

## Article

# Long-Term Growth Trends of 18 Native and Non-Native Tree Species Based on Data from Experimental Plots Since 1878 in Brandenburg, Germany

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**Abstract:** The rapid environmental changes associated with climate change increase the need for adaptation strategies in forest management based on profound knowledge about tree species, particularly in the context of assisted migration. For research purposes, selected native and non-native tree species were planted in Brandenburg, Germany more than 120 years ago. Today, these sites provide an opportunity to gather insights about their performance and growth-response throughout the past century. We analyzed the height growth increment of 18 tree species on 1765 long-term experimental plots, the earliest of which have been monitored since 1878. We additionally investigated the stand-level volume increments on 60 unmanaged plots for two of these species. Our results show increasing trends in forest stand growth for Scots pine (*Pinus sylvestris* L.) and Sessile oak (*Quercus petraea* (Matt.) Liebl.). However, long-term height increment showed positive, negative, and indifferent growth trends in reaction to changing environmental conditions. Remarkably, 16 out of 18 species showed a growth decline between the years 2000 and 2020, likely attributable to increasing frequencies of single and consecutive drought events. We found non-native species to perform comparably to native tree species. Forest management should reconsider the role of native and non-native species in climate-adapted forests. We recommend focusing on provenance and local site adaptability in assisted migration efforts and argue that maintenance of long-term experiments can provide us with valuable insights on species performance in the near future.

**Keywords:** forest growth; growth trend; climate change; assisted migration



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## 1. Introduction

Tree growth dynamics in European forest ecosystems are subject to rapid environmental changes [1], including rising air temperatures [2], disturbance frequencies [3], and varying atmospheric deposition [4]. Recent investigations have shown that resulting growth trends differ between species, European regions, and periods [5–7]. We observe growth declines in some species, such as European beech (*Fagus sylvatica* L.) [8], while other species show growth increases in some areas, such as Norway spruce (*Picea abies* (L.) H. Karst) in Northern Europe [9]. Some species are expected to increase their potential distribution area if the current warming trend continues, such as Black locust (*Robinia pseudoacacia* L.) [10]. The pace of the observed environmental changes is fast and might exceed the genetic and phenotypic adaptability of tree species [11], thus threatening our

goal to increase forest resilience and ensure forest ecosystem services in the future [12]. Assisted migration, which is the transport of forest reproductive material from regions today featuring expected future climatic conditions in the target area, can support rapid forest management responses to climate change challenges [13]. Assisted migration can have positive effects on species adaptation, forest ecosystem stability and productivity, but also comes with risks related to invasive species and maladaptation [14]. The knowledge gap concerning the costs and benefits of assisted migration may be overcome by analyzing data from existing long-term experimental sites with actively “migrated” tree species, some of which have been intensively studied since the end of the 19th century [5,6]. These experiments provide an alternative source of information on the performance of tree species and provenances in a changing environment [15].

In Brandenburg, Germany, the first long-term field experiments were established in 1870 [16]. Since then, they have been dedicated to finding optimal spacing, rotation, and thinning regimes for tree species for the maximum yield, provenance trials, planting experiments, and more [16]. Furthermore, seed sources from various non-native tree species, especially from North America, were transferred to Brandenburg for investigation of their growth, wood quality, and adaptability to local site conditions [17]. Some of these experiments with non-native tree species and provenances are still monitored today and provide insights into the suitability of these species for modern assisted migration efforts.

In contrast, experiments without any treatment are rare, but have been more frequently investigated since 1960. Species-specific, management-independent long-term trends in forest stand growth, such as the change of the self-thinning line, can only be investigated with the help of fully stocked and unmanaged experimental plots [15]. Trends in tree height growth, on the other hand, can be investigated for managed and unmanaged experimental sites if the considered trees are dominant and other factors, such as tree age and site fertility, are accounted for in the analysis [18,19].

This study investigates the height growth trends for 18 tree species on long-term experimental sites and, additionally, the stand growth trend for two major tree species on unmanaged experimental sites in Brandenburg, Germany. Our aim is to reveal the species’ growth reactions to environmental changes, particularly climate warming, on a regional scale and in comparison to changes found in other studies at a European scale. We further investigate if our results are able to classify species to potential “winners” and “losers” under long-term environmental changes and discuss the implications for future assisted migration programs.

## 2. Materials and Methods

### 2.1. Tree Data

Overall, we analyzed 18 tree species which have been measured on experimental plots throughout different time periods ranging from 1878–2024 (Table 1). These periods vary among tree species due to the different establishment eras of the studied experimental plots. The data gathered on those experimental sites includes the diameter at breast height (1.3 m), tree height, tree species, and tree age. Other parameters, such as the individual tree position, tree crown radii, or the seed sources, have only rarely been documented. Typical measurement intervals are 5 years, although exceptions occur due to various environmental, societal, or administrative issues. The majority of these long-term experiments focus on a particular management regime.

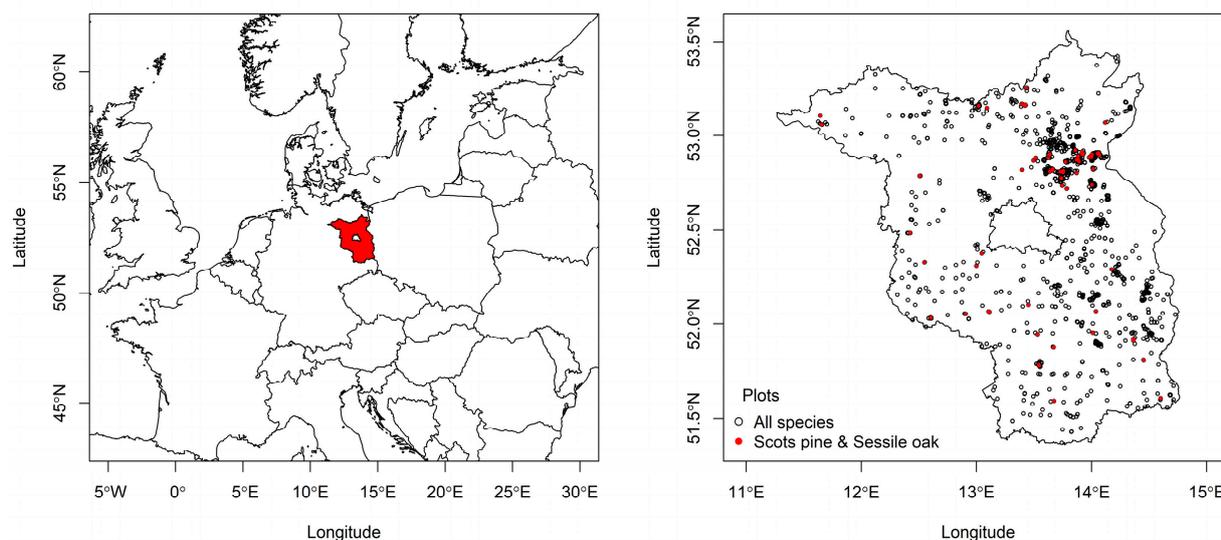
**Table 1.** Tree data summary for 18 tree species used in the analysis and modeling. Orig denotes the species origin: NN in case of non-native, N for native species. Age denotes the age range of trees in the analysis; Years denotes the year range of height measurements in the analysis. Nb Plots denotes the number of plots on which the species occurs, and Nb Incr denotes the number of tree height increments used in the data analysis. Incr denotes the range of annual tree height increments for a particular tree species.

	Species	Orig	Age	Years	Nb Plots	Nb Incr	Incr [m/Year]
1	<i>Abies grandis</i> (Douglas ex D. Don) Lindl.	NN	20–127	1955–2024	32	2298	0.1–1
2	<i>Acer pseudoplatanus</i> L.	N	5–124	1909–2022	14	4739	0–0.5
3	<i>Alnus glutinosa</i> (L.) Gaertn.	N	12–149	1900–2024	31	751	0–0.5
4	<i>Carya ovata</i> (Mill.) K. Koch	NN	43–138	1914–2021	8	1480	0–0.5
5	<i>Chamaecyparis lawsoniana</i> (A. Murr.) Parl.	NN	78–135	1955–2021	14	746	0–0.5
6	<i>Fagus sylvatica</i> L.	N	3–198	1884–2023	194	15,003	0–0.6
7	<i>Larix decidua</i> Mill.	N	22–130	1954–2021	17	852	0–0.6
8	<i>Larix kaempferi</i> (Lamb.) Carrière	NN	14–129	1953–2024	49	3604	0.1–0.7
9	<i>Picea abies</i> (L.) H.Karst.	N	25–139	1915–2023	112	4376	0.1–0.6
10	<i>Pinus sylvestris</i> L.	N	1–187	1886–2024	649	103,070	0–0.8
11	<i>Pseudotsuga menziesii</i> (Mirbel) Franco	NN	1–144	1914–2024	410	23,538	0–0.9
12	<i>Quercus petraea</i> (Mattuschka) Liebl.	N	20–200	1878–2023	96	8650	0–0.5
13	<i>Quercus robur</i> L.	N	12–200	1890–2023	14	1881	0.1–0.4
14	<i>Quercus rubra</i> L.	NN	1–134	1953–2021	33	1496	0.1–0.7
15	<i>Robinia pseudoacacia</i> L.	NN	14–119	1954–2020	13	1648	0.1–0.6
16	<i>Thuja plicata</i> Donn ex D. Don.	NN	13–139	1954–2024	55	3545	0–0.6
17	<i>Tilia cordata</i> Mill.	N	1–81	1954–2021	15	2215	0.1–0.6
18	<i>Tsuga heterophylla</i> (Raf.) Sarg.	NN	31–141	1953–2023	9	413	0.1–0.6

The tree species were selected based on the available tree height increment measurements, setting the minimum at 700 individual height measurements per species. Nine of the tree species in our analysis are considered non-native, as they were introduced into the study area at the end of the 19th century [17]. Classification of native (N) and non-native (NN) tree species is provided in Table 1.

The technology for measuring tree height changed throughout the study period, but the majority of tree heights were obtained using clinometers and laser dendrometers. Tree height measurements were taken on a representative subsample of the experimental plot trees to reduce the measurement effort on the large number of plots. In contrast, tree diameter was measured for all trees using a caliper at 1.3 m height above ground. Missing tree heights were calculated by first modeling the non-linear relationship between tree height and tree diameter, followed by predicting tree height using tree diameter as input variable. For this purpose, different equations have been developed and applied [20]. Usually, a set of non-linear relationships was compared based on the ordinary least squares method and visual inspection of data fit before using a single best non-linear regression for calculating missing tree heights.

We used tree height data from 1765 experimental plots (Figure 1) with individual plot areas ranging from 0.01 to 10 ha, depending on the scientific purpose. In total, 60 of those plots are unmanaged sites with either Sessile oak (*Quercus petraea* (Mattuschka) Liebl.) or Scots pine (*Pinus sylvestris* L.), which we additionally used to analyze stand growth trends. The total experimental plot area in this study amounts to 846 ha.



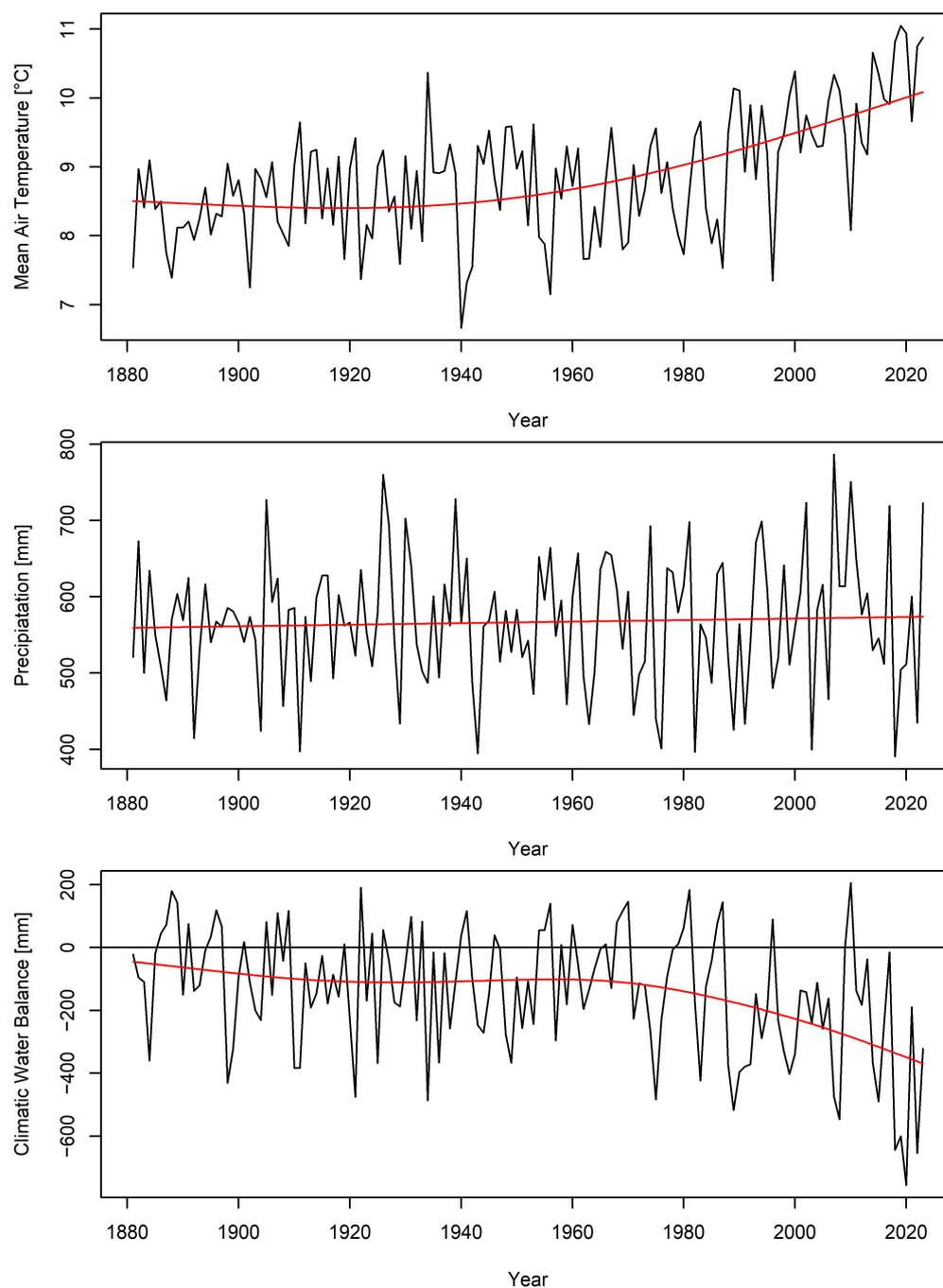
**Figure 1.** Location of the state of Brandenburg (red) in Central Europe (**left**). Plot locations in the state of Brandenburg, Germany (**right**). Hollow circles refer to plots where tree height data was used for analysis; red dots refer to unmanaged plots specifically used for forest stand growth analysis.

We only included tree height data from trees that were dominant and without large neighboring competitors, in order to minimize the error from light competition in the subsequent trend analysis. As tree positions were not readily available for most experimental plots, we relied on written documentation to ensure trees were not suppressed by large neighboring individuals and selected dominant trees greater than or equal to the 0.9 quantile height threshold.

## 2.2. Study Region

The study region is located in Central Europe, featuring a temperate climate with continental influences. The terrain is characterized by small differences in elevation ranging between 0 and 201 m above sea level. The climate has changed drastically between the periods 1880–1910 and 1994–2024: While annual precipitation sums showed very few trend changes, with an annual mean of 560 mm and a standard deviation (sd) of 84.2 mm ([21,22], Figure 2), mean annual air temperatures rose from 8.4 °C (sd 0.56) to 9.8 °C (sd 0.72). A thin-plate regression spline model indicates the observed long-term trend for mean air temperature (Figure 2). Driven by temperature change, the climatic water balance based on the potential evaporation according to Thornthwaite [23] showed a strong negative trend ([21,22], Figure 2). The years 2018–2020 consecutively featured very negative climatic water balances, also classified as severe drought events by other studies [24,25].

Soil conditions in the study region are characterized by prevalent sandy substrates, sometimes with loamy moraine deposits [26]. Most soil types are classified either as cambisols or podzols with low soil pH and nutrient status as well as low water-holding capacity [26]. Soil conditions and tree growth are further influenced by nitrogen deposition, which increased until the 1990s and has decreased ever since [27].



**Figure 2.** Development of mean annual temperature, total annual precipitation, and annual climatic water balance averaged for the state of Brandenburg, Germany, from 1880 to 2024 (black lines). Red lines show a thin-plate regression spline model.

### 2.3. Tree Height Increment Modeling

We calculated the height increments of dominant trees for the particular measurement period on experimental plots, which was typically 5 years. We then calculated annual tree height increments by dividing the periodic height difference by the number of years of the particular period. This approach technically assumes a constant height growth between two consecutive measurements.

We built height increment models based on the calculated annual height increments for every species (Table 1) using hierarchical generalized additive models [28]. Generalized

additive models (GAMs) are a flexible tool using penalized regression splines to model complex real-world phenomena [29]. In general, GAMs can be formulated as:

$$E(Y) = g\left(\beta_0 + \sum_{j=1}^J f(x_j, p_j)\right) \quad (1)$$

where  $E(Y)$  is the expected value of the response  $Y$  (here specified as height increment),  $g$  denotes the link function (here specified as an identity link),  $\beta_0$  is the intercept, and  $f$  denotes the  $j$ th smooth function of the covariate  $x$  and the factor  $p$  (experimental plots). The smooth function ( $f$ ) consists of a number of ( $k$ ) fixed basis functions ( $b$ ) multiplied by a set of coefficients ( $\beta$ ):

$$f_j(x_j) = \sum_{k=1}^K \beta_{j,k} b_{j,k}(x_j) \quad (2)$$

GAMs enable us to investigate the non-linear dependence of tree height increment on several variables, such as tree age or site conditions, while analyzing the variables in an additive manner. The use of a hierarchical model approach gives us the opportunity to analyze smoothing functions that vary between different grouping levels [28], which was necessary in our study in order to estimate long-term trends for all 18 tree species. We tested the application of generalized linear models (GLS), but found model fitting to be inferior to GAMs due to clear non-linear relationships between tree height increment and tree age. Furthermore, we expected a possible long-term trend to be non-linear as well, which can be better estimated using smoothing splines.

Tree species-specific height increment was modeled as dependent on tree diameter, tree age, the experimental plot as a factor and a grouping variable, as well as the calendar year. Tree age was modeled as a smooth that varies between experimental plots (grouping variable), as we assume that site conditions affect the relationship between height increment and tree age [30,31]. We tested another modeling set up using mixed models (GAMMs), which showed many similarities in the random effects calculation. However, due to the high number of factor levels (experimental plots), we decided to implement hierarchical models to enhance performance.

Other variables were modeled as single thin-plate-regression spline smooths [29]. We tested 4 different hierarchical model structures, including tensor-product splines, which differed in the smoothing penalties for the hierarchical tree age effect and the interactions between tree age and the experimental plot as well as the interaction with the calendar year [28]. We chose the best-performing model using the Akaike information criterion (AIC, [32]) and minimized the selection bias [33] by taking the Bayesian information criterion (BIC, [34]) and the root mean square error (RMSE) into consideration. Furthermore, we selected models based on the explained deviance by adding penalties for the null space of all smooths allowing them to be shrunk to zero [35], which has been shown to be superior in a GAM variable selection process compared to forward and backward variable selection using p-values. As a result, we did not include tree diameter in the final height increment models, both because it did not improve model performance and because our main focus was not on demonstrating the diameter effect, but on estimating a possible long-term trend.

The final model form estimated the age effect variation between the grouping variable by implementing a factor-smooth interaction between tree age and experimental plot as factor. This approach estimates a smooth for each factor level, allowing the tree age effect to be site-dependent and entirely random [29]. An additional single smooth term for tree age did not improve model performance and was, hence, excluded. The second smooth was estimated for the variable calendar year. We did not log-transform height increments

before calculations, but instead used an identity-link function [29]. We finally estimated 18 species-specific height increment models of the form:

$$E(H_i) = g \left( \beta_0 + \sum_{i=1}^i (f(\text{Age}_i, \text{Plot}_i) + f(\text{Year}_i)) \right) \quad (3)$$

where  $E(H_i)$  is the expected value of the height increment  $H$  at an instance  $i$ ,  $g$  denotes the identity link function,  $\beta_0$  denotes the intercept, and  $f$  denotes the smooth functions of the interaction between  $\text{Age}$  and  $\text{Plot}$  as well as the single smooth term for  $\text{Year}$ .

We show the long-term trend of the calendar year with the help of partial effect plots [29], in which case the term of the  $\text{Age-Plot}$  interaction is set to zero and the remaining model effect is plotted over the calendar year centered at the overall mean. Model predictions are additionally provided over the calendar year with  $\text{Age}$  set to its median in order to investigate the model estimations on the scale of the response. We provide plots on the interaction between tree age and experimental plot in the appendix, Figure A1. The results of the 18 species-specific models are summarized in Table A1 with detailed information on the AIC, BIC, RMSE, and the share of deviance explained by each model. We additionally provide histograms of the model residuals in Figure A2 and plot the model fits against our height increment data in Figure A3.

Data analysis and modeling were accomplished using R Version 4.3.1 [36] and the package *mgcv* version 1.8–42 [29,37].

#### 2.4. Forest Stand Growth Analysis

We analyzed forest stand growth for unmanaged experimental plots of Sessile oak (6 plots in total) and Scots pine (54 plots in total), both native to the study region. Our analysis focused on the standing volume, which we derived as sum of all single-tree stem volumes on an experimental plot. Single-tree stem volumes were calculated using functions that were specifically developed and calibrated in the study region [38]. These functions provide the estimated volume of all woody components of the tree  $i$  with a diameter greater than 7 cm ( $VD$ ). For Sessile oak:

$$VD_i = \begin{cases} 0.000070436 \times D^{1.8747} \times H^{1.067808} \times 0.98711565 \times e^{-e^{3.627465 - 0.51027 \times D}}, & A < 31 \\ e^{-10.7172 + 2.09058 \times \ln D + 0.97769 \times \ln H}, & A > 30 \end{cases} \quad (4)$$

where  $D$  denotes the tree diameter,  $H$  denotes the tree height, and  $A$  denotes the tree age. For Scots pine:

$$VD_i = e^{-9.675966 + 1.999797 \times \ln D + 0.82493 \times \ln H} - 0.01 \quad (5)$$

where  $D$  denotes the tree diameter and  $H$  denotes the tree height. The single-tree volumes  $VD_i$  were then summed up to the stand total and divided by the experimental plot area, thus yielding the per-hectare standing volume  $VD$  [ $\text{m}^3/\text{ha}$ ]. The standing volume increment  $VI$  for a specific period  $t_1 - t_0$  was then calculated as:

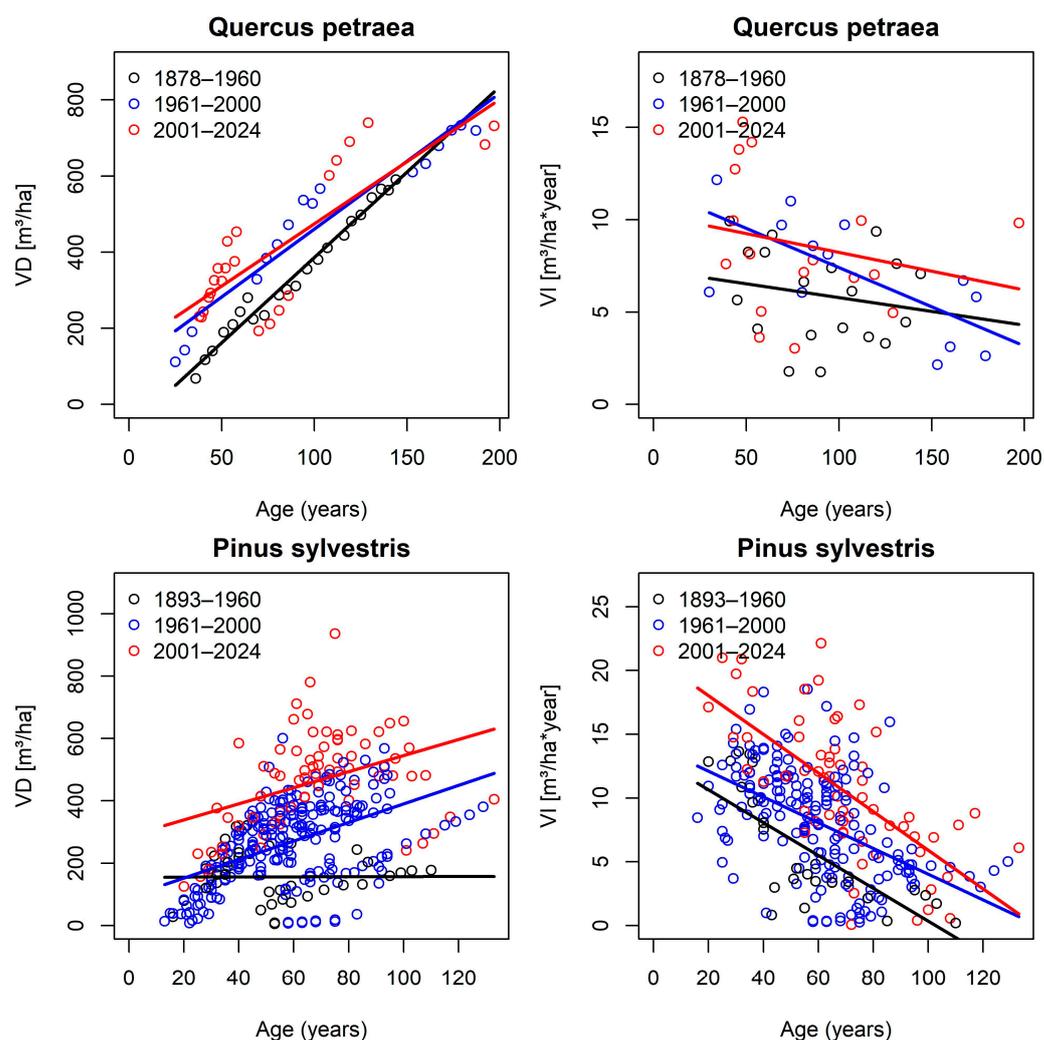
$$VI = \frac{VD_{t_1} - VD_{t_0}}{t_1 - t_0} \quad (6)$$

where  $VD_{t_1}$  is the standing volume at the end and  $VD_{t_0}$  is the standing volume at the beginning of a specific period, respectively. In order to demonstrate changes in the relationships between  $VI$  and tree age, we analyzed three different time periods based on observed mean air temperature and annual precipitation sums in the study region (Figure 2): 1878(1893)–1960, 1961–2000, and 2001–2024. The first period starts in 1878 and 1893 for Sessile oak and Scots pine, respectively. The first and longest period until 1960

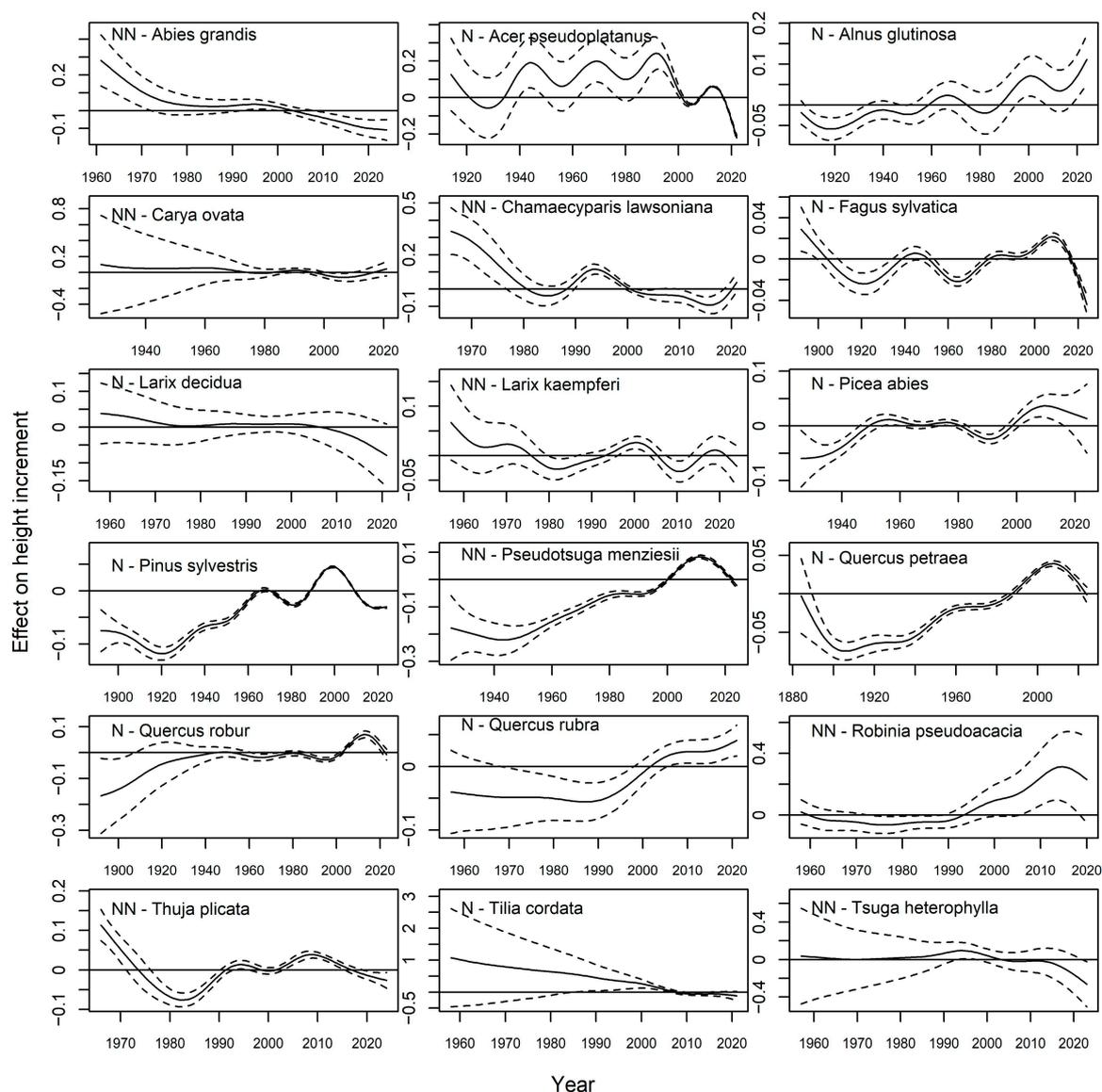
is characterized by very small changes in the temperature and precipitation patterns, followed by a period of rapid temperature change, which we separated by the year 2000 for demonstration purposes only.

### 3. Results

In the case of the native species Sessile oak and Scots pine, both standing volumes  $VD$  and volume increments  $VI$  over tree age increased relative to the first data period of 1878 (1893)–1960 (Figure 3). For Scots pine, the larger number of experimental plots facilitates the distinction between data periods and growth changes, whereas the distinction is less clear for Sessile oak. In contrast to the height growth decline demonstrated in Figures 3 and 4 since the year 2000, neither species shows growth declines in the third period of 2001–2024.



**Figure 3.** Standing volume  $VD$  [ $\text{m}^3/\text{ha}$ ] (left) and volume increment  $VI$  [ $\text{m}^3/\text{ha}\cdot\text{year}$ ] (right) over tree age for Sessile oak (*Quercus petraea*) (top) and Scots pine (*Pinus sylvestris*) (bottom). Red, blue, and black refer to different time periods used for circles and lines. Lines indicate linear trend models for each time period and species.

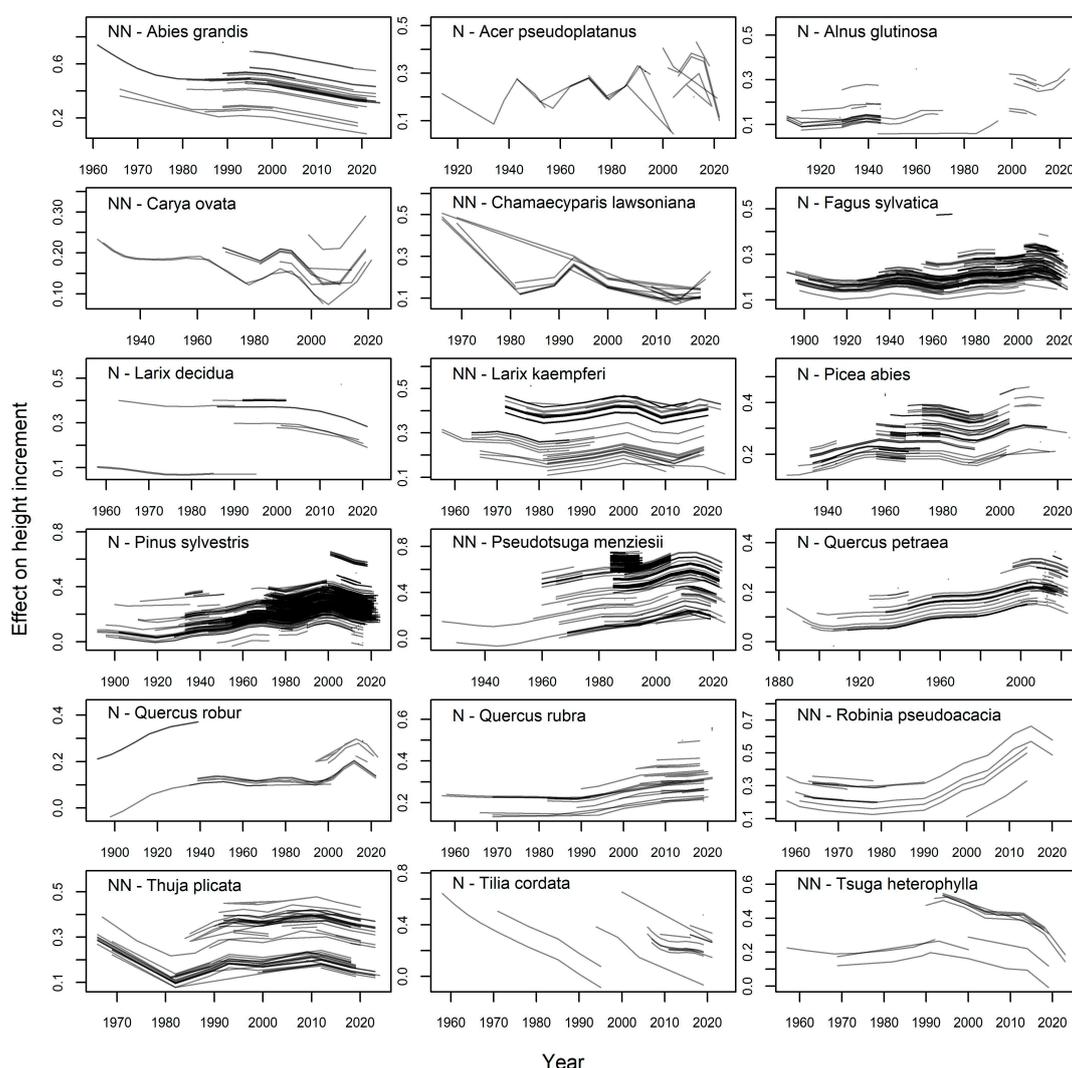


**Figure 4.** Partial effect plots for the effect of the calendar year on tree height increment. The smooth estimate is shown as a solid line; dashed lines indicate 2 standard errors added to the smooth estimate. Partial effect plots are centered at the overall mean. The term for the interaction between tree age and experimental plot is set to zero. NN and N denote the species classifications as non-native and native, respectively.

Figure 4 shows plots of the partial effect of the calendar year on tree height increment. Trends were diagnosed for all tree species except for *Carya ovata*, which shows an almost flat smooth estimate with large standard errors before 1980. Some species show strong fluctuations, but no clear long-term trends, such as *Fagus sylvatica* or *Larix kaempferii*. *Pinus sylvestris*, *Pseudotsuga menziesii*, *Quercus petraea*, and *Quercus rubra* feature long-term increasing trends interrupted by smaller fluctuations. Long-term decreasing trends were observed for *Abies grandis*, *Larix decidua*, and *Chamaecyparis lawsoniana*. Remarkably, a decline between the years 2000 and 2020 was found for almost all species, with only few exceptions, like *Alnus glutinosa* and *Quercus rubra*. The onset of this recent growth decline is, however, very different and can be observed before 2010, such as for *Pinus sylvestris*, or after 2010, such as for *Robinia pseudoacacia*. Some smooth estimates are accompanied by large standard errors, which leaves partial smooth effects very uncertain, such as for *Tilia*

*cordata* and *Tsuga heterophylla*. A clear distinction between the smooth estimates of native and non-native species could not be observed.

Model predictions with tree age set to its median (Figure 5) provide similar observations as the partial effect plots above. However, the additional solid lines for each species indicate the partly substantial experimental plot variation, for instance in the case of *Thuja plicata* or *Pseudotsuga menziesii*. The predictions for *Acer pseudoplatanus*, *Alnus glutinosa*, and *Carya ovata* appear erratic, whereas the predictions for *Tilia cordata* appear to have a clear decreasing trend, which stands in contrast to the partial smooth effect (Figure 3). With few exceptions, most species show a growth decline after the year 2000, although some species, such as *Pseudotsuga menziesii*, showed a long-term increasing trend for more than 60 years before that period.



**Figure 5.** Calendar year effect plots on the model response scale with tree age set to its median. Site-specific variations are depicted with additional lines. NN and N denote the species classifications as non-native and native, respectively.

#### 4. Discussion

Our analysis of unmanaged experimental plots revealed long-term growth increases for the native species Scots pine and Sessile oak since the end of the 19th century, which is in alignment with previous studies on a European scale in the case of Scots pine [6,39]. Our regional study, therefore, reflects large-scale positive effects of environmental changes

like increasing atmospheric CO<sub>2</sub>-concentrations [40], N-deposition [41], and extended growing seasons [42], but no negative growth trends as reported in the Mediterranean area [6,43,44]. It is noteworthy that atmospheric N-depositions decreased for the last two decades, but are still active in the soil, impacting site conditions [41]. For Sessile oak, we are the first to reveal positive long-term growth trends in our study region based on standing volumes of long-term experimental plots. However, the growth increase found in our study is irrespective of frequent forest disturbances and associated tree mortality [3,45], which overall could cancel out productivity gains due to the above-listed environmental changes [46].

The analyzed height growth trends for dominant trees of 18 species revealed both positive and negative effects of the calendar year. We assume the latter to be associated with multifaceted environmental trends including temperature rise, CO<sub>2</sub> increase, and N-deposition. Further investigation on the environmental drivers behind tree growth trends should be focuses to another study and should include accurate data on CO<sub>2</sub> concentrations or N-deposition to unravel a mechanistic understanding of the growth processes.

Based on the calendar year effects, we estimated long-term positive growth trends for 6 out of 18 tree species: *Pinus sylvestris*, *Pseudotsuga menziesii*, *Quercus petraea*, *Quercus robur*, *Quercus rubra*, and *Robinia pseudoacacia*. However, 16 of the 18 species showed growth declines after the year 2000 and 2010, respectively, except for *Quercus rubra* and *Alnus glutinosa*, which, in the latter case, likely experienced positive effects of hydromorphic soil conditions and flooding even in drought years. The observed recent growth declines might be related to increasing drought frequency observed across Europe, culminating in three severe consecutive drought years 2018–2020 in our study region [47–49]. Contrary to the positive long-term trends, *Abies grandis*, *Chamaecyparis lawsoniana*, and *Larix decidua* showed negative growth trends since 1960 and 1970, which could be attributed to the declining climatic water balance in the study region, which possibly exceeded the species adaptive potential [50–52]. Instead of a clear long-term trend, some species such as *Fagus sylvatica* or *Larix kaempferii* showed strong fluctuating responses. For *Fagus sylvatica*, the growth decline in recent years was estimated to be the most severe of all species based on the partial effect of the calendar year, which was also reflected in the drought response reported in other studies [53,54]. Our estimates for *Carya ovata*, *Tilia cordata*, and *Acer pseudoplatanus* showed erratic predictions, wide standard errors of the smooth effects, and implausible age effects (Figure A1), indicating biased model data or shortcomings in the model fitting process. We, therefore, cannot draw any conclusions on growth trends of these species.

Recent studies focusing on the site index [55–57], which is the stand dominant height at a reference age (usually 100 years), reported positive growth trends for various European tree species [58,59], which support our estimated long-term positive trend for some species. However, studies focusing on ring-width analysis also found growth reductions for some species, such as *Picea abies* [60,61], *Pinus sylvestris* [60,62], *Fagus sylvatica* [8], and *Quercus petraea* [63], with growth changes largely varying and depending on local site conditions. Environmental changes affect species differently, especially in rear-edge populations [64]. Hence, for instance, *Fagus sylvatica* might experience negative growth effects through climate change in Northern Germany while *Pinus sylvestris* experiences positive effects, albeit with a higher climate sensitivity [65]. A similar differentiation between species was observed in our study, where some species benefit from environmental changes in the long term, while others react negatively or show almost no reaction at all. Based on our results, there is no clear distinction between non-native and native tree species, as neither group outperformed the other. Rather, in both groups, some species showed long-term benefits, but also reflected growth declines due to recent drought events.

As negative trends since the year 2000 were observable for 16 out of 18 species in our study region, we assume that recommendations on the future tree species choice [66] based on our results are not feasible if the environmental changes continue with the severity observed in recent years. We believe that assisted migration [67] should focus on specific provenances and assisted gene flow instead of simply targeting tree species, as the intra-specific variability and adaption potential in climate-growth responses might outweigh regional or local environmental changes [68–70]. However, local site conditions might exert even more influence on tree growth than provenances [71]. This complexity in tree growth relationships supports our decision to abstain from recommending specific tree species and classifying them as “winners” or “losers”.

Our results question the widespread narrative that non-native tree species can be superior to native species in future climate-adaptive forests. In fact, current forest management programs should be re-evaluated and incorporate current findings on assisted migration and the importance of species provenance and local site conditions on tree growth. However, our regional study focus is not sufficient for altering policy frameworks on a larger scale. Rather, our study supports the need for unraveling a mechanistic understanding of tree growth and environmental factors. This can be improved by forest monitoring networks on a larger scale that enable us to study tree growth reactions over larger environmental gradients.

## 5. Conclusions

We analyzed regional growth trends for 18 native and non-native tree species based on dominant tree height and forest stand volume of unmanaged experimental plots for two native species. Our results support positive growth trends found on a European scale for Scots pine on a forest stand level. We additionally showed positive regional growth trends for stands of Sessile oak. Long-term positive trends in height growth were found for 6 out of 18 species, which correspond with climate warming and nitrogen deposition. The other species showed either negative long-term trends, highly fluctuating species response, or almost steady growth reactions to environmental change. A vast majority of 16 out of 18 analyzed species showed growth declines between the years 2000 and 2020, probably corresponding to increasing frequencies of single and consecutive drought events. We did not find any eminent differences in the performance of non-native compared to native tree species. We conclude that assisted migration aimed at promoting climate change adaptation should not solely focus on tree species, but rather on species provenances and their adaptability to local site conditions. Despite the enormous effort associated with the maintenance of long-term experimental plots, we argue that incorporating insights gathered from those experiments in the development of future adaptive responses in forest management is still a valuable strategy in the future.

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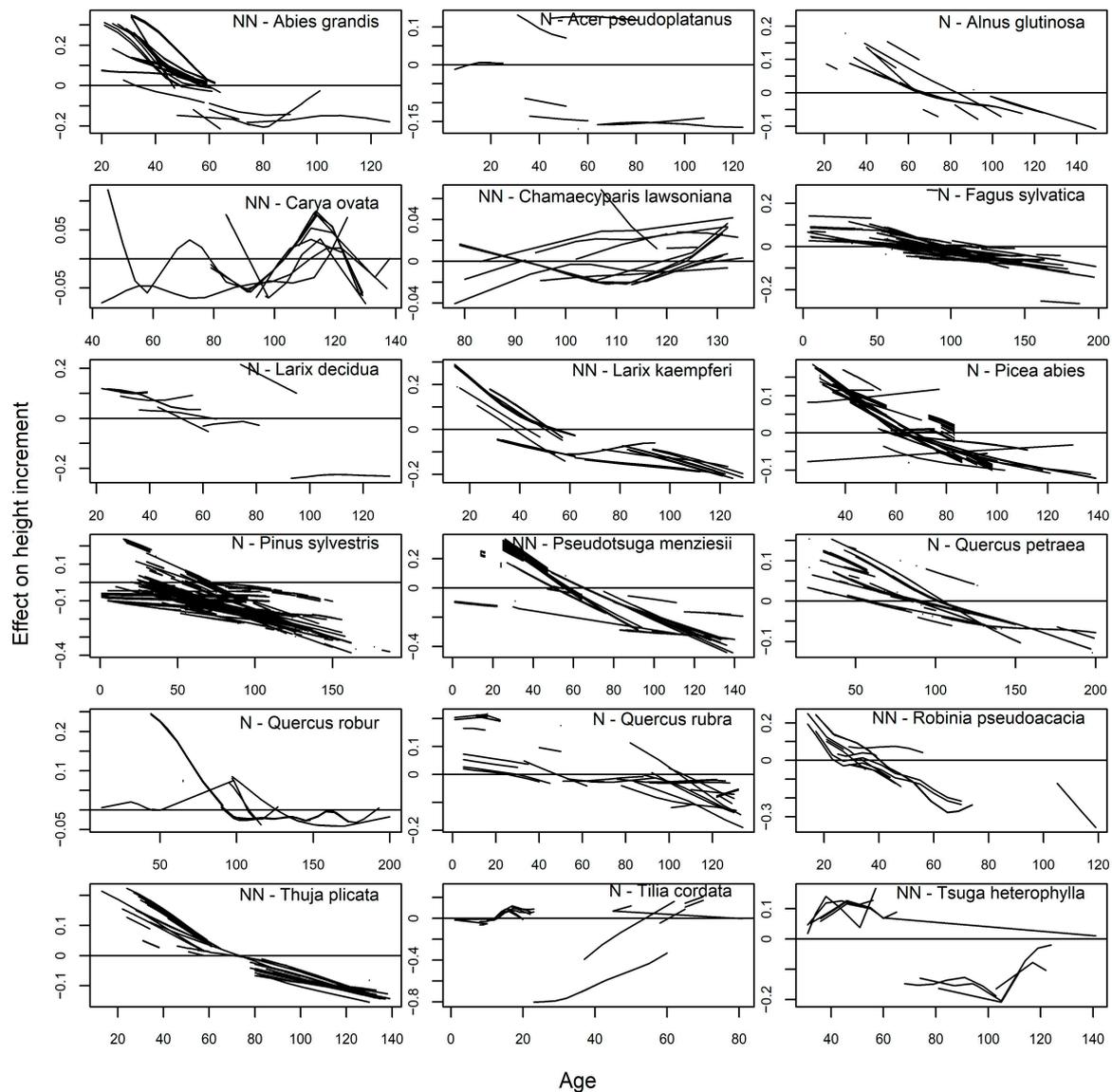
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## Appendix A



**Figure A1.** Effects of the factor-smooth interaction between tree age and the experimental plot as factor. The factor-smooth interaction calculates one single effect smooth for every factor level. NN denotes non-native tree species, N denotes native tree species.

**Table A1.** Model information summary. NbIncr denotes the number of height increments used in the model. Dev.expl. denotes the explained deviance of the model. AIC denotes the Akaike information criterion, BIC denotes the Bayesian information criterion, and RMSE denotes the root mean square error.

	Species	NbIncr	Dev.Expl.	AIC	BIC	RMSE
1	<i>Abies grandis</i> (Douglas ex D. Don) Lindl.	2298	0.66	−3098.89	−2901.86	0.12
2	<i>Acer pseudoplatanus</i> L.	4739	0.28	−8474.64	−8325.57	0.10
3	<i>Alnus glutinosa</i> (L.) Gaertn.	751	0.63	−2030.33	−1898.28	0.06
4	<i>Carya ovata</i> (Mill.) K. Koch	1480	0.37	−4811.24	−4630.23	0.05
5	<i>Chamaecyparis lawsoniana</i> (A. Murr.) Parl.	746	0.63	−2339.16	−2210.56	0.05
6	<i>Fagus sylvatica</i> L.	15,192	0.34	−32,418.84	−32,119.48	0.08
7	<i>Larix decidua</i> Mill.	852	0.77	−2072.77	−1950.82	0.07

Table A1. Cont.

	Species	NbIncr	Dev.Expl.	AIC	BIC	RMSE
8	<i>Larix kaempferi</i> (Lamb.) Carrière	3604	0.64	−6859.32	−6631.49	0.09
9	<i>Picea abies</i> (L.) H. Karst.	4384	0.42	−9854.33	−9611.36	0.08
10	<i>Pinus sylvestris</i> L.	103,078	0.73	−167,620.05	−167,239.88	0.11
11	<i>Pseudotsuga menziesii</i> (Mirbel) Franco	23,538	0.43	−25,536.73	−25,226.38	0.14
12	<i>Quercus petraea</i> (Mattuschka) Liebl.	8651	0.37	−22,097.66	−21,825.20	0.07
13	<i>Quercus robur</i> L.	1881	0.40	−6166.94	−5973.88	0.05
14	<i>Quercus rubra</i> L.	1496	0.54	−2511.86	−2326.67	0.10
15	<i>Robinia pseudoacacia</i> L.	1648	0.53	−3722.69	−3533.86	0.08
16	<i>Thuja plicata</i> Donn ex D. Don.	3545	0.60	−7175.57	−6956.55	0.09
17	<i>Tilia cordata</i> Mill.	2215	0.20	−3485.10	−3314.52	0.11
18	<i>Tsuga heterophylla</i> (Raf.) Sarg.	413	0.67	−789.06	−667.54	0.09

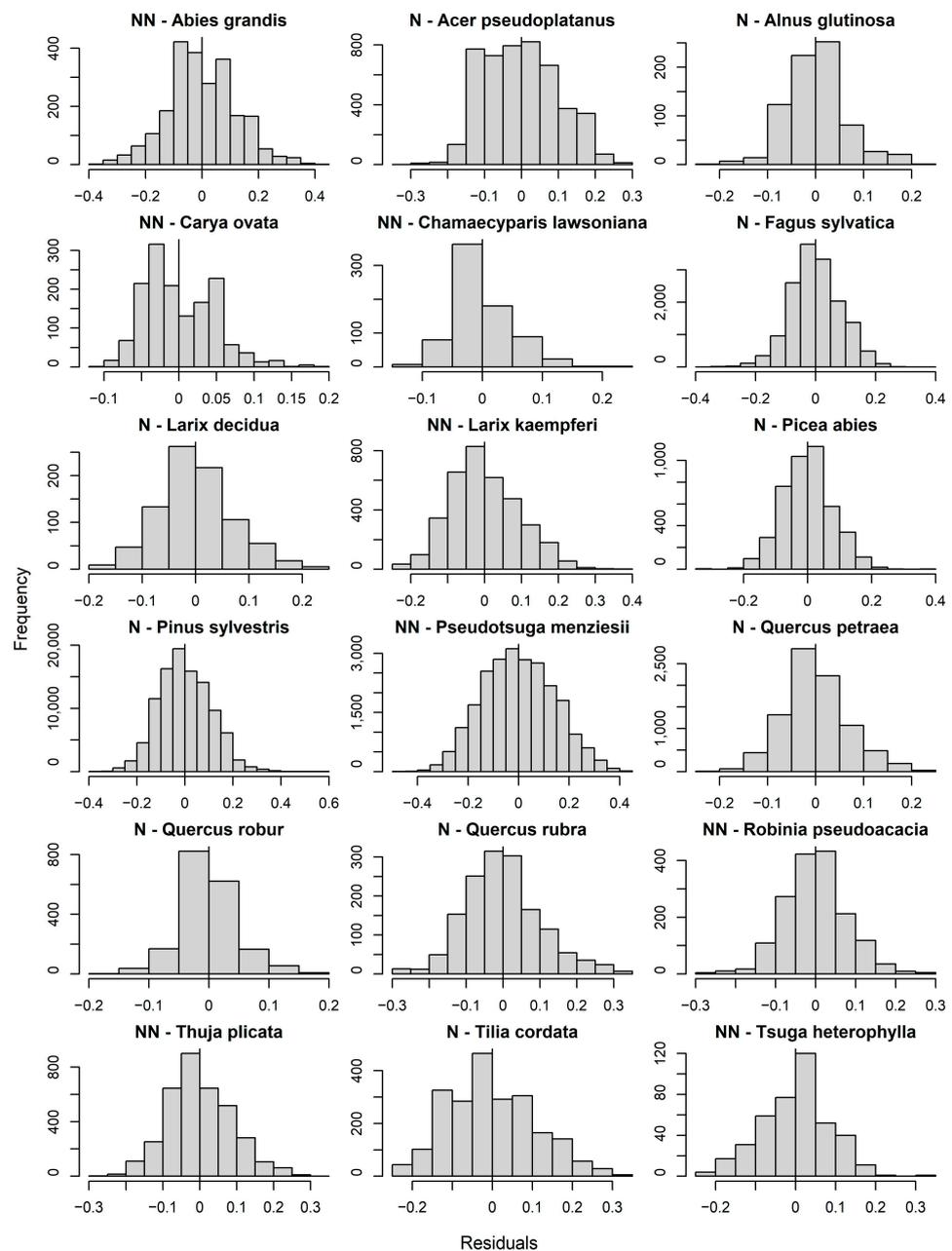
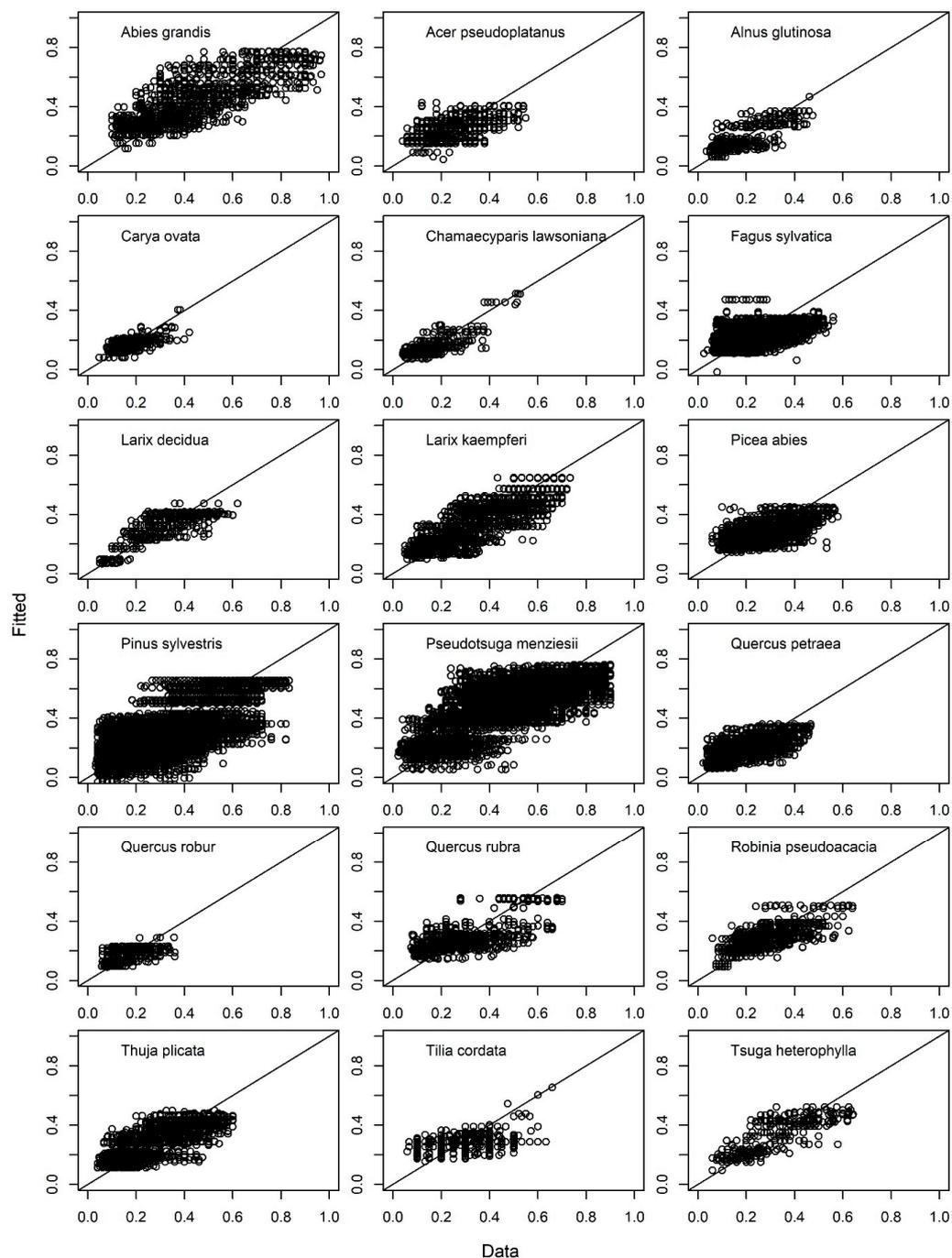


Figure A2. Histograms of model residuals for all species-specific models.



**Figure A3.** Fitted annual tree height increment [m/year] against the actual height increment [m/year] of the model data.

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