi.org/10.1111/ejss.13315.

Patacca, M., M. Lindner, M. E. Lucas-Borja, et al. 2023. "Significant Increase in Natural Disturbance Impacts on European Forests Since 1950." *Global Change Biology* 29: 1359–1376. https://doi.org/10.1111/gcb.16531.

Peltier, D. M. P., and K. Ogle. 2020. "Tree Growth Sensitivity to Climate Is Temporally Variable." *Ecology Letters* 23: 1561–1572. https://doi.org/10.1111/ele.13575.

Ponocná, T., B. Spyt, R. Kaczka, U. Büntgen, and V. Treml. 2016. "Growth Trends and Climate Responses of Norway Spruce Along Elevational Gradients in East-Central Europe." *Trees* 30: 1633–1646. https://doi.org/10.1007/s00468-016-1396-3.

Pretzsch, H., M. del Río, C. Arcangeli, et al. 2023. "Forest Growth in Europe Shows Diverging Large Regional Trends." *Scientific Reports* 13: 1–13. https://doi.org/10.1038/s41598-023-41077-6.

Pretzsch, H., T. Hilmers, P. Biber, et al. 2020. "Evidence of Elevation-Specific Growth Changes of Spruce, Fir, and Beech in European Mixed Mountain Forests During the Last Three Centuries." *Canadian Journal of Forest Research* 50: 689–703. https://doi.org/10.1139/cjfr-2019-0368.

Pretzsch, H., T. Hilmers, E. Uhl, et al. 2021. "European Beech Stem Diameter Grows Better in Mixed Than in Mono-Specific Stands at the Edge of Its Distribution in Mountain Forests." *European Journal of Forest Research* 140: 127–145. https://doi.org/10.1007/s10342-020-01319-y.

R Core Team. 2020. "R: A Language and Environment for Statistical Computing [WWW Document]." Vienna R Foundation Statistical Computing. www.R-project.org/.

Seidl, R., D. Thom, M. Kautz, et al. 2017. "Forest Disturbances Under Climate Change." *Nature Climate Change* 7: 395–402. https://doi.org/10.1038/nclimate3303.

Senf, C., A. Buras, C. S. Zang, A. Rammig, and R. Seidl. 2020. "Excess Forest Mortality Is Consistently Linked to Drought Across Europe." *Nature Communications* 11: 1–8. https://doi.org/10.1038/s41467-020-19924-1.

Sheng, Q., Z. Liu, and L. Dong. 2023. "A Climate-Spatial Matrix Growth Model for Major Tree Species in Lesser Khingan Mountains and Responses of Forest Dynamics Change to Different Representative Concentration Path Scenarios." *Frontiers in Forests and Global Change* 6: 1–18. https://doi.org/10.3389/ffgc.2023.1309189.

Sidor, C. G., I. Popa, R. Vlad, and P. Cherubini. 2015. "Different Tree-Ring Responses of Norway Spruce to Air Temperature Across an Altitudinal Gradient in the Eastern Carpathians (Romania)." *Trees* 29: 985–997. https://doi.org/10.1007/s00468-015-1178-3.

Sommerfeld, A., C. Senf, B. Buma, et al. 2018. "Patterns and Drivers of Recent Disturbances Across the Temperate Forest Biome." *Nature Communications* 9: 4355. https://doi.org/10.1038/s41467-018-06788-9.

St. George, S. 2014. "An Overview of Tree-Ring Width Records Across the Northern Hemisphere." *Quaternary Science Reviews* 95: 132–150. https://doi.org/10.1016/j.quascirev.2014.04.029.

Stolz, J., E. van der Maaten, H. Kalanke, J. Martin, M. Wilmking, and M. van der Maaten-Theunissen. 2021. "Increasing Climate Sensitivity of Beech and Pine Is Not Mediated by Adaptation and Soil Characteristics Along a

13652486, 2024, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17580 by Universidad De Zaragoza, Wiley Online Library on [16/12/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Precipitation Gradient in Northeastern Germany." *Dendrochronologia* 67: 125834. https://doi.org/10.1016/j.dendro.2021.125834.

Takolander, A., T. Hickler, L. Meller, and M. Cabeza. 2019. "Comparing Future Shifts in Tree Species Distributions Across Europe Projected by Statistical and Dynamic Process-Based Models." *Regional Environmental Change* 19: 251–266. https://doi.org/10.1007/s10113-018-1403-x.

Tebaldi, C., K. Debeire, V. Eyring, et al. 2021. "Climate Model Projections From the Scenario Model Intercomparison Project (ScenarioMIP) of CMIP6." *Earth System Dynamics* 12: 253–293. https://doi.org/10.5194/esd-12-253-2021.

Treml, V., J. Mašek, J. Tumajer, et al. 2022. "Trends in Climatically Driven Extreme Growth Reductions of Picea Abies and *Pinus sylvestris* in Central Europe." *Global Change Biology* 28: 557–570. https://doi.org/10.1111/gcb.15922.

Tumajer, J., J. Altman, P. Štěpánek, V. Treml, J. Doležal, and E. Cienciala. 2017. "Increasing Moisture Limitation of Norway Spruce in Central Europe Revealed by Forward Modelling of Tree Growth in Tree-Ring Network." *Agricultural and Forest Meteorology* 247: 56–64. https://doi.org/10.1016/j.agrformet.2017.07.015.

Vacek, Z., S. Vacek, and J. Cukor. 2023. "European Forests Under Global Climate Change: Review of Tree Growth Processes, Crises and Management Strategies." *Journal of Environmental Management* 332: 117353. https://doi.org/10.1016/j.jenvman.2023.117353.

van der Maaten, E., A. Hamann, M. van der Maaten-Theunissen, et al. 2017. "Species Distribution Models Predict Temporal but Not Spatial Variation in Forest Growth." *Ecology and Evolution* 7: 2585–2594. https://doi.org/10.1002/ece3.2696.

Vitasse, Y., S. Ursenbacher, G. Klein, et al. 2021. "Phenological and Elevational Shifts of Plants, Animals and Fungi Under Climate Change in the European Alps." *Biological Reviews* 96: 1816–1835. https://doi.org/10.1111/brv.12727.

Wang, J., A. R. Taylor, and L. D'Orangeville. 2023. "Warming-Induced Tree Growth May Help Offset Increasing Disturbance Across the Canadian Boreal Forest." *Proceedings of the National Academy of Sciences* 120: 2017. https://doi.org/10.1073/pnas.

Weigel, R., H. A. L. Henry, I. Beil, et al. 2021. "Ecosystem Processes Show Uniform Sensitivity to Winter Soil Temperature Change Across a Gradient From Central to Cold Marginal Stands of a Major Temperate Forest Tree." *Ecosystems* 24: 1545–1560. https://doi.org/10.1007/s10021-021-00600-4.

Weiner, J., and S. C. Thomas. 2001. "The Nature of Tree Growth and the "Age-Related Decline in Forest Productivity"." *Oikos* 94: 374–376. https://doi.org/10.1034/j.1600-0706.2001.940219.x.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. "Mixed Effects Models and Extensions in Ecology With R." In *Statistics for Biology and Health*. New York: Springer.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. "A Protocol for Data Exploration to Avoid Common Statistical Problems." *Methods in Ecology and Evolution* 1: 3–14. https://doi.org/10.1111/j.2041-210x.2009.00001.x.

Zald, H. S. J., T. A. Spies, M. E. Harmon, and M. J. Twery. 2016. "Forest carbon calculators: A review for managers, policymakers and educators." *Journal of Forestry* 114: 134–143. https://doi.org/10.5849/jof.15-019.

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