RESEARCH ARTICLE OPEN ACCESS

No Future Growth Enhancement Expected at the Northern Edge for European Beech due to Continued Water Limitation

Stefan Klesse[1,2] | Richard L. Peters[3,4] | Raquel Alfaro-Sánchez[5,6] | Vincent Badeau[7] | Claudia Baittinger[8] | Giovanna Battipaglia[9] | Didier Bert[10] | Franco Biondi[11] | Michal Bosela[12,13] | Marius Budeanu[14] | Vojtěch Čada[15] | J. Julio Camarero[16] | Liam Cavin[17] | Hugues Claessens[18] | Ana-Maria Cretan[19] | Katarina Čufar[20] | Martin de Luis[21] | Isabel Dorado-Liñán[22] | Choimaa Dulamsuren[23] | Josep Maria Espelta[24] | Balazs Garamszegi[25] | Michael Grabner[25] | Jozica Gricar[26] | Andrew Hacket-Pain[27] | Jon Kehlet Hansen[28] | Claudia Hartl[29] | Andrea Hevia[30,31] | Martina Hobi[1] | Pavel Janda[15] | Alistair S. Jump[17] | Jakub Kašpar[32] | Marko Kazimirović[33] | Srdjan Keren[34] | Juergen Kreyling[35] | Alexander Land[36] | Nicolas Latte[18] | François Lebourgeois[7] | Christoph Leuschner[37] | Mathieu Lévesque[38] | Luis A. Longares[21] | Edurne Martinez del Castillo[39] | Annette Menzel[40] | Maks Merela[20] | Martin Mikoláš[15] | Renzo Motta[41] | Lena Muffler[37,42] | Anna Neycken[1,38] | Paola Nola[43] | Momchil Panayotov[44] | Any Mary Petritan[14] | Ion Catalin Petritan[19] | Ionel Popa[45,46] | Peter Prislan[26] | Tom Levanič[26] | Catalin-Constantin Roibu[47] | Álvaro Rubio-Cuadrado[16,22] | Raúl Sánchez-Salguero[31] | Pavel Šamonil[32,48] | Branko Stajić[33] | Miroslav Svoboda[15] | Roberto Tognetti[49] | Elvin Toromani[50] | Volodymyr Trotsiuk[1] | Ernst van der Maaten[51] | Marieke van der Maaten-Theunissen[51] | Astrid Vannoppen[52] | Ivana Vašíčková[32] | Georg von Arx[1,2] | Martin Wilmking[35] | Robert Weigel[37,42] | Tzvetan Zlatanov[53] | Christian Zang[54] | Allan Buras[55]

Correspondence: Stefan Klesse (stefan.klesse@wsl.ch)

ABSTRACT

With ongoing global warming, increasing water deficits promote physiological stress on forest ecosystems with negative impacts on tree growth, vitality, and survival. How individual tree species will react to increased drought stress is therefore a key research question to address for carbon accounting and the development of climate change mitigation strategies. Recent tree-ring studies have shown that trees at higher latitudes will benefit from warmer temperatures, yet this is likely highly species-dependent and less well-known for more temperate tree species. Using a unique pan-European tree-ring network of 26,430 European beech (*Fagus sylvatica L.*) trees from 2118 sites, we applied a linear mixed-effects modeling framework to (i) explain variation in climate-dependent growth and (ii) project growth for the near future (2021–2050) across the entire distribution of beech. We modeled the spatial pattern of radial growth responses to annually varying climate as a function of mean climate conditions (mean annual temperature, mean annual climatic water balance, and continentality). Over the calibration period (1952–2011), the model yielded high regional explanatory power ($R^2 = 0.38$–0.72). Considering a moderate climate change scenario (CMIP6 SSP2-4.5), beech growth is projected to decrease in the future across most of its distribution range. In particular, projected growth decreases by 12%–18% (interquartile range) in northwestern Central Europe and by 11%–21% in the Mediterranean region. In contrast, climate-driven growth increases are limited to around 13% of the current occurrence, where the historical mean annual temperature was below ~6°C. More specifically, the model predicts a 3%–24% growth increase in the high-elevation clusters of the Alps and Carpathian Arc. Notably, we find little potential for future growth increases (−10 to +2%) at the poleward

leading edge in southern Scandinavia. Because in this region beech growth is found to be primarily water-limited, a northward shift in its distributional range will be constrained by water availability.

1 | Introduction

In the context of climate change, droughts, heatwaves, and other climatic extreme events are becoming more frequent and severe—a trend which is likely to continue in the future (Cook et al. 2014; IPCC 2021; Spinoni et al. 2018). Warmer temperatures and increasing water deficits already put a strain on forest ecosystems globally and thus put their contribution to the land carbon sink and the multitude of other ecosystem services they provide at risk (Babst et al. 2019; Pan et al. 2011; Salomón et al. 2022). Accurately predicting how individual tree species and the forests they form will respond in space to increasing drought stress is a central challenge in global change research. The vegetation model ensembles generally project the terrestrial carbon sink to increase. However, these models just recently started to integrate more detailed implementations of critical processes related to drought effects on tree vitality and mortality (Papastefanou et al. 2020; Xu et al. 2016), ultimately leading to a remarkable spread among individual model projections (Schurgers, et al., 2018). To overcome and reduce these uncertainties regarding forest growth responses to climate variability and climate change, large spatiotemporal observations are needed. However, current large-scale observation networks lack temporal resolution (national forest inventories, Evans et al. 2022), have limited temporal depth (eddy-covariance flux towers), and/or yield only indirect measures of tree growth (flux towers, Cabon et al. 2022; remotely sensed metrics of greenness, Arend, Hoch, and Kahmen 2023). Here, tree-ring networks provide a solution since they represent a direct measure of radial tree growth providing data at annual resolution and over much longer time scales (Babst et al. 2018; Klesse et al. 2018). As such, tree rings can improve and constrain vegetation models (Babst et al. 2021). Although several large-scale tree-ring studies have been conducted in the past using multi-species data from the International Tree Ring Data Bank (Zhao et al. 2019), the required large-scale species-specific analyses remain rare (but see e.g., Klesse et al. 2020, Martinez del Castillo et al. 2022).

In recent years, Central Europe has faced two hot and very dry summers in 2018 and 2022, causing drought-induced early defoliation across many tree species, widespread reduction in forest carbon uptake, and enhanced mortality risk (Arend et al. 2022; Bastos et al. 2020; Buras, Rammig, and Zang 2020; Frei et al. 2022; Schuldt et al. 2020; van der Woude et al. 2023). This raised concerns about the future vitality of several tree species in European forests, especially for European beech (*Fagus sylvatica* L.; Leuschner 2020; Frei et al. 2022; Schuldt et al. 2020, Scharnweber et al. 2020), one of the most widespread, ecologically and economically important broadleaved tree species in Europe (Leuschner and Ellenberg 2017; Peters 2013). Across its distribution area, radial growth of beech was found to be mainly driven by water availability (Cavin and Jump 2017; Hacket-Pain et al. 2016; Rozas et al. 2015; Weigel et al. 2023; Martinez del Castillo et al. 2022). Only in cool, mountainous regions at higher elevation was beech shown to be positively related to warmer growing season temperatures (Di Filippo et al. 2007; Dittmar, Zech, and Elling 2003; Dulamsuren et al. 2017). This was also suggested by Bosela et al. (2023) by combining empirical tree-ring-based and process-based mechanistic models. However, there are contrasting findings about how temperature limitation will affect future growth at the northern edge of beech's distribution. Using a large tree-ring dataset, an aridity index, and latitude and elevation as spatial predictors, Martinez del Castillo et al. (2022) projected an increase in growth at the northern range edge of European beech in southern Scandinavia. In contrast, more regionally focused studies in southern Scandinavia showed that beech growth was predominantly water-limited and hence is expected to be under increased drought stress in the future, leading to a decrease in growth (Farahat and Linderholm 2018; Harvey et al. 2020; Muffler et al. 2020).

Motivated by these contrasting findings, we aimed to refine future growth projections of beech using only climatological instead of geographic predictors. We employed an extensive tree-ring network encompassing the entire distribution of European beech to analyze the climate sensitivity of radial growth since 1952 within a linear mixed-effects framework analogous to Cook's aggregate growth model (Cook 1987) and used the output of 10 general circulation models (CMIP6, SSP2-4.5) to project growth for the near-term future (2021–2050; IPCC 2021). In evaluating the model and growth projections, we sought to address the following questions:

- Q1: Which geographic regions of European beech are most sensitive to variability in climate and to which variable and season is growth the most sensitive?

- Q2: Under which mean climatic conditions is growth most sensitive to variations in climate and at which thermal threshold does the primary limiting growth factor change from energy (temperature) to water?

- Q3: How much of the distribution range of beech is energy-limited and can benefit from climate change?

- Q4: What is the magnitude and sign of projected growth changes at the poleward leading edge of European beech?

2 | Material and Methods

2.1 | Study Area and Tree-Ring Data

We compiled a European beech tree-ring data network consisting of 26,430 individual tree-ring time series from 2118 sites, covering almost the entire distributional range of this tree species (Figure 1; Table 1). The dataset consists of previously gathered ring-width data of the European Beech Tree-Ring Network (EBTRN; as used in Dorado-Liñán et al. 2022; Hacket-Pain et al. 2018; Martinez del Castillo et al. 2022) as well as newly collected and other previously published or unpublished data for the clustering approach, see below. (Alfaro-Sánchez et al. 2019; Badeau et al. 1995; Bosela et al. 2019; Camarero et al. 2021; Gillerot et al. 2021; Kašpar et al. 2020, 2021; Klesse et al. 2022;
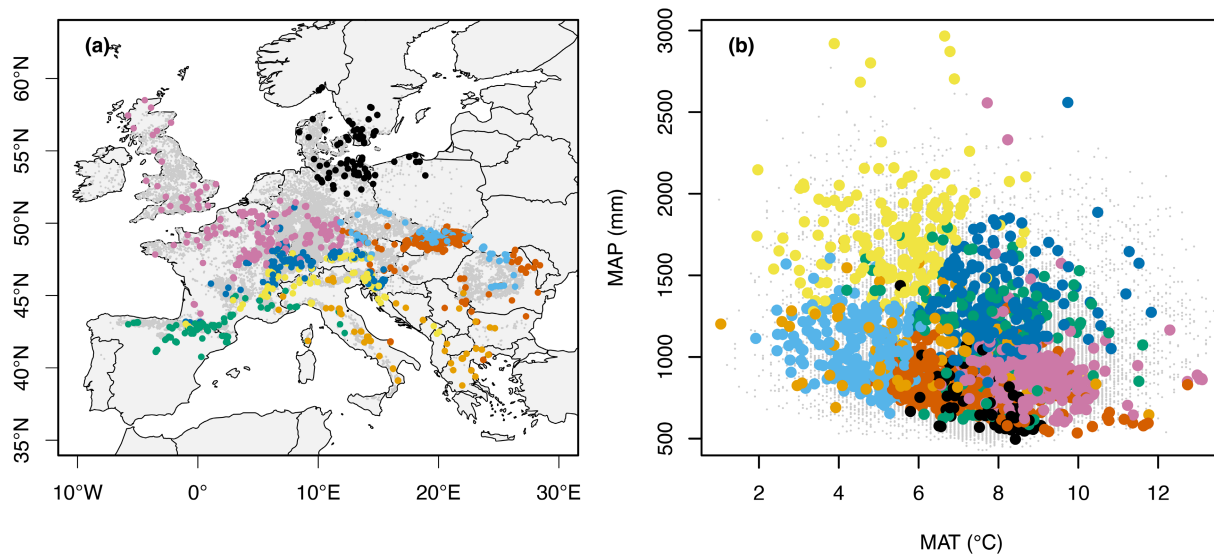
FIGURE 1 | Distribution of the studied sites across geographic (a) and climatic space (b). The different colors refer to the eight self-organized mapping (SOM) clusters across Europe (Table 1; Figure 3). MAT = Mean annual temperature, MAP = mean annual precipitation sum. The dark gray dots show occurrence data based on the EU-Forest dataset of Mauri, Strona, and San-Miguel-Ayanz (2017). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 1 | Supervised-organizing mapping (SOM) clusters and their median and interquartile range (IQR) of mean annual temperature (MAT), mean annual precipitation (MAP), and elevation. "High" and "low" elevation are relative to the distribution of beech occurrence.

SOM cluster	MAT (°C)	MAP (mm)	Elevation (m a.s.l.)	Replication (sites/samples)
SE Europe	6.4 (5.0–7.3)	1092 (886–1217)	1360 (1183–1581)	75/2585
High Elevation E Europe	4.7 (4.0–5.2)	1191 (976–1374)	900 (798–1029)	403/3701
SW Europe	8.1 (6.9–8.9)	1244 (982–1388)	1180 (992–1355)	121/2808
High Elevation Alps	5.6 (4.6–6.2)	1702 (1526–1860)	1007 (930–1210)	179/2567
Central Europe wet	7.9 (7.4–8.6)	1242 (1126–1380)	597 (500–700)	279/3329
Low Elevation E Europe	6.9 (6.2–7.7)	787 (731–869)	520 (400–636)	503/3796
Central-NW Europe	9.2 (8.6–9.6)	867 (818–946)	290 (134–381)	476/5534
Central-N Europe	8.0 (7.2–8.4)	663 (590–762)	85 (52–119)	82/2110

Lévesque, Walthert, and Weber 2016; Martínez-Sancho et al. 2020; Neycken et al. 2022; Šamonil et al. 2013; Serra-Maluquer et al. 2019; Tallieu et al. 2020; Vannoppen et al. 2019; Vašíčková et al. 2019; Vitasse et al. 2019).

To delineate climatically meaningful and geographically coherent regions, tree-ring time series were clustered into eight regions using a supervised self-organizing map algorithm (Wehrens and Buydens 2007), where the inputs were the detrended ring-width time series between 1952 and 1981 (22,577 of 26,430 samples), geographic coordinates (latitude, longitude, and elevation), and climate normals, that is, mean annual temperature (MAT) and mean annual precipitation (MAP). The cluster information was only used to summarize model findings and assess model skill at the regional level. The ring-width detrending for the clustering approach was performed with a cubic smoothing spline with a 50% frequency cutoff at 30 years. Strong weighting toward the geographic and climatic variables was necessary to form

geographically coherent regions (shown in Figure 1; Table 1), that is, no sites belonging to one region were randomly scattered throughout the distribution within other regions: 33% ring width (RW) and 67% geographic and climate information. The number of regions was a compromise between climatically distinct regions across Europe, differences in growth limiting factors, and data availability.

2.2 | Climate Data

Historic climate data were extracted for each of the 2118 sites using CHELSA CRUts (Karger et al. 2017; Karger and Zimmermann 2018), which is based on the CRU TS4.01 gridded historical monthly data product spanning the years 1901 to 2021. We focused on monthly mean minimum and maximum temperatures (t_{min} and t_{max}, respectively) and monthly precipitation sums, with which we calculated climatic water

balance (CWB) using the modified Hargreaves' formulation of potential evapotranspiration (Beguería and Vicente-Serrano 2023; Droogers and Allen 2002; Hargreaves 1994). We used a search radius of 10 km around target grid cells to minimize the elevation difference between the actual elevation of the site as recorded in the field and the elevation of the CHELSA grid cell.

Future climate projections were taken from 10 Atmosphere–Ocean General Circulation Models (AOGCMs) of the CMIP6 multi-model ensemble (Table S1). These data typically have a spatial resolution of more than $1 \times 1°$ in longitude and latitude, which does not allow for a representation of small-scale climate variability, particularly in regions with heterogeneous topography. Therefore, the CMIP6 data were downscaled and bias-adjusted to a spatial resolution of 1×1 km, matching the resolution of the data used for the historical period of analysis (see above). Downscaling was obtained using a monthly quantile-mapping approach. That is, for each available variable-model combination (e.g., precipitation from CanESM2), we determined for each of the 12 months and 2118 site coordinates the quantiles of the corresponding CHELSA CRUts as well as the quantiles of the CMIP6 projections over the historic period 1951–2014 (i.e., 64 quantiles). From these quantile pairs, we derived a transfer function, which allowed for transferring the coarsely resolved and typically biased CMIP6 projections into the statistical density function of the CHELSA CRUts data (see Figure S1 for a validation of the transfer function). By applying the model-variable-specific transfer functions to the projections of the SSP2-4.5 scenario for the period 2021–2050, we obtained bias-adjusted, downscaled projections of t_{max}, t_{min}, and precipitation. The average of the 10 AOGCMs projects an increase of MAT by 1.5°C in the 2021–2050 period relative to the 1981–2010 period and an increase in MAP of 61 mm across all of our sites.

2.3 | Linear Mixed-Effects Model

The modeling approach follows Klesse et al. (2020). In short, because growth rings within a time series, as well as time series within a sampling site, are not independent, we modeled tree RW variation using a linear mixed-effects model. This framework allowed us to simultaneously estimate the (fixed) effects of tree size (TS), climate normals (means of 1952–1981; CN), continentality (Cont), and annually varying seasonal climate (CA) on the annual growth RW, as well as account for unexplained variation between samples and locations (via random intercept and random slope terms). Because these variables potentially influence each other concerning their effect on RW, we also allowed for various interactions. The model has the form:

$$RW_{p,s,t} \sim \beta_0 + \beta_1 TS_{p,s,t-1} + \beta_{2i} CN_{i,p} + \beta_{3i} CN_{i,p} \times TS_{p,s,t-1} + \beta_4 CN_{1p}$$
$$\times CN_{2p} + \beta_{5j,k} CA_{j,k,p,t} + \beta_{6k} CA_{1,k,p,t} \times CA_{2,k,p,t} + \beta_{7i,j,k} CN_{i,p}$$
$$\times CA_{j,k,p,t} + \beta_{8j,k} Cont_p \times CA_{j,k,p,t} + \beta_{9j,k} CN_{1p} \times CN_{2p} \times CA_{j,k,p,t}$$
$$+ \beta_{10j,k} CN_{1p} \times Cont_p \times CA_{j,k,p,t} + \beta_{11j,k} CN_{2p} \times Cont_p \times CN_{2p}$$
$$+ \beta_{12j,k} CN_{1p} \times CN_{2p} \times Cont_p \times CA_{j,k,p,t} + \gamma_{0p,s} + \gamma_{1p,s} TS_{p,s,t-1} + \varepsilon_{p,s,t},$$

where RW of sample s in year t is nested in plot p. $RW_{p,s,t}$ is influenced by $TS_{p,s}$ of the preceding year $t-1$, climate normals $CN_{i,p}$

(climate normals of 1952–1981 that are constant and hence do not include the time index t), annually varying seasonal climate variables $CA_{j,k,p,t}$ (specific to each year t), and random effects γ_0 and γ_1 specific to each sample s nested within each sampling location p. TS is the age-specific cumulative diameter at breast height (DBH) of each sample derived from subtracting twice the RWs from the measured DBH at the time of sampling. When DBH information was missing, TS was summed from the first radial increment, assuming the first measured growth ring originates at the pith ($TS_a = 0$). This fixed effect (TS) serves the same purpose as the dendrochronological practice of detrending and accounts for the growth variability associated with increasing TS. The index i in CN varies from one to two, specifying MAT and mean annual CWB. The index j in CA specifies two climate variables—mean maximum temperature and CWB (precipitation sum minus potential evapotranspiration; where the latter was calculated following Droogers and Allen 2002). The index k specifies eight 2-month seasons, beginning with the previous year's May and June, July and August, up to current year's July and August (noting that the winter period, from previous November to current year February, is a 4-month season because initial model trials showed very similar shapes of the parameters). $Cont_p$ is a measure of continentality and was calculated as the mean difference between July and January mean maximum temperatures over the 1952–1981 period (Noce et al. 2020). It allows for the systematic adjustment of climate sensitivities based on the annual temperature amplitude of each site in our model. We included this term after early model trials showed an improvement in model fit in the SW and SE Europe regions. The scalars β_0, β_1, and β_4 and the vectors $\beta_{2-3,5-12}$, along with the random effects γ_0 and γ_1 are regression parameters estimated by the model.

The influences of TS (β_1) and climate normals CN_i (β_2) on RW were fit using natural cubic splines with a B-spline basis and 2 degree of freedom, with the knot placed at the median (de Boor 1978). Only the linear terms of CN_i were used in β_4. We also included only linear terms for the time-varying seasonal climate variables $CA_{j,k}$ to limit model complexity. These terms (β_{5-6}) capture the plastic response of tree growth to local interannual climate variation. To capture variability across environmental gradients in size-related trends of radial increments, we specified interactions between TS and each of the two CN_i variables (β_3). Expecting climate sensitivity to vary across populations growing under different climatic conditions (Fritts et al. 1965), we also included (two-, three-, and four-way) interactions between CN_i, $Cont_p$, and $CA_{j,k}$ variables (β_{7-12}). These interaction terms (particularly between CN_i and $CA_{j,k}$) capture spatial variation in climate sensitivities driven by variation in MAT and MAP—that is, the growth limiting factors. Only the linear terms of CN_i were used in these three- and four-way interactions. Because of moderately high variance inflation factors (6–8) in early model trials, we also included only the linear term of MAT in the interaction with CWB.

Two kinds of random effects, $\gamma_{0p,s}$ and $\gamma_{1p,s} TS_{p,s,t-1}$, were included for each sample nested within a sampling location. The first is an intercept modification, $\gamma_{0p,s}$, capturing variation in the average RW among sites and samples within sites, caused by unquantified factors such as stand density, soil-, or microsite conditions. The second term, $\gamma_{1p,s} TS_{p,s,t-1}$, is a random slope modification of

the effect of TS, capturing the degree to which the shape of the size-related trend in absolute RWs is influenced by (unquantified) tree- and site-specific factors, adding further flexibility to this detrending analog. These two terms, the random intercept modification and random modification of the influence of TS, have the added benefit that they adjust for error associated with the assumption that the first ring of each time series starts at pith when DBH information is missing. To account for the high variation in per-site replication, we also applied a weighting scheme equal to the inverse square root of the site-specific sample replication, thereby relatively down-weighting heavily replicated sites (> 20 samples) compared to sparsely replicated sites with only 1–5 samples (Klesse et al. 2020).

Because ring-width variability is proportional to the mean RW, we log-transformed the response variable, requiring the transposition of all ring-width values by +0.01 mm to accommodate non-positive (zero) values—that is, missing rings. The model was implemented using the *lme4* package (Bates et al. 2015) in R version 4.3.1; (R Core Team 2023). All predictor variables were normalized to a mean of zero and a standard deviation of one. During the model fitting, we kept track of collinearity in the model predictors and removed interactions with variance inflation factors above 8 (Table S2).

2.4 | Model Calibration and Verification

We evaluated model performance (fit to data), that is, the ability of the model to reproduce temporal (interannual) variability by calculating Pearson correlation coefficients between observed vs. predicted ring-width time series at the regional scale (see supervised-organizing mapping [SOM] clustering above). We defined regions primarily to better visualize the model projections and because regional-scale chronologies have much less individual- and stand-related noise that could mask climate–growth relationships (Klesse et al. 2020).

Focusing on the ability of the model to predict high-frequency, that is, the climate-driven variation in RWs, we divided each observed raw ring-width time series by the (back-transformed) growth curve predicted by the model (including all fixed and random effects), holding all time-varying climate variables (CAs) constant at their site-specific median. This is analogous to the standard dendrochronological practice of detrending (Klesse et al. 2020), that is, the effect of TS changing over time is removed. Predicted (back-transformed) ring-width time series were generated with the same model, with a constant stem DBH of 30 cm (the median cumulative DBH in our dataset) and including interannual climate variability (CAs). Before averaging these observed and predicted time series with Tukey's bi-weight robust mean to form separate region-level chronologies, each individual series was divided by its mean to dampen possible low-frequency distortions in the site-level chronology due to changing sample replication over time.

Finally, we complemented Pearson correlations with calibration-verification trials. Reduction of error (RE) and coefficient of efficiency (CE) statistics (Cook, Briffa, and Jones 1994) were used to evaluate prediction of the full model separately during the 1952–1981 and 1982–2011 periods, where values < 0 indicate limited predictive skill and hence low confidence in model predictions. We chose 2011 as the end of the verification period because of a rapid drop in sample replication afterward. We also calculated the Kling–Gupta efficiency score (KGE, Gupta et al. 2009) across the 1952–2011 period. The KGE is a diagnostic decomposition of CE, facilitating the analysis of the relative importance of its different components (correlation, bias, and variability).

To visualize the climate sensitivities estimated by the model, we calculated the relative sensitivity of radial growth increments to a change in each variable CA_j (CWB or mean maximum temperature) for each season k by increasing the focal $CA_{j,k}$ by 50 mm or 1°C, respectively, holding all other seasonal $CA_{j,k}$ values as well as *TS* constant at their median. 50 mm or 1°C are roughly equivalent to the mean standard deviation of CWB and T_{max}, respectively, across all seasons and sites.

2.5 | Projection of Future Growth

We projected future growth of an average-sized tree (constant DBH of 30 cm) based on the fixed effects of the linear mixed-effects models described above. Model projections used near-term (2021–2050) future values of $CA_{j,k}$ variables. Projected changes in growth were calculated as a percent change compared to the modeled 1952–2011 mean growth rate (also with a constant DBH of 30 cm) at each sampling site; hence, we report *relative* growth change. We used the EU-Forest dataset, a gridded 1×1 km product harmonizing forest plot surveys from National Forest Inventories (Mauri, Strona, and San-Miguel-Ayanz 2017), to spatially extrapolate the beech sites responding positively to climate change across space and sum up their area relative to the entire potential distribution (Q3). Therefore, we regressed the projected growth change at our sites against MAP (linear term) and MAT (quadratic term) and derived the line where the interpolation changes from positive to negative, that is, the energy-vs-water limitation boundary. Based on the combination of historic MAP and MAT values of the Mauri, Strona, and San-Miguel-Ayanz (2017) grid points, we classified them as energy-limited (above the boundary line) or water-limited (below the boundary line).

3 | Results

3.1 | Model Output and Performance

We found the highest average radial growth rates (4.3 mm/year) for a tree of 30 cm in diameter in the mild oceanic climates of NW-Europe (France, UK, Belgium; Figure 2). The lowest average growth rates (< 1 mm/year) were observed at cooler high-elevation sites in mountainous regions of the Alps and Carpathians. Across the distribution of beech, the model adequately reproduced past interannual growth variability; it explained overall 58.8% of the high-frequency variance of the data (Table S2). The median correlation between modeled and observed regional growth variability was $r = 0.75$ and ranged from $r = 0.63$ in south-eastern Europe and $r = 0.56$ in the high-elevation cluster of eastern Europe to $r = 0.86$ in central-NW Europe (Figure 3). Using the full model, all RE and CE statistics are positive, except the late-verification period of the
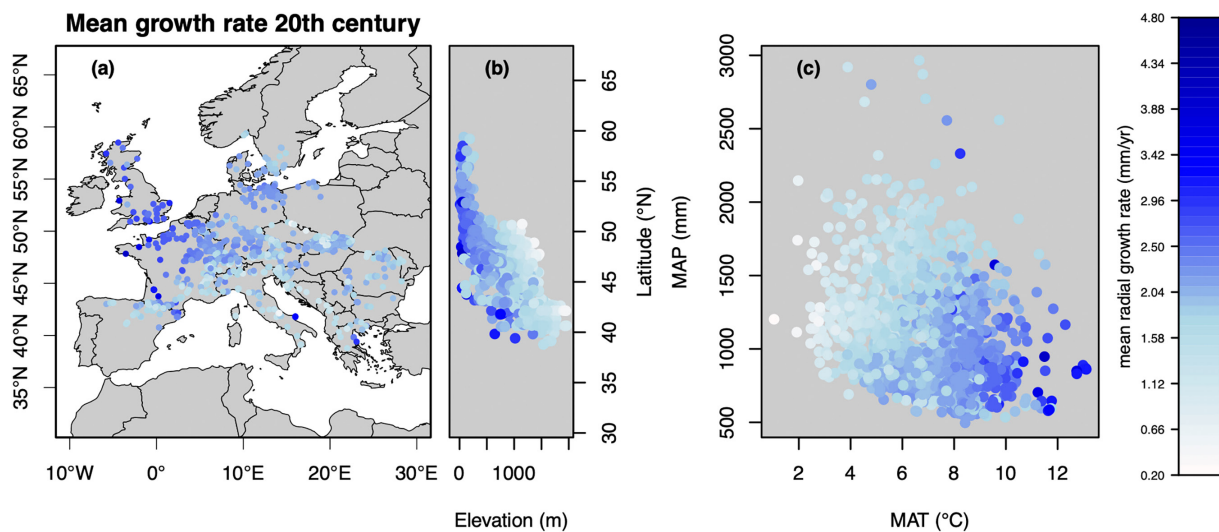
FIGURE 2 | Modeled mean growth rate for a simulated beech tree of 30 cm in diameter during the 1952–2011 calibration period across Europe (a), across latitude and elevation (b), and across climate space (means of 1952–1981) (c). MAT = Mean annual temperature, MAP = mean annual precipitation sum. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

high-elevation cluster of Eastern Europe (RE: +0.21, CE: −0.23; Table S3).

3.2 | Climate Sensitivities

Wetter-than-average seasons appeared to be beneficial for growth across beech's distribution and across seasons (Figure 4; Figures S2 and S3). The most important season of influence regarding CWB is May–June of the same growing season, followed by May–June of the previous year and July–August of the same growing season (Q1). All of these seasonal effects are strongest in the warmest and driest places (Figure 4; Q2). Increased temperatures have a variable effect on growth but tend to negatively impact growth. The strongest negative effect of increased temperatures is in July–August of the previous year, with negative effects across the entire distribution (Figure 5). However, warmer-than-average winter (previous November to February) temperatures positively affect growth. There is a clear gradient in the growth response to higher temperatures, with sites in colder locations responding more positively to increasing temperatures. This even leads to a switch in response sign from colder to warmer MAT at around 6°C MAT (Figure 5c,d), where trees in the coldest locations benefit from higher temperatures. The warmer and drier the location, the higher the sensitivity of trees to an increase in CWB (Figure 4).

Geographically, growth sensitivity to variations in CWB is strongest in NW-Central Europe, whereas temperature sensitivity is highest (most negative) in the Mediterranean region (Q1).

3.3 | Growth Projection

Considering a moderate and currently realistic climate change scenario (CMIP6, SSP2-4.5), European beech growth is projected

to decrease over the period 2021–2050 relative to the calibration period (1952–2011) across most of its distribution area. In Central and Western Europe, the model projects a growth decrease of 12%–18% (range of values represents the interquartile range; Q3), in the Mediterranean region of 11%–21% (Figure 6a, Figure 7), peaking at a 30% growth decrease at the most extreme sites. Notably, also in the northernmost region, growth is projected to decrease by 6%–14%.

In contrast, beech forests growing historically (1951–1980) below a MAT of about 6°C are mostly projected to benefit from climate warming (Figure 6c). The model predicts a growth increase of 3%–24% in the high-elevation clusters of the Alps and Carpathian Arc, with some sites predicted to increase by > 50% (Figures 6c and 7). However, the area where beech growth is projected to benefit from global warming only comprises around 13% of beech's current distributional range and is limited to the high-elevation sites in Central Europe and the Carpathians (Q3; Figure S6).

4 | Discussion

Our study showed that across almost its entire distribution, beech growth is water-limited primarily by summer drought and heat. This widespread drought sensitivity was shown previously (Cavin and Jump 2017; Hacket-Pain et al. 2016; Martinez del Castillo et al. 2022), but our comprehensive study now reveals that northernmost populations will not benefit as previously expected (Q4). Opposite to expectation, we find that only at 13% of beech's current occurrence, areas restricted to higher elevations and colder temperatures, climate warming is projected to be beneficial to growth.

To our knowledge, our study provides for the first time a threshold of MAT at 6°C–7°C, above which beech radial tree growth gradually switches from energy limitation to water limitation (Q2; Figure 5; Figures S4 and S5), independent from latitude or
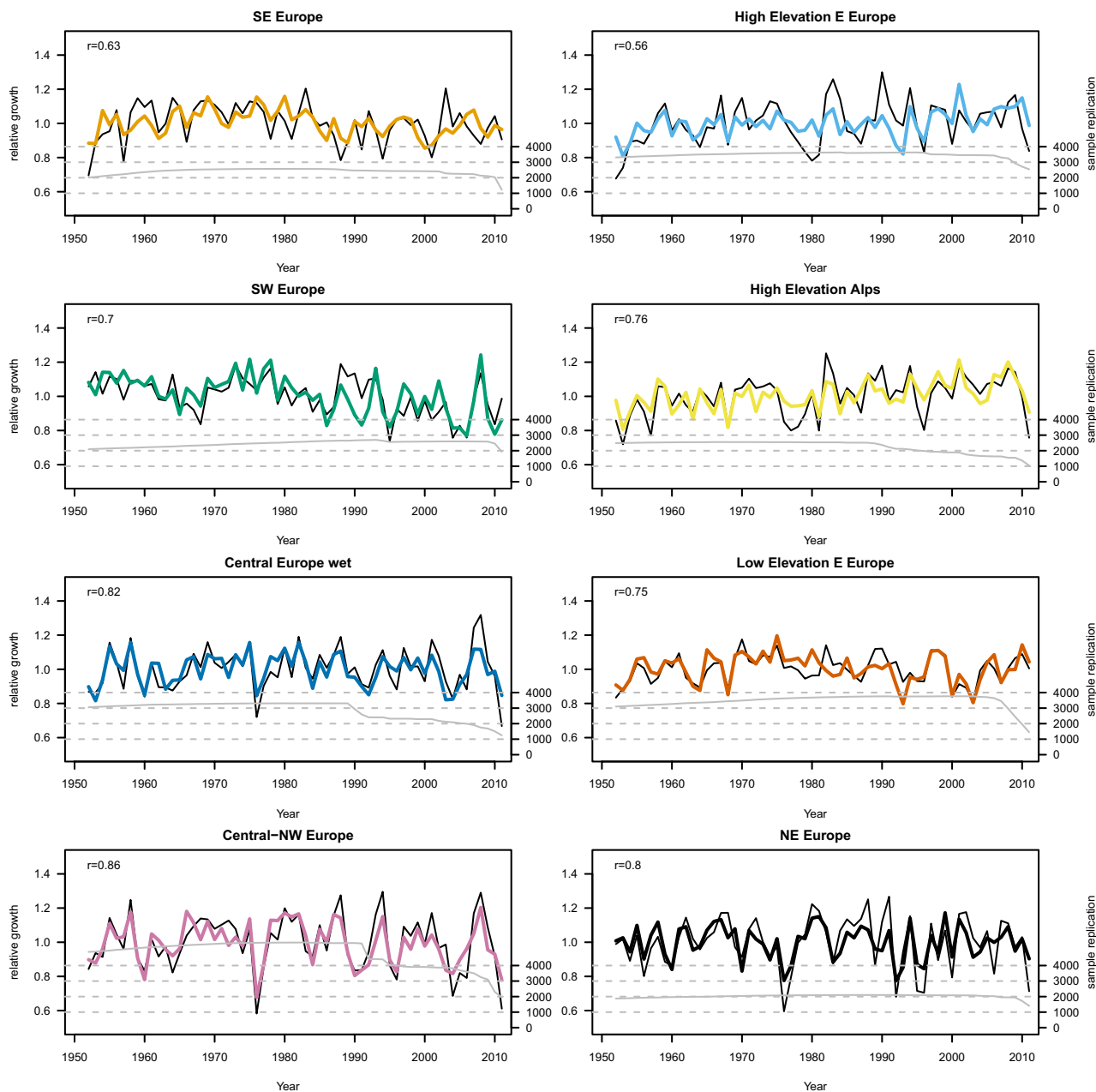
FIGURE 3 | Time series of modeled (color) and observed (black) average regional ring-width indices. Pearson correlation coefficients (*r*) between modeled and observed time series over the 1952–2011 are reported. The sample replication per regional cluster is shown in gray.

elevation. This finding aligns very well with the regional clustering, where the warm edge of the two high-elevation clusters runs at 6°C MAT (Figure 1). These MAT values are equivalent to mean monthly maximum temperatures in May–June of 14°C–17°C (range depends on continentality and moisture availability) or average July–August temperatures between 17°C and 20°C. The beneficial nature of global warming for cooler sites might thus be considered temporary, should warming exceed these above-mentioned thresholds. In all other places, where beech currently dominates forests in Europe, increasing temperatures and the concomitant increase in atmospheric and soil dryness will likely lead to reduced radial growth and hence forest productivity.

4.1 | No Growth Enhancement at the Poleward Leading Edge

Predictions from species distribution models of how species will respond to climate change often assume that variation in growth rates across spatial climatic gradients predicts how individual occurrence and populations will respond to climate change through time (Adler, White, and Cortez 2020). Similar to what was shown previously for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco; Klesse et al. 2020) and Ponderosa pine (*Pinus ponderosa* s.l.; Perret, Evans, and Sax 2024), absolute growth rates of European beech are currently highest on the warm side of the species' distribution, whereas growth
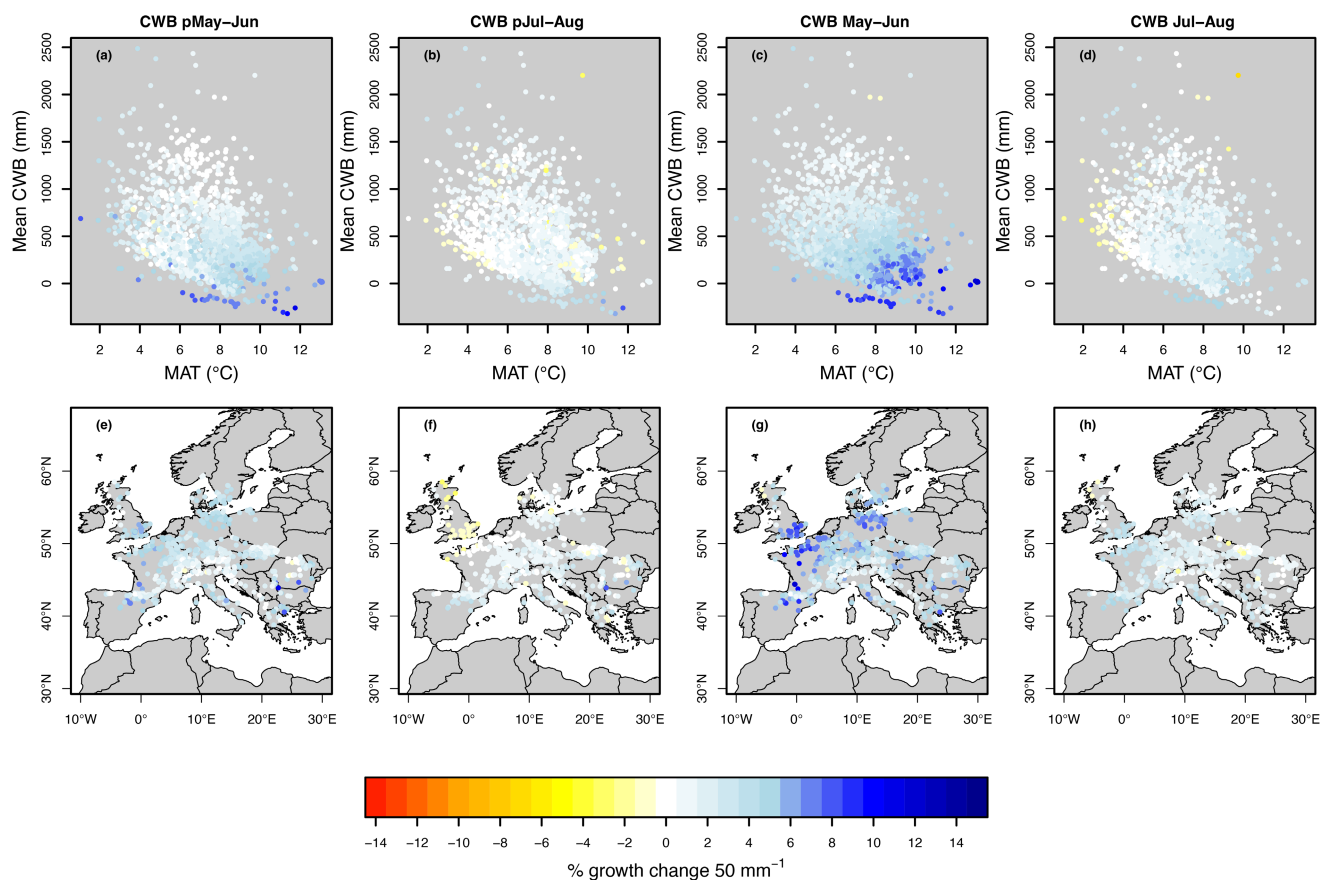
FIGURE 4 | Sensitivity (% growth change) of beech growth to seasonal climatic water balance (CWB) as a function of mean annual temperature (MAT) and mean annual climatic water balance (Mean CWB) (a–d) and across Europe (e–h). Increased growth in response to an increase in CWB of 50 mm is shown in blue; negative changes are yellow. 50 mm roughly corresponds to the average standard deviation of climatic water balance across all seasons and sites. Sensitivities across all seasons are shown in Figures S2 and S3. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

sensitivity to temporally varying temperatures is more negative at warmer sites. Our study thus contributes to the growing body of literature showing that spatial gradients in growth rates are independent of and often opposed to the gradient of climate sensitivity and that simple space-for-time approaches, as they are often used in species distribution models, can lead to severely misleading projections of increased growth with climate change (Perret, Evans, and Sax 2024; Yue et al. 2023).

There are several dendrochronological studies that use latitudinal gradients as the basis for expectations about climate growth response patterns, where latitude is used as a proxy for temperature-related changes in climate sensitivity (e.g., Cavin and Jump 2017; Chagnon et al. 2023; Henttonen et al. 2014; Huang et al. 2010). When assessed in a qualitative way, this latitude-for-temperature substitution often holds true. However, when a geographic predictor such as latitude, longitude, or elevation is included quantitatively as a linear predictor, care must be taken that such a relationship with a climate variable is stable over the application domain. Contrary to a previous study (Martinez del Castillo et al. 2022), we show that there is little chance for growth increases due to climate warming in the northernmost poleward edge of the distribution of beech (Q3; Figure 6). Whereas Martinez del Castillo et al. (2022) projected clear growth increases in southern

Scandinavia (Denmark, Sweden, and Norway), our model shows that beech is still water-limited in this region (Figure 5; Figures S2 and S3). One possible explanation is that Martinez del Castillo et al. (2022) used latitude, elevation, and de Martonne's aridity index as spatial predictors of climate sensitivity, whereas this study employs MAT, mean CWB, and climatically derived continentality and their interactions. Latitude and elevation are ecologically rather indirect predictors to include with a linear term as a proxy for mean climate conditions describing growth limiting factors across large scales. In our network across Europe, these linear geographic rather than climatic predictors create a systematic cold bias at northern latitudes and hence lead to overestimated temperature sensitivity (Figures S7 and S8). Further, the Gulf Stream causes western coastal sites to be 1°C–2°C warmer compared to continental eastern sites at the same latitude and elevation. We show how these effects in combination can create a bias, and we therefore advise against the use of geographical predictors (latitude, longitude, and elevation) for climate sensitivity estimation in large-scale studies. Directly using downscaled MAT and CWB (or other climatic variables relevant for tree growth) can be much more readily physiologically and mechanistically translated and thus should be superior variables when modeling radial growth. We thus see little chance that tree growth at the poleward leading edge can notably
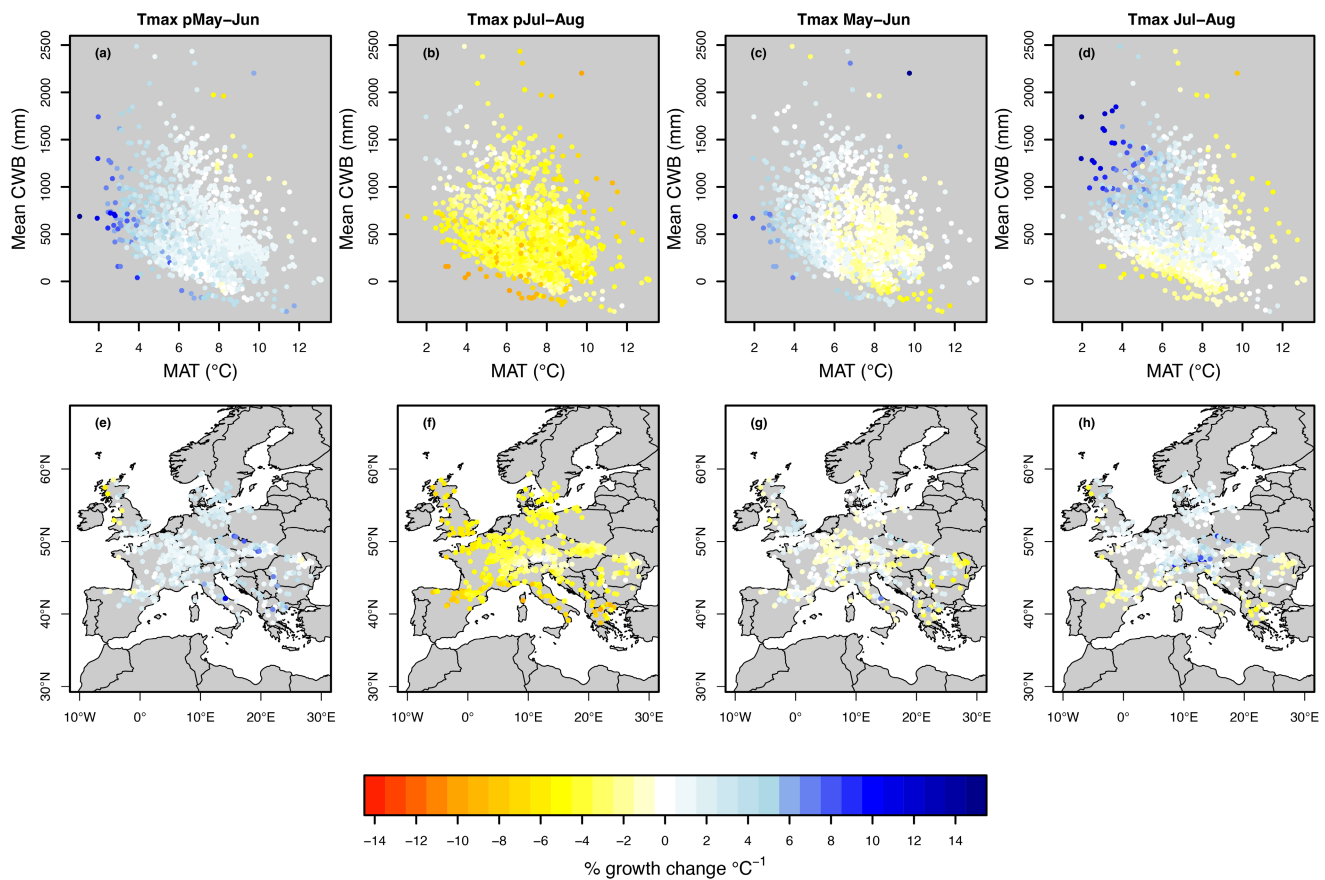
FIGURE 5 | Sensitivity (% growth change) of beech growth to seasonal maximum temperatures (T_{max}) as a function of mean annual temperature (MAT) and mean annual climatic water balance (Mean CWB) (a–d) and across Europe (e–h). Increased growth in response to an increase in T_{max} of 1°C is shown in blue; negative changes are yellow. 1°C roughly corresponds to the average standard deviation of maximum temperature across all seasons and all sites. Sensitivities across all seasons are shown in Figures S4 and S5. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

increase under any future climate change scenario that predicts increasing water deficits. Hypothetically, in more northwestern and coastal locations of isolated beech populations in Norway, higher annual CWB or precipitation sums could allow growth to be less water-constrained, and thus, beech might benefit from warmer projected temperatures in these specific locations.

When considering a north- and northeastward expansion of beech as compensation for productivity and potential range losses in the center and southern part of the distribution, our study dampens expectations because of the observed drought sensitivity of the relatively dry northern and northeastern study sites in our dataset. In a more local study from central to northeastern cold-marginal beech populations, Weigel et al. (2018) pointed out both summer drought and winter cold limitations along this gradient. Thus, radial growth in potential leading edge populations in this area may face two limiting stressors in the future, that is, summer drought and periods of extreme winter cold (Ringgaard et al. 2020). However, tree establishment, that is, germination success and survival, was shown to be strongly positively correlated with winter temperatures and minimum May temperatures (Muffler et al. 2021). More generally, warmer temperatures (Klopčič, Rozman, and Bončina 2022) and a moister climate increases seedling density (Silva et al. 2012).

Concluding, while climate warming might not benefit radial growth rates in northern and northeastern populations, the effect on establishment is very likely to be seen positively.

4.2 | Climate Sensitivity to Drought

We found the highest growth sensitivity to variability in May–June CWB of the same growing season, when cell division and enlargement peak (Q1; Etzold et al. 2022; van der Maaten et al. 2018; Zweifel et al. 2021). The sensitivity is highest in the warmest and driest areas and much weaker in cool and moist places with mean CWB above 1000 mm (Figure 4), underlining the potentially important role of soil moisture and high water vapor pressure deficit (VPD) for turgor pressure to enable and facilitate wood formation processes (Q2; Cabon et al. 2022; Peters et al. 2021). Among the warmest and driest sites in our dataset are the low elevation sites in central to northern Europe, with annual precipitation sums well below 750 mm, in extreme cases even below 600 mm, and MATs above 8°C (Weigel et al. 2023). The recent negative growth trends in northern Central Europe were shown to be strongest in regions with < 350 mm growing season precipitation (or about 660 mm MAP, Knutzen et al. 2017; Leuschner et al. 2023; Weigel et al. 2023). This contrasts with SW and
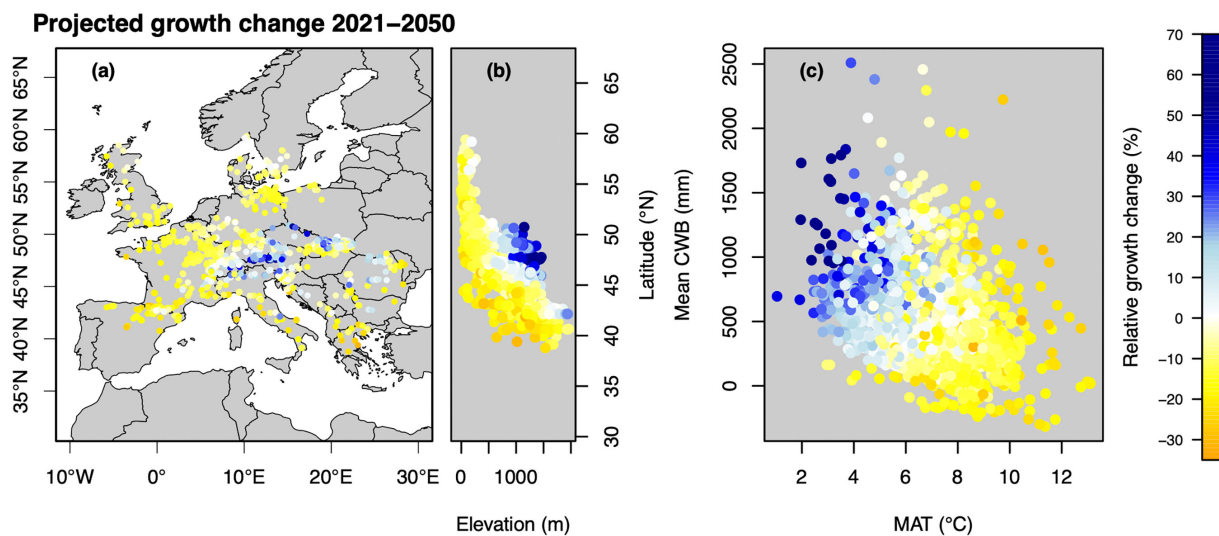
FIGURE 6 | Projected mean growth 2021–2050 relative to baseline growth during the 1952–2011 calibration period across Europe (a), across latitude and elevation (b), and across climate space (c). Map lines delineate study areas and do not necessarily depict accepted national boundaries.
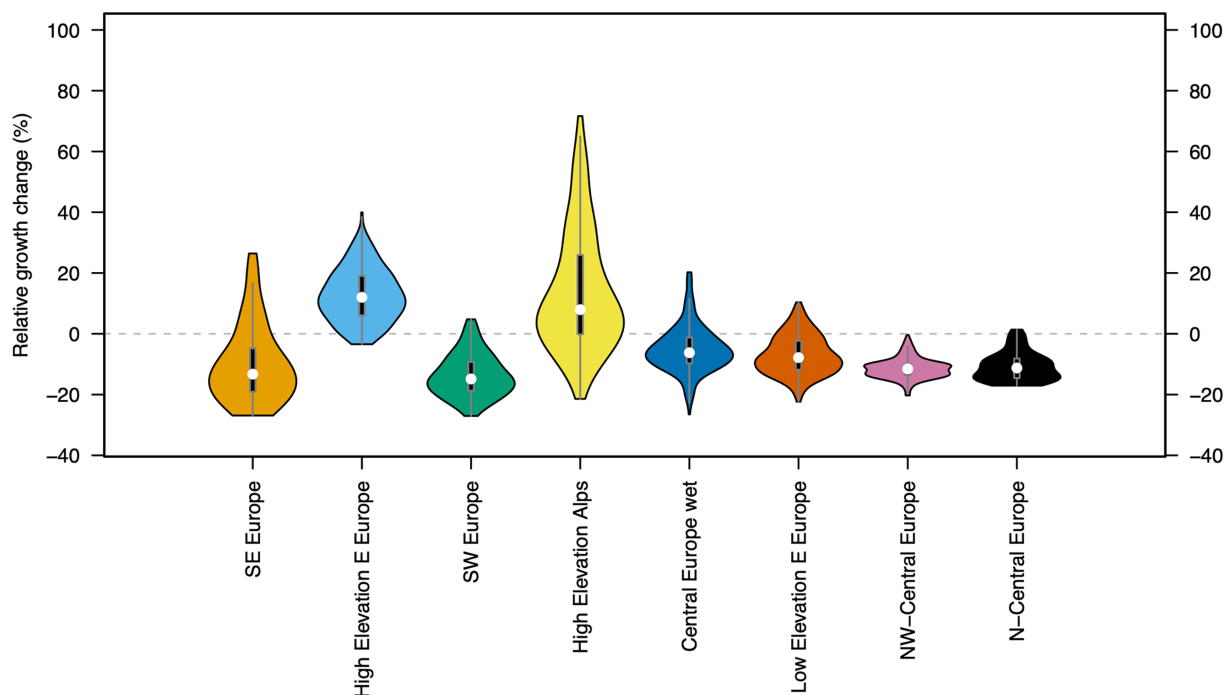

FIGURE 7 | Kernel density distributions of regional projected relative growth changes for the 2021–2050 period compared to 1952–2011 mean growth rates assuming SSP2-4.5 emission scenario. The boxes represent the interquartile range of the distributions, and the whiskers extend to 1.5 times the interquartile range. White circles represent the median of the distributions.

SE Europe, where most beech sites are situated in cooler and wetter higher elevation sites (Figure 5; Figures S4 and S5; Table 1). This could explain why drought sensitivity of beech is among the highest in the center of its geographical distribution and not as often assumed only at the (geographical) rear edge in the Mediterranean region (Q1; Cavin and Jump 2017, Muffler et al. 2020). Moreover, these rear edge sites may be particularly rich in high-quality habitats for beech owing to small-scale environmental variation (e.g., topography, edaphic factors, and vegetation structure) buffering their lower climatic suitability (Vilà-Cabrera and Jump 2019; Bert

et al. 2022). Another reason could be that marginal southern beech populations growing in a warmer and drier climate have developed higher plasticity-induced resistance to embolism than those from northern Europe growing in more favorable conditions (Stojnić et al. 2018).

We interpret the similar (but slightly weaker) responses to May–June CWB and May–June temperature of the previous year (Figure S4) as a statistically integrated biological memory and carry-over effect of our model taking care of some of the positive auto-correlation in tree-ring time series (the climate memory,

as discussed in Peltier, Barber, and Ogle 2018). The strongest response to temperature alone was found in July–August of the previous year. In contrast to the above-mentioned lagged CWB effect interpretation, this is less likely to be a manifestation of auto-correlation. Firstly, in July–August, across most of beech's distribution, most of the tree ring is usually already formed (Etzold et al. 2022; Salomón et al. 2022; Martinez del Castillo et al. 2016; Michelot et al. 2012; van der Maaten, van der Maaten-Theunissen, and Spiecker 2012). For this reason, any climate effect in a season without substantial growth cannot contribute much to the observed auto-correlative characteristics of radial growth (but see Ježík et al. 2021 for a temperature-limited high-elevation site in Slovakia where beech grows well into July). Secondly, the response looks different than that of July–August of the current year, which shows a mean temperature-related switch to positive sensitivity at the coldest locations, making it unlikely to be related to auto-correlation. For it to be a manifestation of climatically caused auto-correlation, the response patterns of the two seasons (current and previous year) should look similar. The most plausible explanations are that warmer-than-average temperatures in peak summer increase fruit production in the coming year, redistributing carbon allocation away from wood production to reproduction in the following year (Hacket-Pain et al. 2018; Nussbaumer et al. 2021), or contribute to spending or depletion of non-structural carbohydrates through respiration or bud formation, or even lead to embolisms that reduce the water-conducting area and hydraulic capacity in the following year (Arend et al. 2022).

4.3 | Caveats

Although we gathered an unprecedentedly rich tree-ring dataset for a single European tree species, the network is far from being perfect. Compared to the site and sample replication in Central Europe, it has a far lower replication density in the mountainous and climatically heterogeneous south-eastern Europe (Italy and the Balkans; see also the large range of projected growth changes in Figure 7 in this region). In our model, this imbalance is reflected in the lowest coefficients of determination of all regions. Further, the high-elevation cluster of Eastern Europe has a negative CE in the late-verification period. The growth projections in these two regions are hence associated with the highest uncertainties. Future modeling and sampling endeavors should focus on these two regions, as well as the generally under-sampled warmest populations, relying on a denser and better-replicated network to reduce uncertainties in the climate response and future projected growth trajectories. The dataset also does not cover well the most recent period (2015–2022), which contained several exceptional summer droughts in Central and Southern Europe with large consequences for tree health (Buras, Rammig, and Zang 2020; Schuldt et al. 2020; van der Woude et al. 2023). A continued updating, expansion, and densification of the beech tree-ring network is desired, but these efforts need to be accompanied by a continued contribution to public data repositories (Babst et al. 2021) by data producers.

4.4 | Outlook: Where to Go From Here

Over the past decade, it has become more and more evident that soil moisture is a crucial factor for wood formation since it is a direct measure of water potential and turgor pressure needed for cell enlargement and division (Fatichi, Leuzinger, and Körner 2014; Kannenberg et al. 2024; Peters et al. 2021). The critical role of microsite conditions—likely characterized by differences in soil water availability—has been shown previously to account for differences in the sensitivity of radial growth to interannual variations in precipitation (Klesse et al. 2018; Schmied et al. 2023). A logical next step in the refinement of statistical growth models would thus be the incorporation of soil moisture, together with other microclimate-, stand structure-, or management-related information that has been shown to affect climate sensitivity of tree growth (Buras et al. 2018; del Río et al. 2017). However, a primary challenge to informing soil-moisture models will be the quality and resolution of large-scale soil data, which can range from $0.5 \times 0.5°$ (Global level, Wang-Erlandsson et al. 2016) to 1×1 km (European level: e.g., Hiederer 2013; global level: Fischer et al. 2008) resolution. Another challenge is the lack of precise site coordinates for samples collected before the widespread availability of GPS, that is, all data collected before and during the early 2000s.

We encourage joint community efforts to continuously collect and compile species-distribution-wide tree-ring datasets and the resulting accompanying analyses to gain insights into gradients, thresholds, and magnitudes of climate sensitivities and the intricate interplay of energy versus water limitation on radial tree growth. Such datasets and analyses are in our view invaluable calibration targets for improving next-generation vegetation models with dedicated wood formation modules. Cross-disciplinary model-data-fusion efforts are hence needed to better constrain the future trajectory of the forest carbon sink.

Author Contributions

Stefan Klesse: conceptualization, data curation, formal analysis, software, validation, funding acquisition, investigation, methodology, visualization, writing – original draft. **Richard L. Peters:** investigation, methodology, conceptualization, writing – review & editing. **Raquel Alfaro-Sánchez:** investigation, writing – review & editing. **Vincent Badeau:** investigation, writing – review & editing. **Claudia Baittinger:** investigation, writing – review & editing. **Giovanna Battipaglia:** investigation, writing – review & editing. **Didier Bert:** investigation, writing – review & editing. **Franco Biondi:** investigation, writing – review & editing. **Michal Bosela:** investigation, writing – review & editing. **Marius Budeanu:** investigation, writing – review & editing. **Vojtěch Čada:** investigation, writing – review & editing. **J. Julio Camarero:** investigation, writing – review & editing. **Liam Cavin:** investigation, writing – review & editing. **Hugues Claessens:** investigation, writing – review & editing. **Ana-Maria Cretan:** investigation, writing – review & editing. **Katarina Čufar:** investigation, writing – review & editing. **Martin de Luis:** investigation, writing – review & editing. **Isabel Dorado-Liñán:** investigation, writing – review & editing. **Choimaa Dulamsuren:** investigation, writing – review & editing. **Josep Maria Espelta:** investigation, writing – review & editing. **Balazs Garamszegi:** investigation, writing – review & editing. **Michael Grabner:** investigation, writing – review & editing. **Jozica Gricar:** investigation, writing – review & editing. **Andrew Hacket-Pain:** investigation, writing – review & editing. **Jon Kehlet Hansen:** investigation, writing – review & editing. **Claudia Hartl:** investigation, writing – review & editing. **Andrea Hevia:** investigation, writing – review & editing. **Martina Hobi:** investigation, writing – review & editing. **Pavel Janda:** investigation, writing – review & editing. **Alistair S. Jump:** investigation,

writing – review & editing. **Jakub Kašpar:** investigation, writing – review & editing. **Marko Kazimirović:** investigation, writing – review & editing. **Srdjan Keren:** investigation, writing – review & editing. **Juergen Kreyling:** investigation, writing – review & editing. **Alexander Land:** investigation, writing – review & editing. **Nicolas Latte:** investigation, writing – review & editing. **François Lebourgeois:** investigation, writing – review & editing. **Christoph Leuschner:** investigation, writing – review & editing. **Mathieu Lévesque:** investigation, writing – review & editing, funding acquisition. **Luis A. Longares:** investigation, writing – review & editing. **Edurne Martinez del Castillo:** investigation, writing – review & editing. **Annette Menzel:** investigation, writing – review & editing. **Maks Merela:** investigation, writing – review & editing. **Martin Mikoláš:** investigation, writing – review & editing. **Renzo Motta:** investigation, writing – review & editing. **Lena Muffler:** investigation, writing – review & editing. **Anna Neycken:** investigation, writing – review & editing. **Paola Nola:** investigation, writing – review & editing. **Momchil Panayotov:** investigation, writing – review & editing. **Any Mary Petritan:** investigation, writing – review & editing. **Ion Catalin Petritan:** investigation, writing – review & editing. **Ionel Popa:** investigation, writing – review & editing. **Peter Prislan:** investigation, writing – review & editing. **Tom Levanič:** investigation, writing – review & editing. **Catalin-Constantin Roibu:** investigation, writing – review & editing. **Álvaro Rubio-Cuadrado:** investigation, Writing – review & editing. **Raúl Sánchez-Salguero:** investigation, writing – review & editing. **Pavel Šamonil:** investigation, writing – review & editing. **Branko Stajić:** investigation, writing – review & editing. **Miroslav Svoboda:** investigation, writing – review & editing. **Roberto Tognetti:** investigation, writing – review & editing. **Elvin Toromani:** investigation, writing – review & editing. **Volodymyr Trotsiuk:** investigation, writing – review & editing. **Ernst van der Maaten:** investigation, writing – review & editing. **Marieke van der Maaten-Theunissen:** investigation, writing – review & editing. **Astrid Vannoppen:** investigation, writing – review & editing. **Ivana Vašíčková:** investigation, writing – review & editing. **Georg von Arx:** investigation, writing – review & editing, funding acquisition. **Martin Wilmking:** investigation, writing – review & editing. **Robert Weigel:** investigation, writing – review & editing. **Tzvetan Zlatanov:** investigation, writing – review & editing. **Christian Zang:** investigation, writing – review & editing. **Allan Buras:** investigation, methodology, conceptualization, writing – review & editing.

Affiliations

[1]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland | [2]Oeschger Centre for Climate Change Research, Bern, Switzerland | [3]Department of Environmental Sciences, University of Basel, Basel, Switzerland | [4]Tree Growth and Wood Physiology, School of Life Sciences, Technical University of Munich, Munich, Germany | [5]Higher Technical School of Agronomic and Forestry Engineering and Biotechnology, University of Castilla-La Ancha, Albacete, Spain | [6]Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada, Edmonton, Alberta, Canada | [7]Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France | [8]Environmental Archaeology and Materials Science, National Museum of Denmark, Copenhagen, Denmark | [9]Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, University of Campania Luigi Vanvitelli, Caserta, Italy | [10]INRAE, University of Bordeaux, BIOGECO, Cestas, France | [11]Department of Natural Resources and Environmental Science, DendroLab, University of Nevada, Reno, Nevada, USA | [12]Technical University in Zvolen, Zvolen, Slovakia | [13]National Forest Centre, Zvolen, Slovakia | [14]National Institute for Research and Development in Forestry "Marin Dracea", Brasov, Romania | [15]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Praha-Suchdol, Czech Republic | [16]Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza, Spain | [17]Biological and Environmental Sciences, University of Stirling, Stirling, UK | [18]University of Liège – Gembloux Agro-Bio Tech – Forest Is Life, Gembloux, Belgium | [19]Faculty of Silviculture and Forest Engineering, Transilvania University of Brasov, Brasov, Romania | [20]Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia | [21]Department of Geography and Regional Planning, IUCA, University of Zaragoza, Zaragoza, Spain | [22]Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, Madrid, Spain | [23]Chair of Applied Vegetation Ecology, University of Freiburg, Freiburg, Germany | [24]CREAF, Bellaterra, Catalonia, Spain | [25]University of Natural Resources and Life Sciences Vienna, BOKU, Vienna, Austria | [26]Slovenian Forestry Institute, Ljubljana, Slovenia | [27]Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, UK | [28]Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark | [29]Nature Rings – Environmental Research and Education, Mainz, Germany | [30]Department of Plant Biology and Ecology, University of Sevilla, Sevilla, Spain | [31]Laboratorio DendrOlavide, Universidad Pablo de Olavide, Sevilla, Spain | [32]Department of Forest Ecology, The Silva Tarouca Research Institute, Brno, Czech Republic | [33]Faculty of Forestry, University of Belgrade, Belgrade, Serbia | [34]Faculty of Forestry, University of Agriculture in Krakow, Krakow, Poland | [35]Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany | [36]Institute of Biology (190a), University of Hohenheim, Stuttgart, Germany | [37]Plant Ecology and Ecosystems Research, University of Goettingen, Goettingen, Germany | [38]Silviculture Group, Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland | [39]Department of Geography, Johannes Gutenberg University, Mainz, Germany | [40]Department of Life Science Systems, Ecoclimatology, Technical University of Munich, Freising, Germany | [41]Department of Agricultural, Forest and Food Sciences (DISAFA), University of Turin, Turin, Italy | [42]Ecological-Botanical Garden, University of Bayreuth, Bayreuth, Germany | [43]Department of Earth and Environmental Sciences, University of Pavia, Pavia, Italy | [44]Faculty of Forestry at the University of Forestry, Sofia, Bulgaria | [45]National Institute for Research and Development in Forestry Marin Dracea, Voluntari, Romania | [46]Center for Mountain Economy (CE–MONT), Vatra Dornei, Romania | [47]Forest Biometrics Laboratory, Faculty of Forestry, "Stefan Cel Mare" University of Suceava, Suceava, Romania | [48]Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic | [49]Faculty of Agricultural, Environmental and Food Sciences, Free University of Bolzano/Bozen, Piazza Università, Bolzano, Italy | [50]Department of Forestry, Faculty of Forestry Sciences, Agricultural University of Tirana, Tirana, Albania | [51]Chair of Forest Growth and Woody Biomass Production, TU Dresden, Tharandt, Germany | [52]Vlaamse Instelling voor Technologisch Onderzoek NV, Mol, Belgium | [53]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria | [54]Institute for Ecology and Landscape, Weihenstephan-Triesdorf University of Applied Sciences, Freising, Germany | [55]Professorship for Land-Surface-Atmosphere Interactions, Technical University of Munich, Munich, Germany

Acknowledgments

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study and code to run the model, as well as the linear-mixed effects model output are openly available in Envidat at https://doi.org/10.16904/envidat.547. Future climate projections were taken from 10 Atmosphere-Ocean General Circulation Models (AOGCMs) of the CMIP6 multi-model ensemble. See supplemental table 1 for access details.

References

Adler, P. B., E. P. White, and M. H. Cortez. 2020. "Matching the Forecast Horizon With the Relevant Spatial and Temporal Processes and Data Sources." *Ecography* 43, no. 11: 1729–1739. https://doi.org/10.1111/ecog.05271.

Alfaro-Sánchez, R., A. S. Jump, J. Pino, O. Díez-Nogales, and J. M. Espelta. 2019. "Land Use Legacies Drive Higher Growth, Lower Wood Density and Enhanced Climatic Sensitivity in Recently Established Forests." *Agricultural and Forest Meteorology* 276–277: 107630. https://doi.org/10.1016/j.agrformet.2019.107630.

Arend, M., G. Hoch, and A. Kahmen. 2023. "Stem Growth Phenology, Not Canopy Greening Constrains Deciduous Tree Growth." *Tree Physiology* 44: tpad160. https://doi.org/10.1093/treephys/tpad160.

Arend, M., R. M. Link, C. Zahnd, G. Hoch, B. Schuldt, and A. Kahmen. 2022. "Lack of Hydraulic Recovery as a Cause of Post-Drought Foliage Reduction and Canopy Decline in European Beech." *New Phytologist* 234, no. 4: 1195–1205. https://doi.org/10.1111/nph.18065.

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, no. 1: 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, no. 3: 210–219. https://doi.org/10.1016/j.tplants.2020.10.002.

Badeau, V., J.-L. Dupouey, M. Becker, and J. F. Picard. 1995. "Long-Term Growth Trends of *Fagus sylvatica* L. in Northeastern France. A Comparison Between High and Low Density Stands." *Acta Oecologica* 16, no. 5: 571–583.

Bastos, A., P. Ciais, P. Friedlingstein, et al. 2020. "Direct and Seasonal Legacy Effects of the 2018 Heat Wave and Drought on European Ecosystem Productivity." *Science Advances* 6, no. 24: eaba2724. https://doi.org/10.1126/sciadv.aba2724.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no. 1: 1–48. https://doi.org/10.18637/jss.v067.i01.

Beguería, S., and S. M. Vicente-Serrano. 2023. "SPEI: Calculation of the Standardised Precipitation-Evapotranspiration Index." R package version 1.8.1 (Version 1.7) [Computer software]. https://CRAN.R-project.org/package=SPEI.

Bert, D., F. Lebourgeois, A. Ouayjan, A. Ducousso, J. Ogée, and A. Hampe. 2022. "Past and Future Radial Growth and Water-Use Efficiency of Fagus Sylvatica and Quercus Robur in a Long-Term Climate Refugium." *Dendrochronologia* 72: 125939. https://doi.org/10.1016/j.dendro.2022.125939.

Bosela, M., L. Kulla, J. Roessiger, et al. 2019. "Long-Term Effects of Environmental Change and Species Diversity on Tree Radial Growth in a Mixed European Forest." *Forest Ecology and Management* 446: 293–303. https://doi.org/10.1016/j.foreco.2019.05.033.

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.

Buras, A., A. Rammig, and C. S. Zang. 2020. "Quantifying Impacts of the 2018 Drought on European Ecosystems in Comparison to 2003." *Biogeosciences* 17, no. 6: 1655–1672. https://doi.org/10.5194/bg-17-1655-2020.

Buras, A., C. Schunk, C. Zeiträg, et al. 2018. "Are Scots Pine Forest Edges Particularly Prone to Drought-Induced Mortality?" *Environmental Research Letters* 13, no. 2: 025001. https://doi.org/10.1088/1748-9326/aaa0b4.

Cabon, A., S. A. Kannenberg, A. Arain, et al. 2022. "Cross-Biome Synthesis of Source Versus Sink Limits to Tree Growth." *Science* 376, no. 6594: 758–761. https://doi.org/10.1126/science.abm4875.

Camarero, J. J., M. Colangelo, A. Gazol, and C. Azorín-Molina. 2021. "Drought and Cold Spells Trigger Dieback of Temperate Oak and Beech Forests in Northern Spain." *Dendrochronologia* 66: 125812. https://doi.org/10.1016/j.dendro.2021.125812.

Cavin, L., and A. S. Jump. 2017. "Highest Drought Sensitivity and Lowest Resistance to Growth Suppression Are Found in the Range Core of the Tree *Fagus sylvatica* L. Not the Equatorial Range Edge." *Global Change Biology* 23, no. 1: 362–379. https://doi.org/10.1111/gcb.13366.

Chagnon, C., G. Moreau, L. D'Orangeville, J. Caspersen, J.-P. Labrecque-Foy, and A. Achim. 2023. "Strong Latitudinal Gradient in Temperature-Growth Coupling Near the Treeline of the Canadian Subarctic Forest."

RIGHTSLINK()

Frontiers in Forests and Global Change 6: 1–12. https://doi.org/10.3389/ffgc.2023.1181653.

Cook, B. I., J. E. Smerdon, R. Seager, and S. Coats. 2014. "Global Warming and 21st Century Drying." *Climate Dynamics* 43, no. 9: 2607–2627. https://doi.org/10.1007/s00382-014-2075-y.

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

Cook, E. R., K. R. Briffa, and P. D. Jones. 1994. "Spatial Regression Methods in Dendroclimatology: A Review and Comparison of Two Techniques." *International Journal of Climatology* 14, no. 4: 379–402. https://doi.org/10.1002/joc.3370140404.

de Boor, C. 1978. *A Practical Guide to Splines.* New York, NY, USA: Springer-Verlag. https://www.springer.com/de/book/9780387953663.

del Río, M., H. Pretzsch, R. Ruíz-Peinado, et al. 2017. "Species Interactions Increase the Temporal Stability of Community Productivity in *Pinus sylvestris–Fagus sylvatica* Mixtures Across Europe." *Journal of Ecology* 105, no. 4: 1032–1043. https://doi.org/10.1111/1365-2745.12727.

Di Filippo, A., F. Biondi, K. Čufar, et al. 2007. "Bioclimatology of Beech (*Fagus sylvatica* L.) in the Eastern Alps: Spatial and Altitudinal Climatic Signals Identified Through a Tree-Ring Network." *Journal of Biogeography* 34, no. 11: 1873–1892. https://doi.org/10.1111/j.1365-2699.2007.01747.x.

Dittmar, C., W. Zech, and W. Elling. 2003. "Growth Variations of Common Beech (*Fagus sylvatica* L.) Under Different Climatic and Environmental Conditions in Europe—A Dendroecological Study." *Forest Ecology and Management* 173, no. 1–3: 63–78. https://doi.org/10.1016/S0378-1127(01)00816-7.

Dorado-Liñán, I., B. Ayarzagüena, F. Babst, et al. 2022. "Jet Stream Position Explains Regional Anomalies in European Beech Forest Productivity and Tree Growth." *Nature Communications* 13: 1. https://doi.org/10.1038/s41467-022-29615-8.

Droogers, P., and R. G. Allen. 2002. "Estimating Reference Evapotranspiration Under Inaccurate Data Conditions." *Irrigation and Drainage Systems* 16, no. 1: 33–45. https://doi.org/10.1023/A:1015508322413.

Dulamsuren, C., M. Hauck, G. Kopp, M. Ruff, and C. Leuschner. 2017. "European Beech Responds to Climate Change With Growth Decline at Lower, and Growth Increase at Higher Elevations in the Center of Its Distribution Range (SW Germany)." *Trees* 31, no. 2: 673–686. https://doi.org/10.1007/s00468-016-1499-x.

Etzold, S., F. Sterck, A. K. Bose, et al. 2022. "Number of Growth Days and Not Length of the Growth Period Determines Radial Stem Growth of Temperate Trees." *Ecology Letters* 25, no. 2: 427–439. https://doi.org/10.1111/ele.13933.

Evans, M. E. K., R. J. 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, no. 3: 233–246. https://doi.org/10.1093/biosci/biab119.

Farahat, E., and H. W. Linderholm. 2018. "Growth–Climate Relationship of European Beech at Its Northern Distribution Limit." *European Journal of Forest Research* 137, no. 5: 619–629. https://doi.org/10.1007/s10342-018-1129-9.

Fatichi, S., S. Leuzinger, and C. Körner. 2014. "Moving Beyond Photosynthesis: From Carbon Source to Sink-Driven Vegetation Modeling." *New Phytologist* 201, no. 4: 1086–1095. https://doi.org/10.1111/nph.12614.

Fischer, G., F. Nachtergaele, S. Prieler, H. T. van Velthuizen, L. Verelst, and D. Wiberg. 2008. *Global Agro-Ecological Zones Assessment for Agriculture [Dataset].* Laxenburg, Austria: IIASA. FAO: Rome, Italy. https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/.

Frei, E. R., M. M. Gossner, Y. Vitasse, et al. 2022. "European Beech Dieback After Premature Leaf Senescence During the 2018 Drought in Northern Switzerland." *Plant Biology* 24, no. 7: 1132–1145. https://doi.org/10.1111/plb.13467.

Fritts, H. C., D. G. Smith, J. W. Cardis, and C. A. Budelsky. 1965. "Tree-Ring Characteristics Along a Vegetation Gradient in Northern Arizona." *Ecology* 46, no. 4: 393–401. https://doi.org/10.2307/1934872.

Gillerot, L., D. I. Forrester, A. Bottero, A. Rigling, and M. Lévesque. 2021. "Tree Neighbourhood Diversity Has Negligible Effects on Drought Resilience of European Beech, Silver Fir and Norway Spruce." *Ecosystems* 24, no. 1: 20–36. https://doi.org/10.1007/s10021-020-00501-y.

Gupta, H. V., H. Kling, K. K. Yilmaz, and G. F. Martinez. 2009. "Decomposition of the Mean Squared Error and NSE Performance Criteria: Implications for Improving Hydrological Modelling." *Journal of Hydrology* 377, no. 1: 80–91. https://doi.org/10.1016/j.jhydrol.2009.08.003.

Hacket-Pain, A. J., D. Ascoli, G. Vacchiano, et al. 2018. "Climatically Controlled Reproduction Drives Interannual Growth Variability in a Temperate Tree Species." *Ecology Letters* 21, no. 12: 1833–1844. https://doi.org/10.1111/ele.13158.

Hacket-Pain, A. J., L. Cavin, A. D. Friend, and A. S. Jump. 2016. "Consistent Limitation of Growth by High Temperature and Low Precipitation From Range Core to Southern Edge of European Beech Indicates Widespread Vulnerability to Changing Climate." *European Journal of Forest Research* 135, no. 5: 897–909. https://doi.org/10.1007/s10342-016-0982-7.

Hargreaves, G. 1994. "Defining and Using Reference Evapotranspiration." *Journal of Irrigation and Drainage Engineering* 120, no. 6: 1132–1139. https://doi.org/10.1061/(ASCE)0733-9437(1994)120:6(1132).

Harvey, J. E., M. Smiljanić, T. Scharnweber, et al. 2020. "Tree Growth Influenced by Warming Winter Climate and Summer Moisture Availability in Northern Temperate Forests." *Global Change Biology* 26, no. 4: 2505–2518. https://doi.org/10.1111/gcb.14966.

Henttonen, H. M., H. Mäkinen, J. Heiskanen, M. Peltoniemi, A. Laurén, and M. Hordo. 2014. "Response of Radial Increment Variation of Scots Pine to Temperature, Precipitation and Soil Water Content Along a Latitudinal Gradient Across Finland and Estonia." *Agricultural and Forest Meteorology* 198–199: 294–308. https://doi.org/10.1016/j.agrformet.2014.09.004.

Hiederer, R. 2013. *Mapping Soil Properties for Europe – Spatial Representation of Soil Database Attributes.* Luxemberg EUR26082EN Scientific and Technical Research Series, 47: Publications Office of the European Union. https://doi.org/10.2788/87286.

Huang, J., J. C. Tardif, Y. Bergeron, B. Denneler, F. Berninger, and M. P. Girardin. 2010. "Radial Growth Response of Four Dominant Boreal Tree Species to Climate Along a Latitudinal Gradient in the Eastern Canadian Boreal Forest." *Global Change Biology* 16, no. 2: 711–731. https://doi.org/10.1111/j.1365-2486.2009.01990.x.

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,* edited by V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou. Cambridge, United Kingdom: Cambridge University Press.

Ježík, M., M. Blaženec, P. Mezei, et al. 2021. "Influence of Weather and Day Length on Intra-Seasonal Growth of Norway Spruce (*Picea abies*) and European Beech (*Fagus sylvatica*) in a Natural Montane Forest." *Canadian Journal of Forest Research* 51, no. 12: 1799–1810. https://doi.org/10.1139/cjfr-2020-0067.

Kannenberg, S. A., W. R. L. Anderegg, M. L. Barnes, M. P. Dannenberg, and A. K. Knapp. 2024. "Dominant Role of Soil Moisture in Mediating Carbon and Water Fluxes in Dryland Ecosystems." *Nature Geoscience* 17: 38–43. https://doi.org/10.1038/s41561-023-01351-8.

Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the Earth's Land Surface Areas." *Scientific Data* 4, no. 1: 170122. https://doi.org/10.1038/sdata.2017.122.

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.

Kašpar, J., P. Šamonil, I. Vašíčková, D. Adam, and P. Daněk. 2020. "Woody Species-Specific Disturbance Regimes and Strategies in Mixed Mountain Temperate Forests in the Šumava Mts., Czech Republic." *European Journal of Forest Research* 139, no. 1: 97–109. https://doi.org/10.1007/s10342-019-01252-9.

Kašpar, J., J. Tumajer, P. Šamonil, and I. Vašíčková. 2021. "Species-Specific Climate–Growth Interactions Determine Tree Species Dynamics in Mixed Central European Mountain Forests." *Environmental Research Letters* 16, no. 3: 34039. https://doi.org/10.1088/1748-9326/abd8fb.

Klesse, S., F. Babst, S. Lienert, et al. 2018. "A Combined Tree Ring and Vegetation Model Assessment of European Forest Growth Sensitivity to Interannual Climate Variability." *Global Biogeochemical Cycles* 32, no. 8: 1226–1240. https://doi.org/10.1029/2017GB005856.

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, no. 9: 5146–5163. https://doi.org/10.1111/gcb.15170.

Klesse, S., R. J. DeRose, C. H. Guiterman, et al. 2018. "Sampling Bias Overestimates Climate Change Impacts on Forest Growth in the Southwestern United States." *Nature Communications* 9, no. 1: 5336. https://doi.org/10.1038/s41467-018-07800-y.

Klesse, S., T. Wohlgemuth, K. Meusburger, et al. 2022. "Long-Term Soil Water Limitation and Previous Tree Vigor Drive Local Variability of Drought-Induced Crown Dieback in *Fagus sylvatica*." *Science of the Total Environment* 851: 157926. https://doi.org/10.1016/j.scitotenv.2022.157926.

Klopčič, M., A. Rozman, and A. Bončina. 2022. "Evidence of a Climate-Change-Induced Shift in European Beech Distribution: An Unequal Response in the Elevation, Temperature and Precipitation Gradients." *Forests* 13, no. 8: 1311. https://doi.org/10.3390/f13081311.

Knutzen, F., C. Dulamsuren, I. C. Meier, and C. Leuschner. 2017. "Recent Climate Warming-Related Growth Decline Impairs European Beech in the Center of its Distribution Range." *Ecosystems* 20, no. 8: 1494–1511. https://doi.org/10.1007/s10021-017-0128-x.

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.

Leuschner, C., and H. Ellenberg. 2017. "Beech and Mixed Beech Forests." In *Ecology of Central European Forests: Vegetation Ecology of Central Europe*, edited by C. Leuschner and H. Ellenberg, 351–441. Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-319-43042-3_5.

Leuschner, C., G. Weithmann, B. Bat-Enerel, and R. Weigel. 2023. "The Future of European Beech in Northern Germany—Climate Change Vulnerability and Adaptation Potential." *Forests* 14: 1448. https://doi.org/10.3390/f14071448.

Lévesque, M., L. Walthert, and P. Weber. 2016. "Soil Nutrients Influence Growth Response of Temperate Tree Species to Drought." *Journal of Ecology* 104, no. 2: 377–387. https://doi.org/10.1111/1365-2745.12519.

Martinez 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.

Martinez del Castillo, E., C. S. Zang, A. Buras, et al. 2022. "Climate-Change-Driven Growth Decline of European Beech Forests." *Communications Biology* 5: 163. https://doi.org/10.1038/s42003-022-03107-3.

Martínez-Sancho, E., L. Slámová, S. Morganti, et al. 2020. "The GenTree Dendroecological Collection, Tree-Ring and Wood Density Data From Seven Tree Species Across Europe." *Scientific Data* 7, no. 1: 1–7. https://doi.org/10.1038/s41597-019-0340-y.

Mauri, A., G. Strona, and J. San-Miguel-Ayanz. 2017. "EU-Forest, A High-Resolution Tree Occurrence Dataset for Europe." *Scientific Data* 4: 160123. https://doi.org/10.1038/sdata.2016.123.

Michelot, A., S. Simard, C. Rathgeber, E. Dufrêne, and C. Damesin. 2012. "Comparing the Intra-Annual Wood Formation of Three European Species (*Fagus sylvatica*, Quercus Petraea and *Pinus sylvestris*) as Related to Leaf Phenology and Non-structural Carbohydrate Dynamics." *Tree Physiology* 32, no. 8: 1033–1045. https://doi.org/10.1093/treephys/tps052.

Muffler, L., J. Schmeddes, R. Weigel, et al. 2021. "High Plasticity in Germination and Establishment Success in the Dominant Forest Tree *Fagus sylvatica* Across Europe." *Global Ecology and Biogeography* 30, no. 8: 1583–1596. https://doi.org/10.1111/geb.13320.

Muffler, L., R. Weigel, A. J. Hacket-Pain, et al. 2020. "Lowest Drought Sensitivity and Decreasing Growth Synchrony Towards the Dry Distribution Margin of European Beech." *Journal of Biogeography* 47, no. 9: 1910–1921. https://doi.org/10.1111/jbi.13884.

Neycken, A., M. Scheggia, C. Bigler, and M. Lévesque. 2022. "Long-Term Growth Decline Precedes Sudden Crown Dieback of European Beech." *Agricultural and Forest Meteorology* 324: 109103. https://doi.org/10.1016/j.agrformet.2022.109103.

Noce, S., L. Caporaso, and M. Santini. 2020. "A New Global Dataset of Bioclimatic Indicators." *Scientific Data* 7, no. 1: 398. https://doi.org/10.1038/s41597-020-00726-5.

Nussbaumer, A., A. Gessler, S. Benham, et al. 2021. "Contrasting Resource Dynamics in Mast Years for European Beech and Oak—A Continental Scale Analysis." *Frontiers in Forests and Global Change* 4: 1–17. https://doi.org/10.3389/ffgc.2021.689836.

Pan, Y., R. A. Birdsey, J. Fang, et al. 2011. "A Large and Persistent Carbon Sink in the World's Forests." *Science* 333, no. 6045: 988–993. https://doi.org/10.1126/science.1201609.

Papastefanou, P., C. S. Zang, T. A. M. Pugh, and A. Rammig. 2020. "A Dynamic Model for Strategies and Dynamics of Plant Water-Potential Regulation Under Drought Conditions." *Frontiers in Plant Science* 11: 373. https://doi.org/10.3389/fpls.2020.00373.

Peltier, D. M. P., J. J. Barber, and K. Ogle. 2018. "Quantifying Antecedent Climatic Drivers of Tree Growth in the Southwestern US." *Journal of Ecology* 106, no. 2: 613–624. https://doi.org/10.1111/1365-2745.12878.

Perret, D. L., M. E. K. Evans, and D. F. Sax. 2024. "A species' Response to Spatial Climatic Variation Does Not Predict Its Response to Climate Change." *Proceedings of the National Academy of Sciences* 121, no. 1: e2304404120. https://doi.org/10.1073/pnas.2304404120.

Peters, R. 2013. *Beech Forests*. The Netherlands: Springer Science & Business Media.

Peters, R. L., K. Steppe, H. E. Cuny, et al. 2021. "Turgor – A Limiting Factor for Radial Growth in Mature Conifers Along an Elevational Gradient." *New Phytologist* 229, no. 1: 213–229. https://doi.org/10.1111/nph.16872.

R Core Team. 2023. "R: A Language and Environment for Statistical Computing [Computer Software]." R Foundation for Statistical Computing. https://www.R-project.org/.

Ringgaard, I. M., S. Yang, E. Kaas, and J. H. Christensen. 2020. "Barents-Kara Sea Ice and European Winters in EC-Earth." *Climate*

Dynamics 54, no. 7: 3323–3338. https://doi.org/10.1007/s00382-020-05174-w.

Rozas, V., J. J. Camarero, G. Sangüesa-Barreda, M. Souto, and I. García-González. 2015. "Summer Drought and ENSO-Related Cloudiness Distinctly Drive *Fagus sylvatica* Growth Near the Species Rear-Edge in Northern Spain." *Agricultural and Forest Meteorology* 201: 153–164. https://doi.org/10.1016/j.agrformet.2014.11.012.

Salomón, R. L., R. L. Peters, R. Zweifel, et al. 2022. "The 2018 European Heatwave Led to Stem Dehydration but Not to Consistent Growth Reductions in Forests." *Nature Communications* 13: 28. https://doi.org/10.1038/s41467-021-27579-9.

Šamonil, P., P. Doleželová, I. Vašíčková, et al. 2013. "Individual-Based Approach to the Detection of Disturbance History Through Spatial Scales in a Natural Beech-Dominated Forest." *Journal of Vegetation Science* 24, no. 6: 1167–1184. https://doi.org/10.1111/jvs.12025.

Scharnweber, T., M. Smiljanic, R. Cruz-García, M. Manthey, and M. Wilmking. 2020. "Tree Growth at the End of the 21st Century—The Extreme Years 2018/19 as Template for Future Growth Conditions." *Environmental Research Letters* 15, no. 7: 074022. https://doi.org/10.1088/1748-9326/ab865d.

Schmied, G., H. Pretzsch, D. Ambs, et al. 2023. "Rapid Beech Decline Under Recurrent Drought Stress: Individual Neighborhood Structure and Soil Properties Matter." *Forest Ecology and Management* 545: 121305. https://doi.org/10.1016/j.foreco.2023.121305.

Schuldt, B., A. Buras, M. Arend, et al. 2020. "A First Assessment of the Impact of the Extreme 2018 Summer Drought on Central European Forests." *Basic and Applied Ecology* 45: 86–103. https://doi.org/10.1016/j.baae.2020.04.003.

Serra-Maluquer, X., A. Gazol, G. Sangüesa-Barreda, et al. 2019. "Geographically Structured Growth Decline of Rear-Edge Iberian *Fagus sylvatica* Forests After the 1980s Shift Toward a Warmer Climate." *Ecosystems* 22, no. 6: 1325–1337. https://doi.org/10.1007/s10021-019-00339-z.

Silva, D. E., P. Rezende Mazzella, M. Legay, E. Corcket, and J. L. Dupouey. 2012. "Does Natural Regeneration Determine the Limit of European Beech Distribution Under Climatic Stress?" *Forest Ecology and Management* 266: 263–272. https://doi.org/10.1016/j.foreco.2011.11.031.

Spinoni, J., J. V. Vogt, G. Naumann, P. Barbosa, and A. Dosio. 2018. "Will Drought Events Become More Frequent and Severe in Europe?" *International Journal of Climatology* 38, no. 4: 1718–1736. https://doi.org/10.1002/joc.5291.

Stojnić, S., M. Suchocka, M. Benito-Garzón, et al. 2018. "Variation in Xylem Vulnerability to Embolism in European Beech From Geographically Marginal Populations." *Tree Physiology* 38, no. 2: 173–185. https://doi.org/10.1093/treephys/tpx128.

Tallieu, C., V. Badeau, D. Allard, L.-M. Nageleisen, and N. Bréda. 2020. "Year-To-Year Crown Condition Poorly Contributes to Ring Width Variations of Beech Trees in French ICP Level I Network." *Forest Ecology and Management* 465: 118071. https://doi.org/10.1016/j.foreco.2020.118071.

van der Maaten, E., J. Pape, M. van der Maaten-Theunissen, et al. 2018. "Distinct Growth Phenology but Similar Daily Stem Dynamics in Three Co-Occurring Broadleaved Tree Species." *Tree Physiology* 38, no. 12: 1820–1828. https://doi.org/10.1093/treephys/tpy042.

van der Maaten, E., M. van der Maaten-Theunissen, and H. Spiecker. 2012. "Temporally Resolved Intra-Annual Wood Density Variations in European Beech (*Fagus sylvatica* L.) as Affected by Climate and Aspect." *Annals of Forest Research* 55, no. 1: 113–124. https://doi.org/10.15287/afr.2012.83.

van der Woude, A. M., W. Peters, E. Joetzjer, et al. 2023. "Temperature Extremes of 2022 Reduced Carbon Uptake by Forests in Europe." *Nature Communications* 14: 1–11. https://doi.org/10.1038/s41467-023-41851-0.

Vannoppen, A., V. Kint, Q. Ponette, K. Verheyen, and B. Muys. 2019. "Tree Species Diversity Impacts Average Radial Growth of Beech and Oak Trees in Belgium, Not Their Long-Term Growth Trend." *Forest Ecosystems* 6, no. 1: 10. https://doi.org/10.1186/s40663-019-0169-z.

Vašíčková, I., P. Šamonil, K. Král, A. E. Fuentes Ubilla, P. Daněk, and D. Adam. 2019. "Driving Factors of the Growth Response of *Fagus sylvatica* L. to Disturbances: A Comprehensive Study From Central-European Old-Growth Forests." *Forest Ecology and Management* 444: 96–106. https://doi.org/10.1016/j.foreco.2019.04.018.

Vilà-Cabrera, A., and A. S. Jump. 2019. "Greater Growth Stability of Trees in Marginal Habitats Suggests a Patchy Pattern of Population Loss and Retention in Response to Increased Drought at the Rear Edge." *Ecology Letters* 22, no. 9: 1439–1448. https://doi.org/10.1111/ele.13329.

Vitasse, Y., A. Bottero, M. Cailleret, et al. 2019. "Contrasting Resistance and Resilience to Extreme Drought and Late Spring Frost in Five Major European Tree Species." *Global Change Biology* 25, no. 11: 3781–3792. https://doi.org/10.1111/gcb.14803.

Wang-Erlandsson, L., W. G. M. Bastiaanssen, H. Gao, et al. 2016. "Global Root Zone Storage Capacity From Satellite-Based Evaporation." *Hydrology and Earth System Sciences* 20, no. 4: 1459–1481. https://doi.org/10.5194/hess-20-1459-2016.

Wehrens, P., and L. M. C. Buydens. 2007. "Self- and Super-Organizing Maps in R: The Kohonen Package." *Journal of Statistical Software* 21, no. 5: 1–19. https://doi.org/10.18637/jss.v021.i05.

Weigel, R., B. Bat-Enerel, C. Dulamsuren, L. Muffler, G. Weithmann, and C. Leuschner. 2023. "Summer Drought Exposure, Stand Structure, and Soil Properties Jointly Control the Growth of European Beech Along a Steep Precipitation Gradient in Northern Germany." *Global Change Biology* 29, no. 3: 763–779. https://doi.org/10.1111/gcb.16506.

Weigel, R., L. Muffler, M. Klisz, et al. 2018. "Winter Matters: Sensitivity to Winter Climate and Cold Events Increases Towards the Cold Distribution Margin of European Beech (*Fagus sylvatica* L.)." *Journal of Biogeography* 45, no. 12: 2779–2790. https://doi.org/10.1111/jbi.13444.

Xu, X., D. Medvigy, J. S. Powers, J. M. Becknell, and K. Guan. 2016. "Diversity in Plant Hydraulic Traits Explains Seasonal and Inter-Annual Variations of Vegetation Dynamics in Seasonally Dry Tropical Forests." *New Phytologist* 212, no. 1: 80–95. https://doi.org/10.1111/nph.14009.

Yue, C., H.-P. Kahle, J. Klädtke, and U. Kohnle. 2023. "Forest Stand-By-Environment Interaction Invalidates the Use of Space-For-Time Substitution for Site Index Modeling Under Climate Change." *Forest Ecology and Management* 527: 120621. https://doi.org/10.1016/j.foreco.2022.120621.

Zhao, S., N. Pederson, L. D'Orangeville, et al. 2019. "The International Tree-Ring Data Bank (ITRDB) Revisited: Data Availability and Global Ecological Representativity." *Journal of Biogeography* 46, no. 2: 355–368. https://doi.org/10.1111/jbi.13488.

Zweifel, R., F. Sterck, S. Braun, et al. 2021. "Why Trees Grow at Night." *New Phytologist* 231, no. 6: 2174–2185. https://doi.org/10.1111/nph.17552.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.