



Modeling adaptive growth in forest trees: Integrating individual variation to understand climate responses in widely-distributed species

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ABSTRACT

An improved understanding of how forest trees may respond individually and differentially to climate across broad environmental gradients, due to adaptation or physiological acclimation, may facilitate more robust forecasts of forest resilience under climate change. We present a framework for modeling stem diameter growth in adult canopy trees that accounts for responses to climate that may be unique for individuals in different ecological settings. We used data from >10,000 tree cores from 888 forest inventory plots distributed across wide climatic gradients in two mountain ranges in Europe. We formulated a suite of nonlinear models for each of the four species to understand factors regulating annual radial growth. The models accounted for the effects of tree ontogeny, competition, nitrogen deposition (Nd), temperature, and precipitation. We compared two approaches to evaluate evidence for adaptation or acclimation in the growth–climate relations of trees. One method tested whether growth responses diverged for individual trees associated with distinct climate regimes. An alternate method fitted climate response functions with the deviation of climate in a given year from the prevailing average conditions at a tree location. We also tested whether the peak height of this function, representing the maximum growth capacity of a tree, depended on local average climate. For all taxa, models that incorporated within-species variation received stronger support relative to simpler models that assumed a consistent species-average growth response to climate. Growth in all but one species was best predicted by models fitted with climate deviations. Trees differed markedly in terms of their peak growth potential and climate optima, and in some cases, occupied suboptimal environments. Growth responses to nitrogen (N) inputs were also modulated by climate. Our framework offers a flexible approach for integrating individual-level climate sensitivity into tree demography models, which may allow for more rigorous investigations of forest dynamics, the outcomes of which may inform adaptive management strategies for mitigating climate change impacts.

1. Introduction

A long-held assumption in community ecology is that climate fundamentally controls the geographic distribution of plants through physiological limitation (Stephenson, 1990). Consistent with this theory, species range limits appear to be predominantly determined by

climate factors, particularly towards the cooler margins of their distributions (Anderegg and HilleRisLambers, 2019; Copenhaver-Parry et al., 2020). Less clear, however, is the role of climate in regulating the abundance and performance of species within their ranges (Canham et al., 2010; Martin and Canham, 2020). Although a wide range of empirical and process-based models have been developed to explore

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these dynamics (Franklin, 2010; Tang and Beckage, 2010; Canham and Murphy, 2016), most assume that species are homogeneous entities that share a single, static growth–climate relationship. This simplification overlooks potentially adaptive mechanisms that may vary among populations, and can, therefore, confound predictions of forest growth and productivity under global change (Moran et al., 2016; DeMarche et al., 2019; Depardieu et al., 2020).

Differentiated trait functions among populations within a plant species may arise through a combination of adaptive evolution and phenotypic acclimation (Angert et al., 2011). Adaptation involves shifts in allele frequencies due to environmental selection (Lind et al., 2018). Acclimation is an adjustment of physiological, biochemical, or anatomical traits in individual plants induced by a prolonged shift in the environment (Smith and Dukes, 2013). An elevated acclimation potential has been associated with more heterogeneous environments that display greater seasonality (Cunningham and Read, 2003; de la Mata et al., 2022). Acclimatory responses may occur within the life span of an organism (Fonti et al., 2010). Evolutionary change occurs over multiple generations, but may be accelerated during periods of episodic tree mortality followed by non-random cohort survival (Kelly et al., 2003; Jump and Peñuelas, 2005).

A large body of evidence indicates that genetic differentiation patterned on geographical variation in climate is common in many plant taxa, even at fine spatial scales (Leimu and Fischer, 2008; Hereford, 2009; Alberto et al., 2013). Concurrently, acclimatory changes in metabolic and physiological processes induced by environmental stress are well documented (Nicotra et al., 2010; Franks et al., 2014). The vast ecological breadth of many forest tree species is likely an expression of adaptive capacity, whereby differentiated functional traits confer viability in suboptimal conditions (Rehfeldt et al., 1999; Lauteri et al., 2004; Lind et al., 2018). Some studies have documented evidence for recent performance declines in tree species, driven by shifting environmental conditions that exceed the physiological optima of local populations (O'Neill and Nigh, 2011; Isaac-Renton et al., 2018). Declines in fitness may be a consequence of genetically fixed traits that continue to be expressed in trees occupying increasingly suboptimal habitats (Kawecki and Ebert, 2004). However, authors have also suggested that a prevalence of high genetic variance within populations will facilitate ongoing adaptation to shifting environments (Lind et al., 2017), thereby promoting *in situ* survivorship (Benito Garzón et al., 2019; Depardieu et al., 2020). Contradictory expectations and findings from disparate studies suggest that climate change outcomes for plant populations that are attuned to particular localized conditions remain uncertain.

Given the ubiquity of evidence for phenotypic trait variation among disjunct populations of a species, inferences derived from forest models regarding the impacts of global change are likely to be improved with an explicit accounting of the effects of intraspecific divergence (Anderegg, 2015; Moran et al., 2016; Exposito-Alonso, 2023). Experimental designs, referred to as common garden or reciprocal transplant trials, are required to quantify the genetic basis of phenotypic differentiation and to attribute the environmental drivers of divergence (Langlet, 1971). Experiments require a substantial investment of resources and may span decades-long time frames. Consequently, relatively few non-commercial tree species have been represented and adult life-stages are necessarily excluded (Aitken et al., 2008). Logistical considerations also limit, with a few exceptions (Rehfeldt et al., 1999), the number and distribution of *in situ* transplant trials that may be established across the wide climatic breadth of many forest trees. Thus, accompanying inferences regarding the scope of potentially adaptive responses to climate change may be constrained (Kawecki and Ebert, 2004; Lind et al., 2018). Due to advances in sequencing technologies, landscape genomic studies are extending results from experimental studies across larger spatial scales (Sork et al., 2013; Mahony et al., 2020). In addition, analytical approaches are emerging that enable an explicit accounting of differentiated climate relationships in both correlative niche models (Benito Garzón et al., 2019; DeMarche et al., 2019) and demographic

regression-based analyses (Canham et al., 2018; Fréjaville et al., 2019). Niche and demographic models are phenomenological, and thus cannot quantify the underlying genetic architecture that may govern phenotypic variation, nor whether differentiated growth responses are shaped by adaptation versus acclimation. Distinguishing between adaptive and acclimatory mechanisms depends on experimentally derived genetic data. However, differentiated niche and demographic models may be parameterized with empirical data from broadly distributed forest inventories, facilitating insights concerning the pattern of growth that may be consistent with adaptation and/or acclimation, which we suggest may extend our understanding regarding the climate change resiliency of populations that are uneven-aged and that span wide environmental gradients.

In this study, we present a framework for accommodating intraspecific variation in growth models. We assumed that the growth capacity of individual trees can be differentially tuned, via prior adaptation or more recent physiological acclimation, to the average climate conditions of their location. We specifically hypothesized that (1) the radial growth responses to temperature and water availability are nonlinear and potentially unimodal, reflecting theory (Schenk, 1996; Loehle, 2009) and prior empirical findings (Canham and Murphy, 2016; Rollinson et al., 2016; Buechling et al., 2017); (2) the climate optima of widely-dispersed individual trees are unique due to adaptation or acclimation to the prevailing conditions of a given site; (3) annual stem growth is determined foremost, not by the absolute values of climate in a given year, but by how anomalous climate is relative to the average conditions of a location; and (4) peak growth capacity of trees is depressed in sites with greater long-term resource- or water-limitation (Rehfeldt, 1987; Schenk, 1996; Rehfeldt et al., 1999; Canham et al., 2006).

To evaluate evidence for these hypotheses, we fit nonlinear models to observations of annual radial growth for four common tree species distributed across broad environmental gradients in Central Europe (Fig. 1). The model-fitting datasets were acquired from a large network of inventory plots located in primary montane forests. As all data were sourced from intact forests, the potentially confounding effects of management were minimal. Previous studies that have evaluated evidence for within-species variation in the growth potential of adult trees have commonly aggregated ring-width data from individual trees to develop standardized chronologies of mean growth for discrete populations. Separate models for each population-level chronology are then developed to understand whether growth responses to climate vary geographically, with any population-level divergence often attributed to adaptation or acclimation (Latreille et al., 2017; McCullough et al., 2017). However, we assume that data aggregation limits inferences regarding the unique behavior of individuals and the consequences of complex interactions between neighbors (Clark et al., 2011; Jeltsch et al., 2025). We offer an alternative analytical framework that fits nonlinear growth models directly with untransformed ring-width data for individual trees. Our models included the effects of tree size and age, neighbor competition, nitrogen deposition (Nd), and climate factors (precipitation and temperature) for both the year of growth and the preceding year. To test for growth responses in trees that may be tuned to local climate, we compared two model forms: one that specified unique model parameters for distinct climate regimes; another that fit nonlinear response functions with the deviation or fluctuation of climate in a given year from the prevailing average climate at the location of each tree (Canham et al., 2018). The height of the function was also adjusted relative to local average climate. The models presented in this study facilitate a flexible, scalable approach for integrating intraspecific variation into demographic analyses using existing large-scale forest inventory and climate datasets. We suggest that an explicit accounting of individual-level responses in models will lead to a more thorough scientific understanding of the possible consequences of climate change for the many ecosystem services provided by forests.

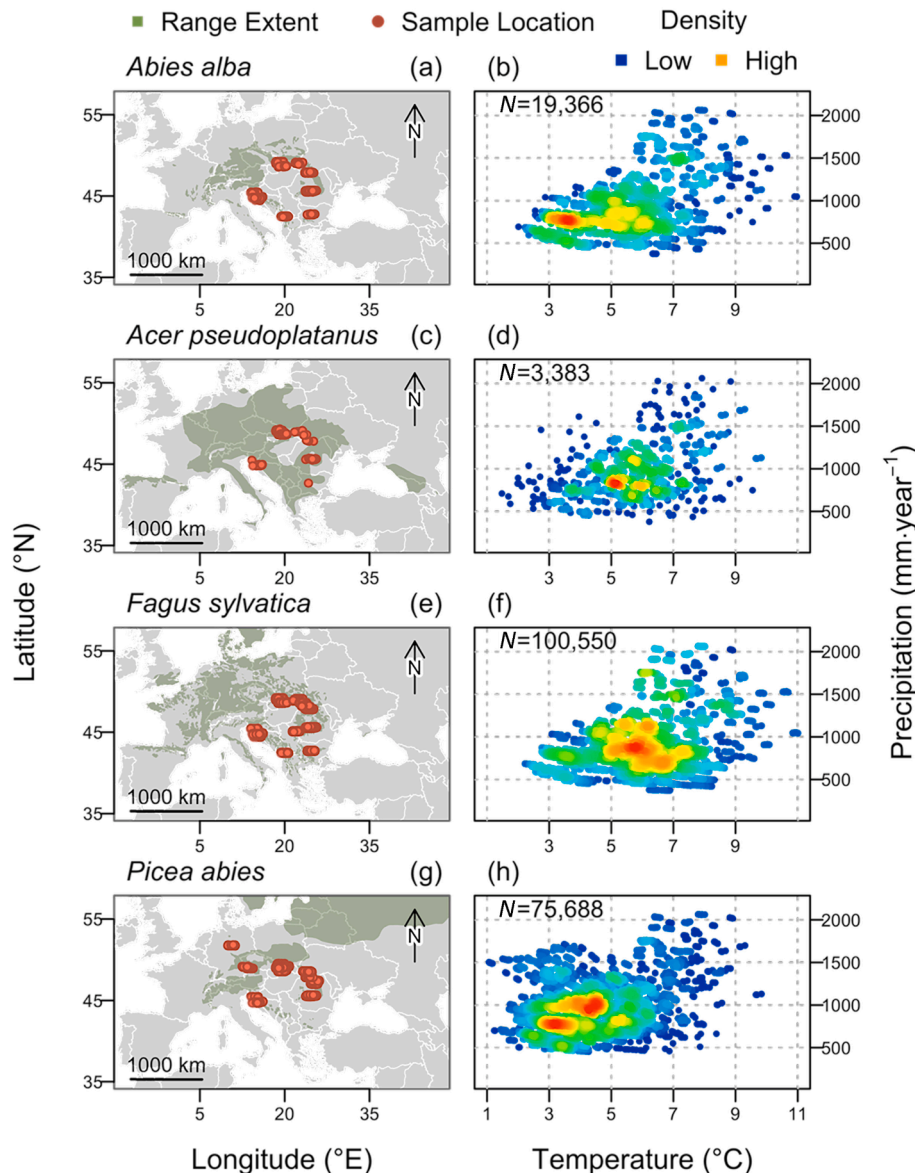


Fig. 1. (a, c, e, g) Geographical locations of tree core samples in Europe for four focal species and (b, d, f, h) the corresponding distributions of samples across gradients of mean annual temperature and total precipitation. Approximate range limits for each focal species in Europe are shaded green. Density heat maps illustrate both the breadth and clustering of samples in climate space; color gradients range from cool (blue) to warm (red) to delineate increasing sample densities. Climate terms describe conditions in 12-month hydrologic year periods (Section 2). Total species-specific sample sizes (N : annual growth measurements) corresponding to datasets used in modeling analyses are shown in the upper left corner of each climate panel.

2. Materials and methods

2.1. Data compilation

We used datasets of tree radial growth rates and corresponding stand structural attributes from the Remote Primary Forest Project (<https://www.remoteforests.org>): A network of permanent forest inventory plots that spans 9 countries and two major mountain regions in central (Carpathians) and southern Europe (Dinaric Alps). Remote plot locations are determined based on geographic information systems (GIS) analyses that randomly distribute survey sites across environmental gradients within primary forest stands (Martini et al., 2025). We used data from circular plots established in the year 2010 or later. Plot sizes varied depending on forest type: 0.1 ha in monodominant conifer stands and 0.15 ha in heterospecific types. Standardized field survey protocols within plots included a mapping of all tree positions, measurements of stem diameters at breast height (DBH), identification of tree taxa, and collection of core samples from 15 to 25 trees for age and radial growth determination. Trees were subjectively selected for coring to represent

the size distribution and species composition of a plot. Data from plots with high observed recent tree mortality rates ($>50\%$) were excluded from our analyses to control for the confounding effects of disturbance on growth responses to climate. We selected the four most common species for analysis: *Abies alba* Mill. (Silver fir), *Acer pseudoplatanus* L. (sycamore maple), *Fagus sylvatica* L. (European beech), and *Picea abies* (L.) Karst. (Norway spruce).

We compiled corresponding time series of annually resolved, rigorously cross-dated diameter growth measurements (tree ring-widths) for all sampled plot trees. The ring-widths were derived from tree core samples, which were processed using standard techniques: Cores were first surfaced with a microtome and then measured on a sliding-stage (Lintab™) equipped with analysis software (TSAP-Win™). A marker year approach was used for cross-dating (Yamaguchi, 1991). Annual dates were verified with CDendro (Larsson, 2015).

Our analyses focus on the growth responses of adult trees. We excluded juvenile trees (DBH <10 cm), as well as adult trees located in highly light-limited conditions (receiving $<50\%$ of full sun due to shading from taller neighboring trees, as assessed by the field crews).

Our lab analyses of the tree cores indicated that shaded understory trees commonly exhibited several multiple-year intervals of highly suppressed growth (near-zero ring-widths or completely absent rings). These observations are consistent with results from a prior investigation of the life history of these species, which demonstrated that understory trees can persist with low growth for long periods in resource-limited, low-light conditions (Pavlin et al., 2021). In this study, we therefore elected to analyze the growth dynamics of canopy and subcanopy trees having at least 50% full sun exposure, as we assumed that these trees are responsive to climate variation in terms of growth. Despite filtering suppressed trees, our dataset spans a considerable range of stem diameters (10 to >90 cm) and tree ages (~45 to >300 years). However, we also acknowledge that the growth–climate relations of juveniles and predominantly shaded adult trees may diverge relative to individuals with more substantial exposure to light (Canham and Murphy, 2016; Rollinson et al., 2021). Whether the climate relations of juvenile or highly-shaded adult trees in our study region are locally differentiated will require further research.

We restricted analyses to a 20-year period (1991–2010). Quality-control filtering produced a final dataset with 10,318 cores from 888 plots that encompassed broad gradients in climate and neighborhood conditions (Fig. 1 and Table 1). Sample sizes of measured annual ring widths ranged from 3,383 for *A. pseudoplatanus* to 100,550 for *F. sylvatica*.

We assessed the performance of trees in response to variation in thermal and moisture conditions. We used mean annual temperature to represent thermal effects, as annual averages were strongly correlated with both monthly and seasonal conditions. Spearman correlations between mean annual temperature and individual monthly means for all months of the year ranged from 0.83 to 0.93 (mean = 0.90). Correlations between annual temperature and each of four seasonal means (average temperature over 3-month intervals) ranged from 0.89 to 0.97 (mean = 0.94). Thus, for the purposes of statistical modeling, mean annual temperature provided a robust representation of the effects of thermal variation on the annual growth potential of trees.

Table 1
Summary of attributes of the model-fitting datasets.

Variable	<i>Abies alba</i>	<i>Acer pseudoplatanus</i>	<i>Fagus sylvatica</i>	<i>Picea abies</i>
Sample sizes				
Stands	29	25	33	51
Plots	218	71	390	512
Tree cores	1016	185	5185	3932
Mean attributes of the target trees (5th and 95th percentiles)				
*Mycorrhizae	EM	AM	EM	EM
Age (years)	134 (46, 273)	114 (48, 216)	177 (63, 314)	138 (50, 243)
dbh (cm)	33.1 (12.7, 71.4)	34.6 (15.7, 63.3)	35.6 (13.7, 69.5)	38.2 (16.2, 65.5)
[†] Tmp (°C)	5.5 (3.1, 8)	5.9 (3.8, 8)	6.2 (3.5, 8.8)	4.3 (2.4, 6.8)
[‡] Water (mm·year ⁻¹)	599 (389, 834)	961 (601, 1484)	176 (0, 410)	974 (578, 1548)
N deposition (kg N·ha ⁻¹ ·year ⁻¹)	13.6 (8.9, 19.8)	14.5 (10.5, 18.6)	14.4 (9.7, 19.9)	14.5 (9.7, 21.4)
Neighborhood density (stems·ha ⁻¹)	575 (174, 1026)	437 (186, 754)	731 (142, 1486)	755 (164, 1422)
^{‡‡} Effective neighborhood radii (m)	12.2	8.8	14.1	8.6

Notes:*Specific mycorrhizal association of each focal tree species, where AM = arbuscular, EM = ectomycorrhizal. [†]Tmp is mean temperature for a hydrologic year. [‡]Water is a species-specific water supply term for a hydrologic year (Water = total precipitation for *A. pseudoplatanus* and *P. abies*, effective water supply for *A. alba*, and water deficit for *F. sylvatica*). ^{‡‡}Maximum threshold distance beyond which competitive effects from neighbors were negligible.

Dendroclimatological studies often select explanatory climate variables based on the relative strength of simple linear correlations between some standardized metric of average growth for a population and a large candidate set of subannual-scale climate terms (Littell et al., 2008; Sedmáková et al., 2019). However, explanatory variable selection based on many simultaneous comparisons performed without a strong mechanistic underpinning, and using variables that are potentially collinear, may lead to spurious or idiosyncratic findings and possible model selection uncertainty (Cook et al., 1987; Johnson and Omland, 2004).

Annual precipitation was less strongly representative of intra-annual or seasonal variation in moisture levels. Nonparametric Spearman correlations (Akoglu, 2018) between total annual precipitation and seasonal sums ranged from 0.53 to 0.85 (mean = 0.72). We therefore tested two alternate, more integrative measures of moisture availability that we derived from water balance equations (Stephenson, 1990): (1) Effective water supply, which combined monthly precipitation inputs, soil water storage, snowmelt losses and evaporative demand (potential evapotranspiration; PET); and (2) water deficit, defined as unmet atmospheric demand, and quantified from the cumulative difference of PET and actual evapotranspiration. Water balance calculations account for factors at a monthly resolution that modify the supply of water from precipitation, including latitude, topography, cold-season runoff, cloud cover, and atmospheric conditions (Appendix S1).

Climate data were obtained from E-OBS (Cornes et al., 2018), a gridded dataset of interpolated daily temperature means and precipitation sums having a spatial resolution of 0.1°. We statistically evaluated and compared several alternative gridded datasets, but E-OBS maximized goodness of fit metrics relative to available meteorological station records in the study region (Fig. S2.1). We extracted daily E-OBS climate values for each tree location using bilinear interpolation. Daily data were aggregated to generate monthly estimates of mean temperature and total precipitation, which were then used to compute annual measures of mean temperature, total precipitation, and the water balance-derived measures of effective water supply and water deficit. Annual periods were defined according to a hydrologic year period, which spans a 12-month window from October of the prior year through September of the current growth year, and therefore better aligns with growth processes in trees relative to a calendar year.

We assumed that species-specific physiological and life history traits, which through acclimation or adaptation, may uniquely determine the growth responses of each species. We thus conducted preliminary analyses to test the sensitivity of each focal species to the three measures of water availability described above. Specifically, we compared competing regression models that parameterized tree size, age, annual temperature, and one of the three alternate precipitation variables. The single water supply term that maximized model performance (based on Akaike information criterion (AIC)) for a given species was used in all subsequent analyses (Table 1).

Effects of anthropogenic Nd were investigated using time-varying, spatially continuous estimates of Nd generated via an atmospheric chemical transport model (MATCH; Robertson et al., 1999). These datasets were acquired from (Theobald et al., 2019) and provide gridded estimates of wet and dry deposition rates for both reduced (ammonium) and oxidized (nitrate) N compounds for the 20-year period of our analyses. In a comparison of six alternate chemical transport models, Theobald et al. (2019) show that MATCH was one of only two models that met all the acceptability criteria suggested by Chang and Hanna (2004) for wet Nd. The fractional bias for MATCH was, for example, ca. +5%, and the number of observations within a factor of two of the MATCH results was close to 90%. We extracted MATCH-derived deposition data for all tree locations. Monthly data were aggregated to annual values, again defined by hydrologic year periods. Estimated rates of deposition via wet and dry pathways were summed, as were oxidized and reduced forms to generate a single measure of total annual Nd for all sample locations (Appendix S3).

2.2. Growth analyses

We extend a nonparametric modeling framework implemented in prior studies (Kobe, 1996; Uriarte et al., 2004a; Canham et al., 2006; Martin et al., 2010; Thomas et al., 2010; Gómez-Aparicio et al., 2011; Coates et al., 2013; Buechling et al., 2016; Valor et al., 2024; Ibrahim et al., 2025). We use a spatially-explicit neighborhood approach where stem growth responses to competition from neighbors, N_d , and climate are estimated at the individual tree level, corresponding to the scale at which these processes operate (Clark et al., 2011; Musters et al., 2023). Our analyses are grounded in likelihood principles (Edwards, 1992; Hillborn and Mangel, 1997), and contrast a null hypothesis significance testing paradigm. Specifically, we quantified the maximum-likelihood values of all unknown model parameters using an iterative global optimization algorithm (Section 2.4). A separate set of models was generated for each focal tree species. We assumed that a given species has a potential growth rate (g_m) that represents expected growth ($\text{mm}\cdot\text{year}^{-1}$) at optimal levels of the other explanatory terms in the model (Canham et al., 2006; Thomas et al., 2010). In our analyses, potential growth is then scaled (i.e., reduced by a finite scalar quantity) by biological and environmental factors. We used a multiplicative model structure:

$$g = g_m^* \times \text{age} \times \text{size} \times \text{competition} \times T \times W \times N_d \quad (1)$$

where the response term (g) is estimated radial growth ($\text{mm}\cdot\text{year}^{-1}$) at breast height (1.3 m) of a target tree, age is the age of a target tree in a specific year, size is the DBH of a target, competition is the effect of resource competition from proximate neighboring trees, T is annual temperature, W is annual water supply, and N_d represents the effect of annual nitrogen deposition at a site. Separate values for potential growth (g_m^*) were computed for each forest stand to capture local variation not accounted for by the specified fixed effects of the model. In effect, the models were multi-level. Each covariate (functional forms defined below) was a unitless scalar quantity that proportionally reduced the estimated potential growth (g_m^*). Our model formulation, one term having actual units of $\text{mm}\cdot\text{year}^{-1}$ while all other terms are scalars bounded between 0 and 1, is an effective means of avoiding parameter tradeoffs during model fitting (Canham and Murphy, 2016). In addition, our framework, which includes an explicit accounting of size and age effects, obviates the need to standardize the growth data (Buechling et al., 2017; Canham et al., 2018). Thus, models were fit with untransformed measurements of annual stem increment (cross-dated ring-widths) from tree core samples.

The age covariate was fit using a single-parameter exponential decay function:

$$\text{Age effect} = \exp(-A_0 \times \text{age}) \quad (2)$$

where A_0 is a species-specific shape parameter that determines the decay rate. Size effects were quantified using a two-parameter exponential function bounded by a horizontal asymptote:

$$\text{Size effect} = 1 - S_0 \times \exp(-S_b \times \text{DBH}) \quad (3)$$

where S_0 and S_b are estimated parameters that determine the initial value (y intercept) and shape of the effect, respectively. The age and size terms in the models were fit with annually resolved reconstructions of age and stem diameter (DBH), respectively.

Competition effects were modeled by extending traditional neighborhood approaches (Bella, 1971; Lorimer, 1983). We formulated an index of crowding that, as in prior studies (Canham et al., 2004; Uriarte et al., 2004b, 2005; Stadt et al., 2007; Coates et al., 2013; Buechling et al., 2017; Ibrahim et al., 2025), integrates information describing the size (DBH), taxonomy, and proximity (distance) of neighboring trees. As the inventory plots were not surveyed annually and not all trees were cored, we used data quantifying the sizes and mapped positions of trees from the initial census of a plot (2010–2014) and assumed a constant

index value for the duration of the 20-year analysis window (due to limited recruitment or mortality of adult trees). We acknowledge that canopy disturbance events (windthrow, insect herbivory) in unmanaged old-growth forests may alter competitive environments within 20 years, even where tree recruitment and mortality rates are generally low. Our size- and distance-dependent index summed the crowding effects of all neighboring trees within a specified radius of a target tree:

$$\text{NCI} = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{(\text{DBH}_{ij})^\alpha}{(\text{distance}_{ij})^\beta} \quad (4)$$

where NCI is a neighborhood crowding index and subscripts i and j denote neighbor taxa and corresponding sample size (number of stems), respectively. To allow for differences among neighbor species in their effects on a target tree, we incorporated a competition coefficient (λ) and estimated unique values of λ for each neighbor species i . The exponents α and β govern the shape of the effects of the DBH and distance of neighbors on NCI. To limit the complexity of the model and the number of parameters requiring estimation, α and β were assumed to be equivalent for all neighbor taxa. For each of the four focal species, we calculated the effective neighborhood radii beyond which crowding effects from neighbors were estimated to be negligible.

Trees beyond plot limits were not measured during field surveys. Thus, data describing the effects of crowding on target trees proximate to plot edges were incomplete. Excluding trees near plot edges would have greatly reduced our sample sizes and the robustness of the analyses. We assumed, as the survey plots were generally located in homogeneous forests and not in fragmented, patchy, or transitional stands, that the competitive environments within plots and external to but directly adjacent to plot boundaries were relatively consistent. Therefore, adopting previous approaches (Uriarte et al., 2005, 2016; Ibrahim et al., 2025), we simulated neighborhood conditions within associated buffer regions contiguous to plot boundaries to capture associated crowding effects for edge trees, as estimated by NCI. NCI incorporated all neighbor trees within a predetermined radius of a given target tree, which ranged from 9 to 14 m depending upon the identity of the target (Table 1). The buffers were sufficient in size to enable a determination of NCI for all target plot trees; specifically, buffer regions extended the plot radii by a factor of two. Buffers were comprised of a simulated population of trees characterized by a size distribution and species composition exactly matching conditions within surveyed plot limits. Simulated trees were randomly located within buffers.

Growth response to competition was encoded as an exponential function of NCI:

$$\text{Competition} = \exp(-C \times \text{BARatio}^\gamma \times \text{NCI}^\delta) \quad (5)$$

where C , γ , and δ are estimated shape parameters. For $\delta > 1$, responses are sigmoidal in form and only decline beyond a threshold NCI level. An initially more rapid decay in growth is observed for $\delta \sim 1.0$. BARatio modifies the response function to account for size-dependent variation in a focal species' sensitivity to crowding and stress tolerance (Goldberg and Landa, 1991). BARatio was estimated from a ratio of the overall mean basal area of a neighborhood to the basal area of a corresponding target tree.

We posited that growth–climate relationships are fundamentally nonlinear and unimodal. We therefore used Gaussian functions to fit the climate as well as the N_d terms of Eq. 1:

$$\text{Effect } (T, W, \text{ or } N_d) = X_a \times \exp\left[-0.5 \times \left(\frac{X - X_c}{X_b}\right)^2\right] \quad (6)$$

where X represents a vector of observations of either annual mean temperature (T ; Kelvin), water supply (W ; $\text{mm}\cdot\text{year}^{-1}$), or total N_d ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) for sampled trees. As described above, species-specific water supply variables were determined from preliminary analyses (Table 1). The shape parameters X_a , X_b , and X_c determine, respectively,

function height, width, and mode (climate or Nd level associated with the peak of the curve). A Gaussian function is unimodal and symmetrical, but, depending on the estimated values of the shape parameters, may also describe relationships that are monotonically increasing, decreasing, or even effectively flat. This flexibility allows for an explicit test of our hypothesis concerning nonlinearity. Preliminary analyses indicated that antecedent climate effects were important for all species except *A. alba*. Therefore, separate Gaussian functions were fit for current (0) and prior (−1) years, and were assumed to be additive in Eq. 1:

$$T = T_0 + T_{-1} \quad (7)$$

$$W = W_0 + W_{-1} \quad (8)$$

2.3. Testing for population-specific responses to climate

To account for unique climate relations among widely dispersed trees, we modified the Gaussian climate functions described by Eq. 6. We compared two approaches that provide tests of our second hypothesis in the Introduction; specifically, that trees respond differentially to the prevailing conditions of their location due to either adaptation or acclimation. These methods adjust the values of the three shape parameters of Eq. 6 (X_a , X_b , and X_c) to optimize the fit between growth and the climate of a given site. Our first approach, adopted from Buechling et al. (2017), computed unique shape parameters for trees exposed to divergent climate regimes. Specifically, we statistically clustered or classified forest plots with similar long-term climate factors (Appendix S4). For the classification, we used a *K*-means algorithm (“kmeans”) from the stats package of the R statistical environment (R Development Core team, 2024). Five distinct clusters were identified for *P. abies* and three for the other species. Differentiated Gaussian functions were then estimated:

$$\text{Effect } (T \text{ or } W) = X_a^* \times \exp \left[-0.5 \times \left(\frac{X - X_c^*}{X_b^*} \right)^2 \right] \quad (9)$$

where X_a^* , X_b^* , and X_c^* are shape parameters that govern function height, width and mode, but whose values were specified uniquely for each cluster. The differentiated parameter values allow for unique responses to temperature or moisture variability.

Our second approach for computing spatially varying climate functions was based on the premise that differentiated growth processes may emerge as a consequence of the magnitude of annual climate fluctuations relative to average conditions at a site (hypothesis 3 of Section 1). This approach does not depend on a clustering or aggregation of data. Instead, following Canham et al. (2018), we adjusted the shape of a Gaussian function to optimize the fit between observed tree growth and the corresponding deviation of local climate in a given year from the average climate at the location of the tree. Annual climate deviations or anomalies were computed as:

$$\Delta X = X - X_{\text{ave}} \quad (10)$$

where $\mathbf{X}$ is a vector of temperature or precipitation values and $\mathbf{X}_{\text{ave}}$ is the 20-year mean (1991–2010) temperature or moisture level at a site. We then fit Gaussian functions (Eq. 6) with anomalies (ΔX) instead of the absolute values of climate ($\mathbf{X}$):

$$\text{Effect } (T \text{ or } W) = X_a^{\dagger} \times \exp \left[-0.5 \times \left(\frac{\Delta X - X_c^{\dagger}}{X_b^{\dagger}} \right)^2 \right] \quad (11)$$

where $X_a^{\dagger}$, $X_b^{\dagger}$, and $X_c^{\dagger}$ are differentiated parameters that adjust the shape (height, width, and mode) of the response curve in relation to the magnitude of local climate fluctuations. Both current and prior year climate terms were fit with anomalies. We also posited that the maximum growth capacity of a tree is inherently constrained by local

prevailing conditions (fourth hypothesis of Section 1). Thus, we adjusted the height parameter ($X_a^{\dagger}$) in Eq. 11 according to local average climate. Specifically, $X_a^{\dagger}$ was computed as a Gaussian function of 20-year mean climate at each tree location:

$$X_a^{\dagger} = X_a^* \times \exp \left[-0.5 \times \left(\frac{X_{\text{ave}} - X_c^*}{X_b^*} \right)^2 \right] \quad (12)$$

where X_a^* , X_b^* , and X_c^* are shape parameters. In summary, our second approach uses hierarchical analyses to generate a family of response curves where each member quantifies annual growth for an individual tree as a function of the magnitude of local climate fluctuations or anomalies relative to expected average conditions.

2.4. Model specification

We formulated a set of hierarchical models (Table 2) based on different permutations of Eq. 1: (1) a base model comprised only of biotic effects (age, size, and competition) estimated using Eqs. 2–5; (2) a climate model that added undifferentiated temperature and water supply terms (from Eq. 6) to the biotic effects of the base model; (3) an undifferentiated full model that combined biotic, climate, and Nd (Eq. 6) variables; (4) a locally differentiated full model (LDcluster, Table 2) where Gaussian climate terms were estimated uniquely for distinct plot clusters (Eq. 9); and (5) an alternative locally differentiated full model (LDtree) where Gaussian climate terms were fit with climate anomalies (Eqs. 10–12). All candidate models, excluding the base model, incorporated both current and prior year climate terms.

Simulated annealing, a global optimization algorithm (Goffe et al., 1994), was used to solve for the maximum-likelihood-based estimates of model parameters. We implemented an annealing schedule with a high initial temperature ($T = 3$), a slow temperature reduction regime ($rT = 0.95$), and a large number of iterations (100,000). We argue that our global optimization procedure facilitates an escape from local optima and eliminates the need to conduct multiple runs with different starting values or convergence criteria. To specify parameter uncertainty, we calculated asymptotic support intervals (Canham and Uriarte, 2006). Support intervals are defined as the range in parameter values corresponding to a two-unit change in likelihood (Edwards, 1992), which approximate traditional 95% confidence limits in parametric regression (Murphy, 2025). A normal probability density function (PDF) was used to calculate likelihood. As model residuals were heteroscedastic, we modified the PDF so that the standard deviation (SD) was computed as a power function of the mean:

$$\text{SD} = a + G^b \quad (13)$$

where a and b are estimated parameters and G is a vector of predicted growth rates. We tested for autocorrelation among model residuals using the function “acf” from the R stats package.

We evaluated model goodness-of-fit via visual inspection of observed versus predicted values, as well as quantitative estimates of bias, root mean square error, and coefficient of determination (R^2). Bias was quantified from the slope of the relationship between observed and predicted values (Table 2). A variety of alternate R^2 type statistics have been developed and used to assess the fit of generalized multi-level linear models (Nakagawa et al., 2017) and nonlinear models (Cameron and Windmeijer, 1997; Clark et al., 1998). In this study, R^2 was computed from residual sums of squares ($R^2 = 1 - \text{sum of squares error} / \text{sum of squares total}$), distinct from the derivation of the coefficient of determination or r^2 (squared correlation between observed and predicted) for ordinary least squares regression (Canham and Uriarte, 2006). This formulation represents a measure of the goodness-of-fit of observed to predicted values, or alternately as the fraction of the total sum of squares explained by a model. The R^2 term is

Table 2
Summary of regression model results for the four focal species. Shown are results for five alternate models (Base, Climate, Full, LDcluster, and LDtree). The explanatory variables for each model are provided below each model name. Models are compared based on AIC values adjusted to account for model complexity (AICc). ΔAICc is the difference between AICc of a given model and the minimum AICc of the model set. The terms *n* and *p* are the sample size of a model-fitting dataset and the parameter count of a model. Derivations of AICc, *R*², and bias are provided in a note below the table.

Species	Statistic	Base	Climate	Full	LDcluster	LDtree
		Age + size + competition	Base + T + W	Climate + N deposition	Full (T and W differentiated by cluster)	Full (T and W fit with anomalies)
<i>Abies alba</i>	<i>n</i>	19,366	19,366	19,366	19,366	19,366
	<i>p</i>	43	49	52	65	56
	ΔAICc	1022	566	261	23	0
	<i>R</i> ²	0.301	0.301	0.316	0.303	0.317
	Bias	1.00	1.00	1.01	1.03	1.01
<i>Acer pseudoplatanus</i>	<i>n</i>	3383	3383	3383	3383	3383
	<i>p</i>	40	52	55	78	62
	ΔAICc	232	212	195	128	0
	<i>R</i> ²	0.277	0.273	0.283	0.289	0.307
	Bias	1.00	0.99	1.01	1.00	1.01
<i>Fagus sylvatica</i>	<i>n</i>	100,550	100,550	100,550	100,550	100,550
	<i>p</i>	48	60	63	87	70
	ΔAICc	2038	995	991	1090	0
	<i>R</i> ²	0.227	0.238	0.239	0.243	0.248
	Bias	1.00	0.99	1.00	1.00	0.99
<i>Picea abies</i>	<i>n</i>	75,688	75,688	75,688	75,688	75,688
	<i>p</i>	68	80	83	114	98
	ΔAICc	2656	1388	914	0	171
	<i>R</i> ²	0.313	0.321	0.325	0.328	0.328
	Bias	1.00	1.00	1.00	1.01	1.01

Notes: *T* is a model covariate representing temperature effects on radial growth. *W* is a covariate representing water supply effects. AICc was calculated as: $AICc = -2\ln(L(\theta|y)) + 2p \times [n/(n - p - 1)]$, where $\ln(L(\theta|y))$ is the log likelihood (Burnham and Anderson, 2004). *R*² was calculated as $R^2 = 1 - \frac{SSE}{SST} = 1 - \frac{\sum_{i=1}^n (obs_i - exp_i)^2}{\sum_{i=1}^n (obs_i - \overline{obs})^2}$, where, exp_i is the expected value of observation *i* given the model, and $\overline{obs}$ is the overall mean of the observations (Cameron and Windmeijer, 1997). Bias was computed from the slope of observed vs. predicted growth: $slope = \sum_{i=1}^n (obs_i)(exp_i) / \sum_{i=1}^n (exp_i)^2$ (Canham and Uriarte, 2006). Unbiased models have slopes approaching 1 (Uriarte et al., 2004a).

bounded at the upper end as 1 (i.e., when observations exactly equal expected values), and declines as the average deviation from expected values increases. Note that this version can assume negative values if the deviations from expected values are on average greater than the deviations from the simple mean of the observations, indicating that model estimates are no better than simply using the mean of the observations (Cook et al., 1987; Clark et al., 1998).

We used standard model comparison criteria, specifically, AIC, to weigh the strength of evidence for a particular model form and climate function (Burnham and Anderson, 2004). AIC values were penalized for the number of parameters in a model (AICc) using a bias correction term (Table 2), and therefore balance model fit versus complexity (Johnson and Omland, 2004). Modeling analyses were conducted in R using the likelihood package (Murphy, 2025).

3. Results

For all four focal tree species, tree ontogeny, resource competition, and Nd were the most important predictors of radial growth capacity. After controlling for these factors, the best-supported models, based on AICc, consistently included climate variables that were differentiated according to either plot clusters or local climate anomalies (Table 2). Model estimates of growth were unbiased (Table 2 and Appendix S5). Model residuals were uncorrelated for all species except *A. alba*, which exhibited minor levels of temporal autocorrelation at a 5% significance level. One of the important strengths of likelihood-based statistical inference is that it does not rely on the notion of “degrees of freedom” that underlie frequentist statistical tests based on sample size. Auto-correlated residuals would inflate the degrees of freedom for a frequentist statistical test relative to the true number of independent observations. However, use of likelihood (and AICc) for inference does not rely on degrees of freedom, so likelihood methods are relatively

robust to autocorrelated residuals (Uriarte et al., 2004a). Therefore, the minor autocorrelation observed for *Abies* is unlikely to substantially affect model ranking. The maximum-likelihood-based estimates of all parameters of the best-supported models are shown in Appendix S6.

The best-supported models provided modest fit to the observational data; *R*² ranged from 0.248 (*Fagus*) to 0.328 (*Picea*), and root mean square error ranged from 0.64 (*Picea*) to 0.95 mm (*Abies*). Various factors may be expected to constrain goodness-of-fit measures, including the high levels of ecological complexity present in natural old-growth forest ecosystems and the influence of unmeasured ecological variables (e.g., microsite conditions) that may vary across spatial-temporal gradients. Considering that our research objective was to further an understanding of patterns and processes, rather than a prediction of a particular outcome, we argue that the models demonstrate reasonable performance. We note also that our individual-based models contrast the still prevailing paradigm of investigating demographic rates, such as plant growth, at coarser community scales (Clark et al., 2011). Aggregating datasets to, for example, develop mean indices of growth for a species or population of trees, reduces individual-level variation and tends to enhance metrics of model fit. However, aggregation also leads to a loss of information and obfuscates the role of unique individual behaviors that may mediate community- and ecosystem-level responses to the environment (Clark et al., 2011; Jeltsch et al., 2025).

3.1. Climate

Although we evaluated the relative sensitivity of growth to alternative permutations of water supply, two species (*A. pseudoplatanus* and *P. abies*) responded most strongly to a simple measure of total annual precipitation (Fig. 2d and h). For the other species, more integrative variables derived from monthly water balance calculations (Appendix S1) maximized model performance: growth in *A. alba* responded to

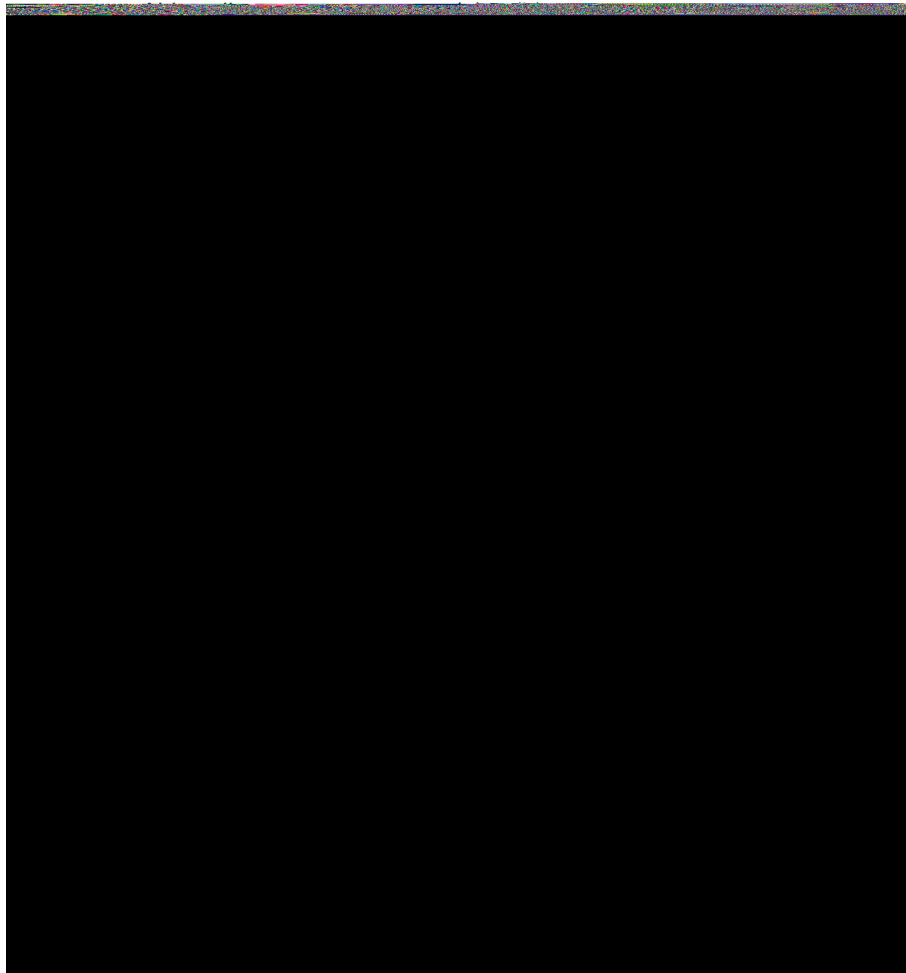


Fig. 2. Predicted radial growth responses in 50 cm diameter trees to mean annual temperature and species-specific metrics of water supply (effective water supply, total precipitation, or water deficit) for the year concurrent with growth. Dashed lines delineate a global mean, undifferentiated growth response to climate. Solid lines are site-specific, differentiated responses to interannual climate variation for individual trees occurring in different local climates; local climates correspond to the 10th, median, and 90th quantiles of observed long-term climate in the whole dataset for a given species (solid circles). In the case of *P. abies* (g and h), solid lines represent locally differentiated responses at the scale of plot clusters. We show growth responses for 3 clusters. Solid circles denote the climate mean of a cluster. The width of all lines corresponds to the breadth of observed climate. Neighborhood factors and Nd rates were fixed at the mean values for a species (Table 1). Tree age was fixed at the species-specific mean for a 50 cm tree. Shaded regions delineate 2-unit asymptotic support intervals. Support limits are values above and below the maximum likelihood estimate that cause the likelihood to drop by 2 units.

effective water supply (Fig. 2b) and *F. sylvatica* was sensitive to water deficits (Fig. 2f).

For all species, Gaussian response functions that were fit to local climate anomalies (LDtree model, Table 2) improved model performance relative to simpler undifferentiated models that estimated a consistent, species-average response to climate drivers (full model, Table 2). For a single species (*P. abies*), response functions that varied across plot clusters (LDcluster) further improved model parsimony relative to either the full or LDtree model.

Results generally support our hypothesis that the shapes of locally differentiated growth–climate relations are nonlinear and often unimodal (Fig. 2c–e). However, the modeling results also reveal approximately linear and monotonic growth responses to climate that lack distinct peaks, at least within the range of the observational datasets. For example, growth in *A. alba* increased monotonically with temperature approaching but not reaching an unambiguous peak level (Fig. 2a). Similarly, *F. sylvatica* growth increased monotonically with decreasing water deficit (Fig. 2f). For *P. abies*, the shapes differed markedly across sites, including approximately linear responses to temperature (Fig. 2g) and, at some sites, unimodal responses to precipitation (Fig. 2h).

Results from the differentiated models reveal substantial variation in the growth dynamics of trees that are distributed across wide climatic gradients. Maximum growth rates (peak of a Gaussian function) for trees at the margins of a species range were not consistently lower relative to growth in trees located in more benign conditions (Fig. 2c, f, and 2h, and

Appendix S7). In addition, optimum conditions for growth (i.e., climate levels corresponding to a function peak) and the climate tolerances of trees (width of a local response curve) varied among trees or populations. For example, differences between local temperature optima for trees at the opposite extremes of the thermal niche of *A. alba* exceeded 4 °C (Fig. 2a).

In some cases, optimum conditions for growth in an individual tree approached the prevailing long-term mean climate for that location (e.g., *Acer*, Fig. 2d). More generally, however, model results indicate a mismatch or divergence between climate optima and local mean conditions of a site (Fig. 3). For example, *F. sylvatica* responded positively to increasing moisture availability (i.e., lower water deficits) well beyond corresponding mean conditions for a location (Fig. 2f and 3c). By species, the average mismatch between temperatures associated with peak growth of a tree and the long-term mean temperature of a corresponding site was 1.9, 0.42, 1.2, and 2.5 °C for *Abies*, *Acer*, *Fagus*, and *Picea*, respectively. For water supply, differences were 66, 10, 266, and 224 mm, though the specific water supply metric varied among the species (Fig. 2). The magnitude of these mismatches differed at the margins relative to the center of the sampled climate gradient of this study in one species (*Picea*). For *Picea*, mismatches were greater at high precipitation and median temperature sites.

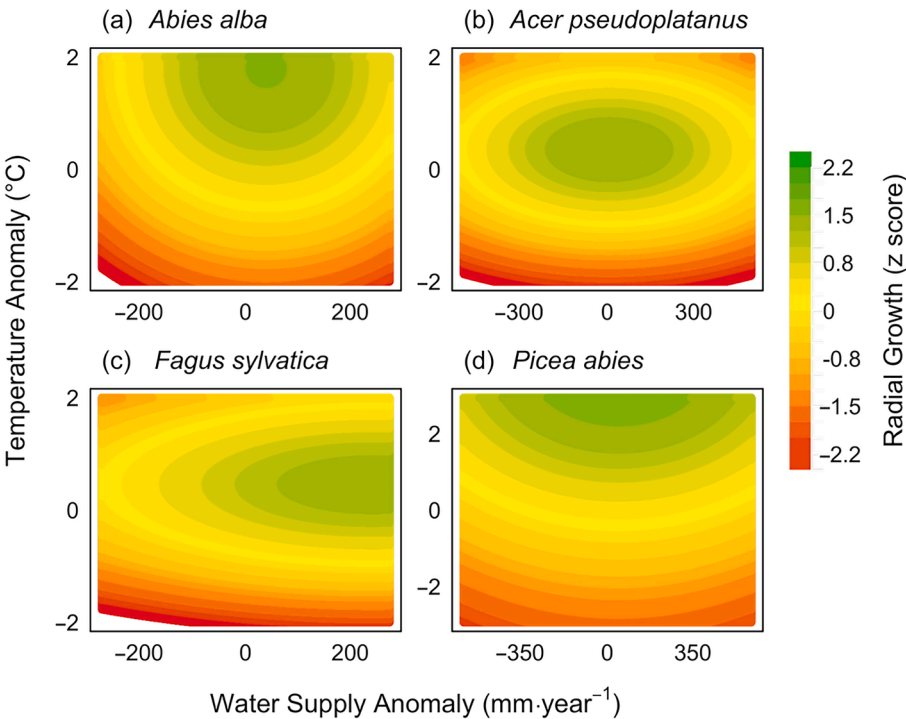


Fig. 3. Species-specific optimized growth responses to climate for an individual 50 cm tree selected from the center of a species climate range. Both temperature and water supply effects are shown as anomalies or departures from corresponding local, long-term mean values for a tree. Both temperature and precipitation mean values are scaled to zero. Species responded to different metrics of water supply (effective water supply for *A. alba*, total precipitation for *A. pseudoplatanus* and *P. abies*, and water deficit for *F. sylvatica*). Predicted annual growth rates are plotted as z scores (SD above or below the mean growth for a given species). Neighborhood factors and Nd rates were fixed at mean levels for a species (Table 1). Tree age was fixed at the species-specific mean for a 50 cm tree. For all species, growth responses are maximized, reflecting a local optima (dark green regions), when climate departs from local average temperature or water supply conditions (zero values).

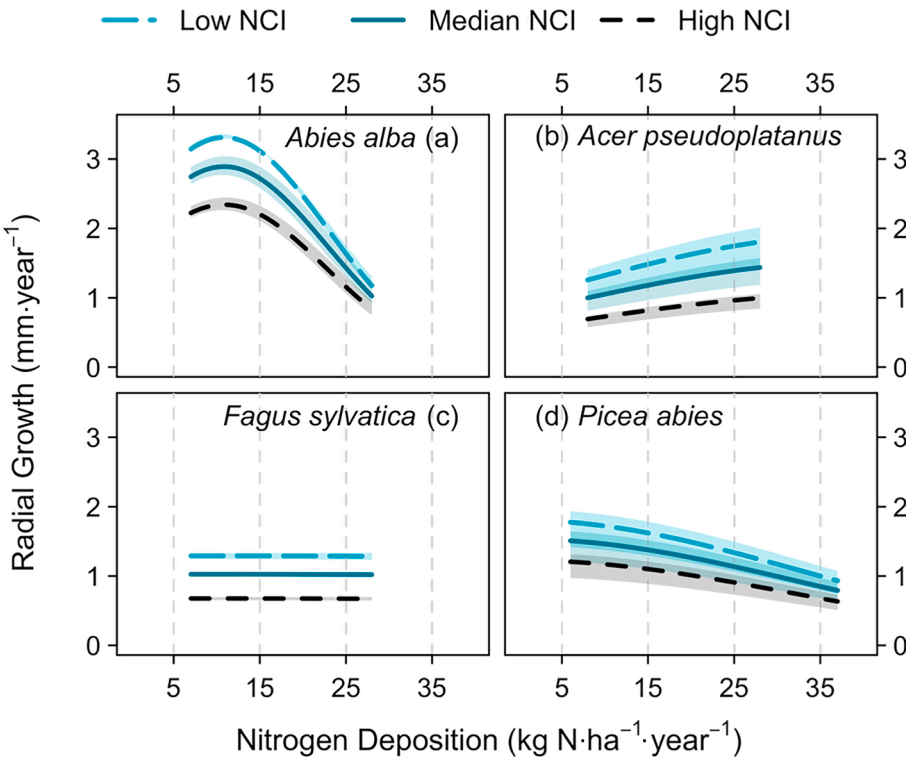


Fig. 4. Effect of total annual Nd on radial growth in a 50 cm diameter tree for three different levels of NCI. Low and high NCI were defined according to the 10th and 90th percentiles, respectively, of observed neighborhood conditions. The deposition flux of N compounds from the atmosphere is comprised of both oxidized (nitrate) and reduced (ammonium) forms, and includes both wet and dry deposition. Predicted responses are based on the observed range of Nd rates in the plots. Climate effects were fixed at species-specific mean levels (Table 1). Tree age was fixed at the mean for a 50 cm tree for a given species. Shaded regions delineate 2-unit support intervals.

3.2. Ontogeny and competition

The datasets used in these analyses spanned a broad range of stem diameters and tree ages (Table 1 and Appendix S8). The average tree age was well over 100 years for all species. Maximum tree ages exceeded 500 years. The derived models indicate that the growth potential of trees declined exponentially with increasing age. In contrast, growth increased monotonically with stem size for all species when controlling for age and other factors (Fig. S8.1a).

In general, radial growth decreased monotonically for all species in response to increasing levels of neighborhood competition, which varied strongly as a function of the proximity of neighbors (Fig. S9.1 and Appendix S9). However, each focal species was also differentially sensitive to the identity of neighbors. Unique lambda coefficient values (λ_i , Eq. 4) for different neighbor taxa of a given focal species (Table S9.1) indicate that the intensity of pair-wise competitive interactions was notably uneven. For example, neighbors of the genus *Acer* had a larger effect on growth in *Abies alba* ($\lambda = 0.67$) relative to the reciprocal effect from a neighbor tree of the genus *Abies* on the growth potential in *Acer* ($\lambda = 0.28$). Contrary to expectations, not all focal species were more sensitive to conspecific neighbors relative to heterospecifics. Results indicate that growth rates in *Abies* and *Picea* were more strongly suppressed by competition from certain broadleaf neighbors than by conspecifics; *Abies* was more sensitive to *Acer*, and *Picea* was more sensitive

to *Fagus*. These patterns may partly reflect species-specific biological traits that confer a differential tolerance of resource limitation. *Fagus sylvatica*, for example, is regarded as a highly stress- and shade-tolerant species (Leuschner and Meier, 2018; Pavlin et al., 2024), and may therefore be less sensitive to neighbor effects on shared resources. Prior research also suggests that a capacity to modify crown shape to maximize light interception may serve as a species-specific strategy for tolerating resource heterogeneity and competition (Canham, 1989); deciduous taxa such as *Fagus* have been shown to exhibit comparatively high plasticity in growth form and crown architecture (Bayer and Pretzsch, 2017; Krůček et al., 2019).

3.3. Nitrogen deposition

Growth responses to Nd differed considerably among the four focal species (Fig. 4). Growth in *A. alba* declined markedly beyond a threshold N level. *A. pseudoplatanus* was the only species studied that responded positively to increasing N additions, and is the only one that forms symbioses with arbuscular mycorrhizal fungi. *F. sylvatica* exhibited an essentially flat response, while growth in *P. abies* gradually declined with increasing rates of Nd.

The effects of Nd were modulated by resource competition and climate variation. For example, high N inputs depressed tree growth in both *A. alba* and *P. abies*, but growth declines were less severe in stands

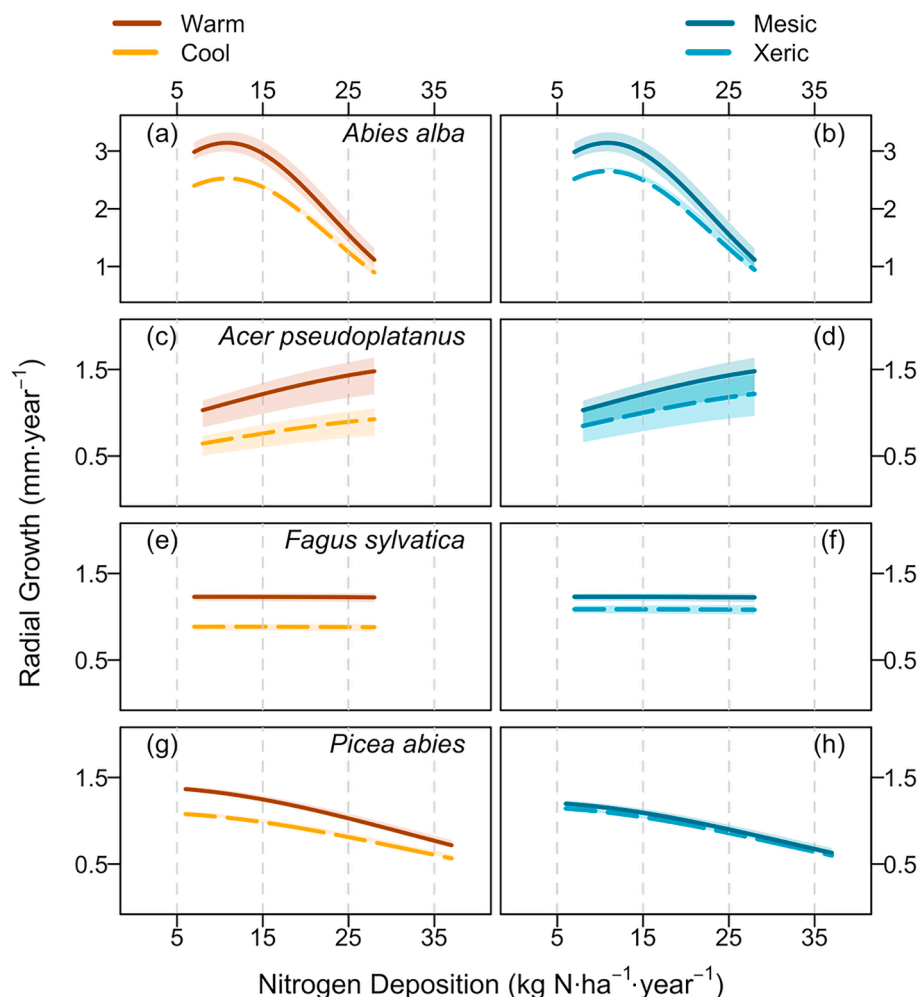


Fig. 5. Thermal and moisture modulation of Nd effects on radial growth. Growth was estimated for hypothetical 50 cm diameter trees at locations where long-term mean climate equals a species region-wide mean climate. N effects span the range of deposition rates observed in the plots. A cool scenario was simulated based on an observed minimum temperature departure ($\sim 2^\circ\text{C}$) below long-term mean conditions for a tree. An average or comparatively warm scenario was fixed at the long-term temperature mean for that tree. Similarly, xeric conditions were simulated using the observed maximum departure of precipitation below mean conditions for a tree. A matching mesic condition was fixed at the long-term, mean precipitation level for that tree. Precipitation variables are species-specific metrics of moisture supply (Table 1). Competition was fixed at species-specific mean levels. Tree age was fixed at the mean for a 50 cm tree of a species. Shaded regions delineate 2-unit support intervals.

where competition for available resources was higher (i.e., the slopes of the N effects were unequal at high vs. low NCI: Fig. 4a and d). Similarly, for most species, the rate of change in growth rates across the range of observed N fluxes was greater in warmer or wetter environments, relative to cooler or drier conditions (Fig. 5).

4. Discussion

The best supported models for all species revealed pronounced variation among individual trees in terms of their climate optima and maximum growth potential, consistent with findings from related research in other forest systems (Canham et al., 2018; Fréjaville et al., 2019; Pederson et al., 2020). We tested two alternative analytical approaches that reflect subtly contrasting assumptions concerning the potential emergence of differentiation among populations. For three of four species, dynamic growth functions that were tuned to the magnitude of site-specific climate anomalies were supported by model selection criteria (AICc). However, for a single species (*P. abies*), the best-supported model used an alternative functional form that optimized the shape of the response curve to fit the growth dynamics of trees associated with distinct long-term climate regimes. The less consistent support for the climate regime approach vs. models fitted with climate anomalies may be attributed to a more complex modeling framework. Specifically, predetermined criteria are required for partitioning the overall climate envelope of a species into homogeneous components. In this study, distinct climate regimes were determined from cluster analyses that grouped forest plots based on patterns of associated long-term climate variation (Appendix S4). We note, however, that this is a purely statistical technique that lacks a mechanistic or biological underpinning. The ensuing classes may not necessarily represent the key drivers or scales of divergence, and may therefore combine data from trees that have evolved distinct responses to climate. Consequently, corresponding models may underestimate the magnitude of growth divergence among the clusters. Integrating data from common garden studies, where available, to iteratively refine the cluster assignments may be one approach for improving this methodology (DeMarche et al., 2019; Fréjaville et al., 2019; Pederson et al., 2020). This approach may be most robust in cases where particular forest stands are distinctly isolated by either distance or physical barriers (mountains, human settlement), and where, consequently, pollen flow and seed dispersal from distant populations are expected to be restricted. Remoteness may provide an ecologically interpretable criterion for discriminating different populations, obviating the need to statistically cluster plot data. More generally, however, our results suggest that fitting nonlinear response functions with local climate anomalies (Eq. 11) and scaling the shape of the response curve according to site-specific average climate (Eq. 12) provides a reliable method for accommodating local differentiation in growth models, and sidesteps somewhat arbitrary data partitioning choices.

A modeling approach based on climate anomalies is flexible and can be adjusted in various ways. For example, the length of the baseline time interval used for calculating local mean climate can be modified to accommodate particular hypotheses. The appropriate baseline interval may depend on the relative role of acclimation versus adaptation in differentiating climate responses, which is unknown in this study. Our 20-year window length partly reflects a parsimonious explanation that responses are mainly determined by phenotypic acclimation (Canham et al., 2018). A longer window length may be more appropriate if differentiated responses are predominantly shaped by adaptation. However, even if differentiation is driven by acclimated phenotypic processes, we do not at present understand whether the mechanisms are physiologically-based (e.g., shifts in the thermal optima for photosynthesis) and potentially rapid, or morphological and therefore slower to develop (e.g., acclimating root/shoot ratios) (Way and Oren, 2010). We therefore argue that the approach presented in this study is limited to testing for the presence of local adaptation/acclimation, and that much

more work is needed to understand the genotypic and phenotypic mechanisms that could produce localized responses (Nicotra et al., 2010).

We elected to use a Gaussian function to model responses to climate, as the fundamental quadratic shape of this function is highly flexible and many fluctuating processes in nature tend towards or can be approximated by Gaussian distributions (McElreath, 2018). The Gaussian can fit a wide range of shapes, including effectively flat or monotonically increasing or decreasing responses to an explanatory variable. We show that the Gaussian can be modified so that its shape varies as a function of local conditions. We adjusted the height parameter according to local climate, but the mode and variance can similarly be differentiated to allow for additional flexibility and heterogeneity in the shapes of growth–climate relationships in different sites. Nevertheless, when a response is unimodal, the Gaussian function imposes symmetry around a modal value and may therefore underrepresent the range of shapes possible. In some cases, asymmetrical hump-based responses to climate may be expected. For example, warming below an optimum may promote growth via positive effects on carbon assimilation or metabolic function (Way and Oren, 2010; Hall et al., 2013). However, temperature deviations above local optimal levels may increase respiration rates, inhibit enzyme function, and/or constrain meristematic activity, potentially triggering steep growth reductions (Saxe et al., 2001), which may be more prominent in trees located near the margins of their thermal niche. Therefore, alternate functional forms capable of fitting asymmetrical distributions (e.g., lognormal or piecewise bivariate Gaussian) may be considered, but were not tested in this study. We also note that we may currently lack a reliable mechanistic basis for selecting an appropriate function. Experimentally-derived relationships between climate and various physiological or metabolic processes occurring at the organ or cellular level, such as unimodal symmetrically-shaped leaf-level photosynthetic responses to temperature (Gunderson et al., 2010), may not necessarily serve as an appropriate basis for model selection, as they are not likely to reliably scale up to reflect the dynamics of whole-plant growth (Canham et al., 2018). For example, a finite supply of photosynthate requires concurrent allocation to multiple plant functions (defense, reproduction, and respiration), among which stem radial growth is only one component (Herms and Mattson, 1992).

We note that the statistical properties of the gridded climate datasets used to fit a given model may affect outcomes. An array of climate data products is available, varying in terms of quality, time frame, temporal and spatial resolution, and the underlying methods used to derive the gridded surfaces. Hence, estimated climate values at a given location may differ across datasets, particularly in remote mountain regions where weather stations are sparse, but few developers of these products offer uncertainty statistics (Davy and Kusch, 2021). We attempted to evaluate the quality of a selection of available gridded datasets covering our study region. Based on our assessment, we used a climate dataset (E-OBS) having a relatively coarse spatial resolution (0.1°), but that exhibited a relatively high degree of fidelity with weather station records (Appendix S2). Based on available weather station data, values of root mean square error between E-OBS and station observations were 1.45 °C for annual temperature and 21 mm for annual precipitation. Our evaluation suggests that finer resolution data do not necessarily provide more reliable estimates of local climate. Nevertheless, both resolution and data quality are important considerations that can influence modeling results (Kusch et al., 2022).

4.1. Consequences of individual variation

Accounting for local differentiation within species provides insights regarding the spatial patterns of demographic processes. Consistent with evidence from common garden experiments (Kremer et al., 2012), our results reveal large differences in the climate optima and tolerances of widely dispersed trees. The climatic tolerances of individuals, as defined by the width of a response curve, were much narrower than the overall

climate niche of a species. In addition, the maximum growth potential of trees (i.e., the peak of the curve) varied markedly depending on local average climate. Trees near the edges of a species' range, and therefore well-displaced from the mean climate conditions within that range, were not consistently less productive relative to other, more centrally located trees. For example, *F. sylvatica* trees in dry environments exhibited higher levels of growth relative to individuals in more benign or mesic sites (Fig. 2f). In general, these patterns suggest a trait optimization capacity that facilitates a tolerance, in terms of growth, of a broad range of climates by disjunct trees within species. We note, however, that growth is only one component of fitness, and tradeoffs may occur between growth capacity and other fitness components, such as survivorship or fecundity, in marginal environments (Rehfeldt et al., 1999; Hereford, 2009; Bordin et al., 2025).

Although trees were differentially tuned to their local environment, our results indicate that in some cases, the ideal conditions for growth did not precisely match the prevailing climate of a site. Instead, growth was often maximized in years when climate departed from local long-term mean conditions; i.e., generally when climate was warmer or wetter than the local average. These patterns suggest a displacement or exclusion of some trees from their climatically ideal environments by competition (Canham et al., 2006). Differences between species in demographic performance and competitive ability may contribute to their differential sorting along environmental gradients (Pérez-Ramos et al., 2019; Marchand et al., 2023). Supporting this premise, our results show that growth responses to competition varied markedly depending on the taxonomic identity of neighboring trees (Appendix S9). Consequently, the growth capacity of trees appears to be concomitantly regulated by environmental selection (local climate) and density-dependent processes (Rehfeldt et al., 1999).

The future climate change consequences for forest productivity may critically be determined by the relative contributions of phenotypic acclimation versus genetic adaptation. These processes may interact (Franks et al., 2014). Acclimation may dampen selection pressure, thereby slowing adaptive evolutionary responses. Conversely, acclimation to rapid environmental changes may promote opportunities for future genetic-based adaptation by prolonging in situ persistence. Additionally, gene expression and acclimation potential are regulated by epigenetic mechanisms, which do not modify the genetic architecture of plants, but are nevertheless putatively heritable (Gugger et al., 2016; Wang et al., 2023). Identifying the relative roles and possible interactions between adaptation and acclimation will promote more robust predictions regarding the impacts of climate change on tree growth and the carbon regulation function of forests. Determining these patterns will depend on experimental work.

4.2. Nitrogen deposition

Growth responses to Nd were strongly individualistic with opposing nonlinear trends among species (Fig. 4). Negative growth responses in two species support posited mechanisms for a coincident shift in resource limitation from N to other mineral nutrients (Aber et al., 1989; Crowley et al., 2012). Chronic N inputs enhance the production and accumulation of highly mobile nitrates, which are expected to saturate plant demand for N, while simultaneously causing a displacement and depletion of soil base cations (Andersson et al., 2002). Plant nutrient deficiency may arise, impacting physiological function (Maathuis, 2009) or causing adjustments in carbon allocation from stem growth to small root production (Waring, 1987). Divergent responses to N inputs among species may be driven by interspecific differences in their physiological requirements for a potentially depleted supply of nutrients, or a disparate sensitivity to accompanying soil acidification processes (Canham and Murphy, 2016).

Mycorrhizal fungi may further mediate N effects. N additions have been found to benefit tree species having symbioses with arbuscular fungi (Thomas et al., 2010). In contrast to ectomycorrhizal fungi, arbuscular

species lack enzymes that facilitate assimilation of organic N, which is the predominant form of stored N in most forest soils (Schulten and Schnitzer, 1997). Thus, trees with arbuscular mycorrhizae—*A. pseudoplatanus* in this study (Kattge et al., 2011)—may experience greater N limitation in unfertilized conditions (Chalot and Brun, 1998), resulting in a comparatively enhanced plant demand and capacity for N absorption across higher deposition loads (Fig. 4b).

In general, the magnitude of growth responses to Nd was modulated by variation in the competitive (Fig. 4) and climatic environment of trees (Fig. 5). For three of four species, responses to accelerating rates of N addition, whether negative or positive, were stronger in warmer or more mesic environments. Possible mechanisms relate to the complex nature of microbial-mediated N transformation in soils. Total nitrate production and ensuing impacts discussed above depend on multiple chemical pathways; in particular, the mineralization of organic N, as well as the oxidation of ammonium (Stark, 2016). These process rates increase nonlinearly with temperature and soil moisture (Shammas, 1986; Agehara and Warncke, 2005) due to concomitant effects on microbial populations (Grundmann et al., 1995; Li et al., 2019). Thus, the consequences of Nd may be accelerated under conditions, such as climate change, that may promote microbial-driven chemical reactions. We note that a confirmation of the mechanisms underlying tree responses to Nd will require experimental investigation and analyses of soil chemistry data.

5. Conclusions

Our analyses provide evidence suggesting that these four tree species have adapted or acclimated, in terms of the growth capacity of individual trees, to the mean climate of their location. The magnitude and direction of growth responses to local climate were found to depend on context, varying markedly across the broad environmental ranges of these species. We also demonstrate the importance of tree ontogeny (age and size) and neighbor competition in determining the growth capacity of individual trees, consistent with prior work (Foster et al., 2016). These patterns underscore the relevance of analyzing ecological processes at the scale of individuals (Clark et al., 2011). Aggregating tree datasets to, for example, compute and examine population-mean indices of growth, may mask the unique behavior of individuals, which can differentially affect whole-system outcomes (Carrer, 2011). Our results support a growing body of evidence highlighting the importance of individual-level variation and adaptive mechanisms in determining the dynamics of a range of ecological phenomena (Grimm et al., 2025; Jeltsch et al., 2025). Accordingly, methods presented in this study can be used to advance a more general understanding of how individual behavior may influence community assembly, as they can be readily modified to understand whether a facility to attune growth responses to local environments also extends to other life-history processes (e.g., survivorship and reproduction) and across life-stages (i.e., adults and juveniles). Our models were fit with observational data, precluding an understanding of whether the patterns observed in this study were underlain by longer-term evolutionary processes or more recent acclimatory mechanisms. The demographic responses of individuals to climate change may vary depending on the relative contributions of adaptation and acclimation. This study therefore, highlights a need for a greater focus and new research on the mechanistic underpinnings of differentiated responses to the environment.

CRedit authorship contribution statement

Arne Buechling: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Charles D. Canham:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Nataliya Korolyova:** Writing – review & editing, Methodology, Investigation. **Melanie Saulnier:** Writing – review & editing. **Patrick H.**

Martin: Writing – review & editing. **Magnuz Engardt:** Writing – review & editing, Methodology, Investigation. **Martin Mikoláš:** Writing – review & editing. **Ondřej Vostarek:** Writing – review & editing, Data curation. **Daniel Kozák:** Writing – review & editing. **Pavel Janda:** Writing – review & editing. **Jenýk Hofmeister:** Writing – review & editing. **Miroslav Svoboda:** Writing – review & editing, Supervision, Resources, Funding acquisition.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2026.100469>.

Data availability

Tree attribute records that were used to fit the models, including annual growth measurements and corresponding environmental data, are available at Zenodo (Buechling et al., 2026).

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