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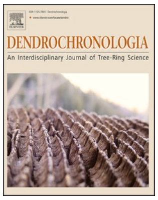

Spatial and temporal variation of *Fagus sylvatica* growth in marginal areas under progressive climate change

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ABSTRACT

The escalating decline in growth trends of European beech (*Fagus sylvatica*) observed across its distribution area pose a major ecological and economic challenge for countries with a high proportion of beech, such as Slovenia. In this study, the effects of climate change were examined at a high-resolution scale, encompassing the large climatic, orographic, and ecological variability of beech forests in Slovenia. Using basal area increment data (BAI) from a tree-ring network (48 sites in Slovenia), modelled climate data, and generalized linear mixed models (GLMM), we found an average growth decline of 11% between the 1953–1985 and 1986–2018 subperiods, affecting 90.5% of the forest stands. Based on climate data, we defined two contrasted marginal areas of beech presence (warm and cold) and analysed the growth changes over time. The warm marginal areas, which predominate near the geographical margin of beech distribution with a sub-Mediterranean climatic regime, were most affected by growth decline, threatening the survival of beech populations in the area. In contrast, cold marginal areas, mainly at high elevations in the Alps, where beech growth had previously been limited by low temperatures, turned out to be the only ones where growth of beech increased under prevailing warming conditions. Consequently, high elevation regions harbour climatic potential for increased beech growth performance, and may represent areas of future expansion of the species.

1. Introduction

European beech (*Fagus sylvatica* L.) is distributed throughout most of Europe, where recent changes in climate have led to higher temperatures, changes in precipitation patterns, and an increase of extreme climate events (ADAPT, 2023; de Luis et al., 2014; Pogačar et al., 2022; Škrk et al., 2021; Twardosz et al., 2021). As a late-successional deciduous tree species, European beech has variable behaviour and responds to climate with plastic and adaptive growth patterns, even in marginal areas (Martinez del Castillo et al., 2016) or those prone to climatic extremes (Decuyper et al., 2020). Some studies have reported the relative high competitive ability of beech to cope with climate change (Hacket-Pain and Friend, 2017), including compared with other pioneer and late-successional species (Dyderski et al., 2018). On the other side, numerous studies have demonstrated that beech populations may become more vulnerable to climate change (Chakraborty et al., 2021; Diers et al., 2022; Leuschner, 2020), particularly at the edge of their distribution range (Martinez del Castillo et al., 2022; Petit-Cailleux et al., 2021). A recent study by Martinez del Castillo and co-authors (2022) using a large tree-ring database of beech covering the entire

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geographic and climatic range of this species and applying various climate change scenarios showed a general current and expected future decline in growth over a great part of its distribution range. The most pronounced growth decline is expected towards the southern distribution limit of the species, mostly in areas with a very probable increase in drought. However, there are areas where growth of beech might increase, depending on the severity of climate change, especially at sites located towards the northern distribution range and at higher elevations in mountain regions. Such studies including the entire species distribution area in Europe can help us understand the main trends in distribution shifts, while numerous smaller, more local studies can highlight changes, trends and the reasons for them at a more detailed level (e.g., Bončina et al., 2023; Camarero et al., 2021; Di Fiore et al., 2022; Stolz et al., 2021; Trifković et al., 2022).

European beech is a predominant forest tree species in Slovenia, a territory where beech survived Pleistocene glaciations in some important refuges and later spread over a larger area (e.g., Brus, 2010; Magri et al., 2006). Slovenia is a geographically and climatically diverse area, with almost twice as strong warming in summer and spring compared to neighbouring countries (de Luis et al., 2014; IPCC, 2022; Kutnar et al., 2021). Currently, beech forests are naturally present in almost all of Slovenia, except on the Pannonian floodplains in the northeast and on warm, dry sites in the sub-Mediterranean southwest, with a wide range of forest communities (Brus, 2012; Dakskobler, 2008). Beech represents 33% of the growing stock and is present in more than 89% of forest sites (ZGS, 2021). It covers a wide range of altitudes, from less than 100 m a.s.l. up to 1600 m a.s.l. (Klopčič et al., 2022), and is well adapted to a wide range of climatic conditions, with different levels of dominance in forest stands (Škrk et al., 2022). It is one of the most widely used industrial wood species as its wood can be used for over 350 different traditional and new, innovative products (Čufar et al., 2017).

As an ecologically and economically important species, European beech has been widely studied, although high-resolution spatial analyses suitable for small-scale forest management are rare. Several studies have discovered the general expansion of beech in recent decades (Ficko et al., 2008; Poljanec et al., 2010), with a substantial shift of beech in juvenile and middle-age stages upwards and towards colder sites compared to mature trees (Klopčič et al., 2022). Given its general susceptibility to climate extremes (Decuyper et al., 2020; Nagel et al., 2016), beech forests are particularly at risk at lower elevations in the southwest of Slovenia, on the transition from the temperate to sub-Mediterranean climate, where high temperatures and summer drought prevail and the proportion of beech is considerably lower compared to other parts of the country (Škrk et al., 2022). Since these areas are located at the geographical margin of the species' natural range, we questioned whether they could be considered also climatically marginal (warm marginal sites) with respect to the future survival of beech. On the other hand, beech growth at higher elevations between 1000 and 1600 m a.s.l. in the Alps has generally been limited by low temperatures (e.g., Čufar et al., 2008b; Di Filippo et al., 2007; Novak et al., 2022), and we wanted to test the hypothesis as to whether they could still be considered marginal (cold marginal sites) as climate change progresses.

Tree-ring data are often used to study the responses of trees to climate (Speer, 2010). They are used in studies of beech growth performance in a changing climate, and thus secondary growth is used as an indicator of past and current tree health and performance (Dobbertin, 2005). The temperature or precipitation conditions in certain periods directly influence tree growth (Čufar et al., 2008b; Di Filippo et al., 2007), and we can identify areas that allow good growth (i.e. wider tree rings) and areas where beech trees find it very difficult to withstand the damaging effects of climatic extremes. Tree rings have also been used to study climatic and geographical marginal areas and their sensitivity to climate (Hacket-Pain et al., 2016).

In this study, we used a modelling approach to estimate beech growth in Slovenia spatially at high resolution, using a dense tree-ring network and corresponding reconstructed climate data. Our aim was to analyse differences in the basal area increment (BAI) of beech between the periods 1953–1985 and 1986–2018 as influenced by climatic conditions depending on progressing climate change. Particular attention was paid to defining and discussing warm and cold marginal areas where beech survival may be threatened or where its growth may even improve with progressing climate change.

2. Materials and methods

We used a beech tree-ring network in Slovenia that includes tree-ring data from 48 sites between 230 and 1600 m a.s.l. with latitudes between 46.5° and 45.5° and longitudes between 13.7° and 15.5° (Fig. 1, Supplementary Table S1). Data were derived in part from previous studies (Čufar et al., 2014, 2008a; Decuyper et al., 2020), which were expanded with 27 recently sampled sites. Twelve sites were sampled near the edge of beech's natural distribution in the southwest with high temperatures and pronounced summer drought (Škrk et al., 2022, 2021), where a progressive growth decline is expected with climate change. An additional 15 sites were sampled across elevational gradients in the Alpine region (Novak et al., 2022), where climate change may locally enhance beech growth (Martinez del Castillo et al., 2022).

The samples of wood were taken by coring at breast height of living trees or by obtaining discs from the basal part (1–4 m above ground) from trees felled during regular harvesting in managed forests. The cross-sections of the wood were smoothed by sanding with increasingly fine grades of sandpaper grits from 80 to 400. All samples were either measured with Lintab and TSAP Win while observed under a stereo microscope or scanned at a resolution of 1200 dpi on a conventional scanner and measured in CooRecorder, and cross-dated using COFECHA, CDendro or TSAP Win software. Ring width was converted into basal area increment (BAI) using the bai.out function from the R package dplR (Bunn, 2008) to better quantify tree growth compared with the one-dimensional measure of the tree-ring width (Biondi and Qeadan, 2008).

For each site daily maximum and minimum temperature and precipitation from 1950 to 2018 were extracted from the nearest point of the SLOCLIM database (Škrk et al., 2020). Climatic parameters – seasonal maximum, minimum temperature, precipitation, and De Martonne aridity index (de Martonne, 1926) – were calculated for each site. Based on the SLOCLIM database (Škrk et al., 2021), the climatic characteristics were derived for each of more than 300,000 forest stands, the smallest management units of the Slovenian Forest Service (ZGS) in Slovenia, where beech is present (Škrk et al., 2022).

Generalized Linear Mixed Models (GLMM) were fitted to predict annual BAI of each tree as a function of altitude, seasonal minimum and maximum temperature, seasonal precipitation and aridity (AI) as well as their interactions assuming a gamma distribution of the response variable. The basal area (BA) of the tree on each given year and the tree identification code were included as random effects in the model to reduce the variability associated with tree size/age and individual tree characteristics. All variables were standardized before model construction to ensure a compensated weight of the independent variables. The R package *lme4* was used for analysis (Bates et al., 2014). A set of models were built, where each one included only one of the explanatory variables (Aridity index (Aim), altitude (Alt), seasonal precipitation (PCP) and temperature (TMAX and TMIN)). Additionally, a second set of models was constructed including all but one of the selected variables. A "full" model including all possible variables and interactions, a "simplified full" model excluding the non-significant variables and a "null" model excluding all independent variables were created. Finally, all models were compared (Table 1) and we selected the "simplified full" one, based on the Akaike information criterion (AIC) scores (Akaike, 1987).

The selected model was applied to each of the forest stands and annual BAI values from 1953 to 2018 were estimated. To compare

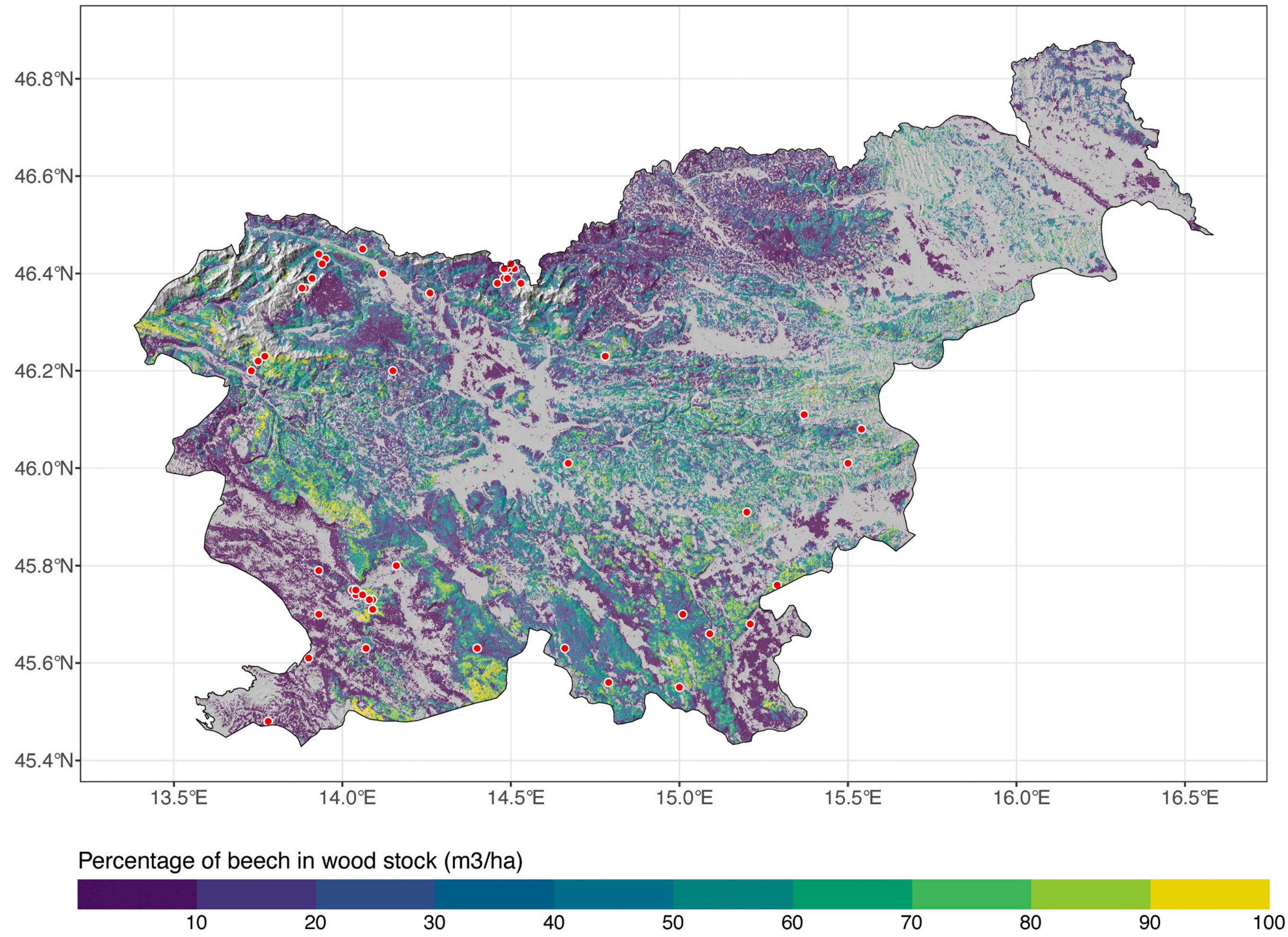

Fig. 1. Locations of European beech sampling sites (red dots), where the colours from blue to yellow represent the percentage of beech in the wood stock (m^3/ha) according to the Slovenian forest service (ZGS).

Table 1
Accuracy assessment of the tested models. Goodness-of-fit measures: AIC (Akaike information criterion), Bayesian information criterion (BIC), logLik (log-likelihood function), deviance (residual deviance), and Df. resid (degrees of freedom—residual). M_null excludes all independent variables (and only includes the random factors), M_full includes all considered variables (Aridity index (AIm), altitude (Alt), seasonal precipitation (PCP) and temperature (TMAX and TMIN)) as well as their interactions. M_full (simplified) is based on M_full but excluding non-significant variables. Two additional groups of models are also tested, including the variables individually and also excluding them individually.

Model	AIC	BIC	logLik	deviance	df.resid
null	84493.7	84538.6	-42241.8	84483.7	58414
Including AIm	84494.3	84548.1	-42241.1	84482.3	58413
Including Alt	84497.6	84551.4	-42242.8	84485.6	58413
Including PCP	83407.6	83497.4	-41693.8	83387.6	58409
Including TMAX	81478	81567.7	-40729	81458	58409
Including TMIN	83146.9	83236.6	-41563.4	83126.9	58409
Excluding AIm	79855.8	80134	-39896.9	79793.8	58388
Excluding Alt	79511.9	79924.8	-39709.9	79419.9	58373
Excluding PCP	80207.4	80458.7	-40075.7	80151.4	58391
Excluding TMAX	81548.3	81844.5	-40741.1	81482.3	58386
Excluding TMIN	80172.3	80468.5	-40053.1	80106.3	58386
full	79463.3	79894.1	-39683.6	79367.3	58371
full simplified	**79460.4**	79810.5	-39691.2	79382.4	58380

growth rates between sites and years, BAI estimates were calculated each time for a theoretical tree with a fixed BA of 650 cm^2 (mean BA of all sampled trees). Lastly, we calculated the mean BAI for two periods, 1953–1985 and 1986–2018, for each stand individually. The relative difference between these two periods at a stand level was calculated by comparing the mean growth values of the studied periods, using the following formula.

$$\text{BAI relative difference} = (\text{Mean BAI}_{1986\text{–}2018} - \text{Mean BAI}_{1953\text{–}1985}) / \text{Mean BAI}_{1953\text{–}1985}.$$

The year-to-year growth variability between marginal versus central areas for the species in the region was additionally compared. Marginal cold areas were defined based on summer maximum mean temperatures as the areas below 1% of the mean values for the entire country. In contrast, marginal warm areas were defined as the 1% of the stands with the highest summer maximum mean temperatures. The central distribution areas were selected using percentiles between 0.49 and 0.51 of the highest summer maximum mean temperatures. The summer maximum temperature was selected for defining marginal areas because it has proved to be the most important climatic factor explaining year-to-year variations in the growth of beech in Slovenia by various studies (e.g., Čufar et al., 2008b; Novak et al., 2022; Škrk et al., 2022).

3. Results

Among the 13 tested models, where we included a list of independent variables and interactions (Supplementary Table S2), the simplified full model proved to be the most accurate to predict the beech growth in Slovenia based on the Akaike information criterion (AIC) scores (Table 1) where the influence of each variable on model estimation is shown in Fig. 2 (complete details of model parameters can be found in Supplementary Table S2).

The BAI estimates derived from the chosen model demonstrated reliability in the stands where the samples for tree-ring analysis were obtained. The growth estimation for all trees and sampled years for the period (1953–2018) showed a significant agreement ($r = 0.8752$) with the observed values (Fig. 3).

The results of the model application across the species distribution from 1953 to 2018 shows large spatial and temporal variability of growth performance. The absolute minimum growth estimates for dominant or codominant trees are of 3.39 cm^2/year, while the absolute maximum is of 107.28 cm^2/year. A global comparison between the periods 1953–1985 and 1986–2018 periods shows a global mean of 20.54 cm^2/year for recent decades and a higher average growth of 23.23 cm^2/year in the past.

The average growth of beech stands varied geographically, showing distinct spatial patterns. During the first period analysed (1953–1985) the minimum growth values (around 10 cm^2/year) are observed in high elevation stands, i.e. in the Alps on the north and northwest and in the Dinaric mountains on the south (Fig. 4a), while during the second period

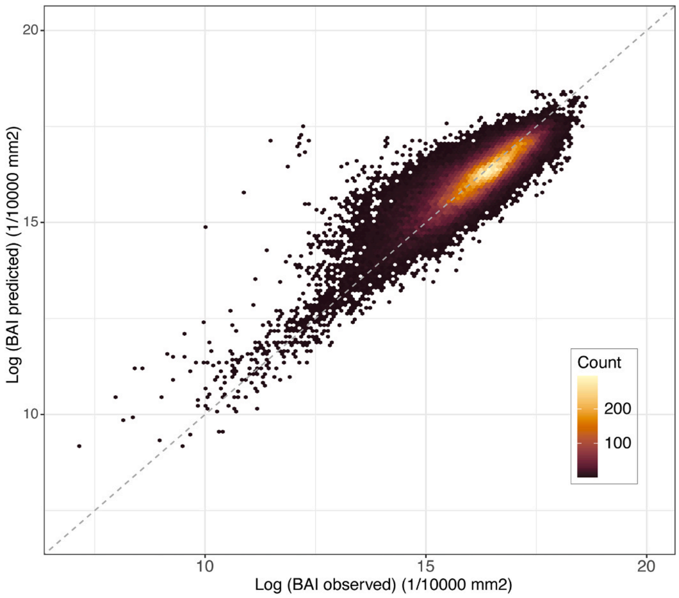

Fig. 3. Comparison between observed and predicted BAI values.

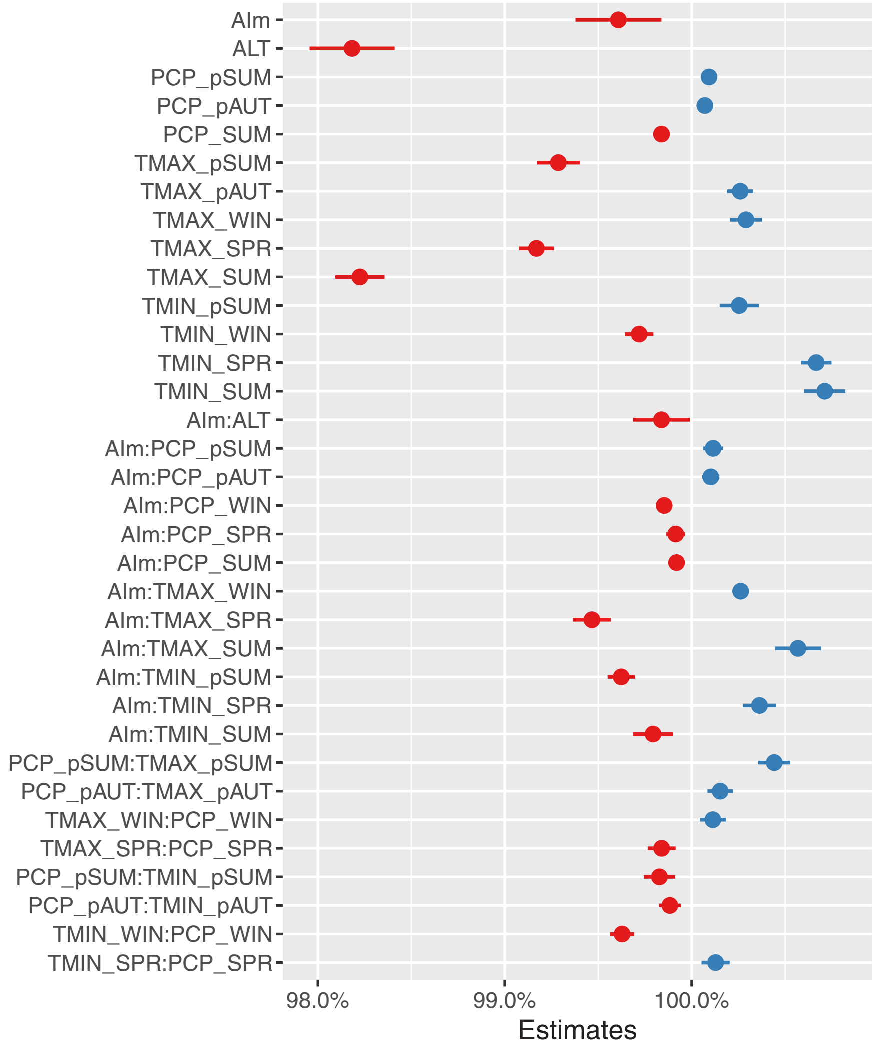

Fig. 2. Influence of each variable on model estimation (M_full (simplified)). AIm represents the Aridity Index, ALT altitude, PCP precipitation, p previous, SUM summer, SPR spring, AUT autumn, WIN winter, TMAX maximum temperature, TMIN minimum temperature.

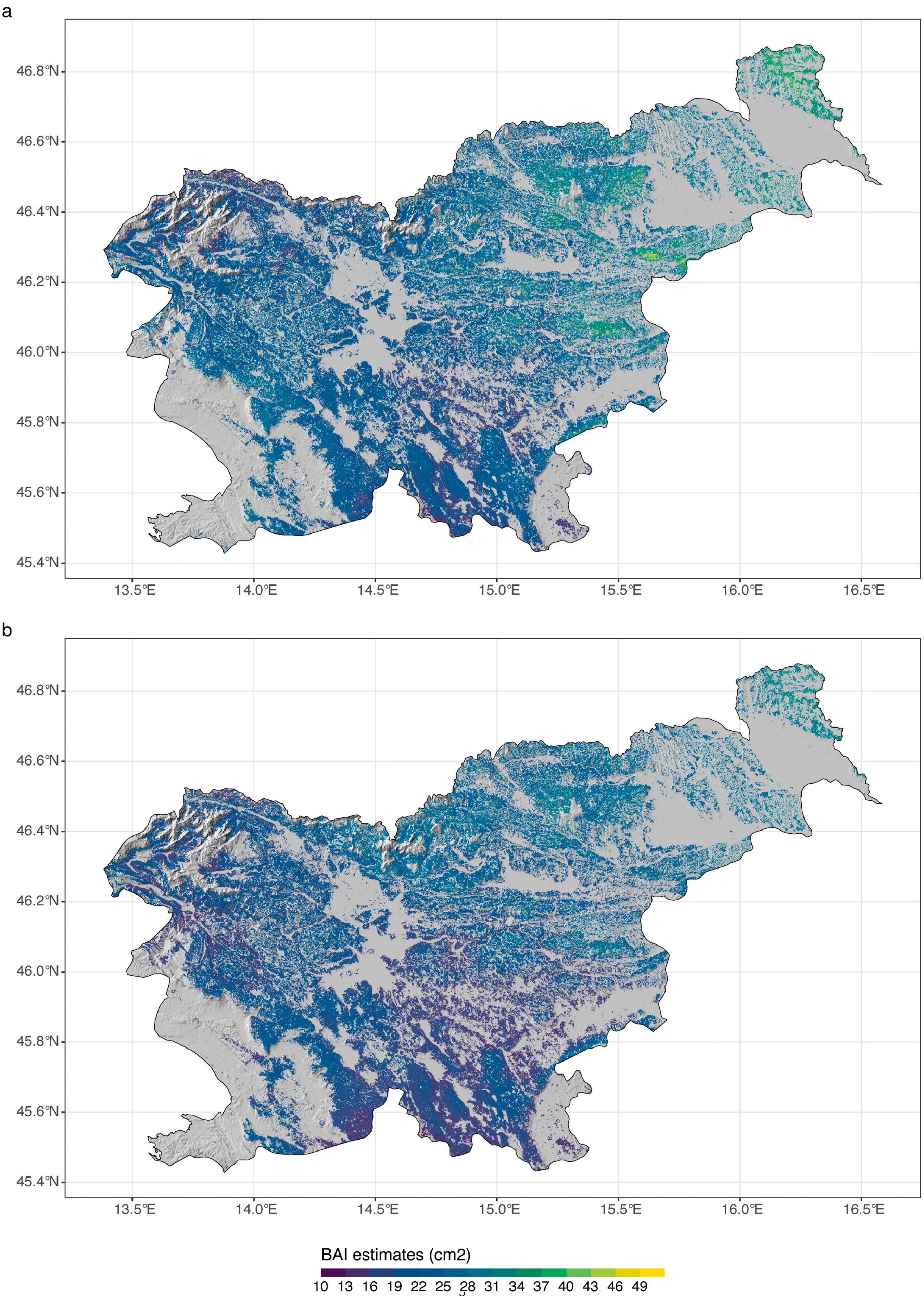

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Fig. 4. Spatial pattern of mean estimates of BAI (in cm^2) of *Fagus sylvatica* for the periods 1953–1985 (a) and 1986–2018 (b) in Slovenia, calculated for a theoretical tree derived from tree-ring chronologies of 48 sites.

analysed (1986–2018) the lowest growth rates (of 11.68 cm^2) are observed in the southwestern ranges of the species, including the Dinaric plateau and the area on the transition from temperate to sub-Mediterranean climatic regimes. In contrast, the higher average growth rates in the central and north eastern hilly area and flatlands did not differ spatially between periods (Fig. 4b).

Relative growth differences calculated between the predefined 33-year periods 1953–1985 and 1986–2018 show an overall growth decline detected in 90.5% of the studied stands in Slovenia. Globally, the average decline is 11%, while in the forest stands in the west, southwest and southeast the growth decline reaches 24% (Fig. 5). These areas include the Dinaric plateaus (west), the area on the transition to sub-Mediterranean climate (southwest) and the hilly area in the Pannonian basin with a temperate continental climate. Only the high-altitude areas of northern and northwest Slovenia which account for 9.5% of the stands, deviate from this general description and have experienced an increase in radial growth of up to 12% in recent decades (Fig. 5). These sites are located in the Julian Alps, Karawanks and Savinja Kamnik Alps where beech grows at altitudes of up to 1700 m a.s.l. (e.g., Novak et al., 2022; Škrk et al., 2022).

The average annual growth of beech in cold marginal and warm marginal areas in relation to those located in central part of the distribution range is shown in Fig. 6. A negative trend in growth pattern, especially in the last decade, is observed at warm lowland sites near the geographical margin of the species distribution in Slovenia (Škrk et al., 2022), while a clear and positive increase in growth rates can be observed at higher elevation (marginal cold areas). These results show how the model presented in this work describes the growth behaviour of species in the cold and warm marginal areas relative to the central areas.

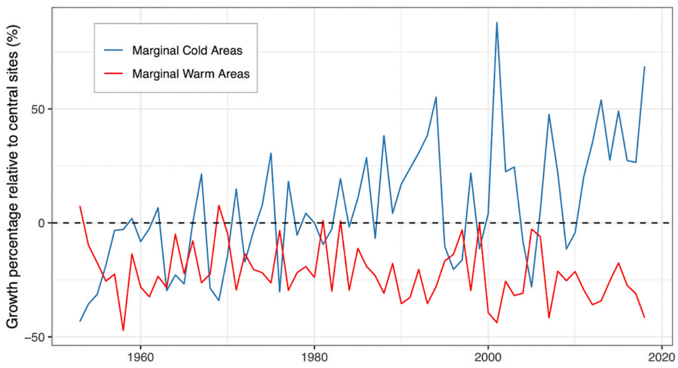

Fig. 6. Relative differences in BAI estimates between marginal cold areas (blue) and marginal warm areas (red) relative to central areas of beech forest populations (black dashed line) from 1953 to 2018.

Modelling also helped us to define the growth behaviour of beech in the warm and cold marginal and central areas of species distribution across Slovenia (Fig. 7). The climatic marginal areas, determined based on extreme 1 and 99 percentiles of summer maximum mean temperatures, are characterized as follows: cold marginal below 16.6 ℃, warm marginal above 27.0 ℃, and the central areas between 23.38 ℃ and 25.5 ℃. The distribution of average summer maximum temperatures across the sampling sites for tree-ring analyses (Figs. 1 and 7, Supplementary Table S1) showed that the dataset is suitable for predictions all over the species distribution in Slovenia.

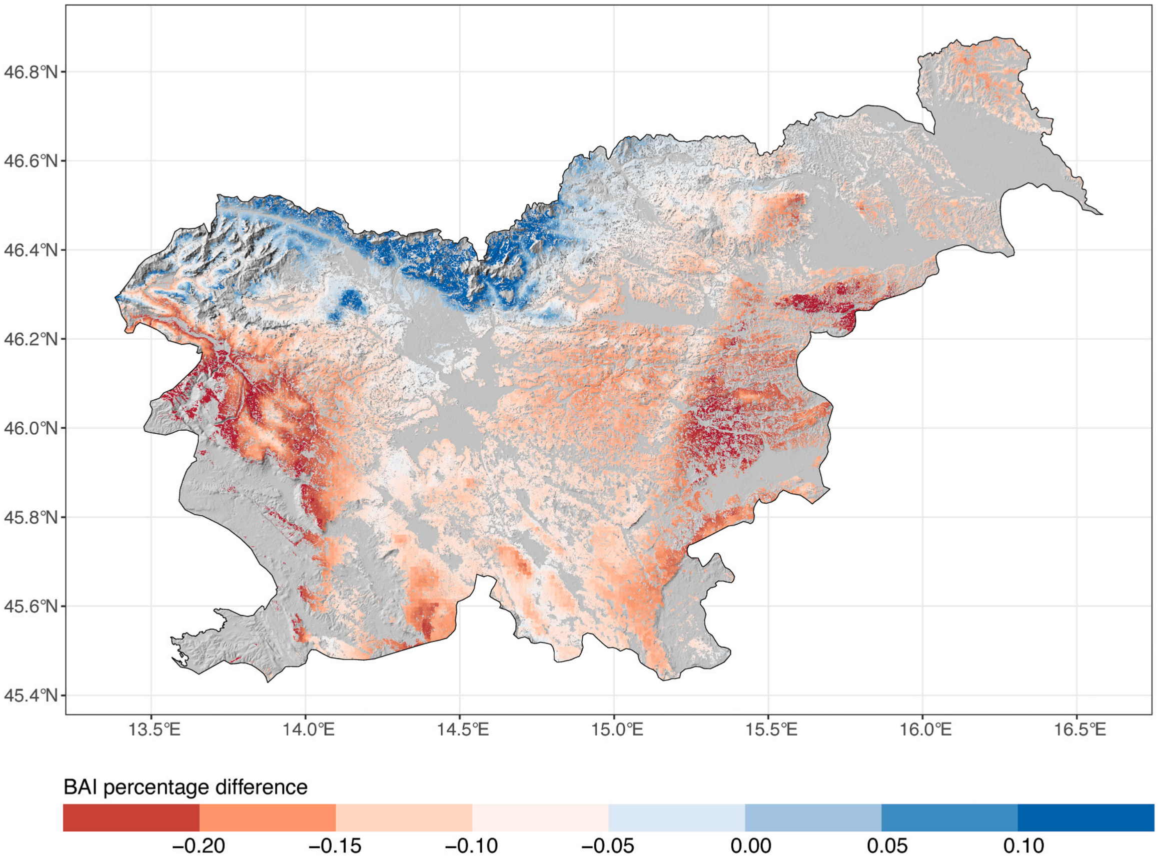

Fig. 5. Relative difference (%) of mean estimates of BAI of *Fagus sylvatica* between the periods 1953–1985 and 1986–2018.

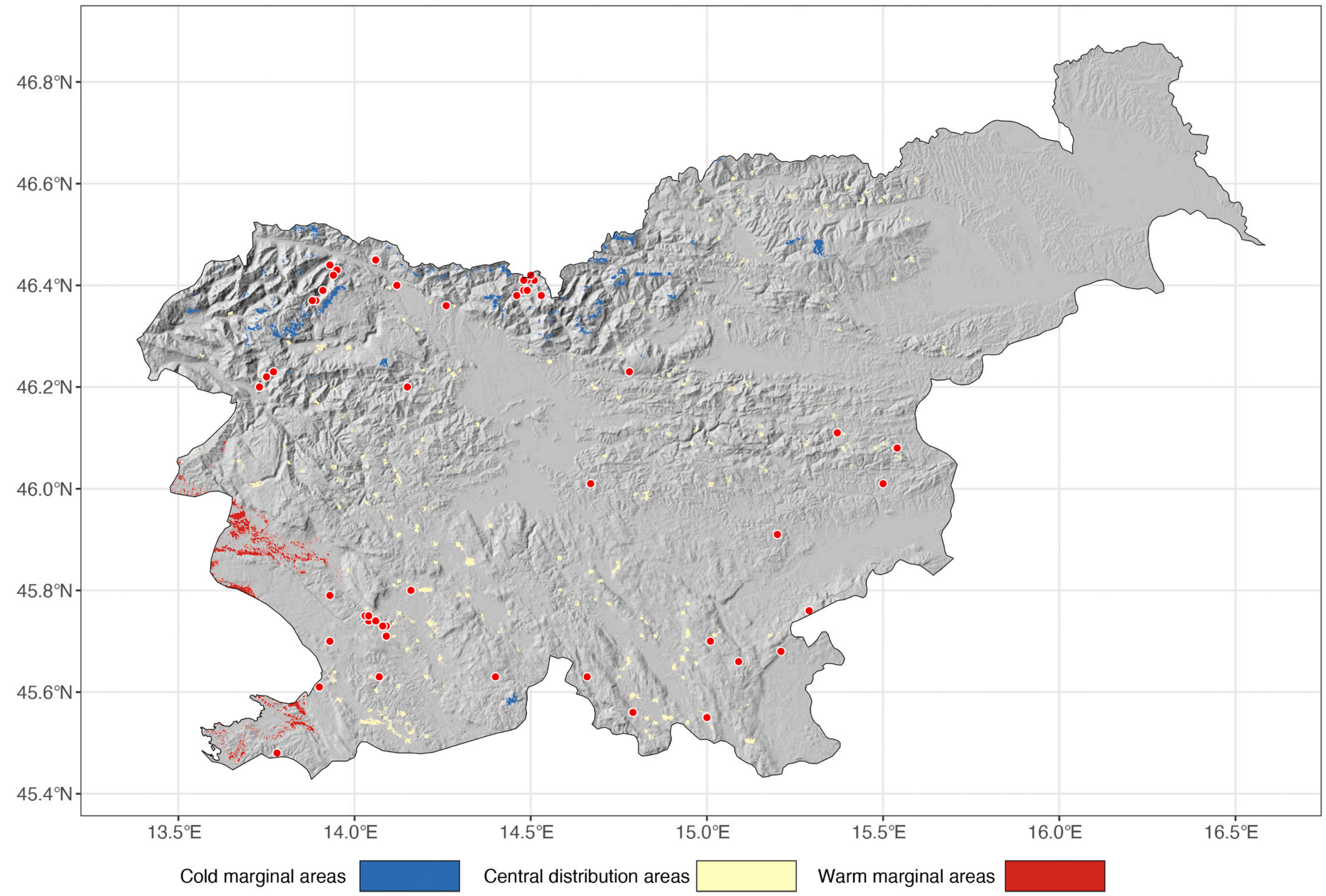

Fig. 7. Warm marginal, cold marginal and central areas for beech growth as defined by extreme 1, 99 and 49–51 percentiles of summer maximum mean temperatures, and sampling sites for tree-ring analyses (red dots).

4. Discussion

Using generalized linear mixed models, we conducted a detailed assessment of beech growth patterns across Slovenia on a fine scale. Our results quantified a persistent reduction in beech growth between the periods 1953–1985 and 1986–2018. Additionally, our analysis showed distinct geographical variations in the growth reduction of the species, highlighting the complex interplay between changing climatic conditions and forest growth trends.

In the last three decades, the highest difference in growth compared to the previous period has been detected in those areas with the highest temperatures, where tree growth was already worse than in other locations. This is consistent with studies of Dulamsuren et al. (2017) and Zimmermann et al. (2015) which discovered a general decline in beech growth in various parts of central Europe. Roibu et al. (2022) and Stjepanović et al. (2018) reported on adverse effects of changing climate on beech growth in Romania and Serbia. Lower elevations and southern areas proved to be especially affected (Martinez del Castillo et al., 2022; Buonincontri et al., 2023). Moreover, our study showed that growth improved only at the highest elevations in the Alps, where average summer maximum temperatures are lower, and their likely increase in the future may allow beech to expand its distribution to new areas that were previously nonviable due to temperatures. This is consistent with several studies showing that elevation plays an important role in beech growth (Di Filippo et al., 2007; Kolář et al., 2017; Martinez del Castillo et al., 2018; Prislan et al., 2013; Roibu et al., 2022; Stjepanović et al., 2018), and that beech has a high potential to advance to higher elevations in European mountain forests (Pretzsch et al., 2021).

Since precipitation in Slovenia is relatively high, exceeding annual totals of 600 mm even in the driest areas (Škrk et al., 2021), differences in annual precipitation do not seem to have a decisive influence on beech growth, although the study of Prislan et al. (2018) demonstrated that the annual precipitation distribution is important in explaining the growth of beech trees, and Trifković et al. (2022) showed that beech responds asymmetrically to precipitation anomalies. High summer temperatures, as shown by our study, seem to become more stressful for beech growth than drought, especially during the recent period of general warming (Cavin and Jump, 2017; de Luis et al., 2014; Kutnar and Kobler, 2011; Weigel et al., 2022). Besides direct impacts, high temperatures also affect the water vapour pressure deficit (VPD), which affects leaf anatomy, stomatal conductance, photosynthesis, nutrient and hormonal status, embolism risk and reduced radial stem growth (López et al., 2021; Vodnik et al., 2019). In addition to climate and altitude, other variables such as soil types and competition can also have a significant effect on tree growth (Meier and Leuschner, 2008; Zimmermann et al., 2015) but are difficult to integrate in our inter-annual modelling approach.

Modelling also helped us define the growth behaviour of beech across climatic marginal areas and distinguish between warm marginal areas, where beech survival is threatened, and cold marginal areas, where its growth could improve as climate change progresses. We also showed that climatic marginal areas do not necessarily correspond to geographical marginal areas, as previously reported by, for instance, Hacket-Pain et al. (2016). The warm marginal areas defined by our model are all located in the southwest near the rear edge of beech distribution in Slovenia, influenced by the sub-Mediterranean climate (Kozjek et al., 2017), affected by the highest temperatures (de Luis et al., 2014), and lower dominance of beech in the forests (Škrk et al., 2022).

By comparing year-to-year variation of BAI estimates, warm marginal and central sites showed consistently lower growth values than in cold marginal areas. Similar observations were previously reported by Jump et al. (2006) and Piovesan et al. (2008).

Increases in temperatures and changes in precipitation patterns are predicted for all of Europe (IPCC, 2021), and future beech expansion and growth will likely be limited by these changes. Although some studies report the drought resilience of marginal beech populations (Muffler et al., 2020; Rose et al., 2009; Stojnić et al., 2018), the net growth performance is expected to decrease in the future in this particular case. Our results support the hypothesis of decreasing beech dominance, especially on warm marginal areas but also in central areas.

The use of GLMM at a very detailed level showed that it can help us to predict the future growth of predominant tree species, such as beech, and consequently adjust current and future forest management which will prevent possible ecological and economic losses. Our results can help identify areas where beech should not be planted for wood production, given the observed decline in growth, which is likely to continue or intensify in the future as the climate warms. The approach to forest management should become consistent with predicted climate changes, avoid planting trees in areas unsuitable for particular tree species and respecting stand structural complexity and tree species diversity (Juchheim et al., 2020).

Slovenian forest management already faces the negative effects of high temperatures and massive decline and mortality of lowland Norway spruce (*Picea abies*), the second most frequent forest tree species with a share of 30% in the wood stock (e.g., Jevšenak et al., 2020; Kutnar et al., 2021). As beech survival may also be endangered in certain areas, as shown in this study, the Slovenian forest management authorities are aware that more thermophilus tree species should be favoured in areas affected by high summer temperatures and drought. On the other hand, beech has the chance to grow better at higher elevations in the Alps, but this will also require adaptation of forest management for timber production.

5. Conclusions

The modelling of tree-ring data using fine-scale climate data in Slovenia showed an overall growth decline of European beech in recent decades. Spatial patterns show a particularly pronounced growth decline in the warm climatic marginal areas defined in this study. These sites are located at the edge of beech's geographical distribution in southwestern Slovenia, characterized by the sub-Mediterranean climate and high average summer maximum temperatures. Here, estimates of BAI are lower and decreases in growth rates are greater than in other areas in the recent period. We also defined cold marginal areas mainly at higher elevations in the Alps, where estimates of beech growth are better than in other areas and growth may even improve as climate change progresses.

CRediT authorship contribution statement

N.Š., E.M., M.d.L. and K.Č. designed the research; E.M., M.d.L. and N.Š. developed the methodological approach; N.Š., K.N., M.M. and K.Č. collected and organized the tree-ring data; N.Š., E.M., M.d.L., and R.S.N. performed the analyses and designed the maps. N.Š., E.M., M.d.L. and KČ designed and wrote the manuscript with important contribution from all co-authors. All co-authors have read and agreed to the published version of the manuscript.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors declare that no AI tools were used to analyse and draw insights from data in any part of the research process.

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.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2023.126135.

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