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Silver fir and its provenances in a climate change perspective

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AA

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A Stranalandia c'è un albero talmente alto che non lo si può misurare, perché la cima si perde tra le nuvole. Anzi, non si è nemmeno sicuri se la sua chioma sia di foglie o di nuvole. Dall'albero cade un enorme frutto giallo, il "bombero". Ogni frutto è deliziosamente fresco anche d'estate, perché lassù dov'era attaccato c'è evidentemente una temperatura da frigorifero.

Alcuni frutti cadono a terra spaccandosi, ed è consigliabile non prenderli in testa. Altri, invece, misteriosamente arrivano giù con il paracadute (una grossa foglia che ne frena la caduta). Questo fece avanzare a Lupus la tesi che sulla cima dell'albero nuvola ci siano degli abitanti. Osvaldo riferì che parecchie volte aveva visto scendere dalla cima dell'albero nuvola aeroplanoni di carta, ma non si riuscì mai a trovarne uno.

L'albero nuvola. Stranalandia - Sefano Benni

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Introduction

The climate crisis, characterized by rising temperatures and altered precipitation patterns, is significantly impacting European forest ecosystems. Mediterranean forests are particularly sensitive to climate change, both due to the significant and rapid climatic variations (Lionello and Scarascia, 2018; Peñuelas et al., 2017) and the presence of forests at the edge of the distribution range of European tree species, which are often more vulnerable to environmental changes (Fady et al., 2016; Peguero-Pina et al., 2007). These combined factors expose Mediterranean forests to the impacts of climate change, which affects their structure, function, and distribution. Challenges such as drought stress, increased tree mortality rates and reduced forest productivity have direct implications for essential ecosystem services such as timber production, carbon sequestration, hydrogeological protection and habitat (Lindner et al., 2010; Thompson et al., 2009).

Resilience and adaptation of forests to climate change impacts must come upfront in forest management and planning, to ensure a healthy future for European forests and related ecosystem services. Through carefully planned and climate-smart management practices, the vulnerability of forests to climate change can be reduced, and their response improved. An increasingly effective strategy is promoting forest diversity, not only under the specific and structural point of view, which are already often taken into consideration during forest management and restoration but also under the genetic perspective. Indeed, genetic diversity plays a crucial role in the adaptation of trees to changing environmental conditions. Forests have always modified their distribution range to follow changes in climate, adapting to new environments over hundreds of years. Recent climate changes produce modifications in the local climate that trigger the natural need for forests to migrate, generation after generation, aiming to occupy the ecological niches best suited to the new conditions. However, the speed at which these changes are occurring does not allow species to respond accordingly, flanking the natural inability to move with increasingly severe environmental stresses (heat waves, droughts, diseases) that put species' survival at risk (Gazol and Camarero, 2022; Lindner et al., 2010). In this context, assisted migration is considered a valid forest management strategy in line with the natural development of forests. This strategy consists of planting specific forest reproductive material in contexts where it will be more suitable in the future, accompanying the natural migration process in a more climate-change-compatible rate (Aitken and Bemmels, 2016; Gömöry et al., 2021). The implementation of climate smart forestry techniques requires special attention in order not to create disruptions in forest ecosystems, due for example to the planting of maladapted genetics or the introduction of pathogens that may compromise forest health (Alfaro et al., 2014). Forest species with high within-species genetic variability can adapt to a wide range of environmental conditions and increase the resilience of forests to climatic stresses, such as extreme temperatures and variations in precipitation regimes (Piotti et al., 2017; Tinner et al., 2013; Vitasse et al., 2019b).

Among temperate conifers with a large degree of genetic variability and promising performances under a warmer climate, silver fir (*Abies alba* Mill.) appears more resistant and resilient than many other species, both in terms of both responses to water stress and stability of the carbon sink (Versace et al., 2020; Vitali et al., 2017; Vitasse et al., 2019a). In European contexts, silver fir is in fact considered an important resource in terms of adaptation to climate change, as it can be implemented for example as a replacement species for the Norway spruce, which is significantly reducing its distribution in many areas (Vieilledent et al., 2010; Vitasse et al., 2019a). At the same time, silver fir is a conifer particularly adaptable to climatic variations due to its degree of genetic diversity, a trait that defines its potential to adapt to a wide range of environmental conditions. Several studies on silver fir provenances have shown that growth responses and drought tolerance differ largely among them, highlighting the importance of intraspecific variability as a key factor in climate change adaptation (Fulín et al., 2023; Kerr et al., 2015; Mihai et al., 2021). A greater understanding of the genetic determinants of climate resilience may be used to support active management strategies such as assisted migration, i.e., the use of forest reproductive material from non-local sources and better adapted to future climate conditions (Aitken and Bemmels, 2016; Gömöry et al., 2021).

The climate resilience of tree species and provenances is usually assessed by looking at how trees respond to stresses, past or present. Common techniques include dendrochronology, which is based on correlations between the width of growth rings and dated exogenous stimuli or disturbances (Oggioni et al., submitted; Zas et al., 2020). Tree-ring analysis can also be used to assess past and current carbon stocks and sinks, especially when complemented by estimating carbon storage and fluxes in other ecosystem components (deadwood, litter, soil) to provide a full ecosystem-scale picture. This can provide indications on the behavior of the different forest provenances and support their use as a tool for forest climate adaptation (Frýdl et al., 2018; Hansen and Larsen, 2004; Mihai et al., 2021).

The assessment of historical responses should also be accompanied by forecasting expected tree growth and its resilience under alternative climate and management scenarios, thus enabling more proactive and adaptive forest management. Process-based forest growth models represent an advanced and essential tool to simulate forest dynamics, offering the possibility to simulate ecosystem responses in a variety of environmental, climatic and management contexts (Bohn et al., 2014; Fischer et al., 2016; Mahnken et al., 2022; Maréchaux et al., 2021). Forest growth models can be developed at the individual, stand or landscape scale, and are able to provide in-depth details on the expected changes in forest structure and demography, highlighting variations in growth dynamics and taking into account interactions between different tree species. Field data collection, including tree morphology, biodiversity observations and soil analysis, provides crucial information to calibrate and validate models, ensuring that they accurately reflect the complex environmental and biological interactions at play within forests (Blanco et al., 2015; Bohn, 2016; Herbert et al., 2023). Forest growth models not only improve our understanding of forest ecosystems but are also valuable tools to support planning decisions and implement sustainable management strategies. Continued evolution and refinement of these models are therefore essential to meet future challenges in forest management.

So far, the role of genetic diversity within tree species has been rarely included as a driver in forest growth models. Given its importance in predicting tree and forest resilience, incorporating genetic diversity into forest dynamic modelling is an important step in ecological research, and will enable the development of more accurate predictions of the ability of forests to adapt and resist climate change. More specifically, incorporating genetic variability into forecasts of forest growth and productivity can reveal how different genotypes respond to environmental stresses, improving our understanding of species resilience and increasing the effectiveness of forest management decisions towards greater environmental health. The integration of genetic diversity into dynamic forest modelling emerges as a promising approach, also charged with a strong multidisciplinary component, needing collaboration among geneticists, ecologists, and modellers to ensure forest resilience in a rapidly changing world (Bohn, 2016; Matyas, 1994).

Objectives

The objective of this thesis is to investigate the relationship between growth and genetic diversity of silver fir under alternative climates and forest management regimes, in order to develop effective guidelines to optimize the response of Mediterranean forests to climate change impacts. The research employs multidisciplinary methods including performance studies of different forest provenances, forest growth modelling, and carbon cycle analysis. This study is divided into four projects, each responding to one of the following specific objectives:

1. ProForesta Project: the objective is to assess the response of silver fir to drought in the territories of the Tuscan-Emilian Apennines (central Italy) by comparing the growth rates of trees with different origin (natural and planted) and provenance. Here, I used dendrochronological analysis to inform local forest management on the performance of commonly planted genetic provenances and to assess which one is better able to support healthier forests that are resilient to climate change.
2. ProForesta+ Project: using the FORMIND growth model, I simulate the future growth of silver fir provenances under different climate change scenarios, with the aim of analyzing expected changes in carbon stocks and sinks of the three silver fir provenances previously analyzed. Through these results, guidelines have been created for implementing assisted migration in local forest management, aiming to provide the highest climate change mitigation in the long term.
3. Forest management in PNATE: The objective of this study is to assess the carbon stocks and sinks of forests in the National Park of the Tuscan-Emilian Apennines (PNATE), comparing carbon stocks and sinks under different forest management regimes and forest compositions, including pure and mixed broadleaves, and mixed broadleaves-conifers stands with silver fir. I analyzed historical carbon stocks and sinks and simulated future ones using the 3PG forest model. These results provide useful information about forest management in the national park and the future resilience of the species that populate these forests.
4. Silver fir provenances in Austria: This study compares the growth, productivity and mechanical stability of Italian and Austrian provenances of silver fir in two provenance trials in Upper Austria. With this project, the best provenances of silver fir for planting in Austria under climate change are evaluated by assessing multiple drivers of tree performance under two different climates.

Summary of research chapters

Silver fir under climate change: four studies to deepen our knowledge.

The first project presented, called "ProForesta" (Forest Provenances), focuses on the analysis of silver fir genetic diversity and its resilience to the effects of climate change. Specifically, I carried out a comparative analysis of the growth performance of three silver fir forest provenances and their response to climate during drought years in natural and planted forests. First, I mapped the genetic diversity of silver fir forests in the Tuscan-Emilian Apennine National Park through genetic analysis, and then focused on the analysis of tree growth in the three main provenances as a function of past climate. I used dendrochronological techniques and climate growth analysis to analyze tree-ring growth as a function of climate, and calculated provenance-specific resilience indices to study the drought response of tree growth. My hypothesis is that southern provenance, which is used to more extreme climatic conditions, may show a high resilience to drought, resulting in potentially adaptable genetic material in climate change contexts. More northern and alpine provenances, on the other hand, might be poorly adapted to drought, resulting in genetic material potentially ill-adapted to the future climate of the Apennines. Local provenance might be well adapted by default to local conditions, alternatively expressing intermediate behavior. Through the analysis of the three provenances under consideration, the project explores not only individual responses to drought and temperature variations, but also how the genetic diversity of this species can influence local forest adaptation. This enables a better understanding of the adaptation mechanisms in silver fir and provides crucial insights for forest management strategies aiming to promote the conservation of natural silver fir forests and the resilience of forest ecosystems in the Tuscan-Emilian Apennines in a context of climate change, offering a valuable perspective for the long-term planning and sustainability of mountain forests.

The second part of this study aims to investigate the response to future climate change scenarios using simulation models. This Project is called "ProForesta+", integrating The ProForesta Project data into a broader context. For this purpose, I used the FORMIND model, an advanced individual based forest gap model that integrates environmental, climatic, geomorphological, and physiological data to predict forest growth and demography in various climatic, environmental or management contexts. This model is able to simulate forest growth and carbon uptake at tree level, and is sensitive to variations in light, water, temperature and competition. The key innovation of our study lies in the use of the morphological and growth data collected for the three provenances analyzed in the ProForesta project to initialize the growth process of FORMIND. The explicit consideration of forest provenances in the simulation makes it possible to examine the range of responses with which silver fir will be able to withstand climate change. The main resilience metrics were forest productivity, carbon sink, and forest ecosystem metabolism (autotrophic respiration). In this paper, I hypothesize that the growth and drought resilience trends identified in ProForesta will be replicated by growth simulations, marking the differences between provenances as the effects of climate change increase. Southern provenance, alongside local provenance, could play a key role in the future adaptation of the species to climate change. It is therefore important to also understand how these trends may vary with changing environmental conditions, such as management type or forest density. Climate scenarios simulated by FORMIND generate a complex picture of potential future forest dynamics, providing forest scientists and managers with essential tools for meeting the challenges of climate change and preserving forest health.

Forest species have a different response to climate based on their morphological and physiological characteristics, and this defines their ability to adapt to their surroundings. In the areas of the Tuscan-Emilian Apennine National Park, silver fir shares its distribution area with other forest species, which can lead to competition for light and nutrients. Beech (*Fagus sylvatica* L.) is the undisputed king of the mountains, occupying a large part of the park's forest territory, and mixing with other broadleaf species at its lower altitudinal distribution limit and with silver fir at its upper limit. However, climate-induced shifts in species' elevational distribution may produce novel competitive dynamics, which should be taken into account in a context of climate change. In our study, the third project was focused on assessing the responses of forest ecosystem processes to changes in forest management and the admixture of competing species. Our hypotheses, based on current literature, consider the mix with fir a great resource for beech forests, possibly more productive and resilient than pure beech in a climate change perspective. This may be valid as long as there are no extreme climate scenarios, under which even fir may easily suffer. In this study, forests of silver fir mixed with beech shows a marked resilience to climate change, increasing its carbon stock and sink in all climate change scenarios compared to historical mean climate conditions, in contrast to beech and other broadleaf species that suffer more from climatic upheaval. These results reveal once again how silver fir is an important resource for local adaptation and should play a prominent role in climate-smart forest management, emphasizing its adaptability and role for climate change mitigation thanks to the stability of carbon stocks and sinks.

Finally, the fourth study compares the growth and productivity of two southern Italian provenances versus two Austrian provenances in two provenance trials located in Upper Austria. This study is set within the broader context of assisted migration as a tool to increase the resilience of European forests to climate change, exploring how the provenance of forest reproductive material influences the performance of silver fir at two different locations. In this study, three key components related to forest growth under climate change are analyzed: productivity, growth rate, and tree mechanical stability. The hypotheses of this study follow those of the ProForesta project with respect to the growth performance and productivity of silver fir provenances in Italy. I expect that the southern Italian provenance may have a better response than the Austrian provenance in locations with warmer climatic conditions, while the Austrian provenance may be more adaptable in more mountainous areas. This evidence may have a direct impact on Austrian forest management, which is interested in the productivity of Mediterranean forests specifically in view of their adaptability in the context of climate change. The performance of southern Italian provenances proved promising under warmer conditions, opening up new possibilities for the planting of forests with non-local genetic heritage to facilitate adaptation to drier climates. Here, I emphasize the importance of understanding the specific responses of provenances in different environmental contexts, with the aim of creating guidelines for the selection of the best provenances in upper Austria under climate change.

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Drought responses of Italian silver fir provenances in a climate change perspective

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Abstract

In a climate change perspective, the resilience of Mediterranean forest ecosystems is closely linked to their ability to cope with drought and rising temperatures. This ability can be influenced by genetic differences between and within species or provenances. In a changing environment, management guidelines should weight the risks associated both to local and/or non-local provenances, to promote the effective conservation and sustainable management of resilient forest genetic resources. In this study, we analyzed the growth responses to drought of silver fir (*Abies alba*) in the Tuscan-Emilian Apennine National Park in natural and planted forests, comparing the growth performance of three provenances of this species in Italy: (a) Western Alpine - (b) Northern Apennine (local) - (c) Southern Apennine. Drought severity was defined by the Standardized Precipitation-Evapotranspiration Index (SPEI). We carried out dendrochronological analyses by assessing climate-growth relationships and applying drought 'resilience indices' (RRR) based on tree-ring width. Planted forests showed faster mean growth than highly fragmented natural forests, higher resilience to severe drought and significantly higher recovery to severe drought. Fir provenances do not differ in mean growth rate, while the Southern Apennine provenance showed significantly better recovery (rec) and resilience (resl) especially compared to the Western Alpine provenance during moderate (rec +5-15 %, resl +13-15%) and extreme (rec +20% %, resl +22%) drought years. The local provenance showed an intermediate behavior. Southern and local provenances showed higher resilience to drought compared to the Western Alpine one, proving to be very important forest genetic resources in the context of climate change response strategies. Finally, the RRR indices trends calculated on the years identified by SPEI6 generally showed greater differences between provenances and regeneration modes than on the years identified by SPEI12, possibly due to the increase in recurrent short-duration droughts in mountainous contexts during the growing season. These results provide important information on the drought response of different silver fir provenances under climate change, highlighting the importance of taking into account the genetic background of forest reproductive materials in forest management and planning. Thanks to the close collaboration with the National Park and local forest managers, these results may find concrete application, e.g., by properly evaluating the usefulness of provenance assisted migration in the National Park forests and providing better management of remnant silver fir natural forests.

Keywords: Genetic diversity, Dendrochronology, Forest resilience, Drought, SPEI

Introduction

The increasing impacts of climate change are severely affecting European forest ecosystems, which have shown signs of drought stress in recent years (Gazol and Camarero, 2022). Recent heat waves have triggered unprecedented mortality episodes in many forest tree species (Schuldt et al., 2020), leading to the loss of ecosystem services (Lindner et al., 2010). A comprehensive understanding of the adaptive strategies that forest tree species can adopt to cope with climate change is therefore required in order to mitigate its effects and inform forest management and planning (Keenan, 2015).

To boost forest resilience against the stressful conditions caused by climatic extreme events, planting new trees is considered a useful tool to increase the specific (Nadrowski et al., 2010) and genetic (Thompson et al., 2009) diversity. Indeed, the study of forest genetic resources (FGR) is an important aspect of forest management in a context of climate change (Knoke et al., 2008; Vinceti et al., 2020), and increasing intra-specific genetic diversity can have positive effects on the adaptive potential of a population (Dorado-Liñán et al., 2020). To increase the adaptive potential and resilience of forests to drought, ‘assisted migration’ is in the portfolio of silvicultural tools (Aitken and Bemmels, 2016), resulting in the use of forest reproductive material (FRM) from non-local provenances that can be better adapted to future climatic conditions (Breed et al., 2013; Mihai et al., 2021; Millar et al., 2007). Indeed, there is solid evidence that different forest provenances can show different eco-physiological and growth-dependent responses to environmental conditions (Correia et al., 2018; Fierravanti et al., 2020) and that some may perform better than others in the face of extreme drought events (Zas et al., 2020).

Planting non-local provenances is nonetheless a challenging task. Possible risks are the use of maladapted FGR or the introduction of new pests and diseases (Alfaro et al., 2014). Another barrier is the restrictions imposed by forest policies, which often limit the transfer of FRM across borders (Gömöry et al., 2021; Konnert et al., 2015). However, increasing scientific knowledge on the current and future species response to climate change may lead to more sensitive policies on these issues and raise awareness among forest managers, reducing the limitations and risks associated with the use of non-local FRM (Vinceti et al., 2020). The European Forest Genetic Resources Programme (EUFORGEN) has highlighted the importance of studies that address the performances of different forest species provenances and facilitate the sustainable use of FGRs and FRMs (Gömöry et al., 2021). These practices could greatly increase the resilience, stability and genetic diversity of forest ecosystems, and provide new insights into when and where assisted migration processes can help to effectively increase the adaptive potential of forests towards climate change (Konnert et al., 2015).

Silver fir (*Abies alba* Mill.) is among the most important forest tree species in Europe (Wolf, 2003). It is distributed in mountainous areas throughout Europe and contributes significantly to maintain biodiversity in forested areas (Dobrowolska et al., 2017), playing a key role in several habitats of conservation importance in the EU, including priority habitats (e.g., 9510*; European Union, 1992). Furthermore, its wood is widely used in construction (Dobrowolska et al., 2017; Mauri et al., 2016). In Italy, it is mainly distributed throughout the Alps while, in the Apennines, it has a highly fragmented distribution (Piotti et al., 2017; Rovelli, 1995). There is evidence that this species is suffering a decline due to climate warming mainly at its southern limits (Robson et al., 2018). Spring and midsummer droughts in both previous and current year significantly impact *A. alba* growth and mortality (George et al., 2015; Lebourgeois et al., 2013; Mazza et al., 2014; Mikulenka et al., 2020). However, the susceptibility of this species to climate change is still debated, as better drought tolerance has been observed in central Europe with respect to other forest species (Latreille et al., 2017; Tinner et al., 2013; Vitasse et al., 2019b).

Little is known about the range-wide levels of local responses of silver fir to climate. However, different silver fir provenances revealed very heterogeneous growth responses to drought, showing different recovery and resilience behaviors after a drought event (Dobrowolska et al., 2017; Lloret et al., 2011; Mihai et al., 2021; Wolf, 2003). Different silver fir provenances have also shown a diverse ecophysological response to drought, in terms of photosynthetic rates and water and nutrient utilization (Konôpková et al., 2020; Matías et al., 2016). Such pieces of evidence reveal that genetically differentiated provenances could impact metabolic and developing ecosystem processes as well as forest growth and health. Differences among silver fir provenances facing drought years suggest the importance of using diverse FRM in reforestation, management, and conservation programmes. Given the lack of local scale data regarding growth responses to drought of genetically differentiated silver fir provenances, it is a priority to deepen our knowledge in order to adopt correct silvicultural measures, especially in the context of climate change. The main factors controlling tree growth are climate, competition and site conditions, which act through close interactions (Calama et al., 2019) and must be taken into account to unravel the genetic component of tree growth.

The main objective of this study is to analyze the growth responses to drought of different provenance of silver fir during drought years. The study area is the National Park of the Tuscan-Emilian Apennines (Northern Apennines) where both natural and planted forests of silver fir occur. By investigating the genetic background of the planted forests, we found that they were established with material of mixed provenance (Southern Apennines, Northern Apennines (local) and Western Alps). This provided us with an ideal experimental setting to test the existence of differences in growth performances among silver fir provenances growing under similar environmental and climatic conditions. The specific objectives are to evaluate the growth responses to climate as a function of (i) the regeneration method of the forest (natural vs planted) and (ii) the silver fir provenances under investigation, while assessing (iii) the effect of competition and environmental factors on the growth response. In order to assess the growth response to changing climatic conditions, three levels of drought were assessed based on the SPEI drought index value (moderate, severe and extreme). The results can provide insights into the relationships between climate and growth, and can be actively useful for local forest management and planning, e.g., in the selection of the most suitable provenance for reforestation or assisted migration programs, and will contribute to study the effect of climate change on silver fir in Italy.

Materials and methods

Abies alba natural and planted stands in the study area

The study area is within the Tuscan-Emilian Apennine National Park in the northern part of the Apennines, a Mediterranean mountain range in the Italian Peninsula. In this area, silver fir has a highly fragmented distribution, with few small and isolated natural populations (Piovani et al., 2010; Avanzi et al., submitted). These stands are the remnants of previously larger populations which were progressively eroded over the last thousand years by a still debated combination of climatic and anthropogenic factors (Di Pasquale et al., 2014; Magri et al., 2015; Morales-Molino et al., 2021). Several silver fir planted forests are present nearby natural populations. Such plantations were established during the 20th century, but no documentation is available about the origin of the planted material. The planted stands ranged from an elevation of 1000 to 1650 a.s.l. while natural populations from 1400 to 1650 a.s.l. From visual assessment, natural populations generally grow on more rocky and difficult terrain with respect to planted stands. Overall, the area is characterized by a Mediterranean Apennine climate, with dry summers and rainy autumns (Fig. S_4). The average annual rainfall is 2100 mm, the average annual temperature of 7.5°C and the average daily temperature range of 6°C. The historical climate data of the study area was derived through the methodology described in (Brunetti et al., (2012) and refers to the period 1957-2017, considered as the study period based on the dominant age of the trees under study.

Reconstruction of the planted individual’s provenance by genetic markers

In July-October 2019, sampling for genetic analysis was carried out. Approximately 24 trees at least 20 meters apart were sampled from ten planted forests, selected to be the nearest and/or the largest stands in the reach of gene flow with natural populations (Fig.1, Table S_1). Each individual was tagged and georeferenced with a metric handheld GNSS device (Garmin Ltd., USA). Fresh needles were collected from each individual for genetic analyses aimed at determining the genetic provenance of the planted trees. For this purpose, we took advantage of a genetic dataset collected through an extensive characterization of silver fir natural populations (Piotti et al., 2017; Santini et al., 2018 Avanzi et al., submitted). The available dataset was enriched by adding further three natural populations from areas that represent potential seed sources for plantations (i.e., CLR, GOU and SUM in Supplementary Materials 1, Fig. S_2).

All sampled trees from planted stands were genotyped at 16 unlinked and null allele free microsatellite markers (SSRs) (Aag01, Aat01, Aat02, Aat03, Aat04, Aat05, Aat06, Aat08, Aat09, Aat10, Aat11, Aat13, Aat14, Aat15 and Aat16: (Postolache et al., 2014, NFF7: Hansen et al., 2005). The multiplexing and amplification procedures are described in Postolache et al. (2014).

A preliminary Bayesian clustering analysis was performed on 1907 silver fir individuals from 39 natural populations by using STRUCTURE v2.3 (Pritchard et al., 2000) to identify the most likely number of genetic clusters (K). STRUCTURE was run varying K from one to 15 and replicating each K ten times. Each run was made up of 1×10^5 burn-in iterations and 2×10^5 data collection iterations. Different runs for the same K were averaged by using CLUMPAK (Kopelman et al., 2015). The most likely K was selected based on the empirical statistic ΔK (Evanno et al., 2005) (Fig. S_1). An assignment test was then performed to compute the probability of silver fir individuals from planted stands to belong to each of the genetic clusters identified by the preliminary Bayesian clustering analysis (Fig. S_2). The assignment test was carried out by running STRUCTURE with the option USEPOPINFO, i.e., using individuals from natural populations as a reference dataset to which individuals from planted stands were to be assigned to. The reference dataset was assembled by selecting only the individuals which were assigned to a genetic cluster with a probability >80% in the previous analysis (Fig. S_3).

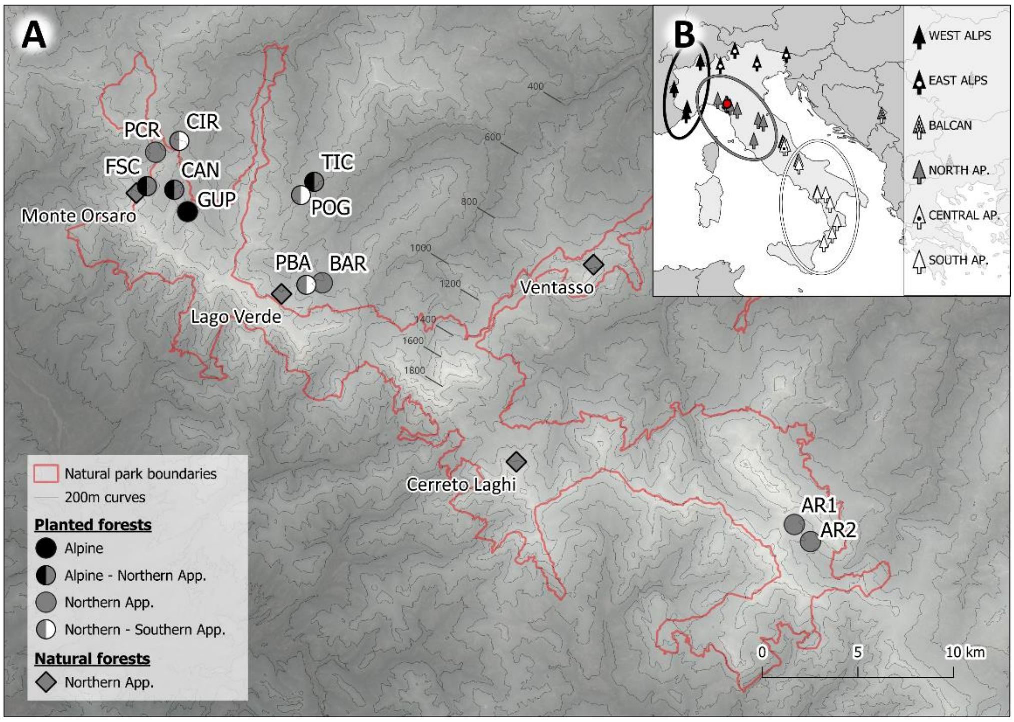


Figure 1. *A) Map of the 15 stands sampled in the National Park of the Tuscan-Emilian Apennine. Diamonds and circles represent natural and planted stands, respectively. Colors represent the provenance of each stand, as reconstructed by means of molecular markers (black: 'Western Alps'; dark grey: 'Northern Apennine' (local); white: 'Southern Apennine'). B) Map of the natural populations used as a reference dataset to reconstruct the provenance of the planted trees*.

Data collection

During July-October 2020, the field survey sampling was carried out. Dendrometric, edaphic, and topographic data were collected in the field from 155 trees in 11 stands (2 natural and 9 planted). Data collection was completed, with an additional sampling of 45 trees in four stands, in June-September 2021 (2 natural and 2 planted, AR1 and AR2, whose local origin was demonstrated by genetic evidence in a previous study, Piotti and Avanzi, 2022). In planted stands, only individuals which had been genetically characterized, and so for which provenance was known, were sampled for subsequent analysis. Each planted individual was assigned to a specific provenance based on two criteria applied on the assignment test results from genetic analyses (Fig. S_3): a probability of belonging ≥ 60% to the first likely provenance, and ≤ 30% probability of belonging to a second likely provenance. Approximately ten trees were sampled from each of the provenances included in that planted stand (Tab S_1). Trees were identified in the forest through the previously affixed tags. Approximately ten trees were sampled also in natural stands, and they were all considered as belonging to the local provenance. The following morphological data were collected for each tree: diameter, height, crown diameter, crown insertion height. Average topographic characteristics of the stand (elevation, exposure and slope) were measured by sampling the data for each of the 10 sampled trees and then averaging the values at stand level. At five points per stand, collected at one meter from the base of some of the measured trees, soil samples were collected to measure some edaphic parameters in the laboratory. Soil texture was obtained by means of the "Pipette Method" (Paturno et al., 1997). Soil samples were sieved at 2mm, grinded <200µm, and organic carbon I and percentage nitrogen (N) content was estimated using an elemental analyzer (Carlo-Erba NA-1500 Elemental Analyzer). C/N ratio has been used as soil fertility proxy. For each sampled tree (i), the neighborhood competition index (NCI) was calculated, which is a distance-dependent competition index that considers the competition experienced by each tree based on the diameter and distance of competing trees within a 10m radius to a subject tree according to the following formula (Canham et al., 2004)

$$1) \qquad \mathrm{NCI} = \sum_{\mathrm{i}=1}^{\mathrm{n}} \frac{DBH_i}{dist_i}$$

Where DBH_i and $dist_i$ are the diameter and the distance of each competitor tree *i* to the subject tree, respectively. Finally, two wood cores corresponding to the trunk radius were collected at breast height (i.e., 1.30m) from each of the surveyed trees using a Pressler's increment borer to perform dendrochronological analyses. When the trees grow on a slope, the woody cores were taken perpendicularly to the slope to avoid wood compression or expansion (Martínez-Sancho et al., 2020).

Dendrochronological analysis

Tree cores were processed manually and analyzed by scanning with an EPSON Perfection v850 Pro scanner at 2400 dpi resolution. Core samples were read using CooRecorder and CDendro software (v. 9.3.1 – Cybis, 2022; Maxwell and Larsson, 2021). The CDendro software was also used for crossdating the samples. Crossdating was carried out at two levels: at tree level, comparing the two cores collected on the same individual, and among trees. Different trees were crossdated by comparing, at the stand level, the two individual mean chronologies with the highest correlation coefficient and then proceeding with the comparison on the remaining trees. A final check was made by comparing the mean chronologies of the different stands. Growth rate of trees from different provenances and forest regeneration mode (natural *vs*. planted) was compared using generalized linear models (GLMs), climate-growth relationships and the application of RRR indices (Lloret et al., 2011).

We built two GLMs with a Gamma distribution including, respectively, tree provenance or forest regeneration mode as explanatory factor (fixed effect), and several environmental and edaphic parameters as continuous predictors: elevation, slope, exposition, NCI (competition), tree age, and edaphic C/N ratio. Exposition was included in the model after a transformation by the cosine of the exposition angle, to have a continuous variable ranging from -1 to 1, whereby 1 means a northern exposure and -1 a southern exposure. Annual Tree-Ring Width (TRW, mm) was transformed into Basal Area Increment (BAI, cm^2) to be used as the main response variable in GLMs. In the GLM, BAI is intended as the mean BAI of each i-th tree. The models have the following formulation:

$$\mathrm{BAI}_i = \alpha + \beta_1 * (\mathrm{Provenance} \mid \mathrm{Regeneration\ mode})_i + \beta_2 * (\mathrm{Elevation})_i + \beta_3 * (\mathrm{Slope})_i + \beta_4 * (\mathrm{Exposition})_i + \beta_5 * (\mathrm{NCI})_i + \beta_6 * (\mathrm{Age})_i + \beta_7 * (\mathrm{C/N})_i + \varepsilon_i$$

Depending on the explanatory factor used, tree provenance or forest regeneration mode, we refer in the text to the specific GLM with the expressions of 'provenance GLM' and 'regeneration mode GLM', respectively. All statistical analyses were performed using the R software (version 4.2.3) (R Core Team, 2022). GLMs were run through the *stats* package. To estimate the model fit, McFadden's R-squared was used. The contribution of individual predictors in explaining BAI variation was quantified by the F-test through the Anova function of the *car* R package and their importance has been assessed by importance plots through the *vip* R package (Greenwell, 2023), quantifying the relative impact of each variable on the model fit. The Variance Inflation Factor (VIF) has been used to evaluate collinearity among predictors, implementing the vif function of the *car* R package (Fox et al., 2023): VIF < 5 indicates no or low collinearity, 5 < VIF < 10 indicates moderate collinearity and VIF values > 10 indicate high collinearity among variables (Dormann et al., 2013). Significant differences among provenances and forest regeneration mode were quantified by Tukey post-hoc tests using the *multcomp* R package (Hothorn et al., 2023).

The climate-growth relationships were conducted over the period 1957-2017 using Ring Width Index (RWI) as the response variable, i.e., TRW data detrended and standardized to a unitless variable to correct for age trend and temporal autocorrelation. Detrending of the growth data from TRW to RWI was performed via the dplR R package using the modified negative exponential function method ('ModNegExp') and the 'Spline' methods (Bunn et al., 2023). The 'ModNegExp' method is used to remove the biological growth effect (increased growth in juvenile stages) from growth series, leaving signals that could be associated with environmental or climatic factors. The further application of the 'Spline' method helps to remove long-term variations, helping to highlight annual or seasonal variations related to climate (Bunn et al., 2023). RWI was correlated with monthly temperature and precipitation for a biological year extending from April of the previous year to September of the current year. Response coefficients from bootstrap correlations were used to analyze the response to climate, taking 1000 bootstrap samples from the original dataset of tree rings and climate data (Zang and Biondi, 2015a). To analyze climate-growth relationships over time, moving plots were produced with a window size of 30 years every year. Climate-growth relationships were carried out using the *treeclim* R package (Zang and Biondi, 2015b) and partial autocorrelation (PACF) was assessed through the *forecast* R package (Hyndman et al., 2023). PACF is considered as a reference variable to analyze possible growth relationships among rings, helping to understand how much previous years' conditions influence current year plant growth, for each of the years analyzed and for an increasing number of lag years between the reference year and previous ones (Dorado Liñán et al., 2011; Monserud, 1986). The presence of a significant autocorrelation suggests that growth may be the result of processes occurring in the growth year and determined by the previous year conditions. This could be due to climate, forest dynamics (e.g., disturbances, cuttings, pest outbreaks) or to the influence of individual genetic background, so subsequent analyses of RRR indices will help to analyze this relationship more specifically.

The sensitivity of silver fir to drought was analyzed in specific drought years. The Standardized Precipitation-Evapotranspiration Index (SPEI) was used to identify drought years of interest (Beguería et al., 2014). Drought years were identified using the SPEI6 and SPEI12 indices, which refer to drought events that occur in the spring-summer period (SPEI6 of September) or that affect the whole year (SPEI12 of December), respectively. A year is defined as droughty when the SPEI value is ≤ -1 (Liu et al., 2021; Mckee et al., 1993). Based on SPEI6 and SPEI12 values, years were classified as moderate drought (-1.5 to -1), severe drought (-1.5 to -2) and extreme drought years (≤ -2) (Fig. S_8, Tab. S_4) (Li et al., 2021; Mckee et al., 1993; Tirivarombo et al., 2018‘). The RRR indices proposed by (Lloret et al., (2011) were used to analyze the sensitivity to drought years. These indices estimate the recovery, resilience, and resistance to a disturbance, in this case drought. They are calculated based on the ratios between growth during the drought year and pre- and post-drought growth, according to the following formulas:

$$\text{Resistance} = \text{Dr}/\text{PreDr}$$

$$\text{Recovery} = \text{PostDr}/\text{Dr}$$

$$\text{Resilience} = \text{PostDr}/\text{PreDr}$$

$$\text{Relative Resilience} = ((\text{PostDr}-\text{Dr})/(\text{PreDr}-\text{Dr}))\ (1-(\text{Dr}/\text{PreDr}))$$

Where *Dr* referred to the growth during the drought year, while *PreDr* and *PostDr* indicate the average growth in the years before and after the drought, respectively. To calculate *PreDr* and *PostDr*, an average increment of the three years before and three years after the drought year is considered (Gazol and Camarero, 2016). The 'Relative Resilience' index is estimated as the resilience to disturbance weighted by the growth during the disturbance. RRR indices among tree provenance and forest regeneration mode were compared via ANOVA and subsequent Tukey post-hoc test. When comparing provenances in the ‘provenance GLM’ and in the RRR indices analysis we only refer to the trees grown in the planted stands, to be able to compare the performances of trees grown in similar conditions. When comparing forest regeneration methods in the ‘regeneration mode GLM’ and in the RRR indices analysis we only refer to the trees from the local provenance (Northern Apennines), to be able to compare the performances of trees with the same genetic background but grown in different environmental and management conditions.

Results

Mean BAI

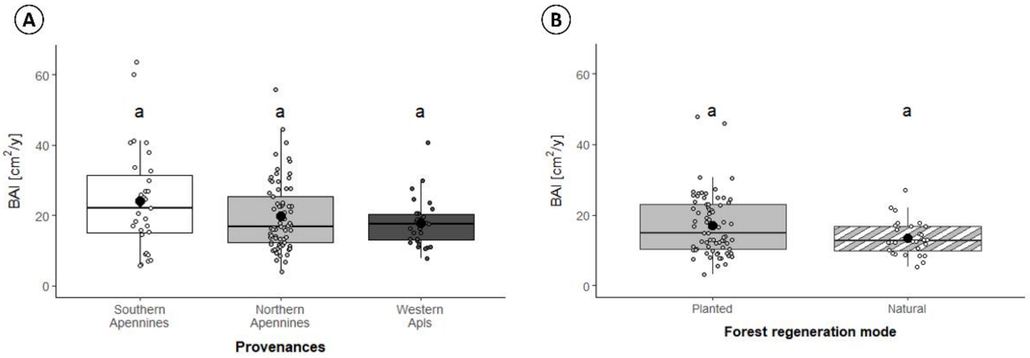


Figure 2. *Distribution of BAI values across A) provenances and B) forest regeneration mode. The black dots represent mean BAI values. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab), according to the results of the GLMs.*

The results from the Generalized Linear Models did not show significant differences among provenances or forest regeneration mode (Fig. 2,3). In the 'provenance GLM', the most significant and important variable was the elevation, with a significant and negative effect on growth and accounting for the 35.2% of the BAI variance explained. The NCI competition index had also a significant and negative effect on growth (p-value = 0.035) and counting as 18.2% of the BAI explained variance. The Southern Apennine provenance showed higher mean BAI (22.8 mm^2/year), followed by the Northern Apennine provenance (19 mm^2/year) and the Western Alps one (17.5 mm^2/year), even if there was no statistical support for these differences (Southern Apennine – Western Alps differed with a p-value of 0.09, while other differences show higher p-values). VIF values did not show any signs of collinearity among model predictors. When comparing provenances, we only refer to the trees grown in planted stands. The 'regeneration mode GLM' showed the tree age as mode as the most important variable that affect tree BAI (29.2% of the variance explained) followed again by the NCI competition index (23.8%) as significant variable (Fig. 3b; Tab. S_3). Planted forests showed higher mean predicted BAI (16.4 mm^2/year) than natural forests (13.2 mm^2/year) even if the difference was not significant (p-value = 0.16). VIF values showed moderate collinearity between C/N and elevation. When comparing the regeneration mode of the forest, we only used trees of local provenance.

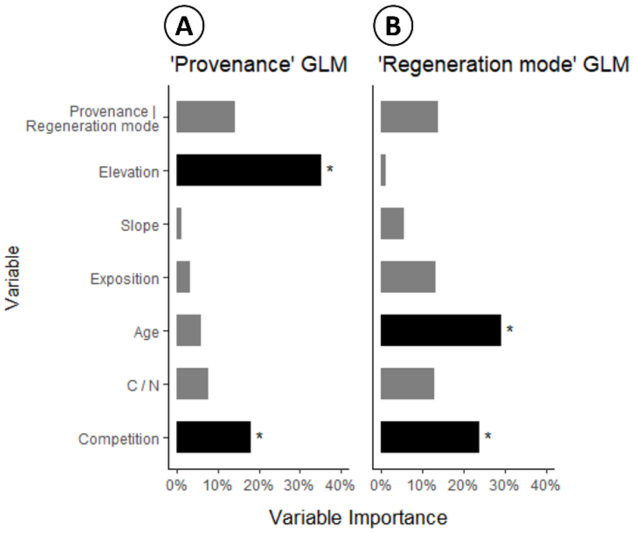


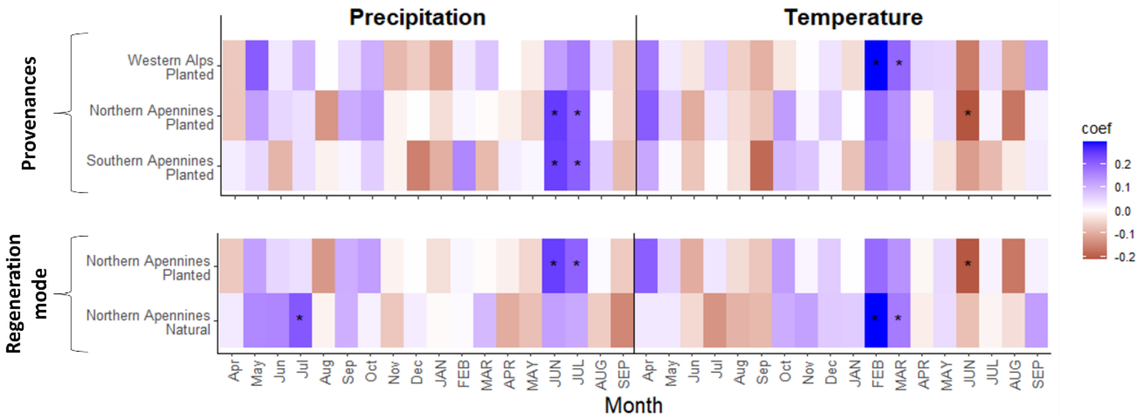
Figure 3. *Importance plots of the predictors of the (A) 'provenance GLM' and (B) 'regeneration mode GLM'. The asterisk (*) indicates the significant predictors in the respective model.*

Tree-ring chronologies and climate-growth relationships

Tree-ring chronologies were quite similar among provenances and between forest regeneration mode (Fig. S_5) and showed no signal of autocorrelation among rings. Partial autocorrelation analysis showed no significant autocorrelation at one year lag among rings, except for the local provenance in planted stands. No significant partial autocorrelation emerged for lags of up to eight years for the Western Alps provenance and up to 15 years for the Southern Apennines provenance (Fig. S_6).

Climate-growth relationships were generally similar among provenances and between forest regeneration mode, although they showed a few differences between the examined trees. In these analyses, positive response coefficients indicate a positive relationship between growth and climate variable (i.e., high temperature -> high growth, but also low temperature -> low growth) while negative response coefficients indicate an inverse correlation (i.e., high temperature -> low growth, and vice versa). The growth of the local provenance (Northern Apennine) and the Southern Apennine provenance was significantly positively influenced by summer precipitation (June and July) of the current year, a trend that was also observed in the trees of the Western Alps provenance and in natural forests, although it was not significant. The Southern Apennine provenance was not significantly limited by any other climatic factor, while the growth of the local provenance (Northern Apennine) in planted forests was also significantly and negatively influenced by the temperatures in June of the current year. This relationship was observed also in the other provenances, but it was not significant. The growth of the Western Alps provenance was significantly and positively correlated with winter temperatures in February and March, as it was for the local provenance in natural forests. This relationship was observed also in the trees of the Southern Apennine provenance and the local provenance in planted forests, but it was not significant. Finally, natural forests showed a positive and significant correlation between growth and June precipitation of the previous year, a trend that was only slightly noticeable in the other levels of analysis (Fig. 4).

Figure 4. *Response coefficients showing the climate-growth relationships of silver fir in the period 1957-2017. * Indicate significant response correlations between RWI and climate data.*



Moving plots analysis revealed some additional differences. The Southern Apennine provenance showed a significant and positive correlation with the June temperatures of the current year (Fig. S_7c), which was also confirmed by the other provenances, albeit to a lesser degree. July temperatures of the current year, on the other hand, showed a negative correlation with the growth of both the Western Alps and the local provenance in planted forests (Fig. S_7a,b), a trend that was reversed in the most recent time windows and it showed slightly positive correlation values. A positive correlation between growth and winter temperatures was observed for all provenances, with less evidence for the Southern Apennine provenance (Fig. S_7c). The positive correlation between growth of the Southern Apennine provenance and the local provenance in natural forests with the temperatures of the previous autumn was notable (Fig. S_7c,d). The positive correlation with summer precipitation (June and July) of the current year was significant and/or continuous especially for the local provenance (Northern Apennine) in planted forests (Fig. S_7b), while it was significant for the other provenances and forest regeneration mode only in the most recent time windows. The sensitivity to the precipitation regime during the whole year was then significant and positive only for the natural forests of local provenance, with emphasis on the summer of the previous year and the spring of the current year (Fig. S_7d). The Southern Apennine provenance was the only one to show negative, though not significant, correlations with precipitation in the summer of the previous year (Fig. S_7c).

Drought years and RRR Indices

Using SPEI6, ten drought years were identified, of which seven were of moderate, two severe and one extreme intensity (Fig. S_8a, Tab. S_6). SPEI12 identified ten drought years as well, of which six were moderate and four were severe (Fig. S_8b, Tab. S_6). Five years coincided between SPEI6 and SPEI12: 1983, 1988, 2003, 2007 and 2011.

Analyses of RRR indices showed more significant differences both among provenances and in drought years identified by SPEI6 than by SPEI12. It should be emphasized that, when comparing the performance of the three provenances, only trees growing in planted forests were compared. For the years identified by SPEI6, the Southern Apennine provenance showed greater recovery, resilience, and relative resilience with respect to the Western Alps provenance in almost all drought intensity classes (except for resilience during severe drought years and relative resilience in moderate drought years) (Fig. S_9). The behavior of the local provenance (Northern Apennine) was generally intermediate. The resistance index showed no significant differences among provenances, while lower resilience for all provenances during the extreme drought year was found (Fig. 5, Fig. S_9a), with average values < 1 (Tab. S_7). Drought resilience was also lower in the extreme drought year for all provenances (Fig. 5, Fig. S_9c), although the Southern Apennine provenance was the only one that showed mean values > 1 (Fig. 8, Tab. S_7). In the years identified by SPEI12, the Southern Apennine provenance showed statistically higher values of resistance and resilience in moderate drought years and higher recovery in severe drought years than the Western Alps provenance (Fig. S_10). The local provenance (Northern Apennine) showed no significant differences compared to the other provenances, except for higher resilience in moderate droughts with respect to the Western Alps provenance (Fig. S_10a).

Forest regeneration mode has a significant effect on RRR indices, with planted forests showing an overall greater capacity to react to drought episodes than natural stands. It should be emphasized that these analyses compared the growth performance of the same provenance (Northern Apennine) between natural and planted conditions. In the years identified by SPEI6, planted forests showed greater recovery, resilience and relative resilience in severe drought years and greater recovery and relative resilience in extreme drought years (Fig. 8, Fig. S_11b,c,d). Resistance and resilience in extreme drought years were significantly lower than in other drought years (Fig. 5, Fig. S_11a,c), also with average values < 1 (Tab. S_5). Resistance in extreme drought years was the only index where natural forests performed significantly better than planted forests (Fig. S_11a). In the years identified by SPEI12, planted forests performed better in terms of drought resistance and resilience in severe drought years (Fig. S_12a,c).

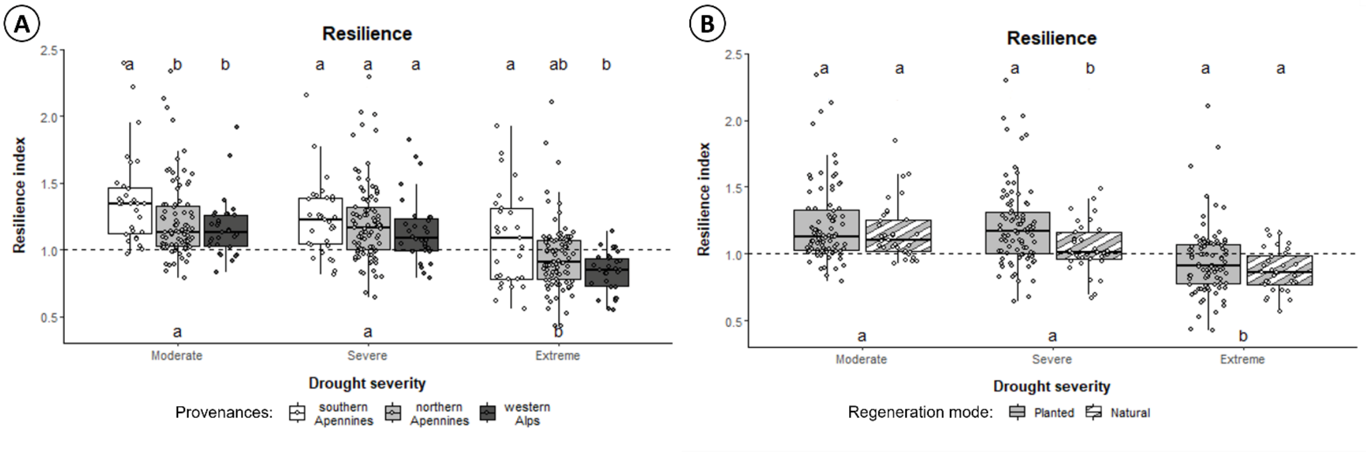


Figure 5. *Distribution of the resilience index calculated for drought years identified by SPEI6 across (A) provenance and (B) forest* regeneration mode*. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab) according to post-hoc tests. The upper line of letters refers to the comparison of (A) provenances and (B) forest* regeneration mode *within the same drought intensity level; the lower line of letters compares the reference mean index (all provenances together) between drought intensity levels.*

Discussion

Our work aims to investigate responses of silver fir to drought in a mountain environment in Italy. By taking advantage of the ideal experimental setting represented by *Abies alba* plantations established during the 20th century in the Northern Apennines, we tested the existence of differences in growth rates, growth-climate relationships, and growth responses to drought among different silver fir provenances (originated from Southern Italy to the Alps) growing under similar climatic and environmental conditions. The results obtained from this study show an influence of the provenance and forest regeneration mode in the growth response of silver fir to climate and drought, although this response may appear more or less clearly depending on environmental conditions. Our results highlight the importance of taking into account the genetic background of forest reproductive materials to valorize forest genetic resources available in the Italian territory and their response to drought.

BAI and environmental drivers of tree growth

Effect of provenance

Analyzing the average growth of the three provenances, we observe that silver fir from the Southern Apennines has a slightly higher growth rate compared to the Western Alps provenance, although the difference is only marginally significant in statistical terms. The absence of a statistically significant difference allows us to proceed with the subsequent analyses with greater confidence, marking the results of the climate-growth relationships and RRR indices as related to climate trends. The constructed model explains only one-third of the variance in the data (Tab S_3), emphasizing the existence of multiple unconsidered factors affecting growth. The BAI data predicted by the GLM were corrected for the effect of multiple environmental parameters, revealing which predictors have a more pronounced effect on growth. Elevation is revealed to be the most limiting factor for growth, confirming previous results from other authors on its negative effect on growth of silver fir (Dinca et al., 2022; Gazol and Camarero, 2016; Jevšenak and Skudnik, 2021). Elevation has also been recognized as one of the main factors shaping recent adaptive and neutral evolutionary dynamics in silver fir (Brousseau et al., 2016; Major et al., 2021). Altogether, our results indicate that the average growth rate is rather uniform among Italian silver fir genetic provenances. The lack of difference in average growth rate, however, does not imply the same physiological response to drought. Therefore, the results call for a more in-depth analysis to study the differences in drought response among provenance found by other authors (Bosela et al., 2016; Dobrowolska et al., 2017; Martínez-Sancho et al., 2021; Mihai et al., 2021; Vitasse et al., 2019b; Walder et al., 2021). NCI index, as a proxy for the competition level experienced by each individual, has a significant effect. The NCI index is widely used to measure competition intensity (Canham et al., 2004; Opgenoorth et al., 2021) and our results confirm its negative relationship with growth and the importance of including competition as a factor in forest growth analysis (Burkhart and Tomé, 2012; Canham et al., 2004).

Effect of regeneration mode

Similarly, the 'regeneration mode GLM' (planted vs. natural) showed age and competition as significant predictors. Even if there are no significant differences in BAI between regeneration modes for this species, the regeneration mode of the forest has been identified as the third most important predictor from the GLM, explaining almost 14% of model variance. Therefore, although not explaining the differences in BAI in our study, regeneration mode needs to be considered when building models to analyze forest data, as suggested by other studies on the Italian territory (Manetti and Cutini, 2006).

NCI competition index has a significant effect, underlying the importance of including it as a predictor in forest data analysis. The inversely proportional relationship between plant age and BAI has already been observed in many tree species (Anning and McCarthy, 2013; Cienciala et al., 2016; Jõgiste, 2000) even though conflicting results can be found in the literature (see Johnson and Abrams, 2008). In this study, the negative relationship is mainly driven by a small number of plants that reach 200-300 years in natural forests. Old individuals are slow-growing and possibly disadvantaged by the difficult micro-environmental conditions, explaining the decreased BAI in this age extreme.

Climate growth relationships

Effect of provenance

The chronology analysis shows partial autocorrelation (PACF) values between tree rings at the first lag level only for the Northern Apennines provenance in planted forests, revealing a possible link between the growth of successive years. The correlation coefficient of the first lag level (PAC1) is often considered as a reference value to analyze possible growth relationships between tree rings (Dorado Liñán et al., 2011; Monserud, 1986). Significant PACF values at lag levels nine and 16, on the other hand, are not considered problematic in the analysis of the results due to the distance from the target tree ring and, thus, not related to climate (Liutsko and Monleon-Getino, 2009; Monserud, 1986). The relationships between climate and growth show common trends among the studied provenances that are positively correlated with summer precipitation and winter temperatures in the current year. These results reflect the sensitivity of silver fir to climate found by other authors, revealing the vulnerability of this species to summer drought and winter frost (Latreille et al., 2017; Lebourgeois et al., 2013). Our results highlight some differences between provenances and regeneration modes of the forest in the response coefficients between climate and growth, further corroborated by previously published work (Carrer et al., 2010; Gazol et al., 2015; Mazza et al., 2014). Silver fir stands from the south-western distribution limit express high correlation coefficients with summer precipitation, while stands from a more continental climate are more limited by winter temperatures (Gazol et al., 2015). Mazza et al. (2014) analyzed some silver fir stands in the Tuscan-Emilian Apennines and found correlation values with precipitation and temperature very similar to those of the Southern and Northern Apennines in planted pure stands shown in the present study. Similarly, Carrer et al., (2010) analyzed natural populations of silver fir from all over the Italian Peninsula, classifying them into three geographical macro categories based on growth response. In Carrer classification, populations from a Mediterranean climate have a high correlation with current summer precipitation. Our results show the same results for the Southern Apennine provenances. The results of our study show high correlation also between the Northern Apennines provenance growth response and summer precipitation. This is in contrast to the classification from Carrer et al (2010), where no correlation was found. Local adaptations and microclimatic conditions can play a significant role in growth responses, potentially overriding broader climatic patterns (Gazol et al., 2015). Mazza et al. (2014) also noted similar responses in varying geographical locations, suggesting a complex interplay of local and regional climate influences. The Western Alps provenance showed a positive relationship between growth and current winter temperatures in Carrer et al., (2010), again in line with our results. It is also interesting to note the effect of the previous year's summer precipitation, which tended to be negative for the Southern Apennines provenance in June and for the local provenance in August, showing signs of positive response to the summer drought in relation to the previous year's rainfall regime. The local provenance, at the same time, seems to suffer more from high temperature of the current year.

Effect of regeneration mode

Natural forests are particularly sensitive to winter temperatures, possibly being penalized by very cold winters, probably due to local conditions in high mountain environments (Carrer et al., 2010; Gazol and Camarero, 2016; Mihai et al., 2021). Climate susceptibility may not only be related to the climatic regime at higher elevations, but also to environmental differences. In our case, natural forests grow on more impervious soils, with higher rockiness and reduced depth. This may affect the ability to effectively absorb water and nutrients, and thus the ability to respond effectively to climate stresses in certain contexts. Furthermore, these forests showed a positive growth response in relation to the previous year's summer precipitation, showing a possible vulnerability to summer drought. Natural forests appear to be less constrained by the climatic conditions of the current year than planted forests of the same provenance, which may be due to the lower climatic sensitivity of high-elevation marginal silver fir forests found by other authors (Mazza et al., 2014).

RRR Indices

Effect of Provenance

Analyses of RRR indices show a high drought tolerance of silver fir, with average values of resistance, recovery and resilience indices tending to be higher than 1. This suggests that silver fir tends not to be impacted by drought in the first place but, when it is, it has the ability to recover from such stressful episodes (Tab S_5). This trend, already observed by other authors in silver fir, suggests a high resilience of the species to the climatic threats imposed by climate change (Bottero et al., 2021). However, our results show a general sensitivity of silver fir to extreme drought, identified with SPEI6 in the year 2003, then to moderate or severe drought events. Extreme droughts affect both the resistance and resilience of silver fir to drought, always resulting in average values below 1. This result is in line with current literature on silver fir (Lloret et al., 2011; Serra-Maluquer et al., 2018), emphasizing that extreme drought events can negatively affect growth and the ability of silver fir trees to respond to it. Regardless, when considering specific provenances, the picture shows interesting differences. For instance, Western Alps provenance shows RRR indices around 1 or lower, with a particularly low recovery ability. On the other hand, the Southern Apennines provenance is the only one with average resilience index values above 1 during extreme drought, even indicating slightly improved growth. The main trend that can be observed in the RRR indices analyses is a generally better response, in almost all its components, of the Southern Apennines provenance than the Western Alps provenance, confirming diversified drought responses among provenances (Dobrowolska et al., 2017; Mihai et al., 2021). This trend is respected in both SPEI6 and SPEI12 analyses, especially for the recovery and resilience components. The non-significant effect between provenances in the resistance index may be related to the results of the climate-growth relationships, which show a high sensitivity of the Southern Apennines and local provenances in planted stands to summer precipitation. This may denote a limitation of growth during drought years, however, it is compensated by a generally high resilience. Silver fir provenances from southern Italy (Calabria and Molise regions) have demonstrated high production yields in provenance trials in Europe in recent decades, both in terms of growth and adaptation to climate change (Hansen and Larsen, 2004; Kerr et al., 2015), besides high genetic diversity (Piotti et al., 2017), underlining the importance they can play in forestation or assisted migration programmes to increase forest resilience. However, this is not the case in all locations or climates, as demonstrated in continental climate sites in the Czech Republic (Fulín et al., 2023). However, the differences between provenances found in the results based on SPEI6 drought years are sometimes not confirmed by those based on SPEI12 years, such as differences in growth recovery during moderate droughts or in relative resilience during severe droughts. This may be due to the ability of the SPEI index to identify the intensity and duration of droughts according to the time scale at which it is calculated. SPEI 6, in fact, is better able to identify droughts of short duration and variations in water availability, while SPEI 12 is generally used to study droughts over longer periods and long-term impacts on vegetation (Eris et al., 2020; Pei et al., 2020). This is further supported by the occurrence of a drought year of extreme intensity in SPEI6 analyses (SPEI62003 = -2.4), whereas in SPEI12 years the maximum drought intensity is 'severe' (SPEI12 > -1.9). Our results suggest that the different provenances may respond similarly to long-term climatic variations, while showing higher differences when subjected to sudden climatic stress. Other authors have found a diversified response of forest provenances when varying the scale at which climate vulnerability is analyzed, indicating the importance of analyzing the appropriate scale for the specific case study (George et al., 2019; Stefanidis et al., 2023).

Effect of regeneration mode

When discussing the effect of the genetic background on growth performance, also the regeneration mode should be taken into account. In the study area, both natural regenerated forests and planted forests of local provenance can be found. Average growth of local natural forests was not different from the same provenance in planted forests, but their ability to respond to water shortage can vary with drought intensity. Natural forests, in fact, suffer from extreme drought levels, showing values below the threshold of 1 in all indices, exhibiting susceptibility to drought similar to that of the Western Alps provenance in this study. The only index where the natural forests show better performance than the planted ones is the resistance with SPEI6. However, due to the lower recovery to drought years (considering SPEI6) the natural forests have a resilience index lower than the threshold value 1 and no significant differences than planted forests. When considering SPEI12, the natural forests show consistently lower RRR indexes compared to planted ones(Carrer et al., 2010). The poorer resistance to drought of natural population might be related to the difficult environmental conditions in which the natural populations grow (assessed in the field using a visual approach): Higher elevation characterized by rocky substrate, resulting in reduced water availability in the soil and a very thin edaphic organic layer. In a climate change perspective, planted Northern Apennines populations outperform natural ones when considering drought resistance, probably due to the more favorable conditions of the stands and the historical management, avoiding high competition among individuals. Similarly to the provenance analysis, the differences between the regeneration modes are more abundant in the analyses of the RRR indices of the years identified by SPEI6, not confirmed by the SPEI12 results as in the case of recovery and resistance. This could be due to the general high adaptability of silver fir to the surrounding environmental conditions. Silver fir is considered to be a conifer with high climate plasticity when translocated to different climates, allowing for good long-term adaptation, but possibly susceptible to sudden changes (Dobrowolska et al., 2017; George et al., 2019). The differences between natural and planted forests could also follow this trend, both generally responding well to drought in the long term (mean RRR > 1 in SPEI12 analysis), while showing a negative response of natural forests to severe or extreme droughts. These differences, in addition to the management methods of the two forest types, can be related once again to the difficult soil conditions in which the trees grow, marking the role of the environment in climate adaptability. Droughts of high intensity over short periods can have a marked effect on the ability of trees to respond to climate, highlighting the importance of proper forest management in natural forests. These nucleus of natural forests in the Apennines needs to be protected as they represent a very important genetic heritage, both historically and for the future adaptation of the species. Northern Apennines are proven to be one of the glacial refugia from which silver fir recolonized parts of Central Europe, revealing natural forests as a reservoir of potentially distinctive and diverse forest genetic material (Konnert and Bergmann, 1995; Piotti et al., 2017; Piovani et al., 2010). The conservation of these natural stands is therefore of paramount importance, both for the functioning of local forest ecosystems and for the conservation of the forest genetic heritage. For these reasons, active management to maintain and improve health and growth status of natural silver fir stands is suggested (Gentilesca and Todaro, 2008; Piovani et al., 2010).

Future for *Abies alba* under climate change pressure and possible management perspectives

From these results we can generalize a positive ability of silver fir to respond to drought, showing a marked ability to recover its growth and being resilient, at least for its Northern and Southern Apennine provenances. Indeed, the literature about silver fir shows that the species is particularly plastic in its response to drought (Mihai et al., 2021) and possibly well adaptable to future climatic conditions (Vitasse et al., 2019b; Walder et al., 2021). The resilience of silver fir to drought is usually higher as compared to other forest tree species, such as spruce or beech (Gillerot et al., 2021; Mikulenka et al., 2020; Vitasse et al., 2019a). Our results show a decline in silver fir growth responses to drought under extreme drought conditions, showing that, beyond certain climatic thresholds, the ability of the species to functionally respond to drought is limited by physiological processes (Larysch et al., 2021). In addition, the effect of genetic provenance on drought responses is clear, highlighting how material from southern Italy and of local provenance can perform in terms of production and drought resilience in mountainous territories of Tuscan-Emilian Apennines. These results also confirm that silver fir stands in the Tuscan-Emilian Apennines include trees that are highly adaptable to drought, that may be linked to high neutral genetic diversity of this species in this area despite the extreme fragmentation of natural stands (Piotti et al., 2017). Forest planning should value and maintain the genetic diversity of forest stands, increasing their functional traits and resilience in the face of environmental and climatic stresses (Mihai et al., 2021).

One of the tools of sustainable silviculture is the translocation of forest reproductive material that is more adaptable to future climates through assisted migration, adopting forest provenances that can be more resilient to drought. Assisted migration is a silvicultural option to improve the climate performance of forest species (Aitken and Bemmels, 2016; Breed et al., 2013; Millar et al., 2007), not only at the scientific level but also by forest owners and managers (Gömöry et al., 2021; Vinceti et al., 2020). The assisted migration accidentally put in place in the postwar period to reforest the Tuscan-Emilian Apennines has resulted in some provenances (i.e., Southern Apennines) showing similar drought responses with respect to the local genotypes, and others (i.e., Western Alps provenance) showing a different behavior. This evidence can be employed by local forest management to adopt sustainable silvicultural management in a climate change context, with respect to both the management of existing forests and the future planting of new forest stands by translocating more adaptable material for the future. Thus, the use of tested provenances to mitigate the effects of climate change is recommended, as long as specific local conditions are taken into account (Dobrowolska et al., 2017). However, future assisted migration projects will need both further evidence about the performance of regeneration from external provenances in the current climate and to be accompanied by sound sustainable forest management plans, as there is already evidence that assisted migration under extreme climate scenarios can only partially improve widespread adaptation to climate change (Gustafson et al., 2023). The loss of ecosystem services related to climate crisis could be only partially mitigated by planting provenances more adapted to future climate, especially in Mediterranean settings, enhancing the role of local sustainable forest management (Mauri et al., 2023).

Conclusions

This work analyses the ability of silver fir trees of different genetic provenance (Southern Apennines, Northern Apennines, Western Alps) and regeneration mode (natural populations and planted forests) to respond to drought, a topic of pivotal importance given the relevance of the species at the European level and the threat of climate change. We thus attempt to define some guidelines for local silvicultural management that can foster the provision of ecosystem services linked to silver fir and mitigate the effects of climate change on local forests. An analysis of growth according to tree provenance shows that silver fir trees from local provenance and from Southern Apennines result in greater resilience to drought and greater ability to take advantage of summer rains when compared to the Western Alps provenance. Similarly, local material in planted stands is found to have greater drought resilience than trees from natural stands, and a possible explanation is related to the difficult soil conditions in which natural silver fir forests grow. This evidence reveals the potential of using non-local forest reproductive material to maintain or improve the response of forests to climate change, as long as the origin and the performances of the FRM is thoroughly tested (e.g. through genetic tests and common garden experiments). Future silver fir assisted migration programmes should consider the use of local material accompanied by material from the southern distribution limit of the species, in particular after assessing possible issues related to outbreeding depression and maladaptive gene flow. In addition, in order to functionally employ local genetic resources, timely silvicultural management is necessary to effectively conserve the local genetic heritage in the original natural stands, so as to be able to benefit from them in the future. These results add to a growing body of information on the growth response mechanisms of silver fir to climate change, and it is hoped that local silvicultural management will benefit directly from them.

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Supplementary Materials

Genetic analysis

A total of 2147 silver fir individuals (1907 from 39 natural populations and 240 from 10 plantations) were used for genetic analyses. All microsatellite markers were polymorphic, and the mean number of alleles per locus varied between 1.59 and 14.85.

The Bayesian clustering analysis showed the presence of a genetic structure within natural populations, with an optimal grouping at K=2 and K=5 according to Evanno et al (2005)'s ΔK (Fig. S_1).

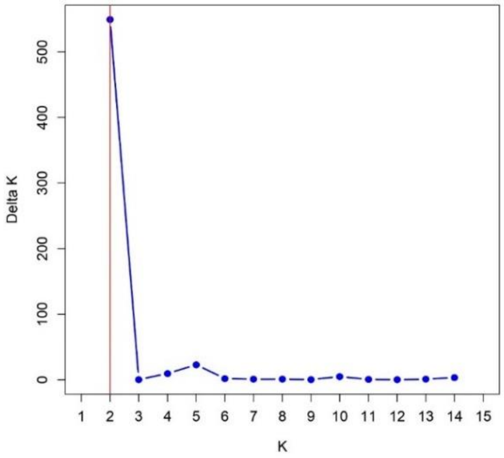


Figure S_1 *– Distribution of ΔK values for each number of genetic clusters (K) tested in the Bayesian clustering analysis on silver fir natural populations.*

At K=5, the five genetic clusters were represented by Eastern Alps and Northern Apennine populations, Western Alps populations, Central Apennine populations, Southern Apennine populations, and Eastern Europe populations (Fig. S_2). The genetic cluster made up of Eastern Alps and Northern Apennine populations can be considered as the 'local' one with respect to the plantation analyzed in the present study.

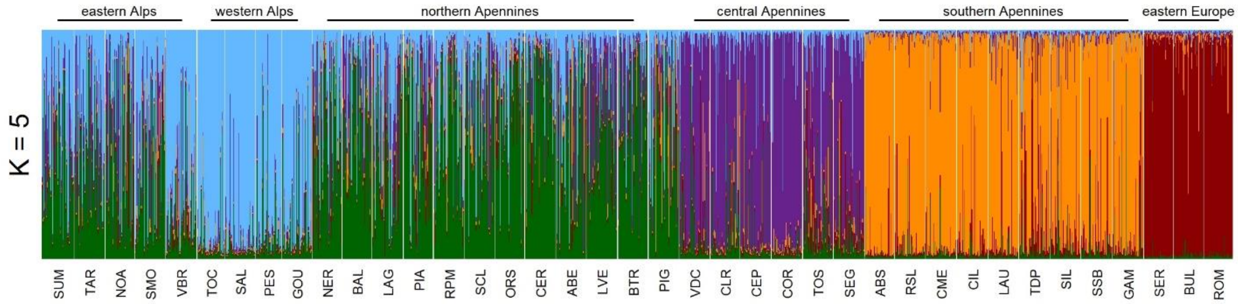


Figure S_2 *- Results of Bayesian clustering analysis on natural populations. Each bar represents an individual, and its probability of being assigned to each of the five genetic clusters (dark green: Eastern Alps and Northern Apennines; light blue: Western Alps; violet: Central Apennines; orange: Southern Apennines; dark red: Eastern Europe).*

The genetic clusters identified by STRUCTURE at K=5 were used as reference dataset to assign individuals from plantations. The reference dataset was made up of 1053 trees, i.e., those trees with a probability >80% of being assigned to one of the five clusters.

The results of the assignment test on the 240 trees from plantations are shown in Fig. S_3, where the probabilities of each tree to belong to the five genetic clusters are shown. Some plantations harbored a single gene pool (e.g., GUP is almost entirely made up of trees with a Western Alpine origin), while others had a mixed origin (e.g., PBA is made up of both 'local' and Southern Apennine genotypes).

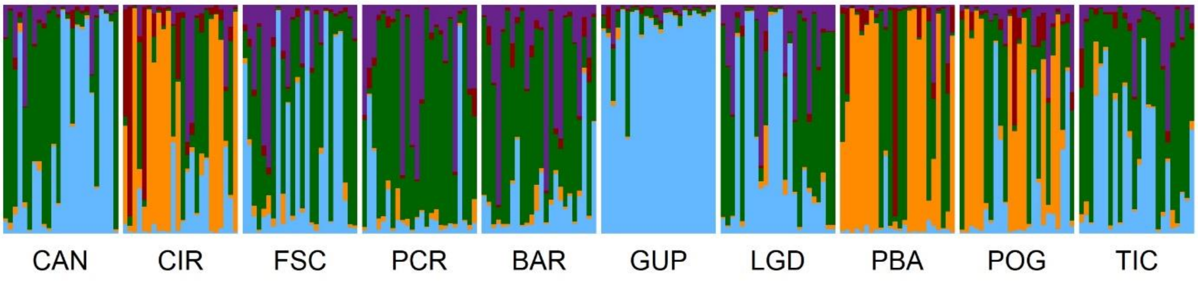


Figure S_3 *- Results of the assignment test on the 240 planted trees. Each bar represents a tree, and its probability of being assigned to each of the five genetic clusters (dark green: Eastern Alps and Northern Apennines; light blue: Western Alps; violet: Central Apennines; orange: Southern Apennines; dark red: Eastern Europe).*

The probabilities shown in Fig. 3 were used to select the trees for the dendrochronological analyses. A tree was selected based on two criteria: a probability >60% of being assigned to the most likely gene pool and <30% of being assigned to the second most likely gene pool. This resulted in 57 trees assigned to the Western Alps cluster, 33 trees assigned to the Southern Apennine cluster, 79 to the 'local' cluster, 3 to the eastern Europe cluster and 9 to the central Apennine cluster. Additional 30 trees from AR1 and AR2 stands were considered as trees of local provenances based on the results of Piotti and Avanzi (2022), which revealed the almost complete local origin of the planted materials.

GLM and Dendrochronological analysis

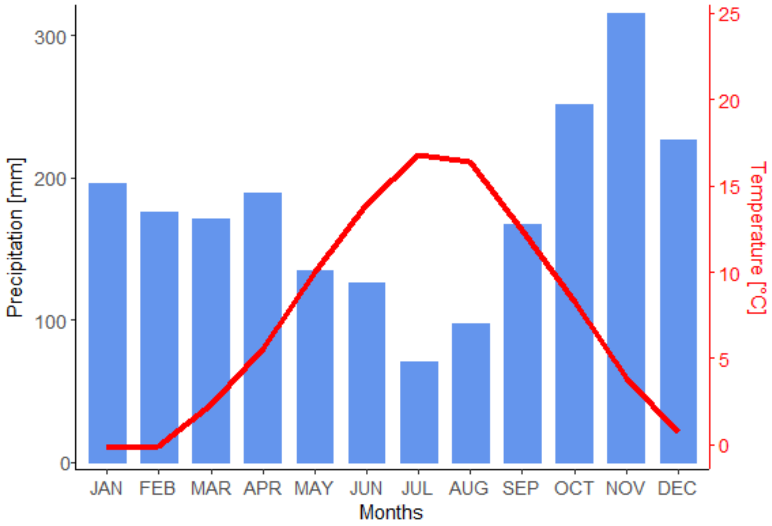


Figure S_4. *Mean climatic conditions of the study area in the Tuscan-Emilian Apennine National Park. Reference period 1957-2017*

Table S_1. *Topographic characteristics and number of sampled trees of the sampled plots.*

Plot	Regeneration mode	Slope	Elevation	Exposition	Year of sampling	Provenance	Number of sampled trees
		deg	*m asl*	*deg*			
AR1	Planted	9	1653	91	2021	Northern Apennines	15
AR2	Planted	17	1526	168	2021	Northern Apennines	15
BAR	Planted	24	1144	169	2020	Northern Apennines	10
CAN	Planted	17	1227	296	2020	Northern Apennines	11
						Western Alps	9
CIR	Planted	24	1015	152	2020	Southern Apennines	11
						Northern Apennines	6
FSC	Planted	25	1633	96	2020	Northern Apennines	10
						Western Alps	7
GUP	Planted	14	1189	204	2020	Western Alps	10
PBA	Planted	32	1227	78	2020	Southern Apennines	11
						Northern Apennines	7
PCR	Planted	20	1318	175	2020	Northern Apennines	10
POG	Planted	19	1130	105	2020	Southern Apennines	10
						Northern Apennines	5
TIC	Planted	9	1083	130	2020	Northern Apennines	12
						Western Alps	6
CL	Natural	19	1627	324	2021	Northern Apennines	5
LV	Natural	32	1430	35	2020	Northern Apennines	15
MO	Natural	29	1641	10	2020	Northern Apennines	10
VN	Natural	31	1493	350	2021	Northern Apennines	5

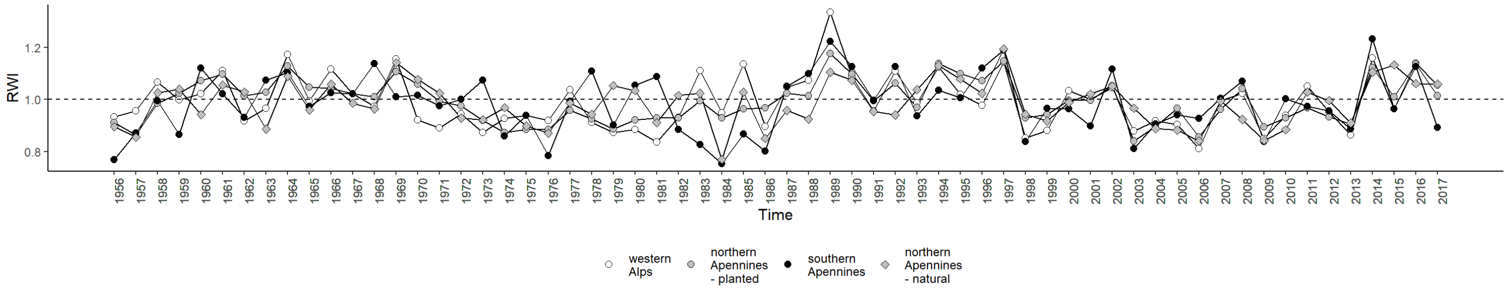
Table S_2. *Topographic characteristics and number of sampled trees by each provenance and regeneration mode.*

Provenance	Regeneration mode	Slope	Elevation	Exposition	Number of sampled trees
		deg	*m asl*	*deg*	
Western Alps	Planted	16.3	1283	181	32
Northern Apennines	Planted	19.6	1296	146	101
Northern Apennines	Natural	27.8	1548	180	35
Southern Apennines	Planted	25	1124	111	32

Table S_3. *Statistics of the two GLMs. Estimate coefficients indicate if the relationship between BAI and the predictor is positive or negative. The importance shows the amount of relative variance explained by each predictor. VIF is the Variance Inflation Factor.*

	Provenance GLM					**Regeneration mode GLM**				
Variable	*estimate coefficient*	*importance*	*F statistics*	*p-value*	*VIF*	*estimate coefficient*	*importance*	*F statistics*	*p-value*	*VIF*
Provenance | Regeneration mode	-	14.15%	1.68	0.191	1.79	-	13.79%	1.83	0.180	2.27
Elevation	-0.001	35.22%	14.67	**0.0002 ***	2.92	6.54E-05	1.23%	0.01	0.908	**6.59**
Slope	-0.001	1.32%	0.02	0.881	1.45	-0.003	5.65%	0.32	0.572	1.51
Exposition	-0.036	3.30%	0.14	0.713	2.29	-0.129	13.28%	1.66	0.201	2.22
Age	0.002	6.05%	0.45	0.504	3.22	-0.004	29.19%	7.00	**0.010 ***	1.62
C/N	0.019	7.66%	0.77	0.383	4.15	-0.038	13.02%	1.54	0.218	**7.78**
NCI	-0.003	18.15%	4.53	**0.035 ***	1.48	-0.004	23.84%	5.51	**0.021 ***	1.51
McFadden's R^2	0.32					0.38				

Figure S_5. *RWI standardized chronologies for the different levels of analysis.*



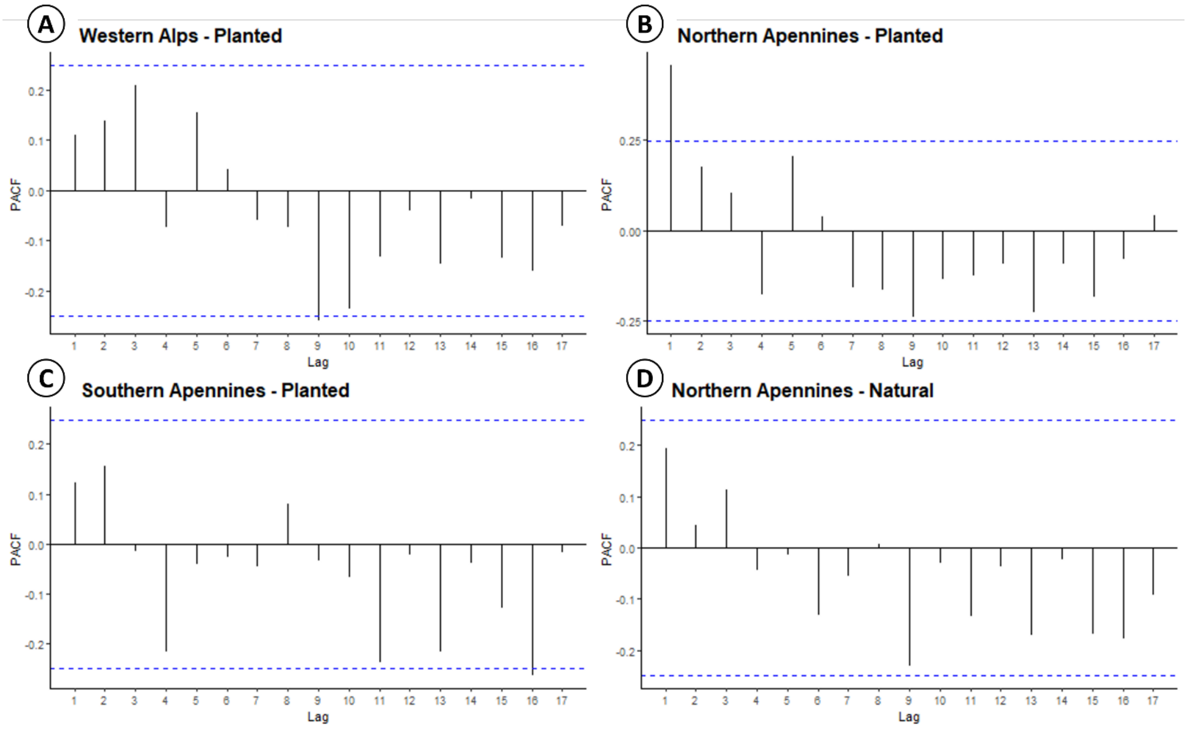


Figure S_6. *Partial autocorrelation plots for the chronologies of every level of analysis. Correlation coefficients higher than 0.25 or lower than -0.25 indicate significant positive or negative correlation, respectively.*

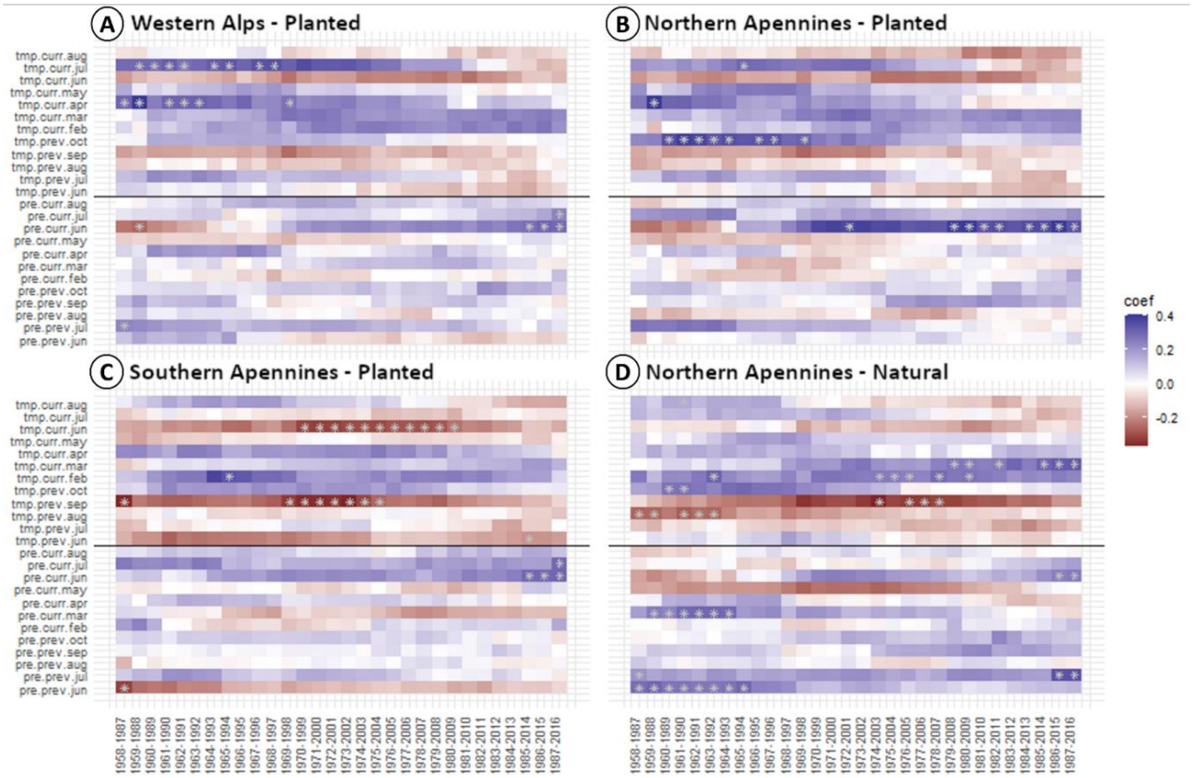


Figure S_7. *Climate-growth relationship moving plots of response coefficients. They represent a window of 30 years shifted every year. * Indicate significant correlations between RWI and climate data in the reference time window. Blue colors indicate positive correlations while red colors indicate negative correlations. Color continuity in a single month between all analyzed windows indicates constancy and continuity of the trend over time.*

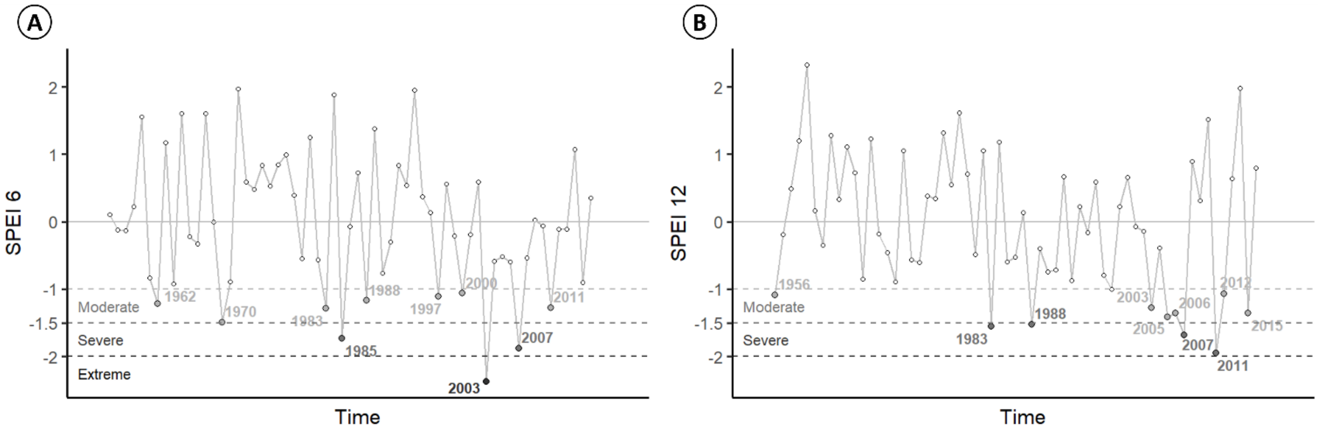


Figure S_8. *A) SPEI6 and B) SPEI12 reference values for each year. If -1 < SPEI < -1.5 the year is defined as 'moderate drought', if -1.5 < SPEI < -2 the year is defined as 'severe drought', if SPEI < -2 the year is defined as 'extreme drought'.*

Table S_4. *Drought years for SPEI6 and SPEI12 analysis, grouped by drought intensity.*

	SPEI6	SPEI12
Moderate ***-1 < SPEI < -1.5***	1962, 1970, 1983, 1988, 1997, 2000, 2011	1956, 2003, 2005, 2006, 2012, 2015
Severe ***-1.5 < SPEI < -2***	1985, 2007	1983, 1988, 2007, 2011
Extreme ***SPEI < -2***	2003	-

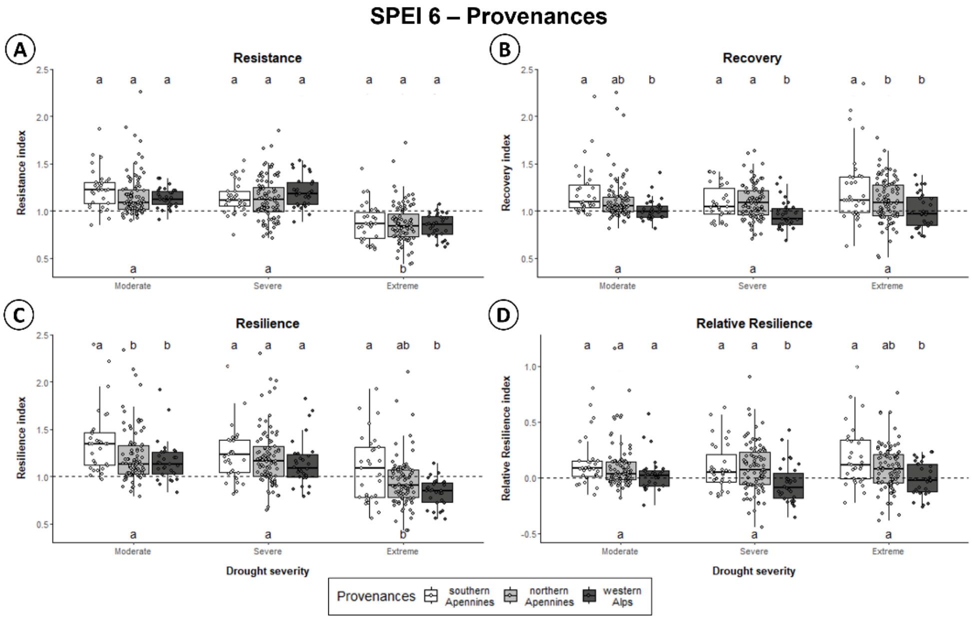


Figure S_9. *RRR indices calculated for drought years identified by SPEI 6, provenance comparison. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab). A) Resistance index, B) Recovery index, C) Resilience index, D) Relative Resilience index. For each chart: the upper line of letters refers to the comparison of (A) provenances and (B) forest regeneration mode within the same drought intensity level; the lower line of letters compares the reference mean index (all provenances together) between drought intensity levels.*

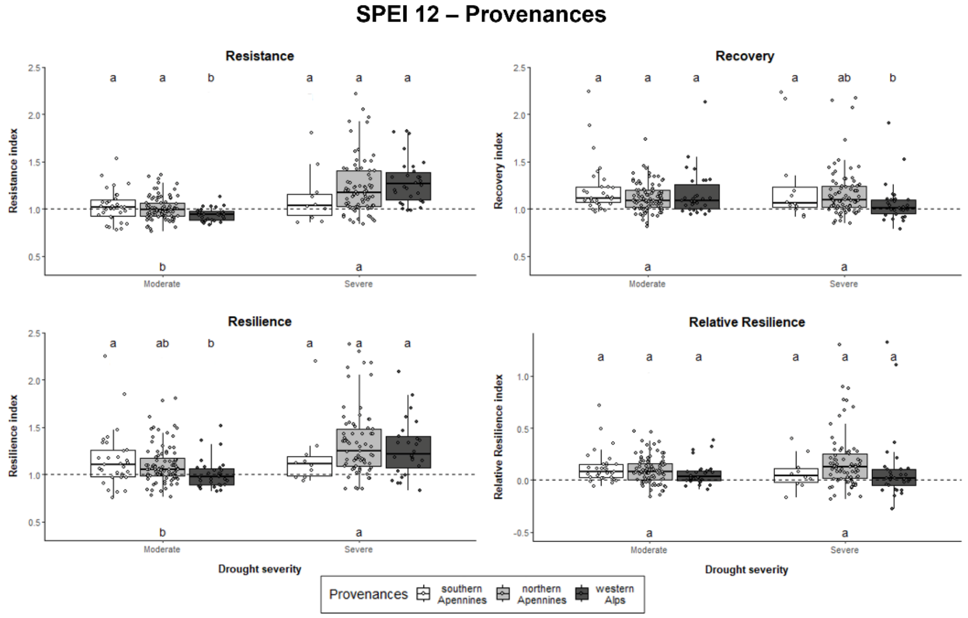


Figure S_10. *RRR indices calculated for drought years identified by SPEI 12, provenance comparison. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab). A) Resistance index, B) Recovery index, C) Resilience index, D) Relative Resilience index. For each chart: the upper line of letters refers to the comparison of (A) provenances and (B) forest regeneration mode within the same drought intensity level; the lower line of letters compares the reference mean index (all provenances together) between drought intensity levels.*

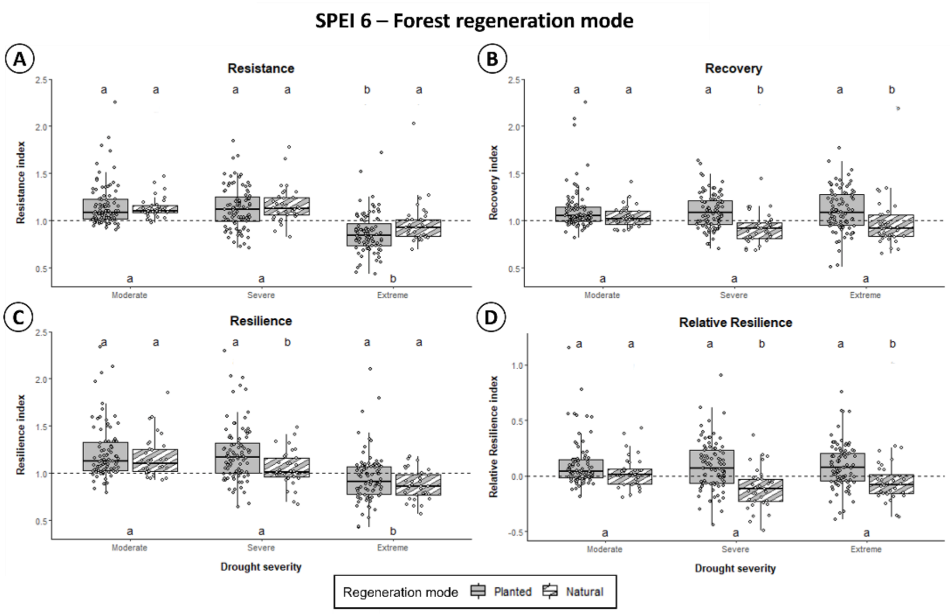


Figure S_11. *RRR indices calculated for drought years identified by SPEI 6, forest regeneration mode comparison. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab). A) Resistance index, B) Recovery index, C) Resilience index, D) Relative Resilience index. For each chart: the upper line of letters refers to the comparison of (A) provenances and (B) forest regeneration mode within the same drought intensity level; the lower line of letters compares the reference mean index (all regeneration mode together) between drought intensity levels.*

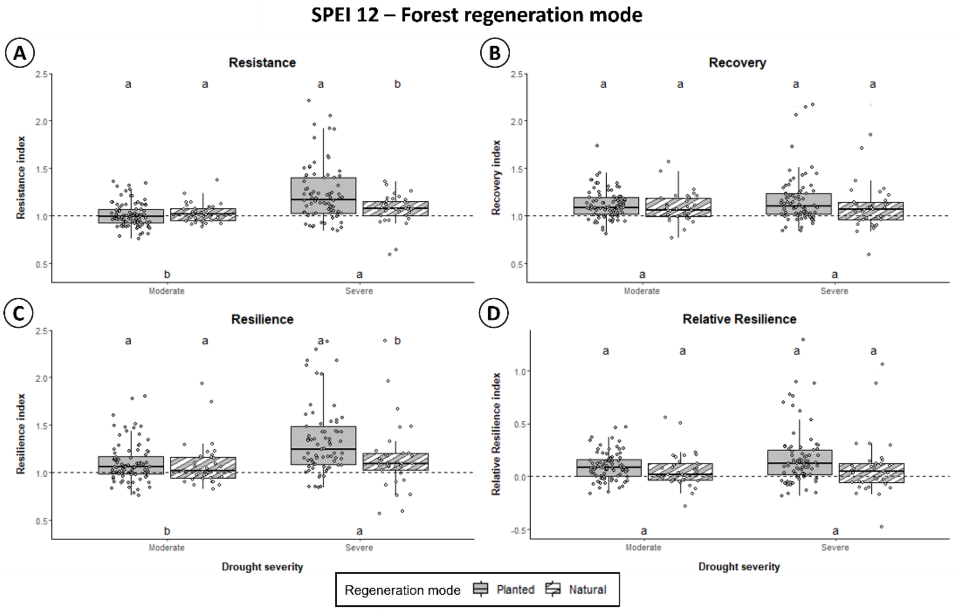


Figure S_12. *RRR indices calculated for drought years identified by SPEI 12, forest regeneration mode comparison. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab). A) Resistance index, B) Recovery index, C) Resilience index, D) Relative Resilience index. For each chart: the upper line of letters refers to the comparison of (A) provenances and (B) forest regeneration mode within the same drought intensity level; the lower line of letters compares the reference mean index (all regeneration mode together) between drought intensity levels.*

Table S_5. *RRR indices values for drought years identified by SPEI6 and SPEI12.*

	RRR Index →	**Resistance**						**Recovery**						**Resilience**						**Relative Resilience**					
	Drought severity →	Moderate		Severe		Extreme		Moderate		Severe		Extreme		Moderate		Severe		Extreme		Moderate		Severe		Extreme	
SPEI ↓	**Provenance ↓**	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*	*mean*	*sd*
SPEI 6	**Western Alps – planted**	1.13	0.10	1.20	0.17	0.84	0.12	1.01	0.11	0.96	0.15	1.00	0.19	1.16	0.22	1.15	0.25	0.83	0.15	0.03	0.16	-0.05	0.18	-0.01	0.15
	Northern Apennines - planted	1.16	0.23	1.13	0.22	0.86	0.21	1.12	0.23	1.10	0.19	1.11	0.23	1.22	0.29	1.22	0.32	0.95	0.31	0.10	0.21	0.09	0.22	0.09	0.20
	Northern Apennines - natural	1.13	0.11	1.16	0.19	0.97	0.23	1.04	0.11	0.92	0.16	0.98	0.28	1.17	0.21	1.05	0.19	0.87	0.16	0.03	0.14	-0.11	0.19	-0.07	0.16
	Southern Apennines – planted	1.23	0.21	1.14	0.16	0.87	0.20	1.20	0.27	1.08	0.18	1.25	0.38	1.37	0.34	1.23	0.28	1.06	0.37	0.14	0.22	0.09	0.22	0.19	0.27
SPEI 12	**Western Alps – planted**	0.94	0.07	1.29	0.24	-	-	1.16	0.24	1.06	0.21	-	-	1.01	0.16	1.28	0.30	-	-	0.06	0.11	0.10	0.33	-	-
	Northern Apennines - planted	1.01	0.13	1.23	0.29	-	-	1.12	0.15	1.17	0.26	-	-	1.10	0.20	1.39	0.44	-	-	0.09	0.13	0.18	0.27	-	-
	Northern Apennines - natural	1.03	0.10	1.07	0.16	-	-	1.09	0.16	1.09	0.24	-	-	1.09	0.23	1.15	0.35	-	-	0.06	0.17	0.08	0.28	-	-
	Southern Apennines – planted	1.03	0.17	1.13	0.30	-	-	1.21	0.27	1.36	0.58	-	-	1.15	0.30	1.20	0.37	-	-	0.12	0.16	0.07	0.16	-	-

Modelling the growth of three silver fir provenances in the Northern Apennines

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Abstract

This study models the dynamics of Italian silver fir (*Abies alba*) forests under varying climate change scenarios using the forest gap model FORMIND. Focusing on three distinct silver fir provenances (Western Alps, Northern Apennines, and Southern Apennines), the study simulates forest growth in the Tuscan-Emilian Apennine National Park under different Representative Concentration Pathways (RCP). The individual-based model FORMIND was parameterised and validated with field data for each of the provenances, demonstrating its ability to accurately reproduce key forest metrics and dynamics. Our results reveal significant differences in expected growth patterns, productivity, metabolism, and carbon storage capacity among the silver fir provenances in pure and mixed stands. In the simulations, the Northern Apennines provenance showed higher biomass production (biomass > 10 ± 1%) and carbon uptake (NPP > 8 ± 1%) at the end of the century compared to the Western Alps provenance in the pure provenance and no regeneration scenario. Conversely, the Southern Apennines provenance showed higher biomass (biomass > 5-10%) and net primary productivity (NPP > 15-18%) in mixed provenance and regeneration scenarios. These variations highlight the importance of considering genetic diversity in forest modelling, as it significantly influences forest growth and resilience to environmental changes. The study also demonstrates the resilience of silver fir to climatic stressors, emphasizing its potential as a robust species in multiple forest contexts. The integration of forest provenance data into the FORMIND model represents a significant advancement in forest modelling, enabling more accurate and reliable predictions under climate change scenarios. The study's findings advocate for a greater understanding and consideration of genetic diversity into forest management and conservation strategies, in support of assisted migration strategies aiming to enhance the resilience of forest ecosystems in a changing climate.

Keywords: Silver fir, genetic diversity, climate change, forest modelling, FORMIND

Introduction

The growing impact of climate change on European forest ecosystems is increasingly evident, mainly due to rising temperatures and altered precipitation patterns, with significant implications for ecosystem services (Anderegg et al., 2013; IPCC, 2022; Lindner et al., 2010). European forests are showing signs of vulnerability, evident in increased drought stress and susceptibility to pests and diseases, resulting in increased tree mortality rates (Charru et al., 2017; Gazol and Camarero, 2022). Furthermore, a reduction in productivity and carbon sink reduction is generally observed in Europe in the Mediterranean area, where the effects of climate change are particularly evident (Peñuelas et al., 2017; Vitasse et al., 2019a). This trend represents a serious problem for the range of ecosystem services provided by forests, such as timber production, carbon sequestration, biodiversity maintenance and water cycle regulation, which are essential for environmental stability and human well-being (Lindner et al., 2010). In this context, understanding the dynamics of forests under climate change pressure becomes crucial.

Forest modelling emerges as a functional tool for forecasting and understanding future forest dynamics. Forest models integrate climatic, ecological and biogeographic data, and make it possible to simulate how forests will respond to rising temperatures, changes in precipitation regimes and in the intensity of extreme events (Bohn et al., 2014; Fischer et al., 2016). The effectiveness of forest growth models in predicting and understanding the dynamics of forest ecosystems under the influence of climate change is highly dependent on the accuracy of the inputs used. Climate data must accurately reflect regional and local variations, similarly local field data are essential to calibrate and validate models to accurately reflect real-world conditions. Given the complex topography and the sensitivity of mountain forests to climatic variations, precise and localized climate data become crucial for effective management and conservation strategies (Charru et al., 2017; Gentilucci and D’aprile, 2021; Pepin et al., 2015). In this context, climate downscaling is a valuable tool for refining climate data to a more relevant scale (Terzago et al., 2018).

Climate change has profound impacts on coniferous forests in Italy, influencing the rise in the altitudinal tree line, the species composition, and the availability of nutrients. Due to global warming, conifers are competing with species that are more resistant to warmer climates, progressively moving to higher altitudes (Bottero et al., 2021; Vitali et al., 2017). Among the various conifer species, silver fir (*Abies alba*) emerges as a valuable resource in a climate change context. This species, widespread in mountainous areas of Italy, shows greater tolerance to heat stress and changes in precipitation regimes than other conifers, such as Norway spruce (Vitasse et al., 2019a). In addition, the Silver Fir can play a significant role in reforestation and sustainable forest management projects due to its high carbon storage and climate resilience. The genetic diversity of the silver fir (Abies alba) plays a crucial role in its ability to adapt to the effects of climate change. The high genetic variability of this species allows it to adapt to a wide range of environmental conditions, ensuring the resilience of silver fir forests to climatic stresses such as extreme temperatures and variations in precipitation regimes (Piotti et al., 2017; Tinner et al., 2013). Southern genetics, in particular, have shown a remarkable ability to adapt to warmer and drier conditions in provenance trials in Europe (Hansen and Larsen, 2004; Kerr et al., 2015; Mihai et al., 2021), essential skill in a context of global warming (Vitasse et al., 2019b). To optimise the adaptive capacity of forests in a rapidly changing climate, 'assisted migration' is a particularly useful forest management strategy. This consists of translocating tree populations to areas where the expected future climatic conditions are more suitable for their survival and growth, aiming to increase the resilience and adaptive capacity of forests (Aitken and Bemmels, 2016; Alfaro et al., 2014). This approach proves to be a proactive solution for counteracting the effects of global warming on essential tree species, as long as the environmental and climatic response of the translocated species or provenance is pre-tested, thus limiting possible environmental threats resulting from the spread of poorly adapted genetics or associated diseases (Alfaro et al., 2014).

However, we still know little about the climatic adaptability potential of different forest provenances. Despite the critical importance of this evidence, our knowledge remains limited, with few long-term observations or dedicated experiments. In Italy, in fact, provenance-specific trials are almost non-existent, apart from a few isolated cases (Bantis et al., 2021; Ducci and Tocci, 1987). This lack of information poses significant challenges in the field of sustainable forest management and climate change adaptation. Predictive forest growth models could support the design of future-oriented guidelines but, despite the increasing relevance of genetic diversity in climate change adaptation strategies, it is surprising to observe that forest growth models poorly incorporate the genetic diversity of forest provenances (Bohn, 2016; Bohn et al., 2014; Collalti et al., 2014; Seidl et al., 2012). Modelling the growth of forest provenances could facilitate the implementation of innovative management strategies such as assisted migration, serving as an additional tool to assess the performance of specific provenances in specific locations with a future vision (Benito-Garzón and Fernández-Manjarrés, 2015). We believe that incorporating genetic diversity into growth models could significantly improve our ability to predict forest dynamics under climate change, adding intraspecific variability to the environmental response.

The objective of this study is to simulate the growth of different Italian silver fir provenances under different climate change scenarios in the territories of the Tuscan-Emilian Apennine National Park. Specifically, we simulate the growth of three Italian silver fir provenances (Western Alps, Northern Apennines and Southern Apennines) under three climate change scenarios (RCP 2.6, 4.5 and 8.5) in comparison with historical climate. Both pure (PP) and mixed provenance forests (MP) were simulated. The growth simulations were carried out using the FORMIND forest growth model and will provide guidance to local forest management on the growth performance of silver fir and the role of its genetic diversity in adapting to a changing climate.

Materials and Methods

In this study, the growth of three Italian silver fir provenances was simulated using the FORMIND model, an individual, process-based forest growth model that allows the simulation of forest dynamics given a series of input data. The three provenances were parameterised within the model thanks to the collection of tree morphological data in the field, making it possible to develop valid simulations and forecasts for the national park and the surrounding territories.

FORMIND

FORMIND is an individual based forest gap model, useful for studying and predicting forest dynamics in response to various environmental factors (Bohn et al., 2014; van Oijen et al., 2013). Its application is particularly relevant in the context of climate change, where the ability to predict how forests will respond to rapidly changing environmental conditions is crucial (Blanco et al., 2015; Mahnken et al., 2022; Morin and Thuiller, 2009). FORMIND has been used in various studies to explore the susceptibility of forests to climate change, highlighting how different species and forest types may react differently to such stresses (Bohn et al., 2018; Fischer et al., 2016). The FORMIND model divides 1 ha of forest into 25 patches (20x20 m). Within each patch trees compete for light, other resources, and space. To model forest growth and its internal dynamics, FORMIND simulates different processes, allowing a detailed and flexible representation of ecological processes in forests (Fig. 1). The main processes regulate tree establishment (seed distribution and light conditions), growth (determined by GPP, respiration, and specific physiological parameters), mortality (described by specific mortality rates and to crowding in dense forest stands), and competition (one of the main factors in tree growth, with calculation of light conditions in different forest height layers). The model calculates GPP, growth, respiration, and NPP for each tree, allowing the carbon balance of a forest stand to be estimated considering the fluxes between soil, forest, and atmosphere. Plant mortality follows two parallel processes: background mortality and crowding mortality. Background mortality has been parametrized based on current literature while mortality due to crowding is calculated by the model based on crown area competition among trees, as a result of spatial competition. The horizontal and vertical distribution of plants in space is thus the result of several interactions between individuals and their growth parameters, resulting in a simulation with year-scale output of various ecosystem processes. Modelling, such as that offered by FORMIND, is fundamental to informing sustainable forest management. Modelling provides forest managers and policy makers with valuable information on how management practices can be adapted to mitigate climate change impacts and promote forest resilience (Bohn, 2016).

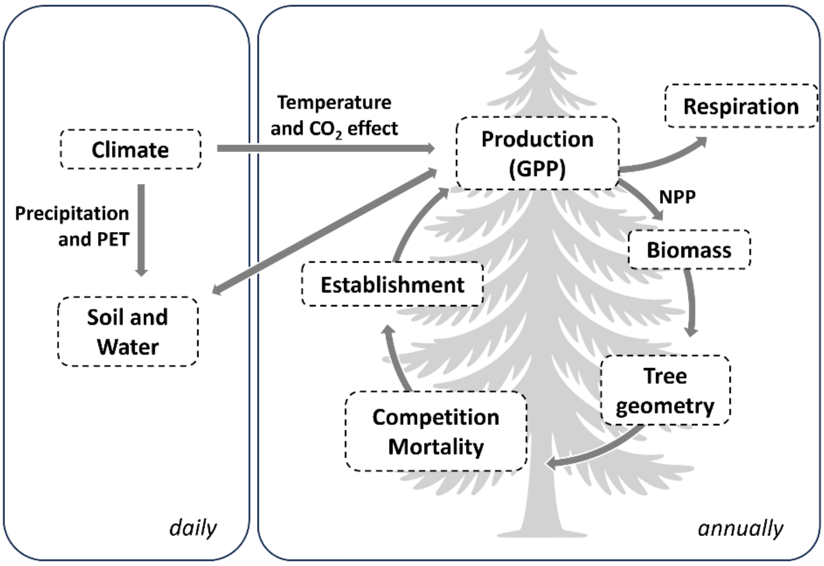

Figure 1. General working scheme of FORMIND and main connections between modules. *All input climatic and edaphic variables are the same for the entire simulated area. Precipitation and PET are used to limit GPP through the soil while temperature and CO2 are used to regulate photosynthesis. GPP is divided into NPP and respiration. Biomass determines allometry, which influences individual competition within the study area. Simplified scheme from* (Bohn et al., 2014).

Input data

Study area

Data for the model parametrization have been collected within the Tuscan-Emilian Apennine National Park area, in the northern section of the Apennines (Fig. 2). In the northern Apennines the distribution of silver fir exhibits notable fragmentation, with limited and isolated natural populations. In the Tuscan-Emilian Apennine National Park silver fir is distributed in natural and planted forest stands. Planted forests were established during the 20th century after the Second World War, although the origin of the planted material has so far been undocumented. Planted stands are located at elevations ranging from 1000 to 1650 meters above sea level (a.s.l.), on a diatomite marls substrate. The study area experiences a Mediterranean Apennine climate, characterized by dry summers and rainy autumns, with an average annual rainfall of 2100 mm, an average annual temperature of 7.5°C, and an average daily temperature range of 6°C.

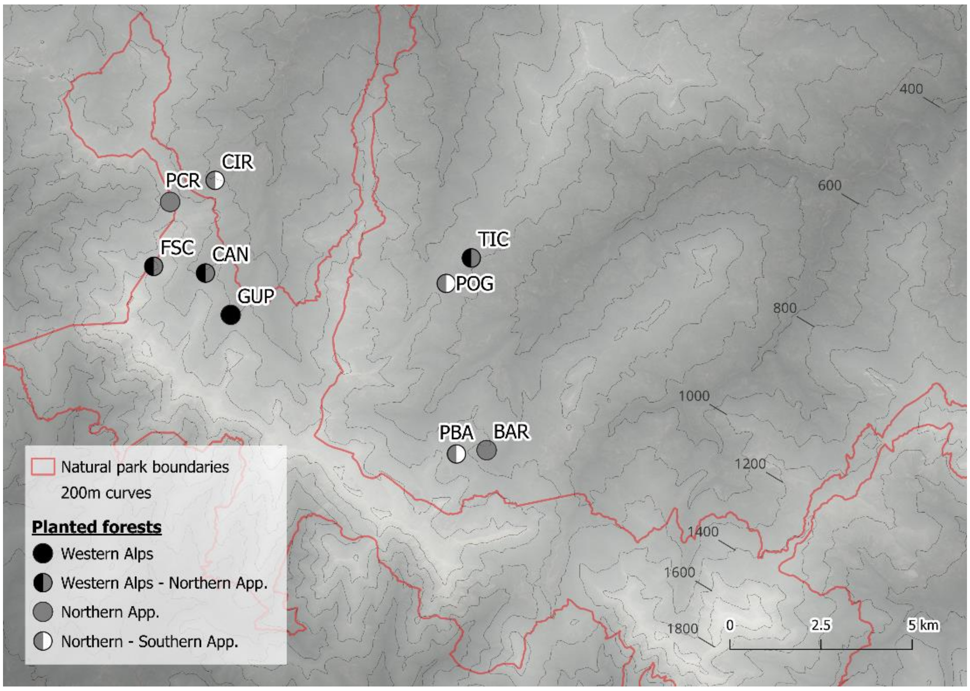

Figure 2. *A) Map of the 9 stands sampled in the National Park of the Tuscan-Emilian Apennine for FORMIND model parametrization. Circles represent silver fir planted stands. Colours represent the provenance of each stand, as reconstructed by means of molecular markers (black: 'Western Alps'; dark grey: 'Northern Apennine' (local); white: 'Southern Apennine').*

Field data

In a previous work (Oggioni et al., submitted), we analysed the genetic makeup of the silver fir trees present in the planted forest stands of the Tuscan-Emilian Apennines National Park, identifying three main Italian genetic groups of this species within the planted stands, distinctive of specific Italian geographic areas: Western Alps (W_Al), Northern Apennines (N_Ap - local) and Southern Apennines (S_Ap) (Oggioni et al., submitted; Piotti and Avanzi, 2022). Genetic analyses at the individual level allowed the assignment of the individuals of silver fir found in all sampled plantations to the three provenances mentioned above, thus allowing the univocal assignment of individuals to their area of origin (Oggioni et al., submitted). The three provenances were used as the main factor of comparison in this study, simulating their growth over time in different climatic scenarios and forest contexts.

To parameterise the three provenances within the FORMIND model, during July-October 2020 dendrometric, edaphic, and topographic data were collected in the field from 135 trees in 9 planted stands (Fig. 2). Each tree was assigned to a specific provenance based on the genetic analyses of Oggioni et al. (submitted). Only individuals which had been genetically characterized, and so for which provenance was known, were sampled for model parametrization. Approximately ten trees were sampled from each of the provenances included in each planted stand, varying the number of sampled trees per forest stand as not all stands contained all provenances together (Tab S_1). Trees were identified in the forest through the previously affixed tags. The following morphological data were collected for each tree: diameter, height, crown diameter, crown height. In (Oggioni et al., submitted) individual tree competition was assessed through sampling areas of 10m radius around each subject tree, performing full diameters assessment. These data were used to assess the forest density in each sampling plot by calculating tree density per hectare based on each of the sample areas used for the competition and then deriving an average value per stand. Soil depth was sampled at 3 random points around each sampled tree within 2 meters from the tree stem, using a hammer and a sharp stick/pike till 90cm whenever possible. The measurements were sometimes repeated to avoid confusing bedrock with buried or near-surface rocks. Soil samples were collected at five points per stand to measure some edaphic parameters in the laboratory, collected at one meter from the base of some of the measured trees. Soil texture was obtained by means of the "Pipette Method" (Paturno et al., 1997) and was used to derive edaphic parameters needed for FORMIND parametrization following (Rawls et al., 1993) mean reference values: Permanent wilting point, field capacity, soil porosity, fully saturated conductivity, pore size distribution index, residual soil water content.

Climate data and downscaling

To create reliable projections of forest growth that cover a range of realized climates, climate data from multiple global climate models were used in this study. We relied on the ESGF CORDEX database for the selection of the climate models and data to be used (ESGF, 2023). The climate models were chosen based on the following characteristics. (i) The climate models had to include historical data and climate change simulations under three RCP scenarios (2.6, 4.5 and 8.5). (ii) The global climate models had to be regionalised according to the same regional model to produce consistent results. In this study, the RCA4 model was used as the regional reference model (Rossby Centre Regional Atmospheric Climate Model, Strandberg et al., 2014). (iii) Climate models were finally chosen by selecting the EUR-11 domain, given its geographical location, and the r1i1p1 ensemble. Through these criteria, 3 valid global climate models were identified for our study: HadGEM2 (Hadley Centre Global Environment Model version 2, Collins et al., 2011), NorESM1 (The Norwegian Earth System Model, Bentsen et al., 2013; Iversen et al., 2013), MPI-ESM1 (Max Planck Institute Earth System Model, Müller et al., 2018). All three proposed models are based on the model experiments CMIP5, with a horizontal resolution of 0.1 deg. From these climate datasets we extracted daily average temperature and precipitation data to be used as input for forest growth simulations. Climate data, in NetCDF format, were preliminarily processed through the CDO software (Schulzweida, 2023) to perform merge (between NetCDFs of the same climate model and scenario), rotation (from EUR-11 rotated latitude-longitude grid to regular co-ordinates) and cropping operations (on smaller surfaces to limit climate file weight). Subsequent statistical and calculation operations were all performed using R software (version 4.3.1) (R Core Team, 2023).

Climate data used in this study have been downscaled to finer resolution for better represent at local level the climate condition in which silver fir is currently distributed. The CSTools R package (Perez-Zanon et al., 2023) has been used for downscale temperature and precipitation data (Pérez-Zanón et al., 2022; Terzago et al., 2018). To downscale temperatures CSTools apply a fixed lapse rate to temperature data following elevation data provided by a Digital Elevation Model (DEM). For temperature downscaling the SRTM30+ Global 1-km DEM has been used (Sandwell et al., 2021), applying a constant lapse rate of -6.5°C / 1 Km (International Civil Aviation Organization, 1993). For temperature downscaling the CST_RFTemp function has been used. To downscale precipitation data, we used the CST_RainFARM function, which downscale precipitation following a stochastic downscaling implemented with orographic adjustment. precipitation downscaling was performed according to a refinement factor of 10 (the output resolution is increased from 0.1 deg to 0.01 deg). As orographic adjustment for precipitation WorldClim 2.1 at 30sec resolution has been used (Fick and Hijmans, 2017), using available precipitation climatology as correction weights for downscaling outputs following the methodology in Terzago et al., 2018). Weights from WorldClim 2.1 have been derived through the CST_RFWeights function for each month, which were used to downscale the data for the respective month. For precipitation downscaling the CST_RainFARM function requires a spectral slope value for each monthly dataset, which describes how precipitation changes with spatial scale (Perez-Zanon et al., 2023). CST_RFSlope function has been used for spectral slope calculation.

The downscaling methodology described here was applied to all global climate models (HadGEM2, NorESM1, MPI-ESM1) and all climate scenarios (historic, RCP 2.6, 4.5, 8.5). The historic data cover the period 1970-2005 while the RCP scenarios produce differentiated outputs over the period 2006-2100. To design a future climate projection that emulates historical temperature and precipitation parameters, we extended existing datasets over future time horizons. Specifically, temperature and precipitation data over the period 1970-2005 were used as the basis for simulating the climate up to 2100. This was achieved through a randomisation process, where annual datasets were randomly selected and replicated over the period 2006-2100. It was crucial to maintain the integrity of the annual datasets to ensure temporal consistency. Through this approach, we generated a 'historical future climatology', using a random distribution of historical years to model potential future climate. The historical future climatology was used to validate model output on existing forest plots and as a comparison value in the analysis of differences in silver fir provenances under different climatic scenarios. In addition to mean temperature and precipitation, the FORMIND model requires irradiance (µmol s-1 m-2), potential evapotranspiration (PET - mm), day length (daylight hours) and the concentration of CO_2 in the air (CO_2 - ppm) as additional climate inputs. Daily irradiance values (1951-2100) for the Italian territory in all climate scenarios (historic, RCP 2.6, 4.5, 8.5) based on the CMIP5 model experiments were obtained from the Copernicus database (C3S, 2023). Daylength values were derived using the daylength() function of the R package geosphere (Hijmans et al., 2022). The PET values were obtained on a monthly scale using the thornthwaite() function of the SPEI package of R (Beguería and Vicente-Serrano, 2023), then scaled to a daily level dividing by the number of days of each month. Annual CO2 values were obtained for the different climate scenarios through the dataset provided by (Meinshausen et al., 2011) available online. Irradiance, PET, day length and CO2 values remained unchanged when precipitation and temperature values were modified between simulations of different global climate models.

Parametrization

To simulate the growth of the three silver fir provenances in similar ecosystems to those of the Tuscan-Emilian Apennines, field data were used to parameterise the three provenances as part of the model inputs. The three provenances were differentiated according to the following geometric and morphological characteristics: ratio Tree Height : Stem Diameter, Crown Diameter : Stem Diameter, Crown Length : Tree Height, Aboveground biomass : Stem Diameter and Diameter increment : Diameter. Table S_1 shows the allometric equations used and their coefficients used as model input. For physiological parameters that cannot be found in the field, parameters found in the literature or default model parameters used for conifers were used. Table S_2 shows the generic parameters used for the three provenances. The background mortality is modelled on the basis of the diameter of the plants (D) and their diametric increment (ΔD), following the indications on the mortality rates of silver fir found by (Vieilledent et al., 2010), obtained in mountainous contexts similar to our case study. The specific equations and coefficients for the parameterisation of D- and ΔD-dependent background mortality are given in Table S_3.

Finally, FORMIND modifies photosynthesis and thus productivity through an effect dictated by the minimum and maximum temperature of the warmest month that the species is used to. In our case, this made it possible to parameterise the response of the different forest provenances of silver fir as a function of the minimum and maximum temperatures of the provenance's places of origin, hypothesising a diversified adaptation according to the geographical origin of the forest material. In order to define these values, historical temperature data of the three global climate models were overlaid on the distribution range of the species in the native areas of the three forest provenances used in this study. The distribution of silver fir has been derived from European forest species distribution maps database (Caudullo et al., 2023), while the locations used as reference for the genetic analysis (Oggioni et al., submitted; Piotti et al., 2017) are considered as the native areas of the three forest provenances. Average value of maximum and minimum temperature data of the warmest month related to the area of origin of the forest provenances of silver fir considered are summarised in Table S_4, together with the coefficients identified by FORMIND used to define photosynthesis limitations.

Model simulations

Validation

Model simulation outputs may over- or underestimate realistic values, making it important to compare the growth dynamics observed in forest provenances with the values expected by the model, in order to obtain accurate and informative estimates of forest growth metrics (Herbert et al., 2023; Jagiełło et al., 2022). Model validation is also relevant in environmental management to establish confidence in the accuracy and reliability of ecological models. These models are often instrumental in shaping policy decisions and directing management practices (Rykiel, 1996) and the validation of growth and yield models is crucial for ensuring the fidelity of forest management to the actual dynamics of forest ecosystems, thereby enabling well-informed decisions in forest resource management (Herbert et al., 2023). To validate the parameterisation of the FORMIND model, the growth of the nine forest plots in the national park, which were originally used to sample the data used to parameterise the provenances in use, was simulated, attempting to replicate their productivity (Volume and Biomass). For this purpose, nine simulations were carried out with the aim of replicating the conditions of the original plots, retrospectively. The simulations were initialised from bare ground, simulating the planting of a new forest with a variable plant density based on the data observed in the field. Several runs were attempted with variable initial tree density (from 1100 to 1500 plants / ha), choosing for the final run the value that resulted in the closest approximation of current number of trees per hectare at the end of the historical simulation. The simulations used the 'historical future climatology' and an end age of the simulation equal to the mean age of the reference forest plot. No forest regeneration was included in the validation simulations (almost absent in the original plots under forest management) while forest mortality was kept active in order to reliably replicate the dynamics of forest growth and development. Each simulation included the mix of provenances found in the actual forest plots (e.g. the BAR plot was simulated as pure N_Ap provenance stand, while the CAN plot was simulated as mixed between W_Al and N_Ap provenances). When multiple provenances shared a plot, their distribution in terms of plant numbers was set as equal. This simplification of proportionality was adopted because originally only 24 trees were used to define the origin of the provenances by genetic analysis (Oggioni et al., submitted), resulting in too few trees to be representative of the numerical distribution of provenances in each forest plot. Model results were validated by comparing predicted against observed stem volume and biomass per hectare (one-way ANOVA, using the R stats package).

Pure and mixed provenances simulation

To simulate growth and dynamics of different provenances, we initialised FORMIND with two different types of virtual stands: managed single provenance forests (without regeneration) and mixed provenance forests with natural regeneration. In both cases, simulations were carried out in ideal contexts of pure silver fir, avoiding the simulation of competition with other forest species. All simulations were repeated for each of the three global climate models (HadGEM2, NorESM1, MPI-ESM1) and for each considered climate scenario (historic, RCP 2.6, 4.5, 8.5). The simulations were initialised in 2006 (start of climate data availability for RCP scenarios) from bare ground, and concluded in 2100 (limit of climate data availability)

The simulations of single provenance forests, henceforth referred to as PP (pure provenance), were set up similarly to the validation simulations: no regeneration and active mortality. These predictions consider a productive context under forest management, with no regeneration before the end of the rotation and consequently limited competition dynamics compared to forests with high forest regeneration. All simulations were carried out by setting an initial planting density of 1500 plants/ha, identified as the maximum initial density set for the validation simulations and considered a plausible density value for a young silver fir forest (Vacchiano et al., 2005), and therefore realistic for our study context.

For the simulations in forests with mixed provenances, henceforth referred to as MP (mixed provenances), three arbitrary densities of established seedlings (SD, seedling density) per year per hectare were used in the simulation: 90, 150 and 210 plants per hectare. These numbers define the number of plants actually established each year, initialised with a diameter of 5 cm (established regeneration diameter). The distribution of the regeneration rate between the three provenances is uniform in all simulations, i.e. the same number of plants per provenance becomes established each year. The choice of simulating multiple initial density conditions will allow a comparison of different competition intensities, also serving as a sensitivity analysis of the FORMIND model in provenance mix contexts.

In order to assess the differences in growth and productivity of the three fir provenances under investigation, several response variables were selected: Basal area (BA - m^2 ha^{-1}) was used as an index of stand density and maturity, biomass per hectare (B - Mg_{ODM} ha^{-1}) was used as an index of productivity, net primary production (NPP - Mg_C ha^{-1}) as a proxy for annual net carbon storage and tree respiration (R - Mg_C ha^{-1}) as an index of plant metabolism.

The results of the PP and MP simulations were statistically compared by means of ANCOVA tests, using the data from each of the 25 FORMIND simulation patches, (upscaled at hectare level), as replicates of each simulation. The tree provenance was used as a comparison factor and the three global climate models were included to express the range of possible outputs of the model. In the PP runs the global climate model was used as a covariate in the ANCOVA tests, while in the MP runs both global climate model and established regeneration density were used as covariates. The interaction between provenance and established regeneration density was also analysed in the MP runs. Differences between the global climate models were not discussed for any of the simulations, using the differences in simulation results of different climate models as an expected range of simulation outputs. The ANCOVA analyses were performed in two-time steps, analysing model outputs at the year 2060 and 2100.

Results

Model validation

The results of the model validation showed results congruent with the data observed in the field. The results of the FORMIND simulations of Volume and Biomass per hectare of the BAR, CAN, CIR, GUP, PBA, POG and TIC plots revealed higher values than those observed in the field (> 14-40%), while the PCR and FSC plots showed lower simulated Volumes and Biomass per hectare than those observed (< 12-36%) (Fig. 3, S_2). The observed volume per hectare data showed no significant differences with the simulated forest values (F-statistic = 1.175, p-value = 0.294) (Fig. S_3a), similar to the Biomass per hectare data (F-statistic = 0.751, p-value = 0.399) (Fig. 3, S_3b). As expected, the data on the number of stems per hectare at the end of the simulation did not differ statistically between the observed and simulated data (F-statistic = 0.491, p-value = 0.494) (Fig. S_3c).

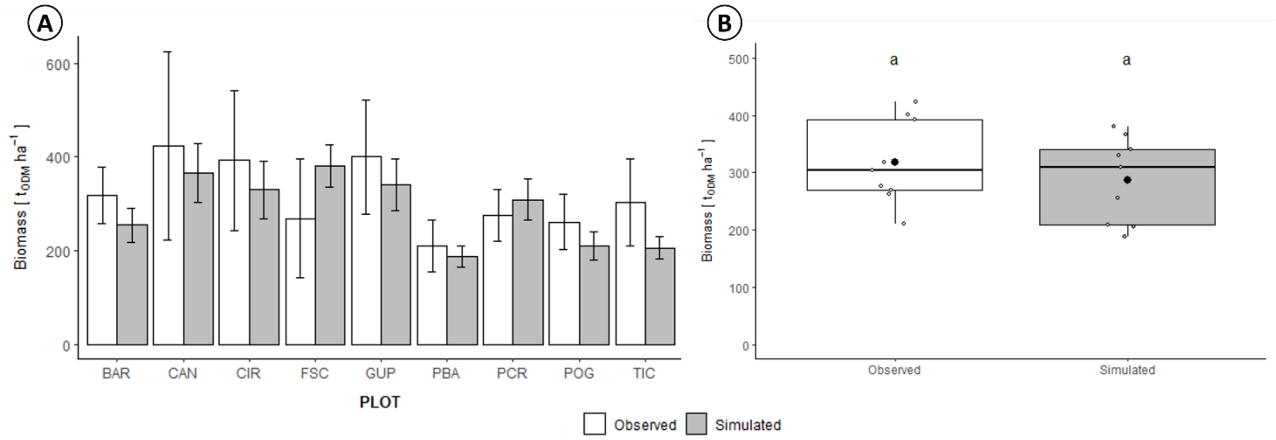

Figure 3. Validation of biomass results at plot level and for whole the study area. *Observed (white) vs simulated (grey) biomass values per hectare for each plot used for model parametrization (a) and mean biomass values per hectare (b).*

Pure Provenance (PP) simulations

The PP simulations generally showed better growth and productivity performance for the local provenance (N_Ap), especially compared to the W_Al provenance. The Basal Area (BA) values showed differences depending on the tree provenance (Tab. S_6), with higher BA values for the S_Ap provenance than for the local provenance in 2060 ($p < 0.001$), which again showed higher values than the W_Al provenance ($p < 0.001$). In 2100, the differences between the S_Ap and N_Ap provenance disappear ($0.9 \geq p \geq 0.6$), while both show higher BA values than the W_Al provenance ($p \leq 0.001$). These trends are maintained in all 4 climate scenarios, and the climate change scenarios do not particularly affect the BA values, revealing higher BA values in RCP scenarios compared to the historical scenario but not particularly different between each RCP (Fig. S_4a, Tab S_7). Biomass values (B) also show differences according to forest provenance (Tab. S_6), showing higher forest yield for the local provenance compared to the S_Ap ($p \leq 0.04$) and W_Al ($p \leq 0.002$) provenances in all climate scenarios and time steps (2060 and 2100). As for BA, Biomass forecasts are also consistent between the climate scenarios, with forecasts under RCP scenarios showing higher BA than the historical scenario and rather consistent between them (Fig. S_4b, Tab S_7). The NPP values also show differences between the provenances under investigation in some of the analysis levels (Table S_6). In 2060 we found higher NPP values for the local provenance than for the S_Ap provenance in the historic scenario

(2.95 > 2.77 Mg C ha^{-1} yr^{-1}, p = 0.011), and higher than the W_Al provenance in the RCP 8.5 scenario (3.38 > 3.18 Mg C ha^{-1} yr^{-1}, p = 0.013). In the 2100 the Biomass of the N_Ap provenance is higher than the S_Ap (0.02 ≥ p ≥ 0.002) and W_Al (0.003 ≥ p ≥ 0.004) provenances in the historic and 2.6 scenario, while no differences have been found in the RCP 4.5 and 8.5 scenarios. NPP increases with more severe climate scenario, especially in 2100, resulting in increasing values towards scenario 8.5 compared to the historic scenario (Fig. 4, S_4c). Finally, the respiration (R) results show different values between the provenances too (Tab S_6), favouring the N_Ap provenance over the S_Ap (p ≤ 0.02) and W_Al (p ≤ 0.01) provenances. Differences between the local and W_Al provenance are absent in all 2060 data, while no differences between the local and S_Ap provenance has been found in 2100 in the RCP 4.5 and 8.5 scenarios (Fig. S_4d).

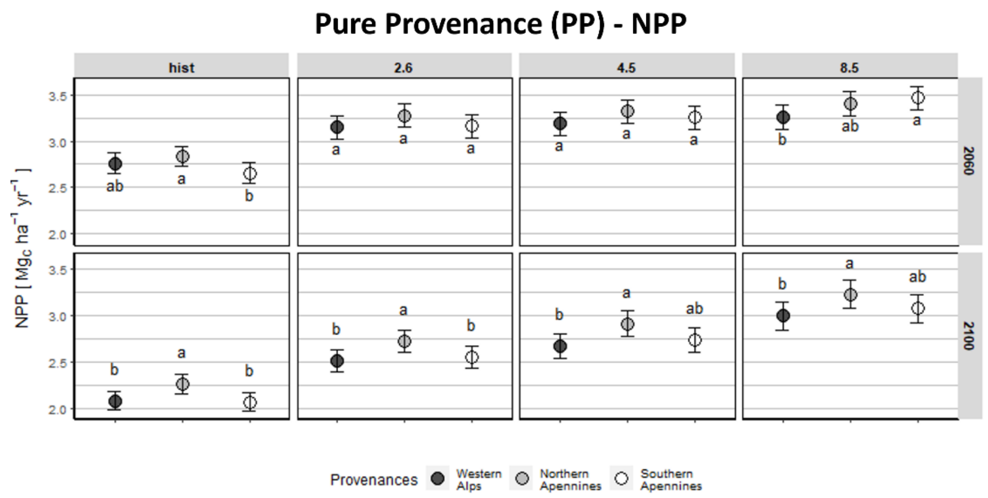

Figure 4. Pure Provenance (PP) simulations NPP results. *Different letters above the boxes indicate significant differences between provenances (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

Mixed Provenances (MP) simulations

The results of the MP simulations show generally better growth performance and productivity for the S_Ap provenance, especially compared to the W_Al provenance. The BA values differ for the three provenances under examination (Tab. S_7), revealing higher values for the S_Ap provenance than for the other two provenances (p < 0.001), in all climatic scenarios and time steps. Similarly, the N_Ap (local) provenance shows higher BA values than the W_Al provenance in all BA results of the MP simulations (p < 0.001) (Fig. S_4a). The model results indicate a significant interaction between BA and SD in 2060 and 2100 for RCP 2.6 (p = 0.01 and p = 0.001, respectively) and 8.5 (p = 0.01 and p < 0.001, respectively), and in 2100 for the historic scenario (p = 0.008). Analysis of the unbundled results of the three seedling densities reveals that for the RCP 2.6 scenario the previously observed trend repeats in all SDs and years of interest, with the exception of SD 210 in 2100 where the difference in BA between N_Ap and W_Al disappears. The same happens for the historical scenario at 2100, where no differences have been found in BA between N_Ap and W_Al for SD=210. For RCP 8.5, on the other hand, the observed trend (i.e. BA S_Ap > N_Ap > W_A) remains unchanged for all levels of SD (Fig. S_5a). Biomass (B) results generally show higher values for the N_Ap (p < 0.004) and S_Ap (p < 0.001) than for the W_Al provenance at 2060, while at 2100 the differences disappear in the RCP 2.6 and 4.5 scenarios (Fig. S_5b). Again, the results indicate a significant interaction between provenance and SD in 2060 and 2100 for RCP 2.6 (p = 0.012 and p = 0.001, respectively) and 8.5 (p < 0.001), and in 2100 for the historic scenario (p

= 0.001) (Tab. S_7). In 2060, the general trend is changed only in scenario 2.6 with SD=150, showing higher B values for the Northern Apennines than for the S_Ap (70.5 > 64.9 Mg ODM ha^{-1}, $p = 0.018$), which in turn results in higher B than the W_Al (64.9 > 49.2 Mg ODM ha^{-1}, $p < 0.001$). In 2100, at the end of the simulation, the trend varies considerably according to SD: with SD=90 significant differences between the provenances appear, with S_Ap biomass greater than the other two provenances in the historic, RCP 2.6 and 8.5 scenarios ($p < 0.03$), while for SD=150 and 210 no differences in biomass values were noted between the provenances in any of the climate scenarios. At SD=90, biomass also increases with increasing climate scenario, while this trend disappears at higher seed densities (Fig. S_6b). The results for the NPP values show differences according to provenance (Tab. S_7), following the trend S_Ap > N_Ap > W_Al in all scenarios and time steps except for scenario 8.5 in 2100, where the NPP difference of Southern Apennines and N_Ap disappears (Fig. 5, S_5c). In 2060, the NPP increases with the climate scenario, while by 2100 the differences in NPP between climate scenarios are less pronounced. In the NPP ancova results the interaction between provenance and SD is significant for the historic ($p = 0.004$) and RCP 2.6 ($p = 0.018$) scenarios in 2060, while in both 2060 and 2100 for the RCP 8.5 scenario ($p = 0.042$ and $p < 0.001$, respectively) (Tab. S_7). Analysing the decoupled NPP values for each SD we see that the difference in NPP between S_Ap and N_Ap disappears with SD=90 in the historic scenario in 2060, with SD=150 in the 2.6 scenario, and in several cases of the 8.5 scenario (Fig. S_6c). Finally, the respiration (R) results follow the same trend as the NPP results, with a clear increase in R as the climate scenario increases in both 2060 and 2100 (Fig. S_5d). The interactions between provenance and SD are significant for all scenarios in 2060 ($p < 0.034$) and for RCP 2.6 and 4.5 in 2100 ($p = 0.044$ and $p = 0.027$, respectively) (Tab. S_7). which can be explained by the absence of differences between the R values of S_Ap and N_Ap in several cases (Fig. S_6d).

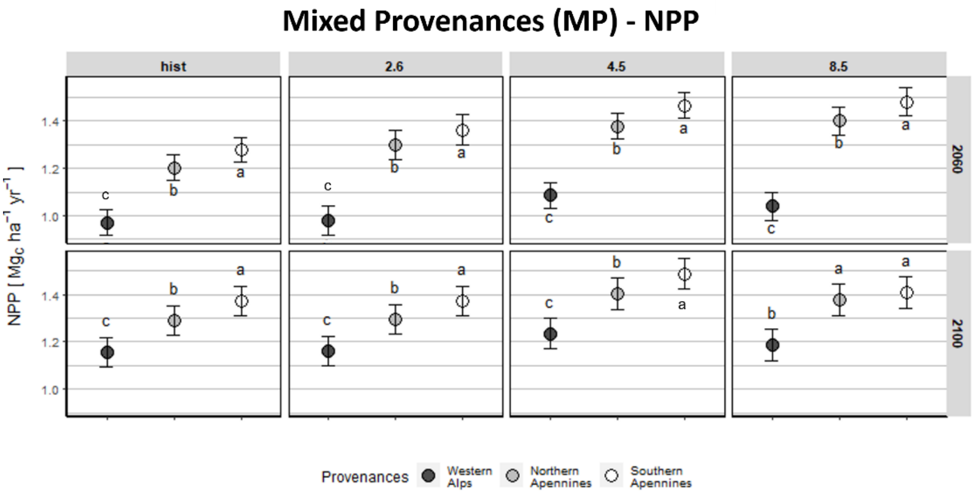

Figure 5. Mixed Provenances (MP) simulations NPP results. *Different letters above the boxes indicate significant differences between provenances (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

Discussion

Model validation

The successful validation of the FORMIND model is evident by its performance across the different forest plots. The congruence between the model's output and field data is indicative of the model's robustness and suggests that the model is capturing the essential dynamics of forest ecosystems, replicating key forest metrics with a high degree of accuracy, which is crucial for reliable forest ecosystem modelling. The fact that the model performs well across different mixed silver fir provenance plots is also noteworthy, underlying the model's robustness in capturing forest dynamics across heterogeneous environments, important for subsequent simulations. With the confirmation of its accuracy, FORMIND can be applied with greater confidence in subsequent PP and MP forecasts, simulating different forest contexts under various scenarios, including climate change impacts and forest management strategies. Finally, FORMIND's ability to replicate local conditions is indicative of a correct and functional climatic downscaling procedure, which is important for replicating climate patterns in areas with high topographical variability. Mountainous topography plays a pivotal role in shaping local climate conditions, introducing a high degree of spatial variability due to its complex terrain (Beniston, 2003). This topographic effect results in unique microclimates within mountain regions, needing localized attention to understand the relations between forest growth and climate. Downscaling enables the acquisition of high-resolution climate projections that are crucial for addressing the specific needs (Terzago et al., 2018). Thus, downscaling serves as a critical methodology for providing detailed, area-specific climate predictions, which are essential for the sustainable management and preservation of mountain ecosystems under changing climatic conditions.

Performance of silver fir provenances

The results of our study show significant differences in the growth patterns, productivity, metabolism and carbon storage capacity of the silver fir provenances considered in this study, confirming how silver fir forest material of different origins can be associated with a diverse environmental response (Hansen and Larsen, 2004; Kerr et al., 2015; Konôpková et al., 2020; Oggioni et al., submitted) and underlining the role of forest genetic diversity in climate change adaptation (Ducci et al., 2021; Kerr et al., 2015). Moreover, the differences observed in basal area, biomass, NPP and respiration in MP simulations are in line with other works that have found for southern Italian provenances high performance in drought response and productivity (Hansen and Larsen, 2004; Kerr et al., 2015; Mihai et al., 2021; Oggioni et al., submitted). Basal area values were statistically higher for the Southern Apennine provenance than for the other two provenances also in PP simulations, identifying it as the provenance that exhibited larger diameters and greater space occupation in the horizontal plane. In parallel, our simulations in pure provenance plots indicate superior production and carbon sink of the Northern Apennines provenance (local), particularly when compared to the W_Al provenance. In the PP simulations the higher biomass and NPP values of the local provenance are often consistent with the performances of the Southern Apennine provenance, similar to the MP simulations, where the high biomass and NPP values of the Southern Apennine provenance are similar to the performance of the local provenance. Despite the excellent performance of provenances that are more accustomed to drier climates and higher temperatures, the local provenance may nevertheless be a valid choice, if not the best choice, based on the evolutionary history of the species in the geographical area of interest and on the adaptability of the local genetics to the surrounding environment. Studies in the Czech Republic have shown that local provenance may in fact perform better in terms of growth and productivity when compared to other European provenances (Frýdl et al., 2018; Fulín et al., 2023), especially when the ability to adapt to the climate meets the environmental optimum of a certain genetics. Furthermore, climate stability plays a key role in climate resilience, favouring continental climates such as the Czech Republic over rapidly changing Mediterranean climates (Lionello and Scarascia, 2018). The different trends between pure and mixed provenance forest simulations reveal how growth and carbon storage capacity can be partly influenced by the dynamics of intraspecific competition and the establishment of regeneration, highlighting how genetic composition a forest stand can influence its ability to adapt to its environment. Different genetic mixtures, in fact, can produce different yields, depending on forest provenance (Gömöry et al., 2021; Matyas, 1996). Our results underline how the Northern Apennine and the Southern Apennine provenance better respond during forest growth simulations, marking these two provenances as valuable resources for forest management in the territories of the Tuscan-Emilian Apennine National Park. This confirms the results of previous studies on the performance of these same provenances in the same study area (Oggioni et al., submitted), making clear the potential of silver fir genetic diversity in adapting to a changing climate (George et al., 2015; Vitasse et al., 2019b). The conservation and enhancement of silver fir genetic diversity is crucial to sustaining the function of silver fir forests as important carbon sinks and drought barriers, thus contributing to climate change mitigation (Dobrowolska et al., 2017; Mihai et al., 2021). The use of local and southern provenances in reforestation and sustainable forest management programmes can therefore offer effective strategies to preserve the biodiversity and health of forest ecosystems in a rapidly changing climate (Gömöry et al., 2021; Hansen and Larsen, 2004).

Climate change effects

Resilience of silver fir growth to varying climatic conditions, as indicated by the consistent BA and Biomass values across different Representative Concentration Pathway (RCP) scenarios, is evidence for silver fir's remarkable adaptability and resilience to drought conditions (Gazol et al., 2015; Gazol and Camarero, 2016; Oggioni et al., submitted). Silver fir response to warmer and drier climates revealed higher resilience compared to other conifers like Norway spruce, highlighting its adaptability to a range of climatic conditions (Vitali et al., 2017; Vitasse et al., 2019a). Resilience to climatic stressors is crucial for species to be used in forest management under changing climate scenarios, highlighting the potential of silver fir as a robust species in diverse forest ecosystems. At the same time, our results showed a general increase in the amount of carbon sequestered from the atmosphere (NPP) as a function of climate scenario, especially in the pure provenance simulations where the effect of climate is less masked by intraspecific competition and regeneration dynamics. Simulations of forest growth under climate change carried out by other authors have shown a possible increase in growth and NPP of silver fir under climate change scenarios, especially under scenarios with high temperatures as the RCP 8.5 scenario (Sperlich et al., 2020). On the contrary, we did not notice any signs of growth reduction of this species compared to the historical scenario in the next decades in the territories studied, assuming a good response of silver fir to a rise in temperatures and aridity in the territories of the Tuscan-Emilian Apennines. However, NPP values in single-provenance simulations (PP) were higher in 2060 than in 2100, indicating a greater carbon sequestration capacity in younger forest stands rather than in older forests (Desai et al., 2005). Carbon sequestration capacity of older forests, in fact, may decrease over time, while young and regrowth forests absorb large amounts of carbon (Zhu et al., 2019). Our results in fact reveal that while maintaining a good regeneration rate (MP simulations) NPP does not vary between 2060 and 2100 while it decreases in PP simulations without regeneration, underlining a possible effect of forest age. However, the role of mature forests should not be underestimated and their reduced capacity to store carbon annually in our simulations could be due to the general underestimation of forest growth models (Carey et al., 2001). Our results showed also an increase in plant respiration as a function of the severity of the climatic scenario, emphasising the positive relationship between increased temperatures and plant metabolism. The positive relationship between temperature and respiration indicates that silver fir actively responds to temperature increases by modifying its metabolic process (Gazol et al., 2015; Gazol and Camarero, 2016). In physiological terms, increased temperature stimulates plant respiration, influencing photosynthesis and thus production processes (Bohn et al., 2014). In the context of climate change, increased respiration could have significant implications for carbon uptake and overall plant health. On the one hand, under optimal conditions, an increase in respiration may indicate a more active metabolism and thus potentially higher growth and productivity, especially if the increase in respiration is accompanied by an increase in photosynthesis (Lin et al., 2012). On the other hand, if the increase in respiration is large, or if it occurs under stressful conditions (such as high temperatures), it may lead to a reduction in the plant's energy reserves, thus reducing its overall productivity (Zha et al., 2004). In brief, the relationship between increased plant respiration and plant productivity is complex and depends on a balance between various physiological processes and environmental conditions (Collalti et al., 2020b, 2020a). In our case, an increase in respiration as the climate scenario increases is accompanied by an increasing NPP, especially in PP simulations with lower intraspecific competition and regeneration dynamics. An increase in carbon sinks with more severe climate change suggests that silver fir could become an important resource in the near future, also proving to be a key indicator of the effects of climate change on European forests (Vitasse et al., 2019b). Silver fir is a conifer that is particularly adaptable to climate change, thanks to its positive growth under drought conditions and ability to ensure carbon sink (Oggioni et al., submitted; Vitasse et al., 2019a), and should therefore be promoted on suitable sites to ensure healthy forests providing multiple ecosystem services (Vitasse et al., 2019b).

The inclusion of forest provenance data is a fundamental aspect in forest modelling. Genetic diversity, which is often overlooked in traditional modelling, in this study emerged as a crucial factor in understanding and predicting forest dynamics. The results of our study show significant differences between different provenances, both in terms of forest maturity (BA), productivity (biomass and NPP), and metabolism (respiration). These differences persist across different climate scenarios, suggesting that climate change may not alter the distinctive patterns between provenances in the simulated territories. It is therefore clear that forest modelling can greatly benefit from the integration of provenance-specific parameters, providing more reliable predictions under climate change scenarios and informing more sustainable and resilient forest management. Integrating forest provenance data into forest models can present significant challenges. Parametrising different provenances can include a wide range of parameters, which requires a thorough understanding of the complex interactions between morphology, genetics, plant physiology and environmental variables. Nevertheless, our study represents an important step towards integrating genetic diversity into forest modelling, serving as a robust approximation for future experiments. The simulations proposed in this study do not explicitly include forest management, which may play an important role in climate adaptation. We suggest that future simulations that include the effect of provenances take into account multiple management scenarios, analysing the role of climate-smart forestry practices on the response of species to climate.

Conclusion

In this study, we comprehensively explored the dynamics of Italian silver fir forests and three of its provenances in a climate change context, through the application of the FORMIND model. The FORMIND model, through its valid reproduction of forest dynamics, proves to be a crucial tool for ecological modelling, offering reliable forecasts for forest management under climate change scenarios. Silver fir proves to be particularly resilient to changing climate scenarios: The resilience of silver fir to varying climatic conditions, evidenced by consistent values of basal area and biomass across different RCP scenarios, indicates its potential robustness as a species under different forest contexts and climate scenarios. Furthermore, the carbon sequestration capacity of silver fir forests, which increases with climate scenarios, underlines their crucial role in climate change mitigation. However, it is important to consider that this potential may vary according to the age and maturity of the forest, with young and growing forests absorbing greater amounts of carbon than older ones in our pure provenance simulations without regeneration.

The results on the performance of different silver fir provenances showed significant variations in growth, productivity, metabolism and carbon storage capacity, emphasising the higher growth performance of the local provenance (Northern Apennines) and Southern Apennines compared to the W_Al provenance in the territory under investigation. These differences, persisting through various climate scenarios, emphasise the importance of genetic diversity in influencing the adaptability and resilience of forests to environmental changes. Finally, our study emphasises the importance of integrating forest provenance data into forest models, overcoming the challenges of parameterising a wide range of morphological and environmental variables. Integrating genetic diversity into forest modelling is a key step in understanding and predicting forest dynamics, informing more sustainable and resilient forest management in the face of climate change. We hope that the results will stimulate further investigations, encouraging the development of models that more effectively combine genetic diversity and forest modelling. This integrated approach would not only increase the accuracy and effectiveness of forest models, but also contribute to a better understanding of forest dynamics in a rapidly changing world.

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Supplementary Materials

Table S_1. FORMIND Model parametrization: *Geometry coefficients that differs by provenance. All coefficients have been derived from field data.*

Variable	Provenance									Equation
	Western Alps (W_Al)			Northern Apennines (N_Ap)			Southern Apennines (S_Ap)			
Tree Height - Stem Diameter	*h0*	*h1*		*h0*	*h1*		*h0*	*h1*		*Saturation approach*
	102.811	80.42099		115.8351	48.7984		85.45171	55.65025		$H = D/(1/h0 + D/h1)$
	$R^2 = 0.331606$			$R^2 = 0.4311977$			$R^2 = 0.8043591$			
Crown Diameter - Stem Diameter	*cd0*	*cd1*		*cd0*	*cd1*		*cd0*	*cd1*		*Saturation approach*
	18.3223	29.12556		33.00853	10.56288		28.293	13.49669		$CD = D/(1/cd0 + D/cd1)$
	$R^2 = 0.3420063$			$R^2 = 0.2983323$			$R^2 = 0.326318$			
Crown Length - Tree Height	*cl0*			*cl0*			*cl0*			*Constant approach*
	0.453405			0.534414			0.700087			$CL = c0$
Aboveground Biomass - Stem Diameter	*b0*	*b1*		*b0*	*b1*		*b0*	*b1*		*Power-law approach*
	7.50032	2.33375		5.73942	2.21526		6.64028	2.56054		$AGB = b0*(D\hat{}b1)$
	$R^2 = 0.9344819$			$R^2 = 0.9370445$			$R^2 = 0.9919445$			
Diameter increment - Stem Diameter	*a0*	*a1*	*a2*	*a0*	*a1*	*a2*	*a0*	*a1*	*a2*	*Richards approach*
	0.00246	1.85193	1.4121	0.00279	1.86263	1.32254	0.00616	0.69914	1.10171	$\Delta D = a0*a1*a2*\exp(-a1*D)*(1-\exp(-a1*D))\hat{}(a2-1)$
	$R^2 = 0.880088$			$R^2 = 0.9071112$			$R^2 = 0.368657$			

Table S_2. FORMIND Model parametrization: *Model parameters uniform across provenances.*

Module	Variable	Value	Unit	Reference
Geometry	Max Diameter	200	cm	arbitrary
	Fraction of stem biomass to total biomass	0.7		default
	LAI	6.2		default
Production	Maximum leaf photosynthesis	8.9014	μmol(CO_2) / (m^2*s)	default
	Slope of light response curve	0.0402	μmol(CO_2) / μmol(photons)	default
	Light extinction coefficient of leaves	0.7		default
	Wood density	0.353	Mg(odm) / m^3	(Zanne et al., 2009)
Soil / Water	Water Use Efficiency	6	g (odm) / kg (H2O)	default
	Permanent wilting point	11.7	Volume %	from (Rawls et al., 1993)
	Field capacity	27	Volume %	from (Rawls et al., 1993)
	Interception constant	0.2		default
	Soil porosity	46.3	Volume %	from (Rawls et al., 1993)
	Hours of rainfall per day	24		
	Fully saturated conductivity	0.00132	m / s	from (Rawls et al., 1993)
	Pore size distribution index	0.252		from (Rawls et al., 1993)
	Residual soil water content	2.7	Volume %	from (Rawls et al., 1993)
	Soil depth	71.73	cm	field data
Temperature effects	Minimum temperature for photosynthesis	-2	°C	default
	Maximum temperature for photosynthesis	36	°C	default
	Minimum temperature to start the vegetation period	5	°C	default
	Minimum temperature to end the vegetation period	9	°C	default

Table S_3. FORMIND Model parametrization: *Coefficients to model tree mortality based on data from* Vieilledent et al. (2010).

Variable	Coefficient		Equation
Mortality D	*ao*	*a1*	$M_D = a0*exp(a1*D)$
	0.002	-1.03816	
	R^2 = 0.8562977		
Mortality ΔD	*b0*	*b1*	$M_{\Delta D} = b0*exp(b1*\Delta D)$
	0.16004	-4687.976	
	R^2 = 0.989772		

Table S_4. FORMIND Model parametrization: *mean historical temperatures data (1970-2005) and temperature effect on photosynthesis.*

Temperature	**Western Alps**	**Northern Apennines**	**Southern Apennines**
Maximum temperature of the warmest month (°C)	22.4	23.1	25.3
Minimum temperature of the warmest month (°C)	11.1	11.9	13.8

Tree gross photosynthesis reduction due to temperature effects and soil water deficit effects				
Global climate model	**RCP scenario**	**Western Alps**	**Northern Apennines**	**Southern Apennines**
HadGEM	8.5	0.726	0.707	0.664
	4.5	0.700	0.680	0.635
	2.6	0.688	0.669	0.624
	historical	0.613	0.594	0.549
NorESM	8.5	0.743	0.720	0.668
	4.5	0.716	0.693	0.640
	2.6	0.699	0.676	0.622
	historical	0.653	0.629	0.575
MPI	8.5	0.722	0.701	0.654
	4.5	0.687	0.666	0.618
	2.6	0.677	0.656	0.607
	historical	0.632	0.612	0.565

Mean yearly radiance during the day-length of the reference year(s)				
Global climate model	**RCP scenario**	**Western Alps**	**Northern Apennines**	**Southern Apennines**
ALL	8.5	788.923	788.923	788.923
	4.5	790.053	790.053	790.053
	2.6	785.512	785.512	785.512
	historical	780.079	780.079	780.079

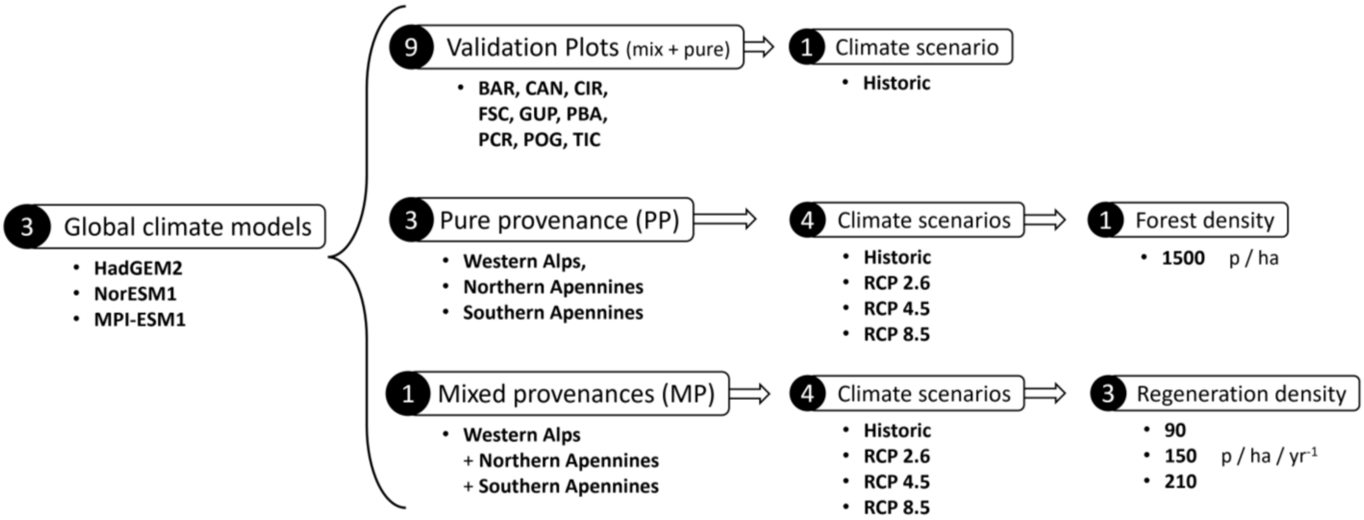

Figure S_1. Scheme of model simulations.

Table S_5. Validation results. *Age, stem number, volume, and biomass of the 9 plots used for the FORMIND parametrization and related validation results.*

Plot	Provenance	Age		Stem number			Volume / ha [$m^3\ ha^{-1}$]		Biomass / ha [$Mg_{ODM}\ ha^{-1}$]	
		observed	simulated	observed	simulated initial	simulated final	observed	simulated	observed	simulated
BAR	**Northern Ap.**	50	50	701	1300	692	627.33	468.45	318.65	255.05
CAN	**Western Alps** **Northern Ap.**	91	91	512	1300	530	863.35	720.09	423.63	366.69
CIR	**Northern Ap.** **Southern Ap.**	79	79	566	1250	588	785.16	674.31	392.92	329.84
FSC	**Western Alps** **Northern Ap.**	77	77	659	1500	665	528.39	722.80	268.95	381.11
GUP	**Western Alps**	96	93	450	1250	486	753.22	627.62	400.61	341.36
PBA	**Northern Ap.** **Southern Ap.**	45	45	629	1100	612	408.30	351.08	210.76	187.95
PCR	**Northern Ap.**	69	69	587	1250	593	546.71	613.92	276.59	309.57
POG	**Northern Ap.** **Southern Ap.**	44	44	595	1150	622	510.71	407.07	261.69	214.10
TIC	**Western Alps** **Northern Ap.**	46	46	550	1100	568	603.02	353.33	303.77	206.01

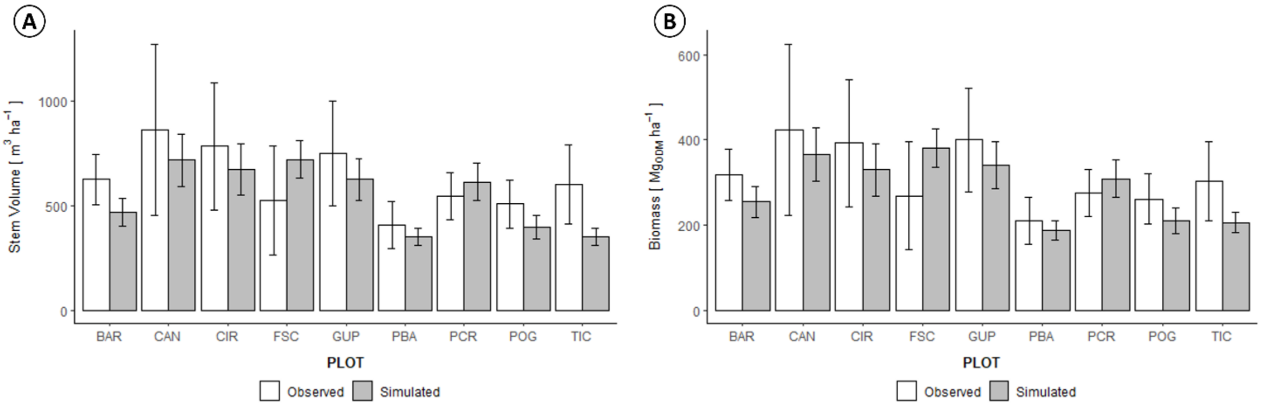

Figure S_2. Validation results at plot level. *Observed (white) vs simulated (grey) stem volume and biomass values per hectare for each plot used for model parametrization.*

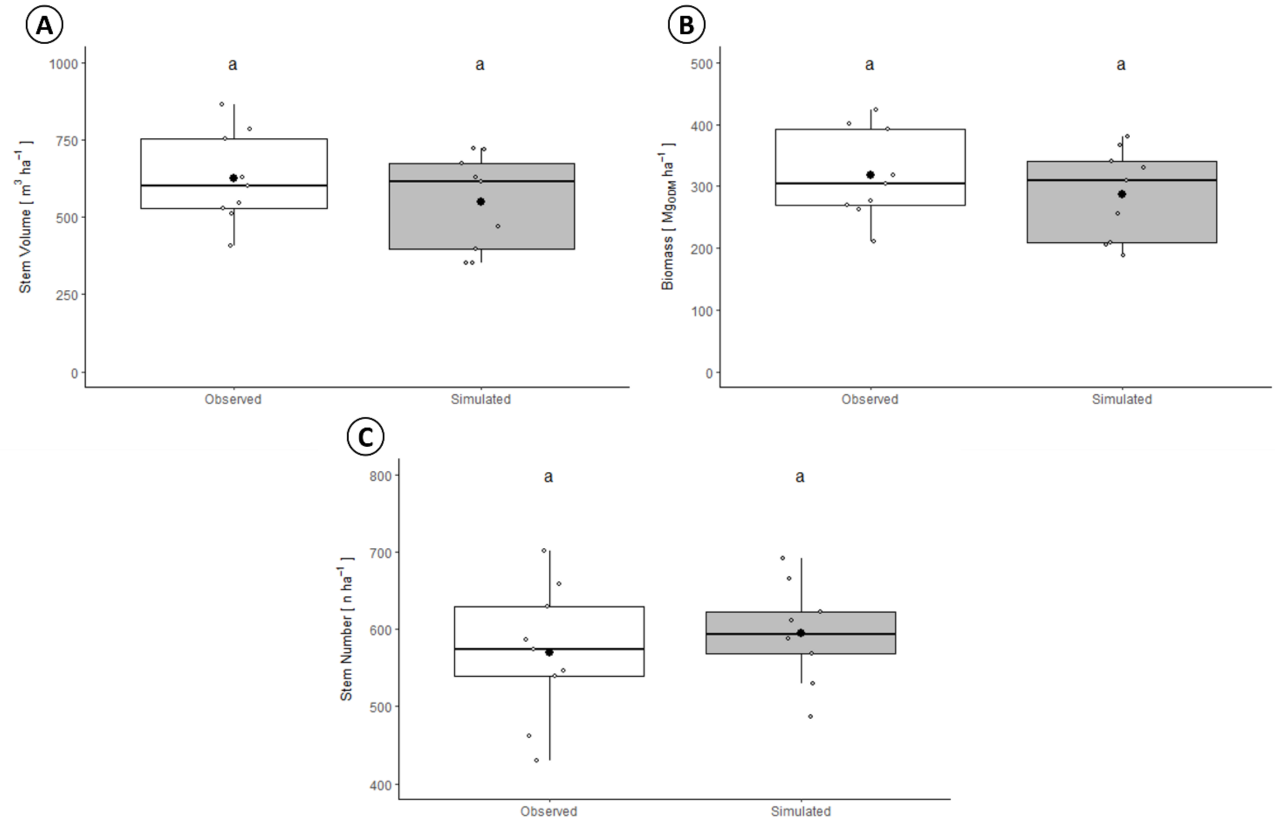

Figure S_3. Validation results for the study area. *Observed (white) vs simulated (grey) stem volume and biomass mean values per hectare of the nine forest plots used for model parametrization. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

Table S_6. Pure Provenance (PP) simulations results. *Basal area, Biomass, NPP and Respiration ANCOVA results. F-statistics and p-value for each model predictor are shown for each climate scenario (historic, RCP 2.6, 4.5, 8.5) and time steps (2060, 2100).*

Var	Factor	historic		2.6		4.5		8.5		Year
		F_statistic	p	F_statistic	p	F_statistic	p	F_statistic	p	
Basal Area	Provenance	119.00	**<0.001**	146.41	**<0.001**	125.53	**<0.001**	131.91	**<0.001**	2060
	Climate Model	2.06	0.129	1.02	0.362	1.48	0.230	5.11	**0.007**	2060
	Provenance	78.10	**<0.001**	88.14	**<0.001**	79.88	**<0.001**	78.31	**<0.001**	2100
	Climate Model	3.06	**0.049**	1.18	0.309	0.93	0.397	1.18	0.309	2100
Biomass	Provenance	8.58	**<0.001**	8.34	**<0.001**	7.00	**0.001**	7.22	**0.001**	2060
	Climate Model	2.64	0.074	1.31	0.273	1.87	0.157	6.43	**0.002**	2060
	Provenance	11.58	**<0.001**	10.34	**<0.001**	9.15	**<0.001**	7.24	**0.001**	2100
	Climate Model	3.94	**0.021**	1.39	0.251	1.16	0.315	1.45	0.238	2100
NPP	Provenance	4.28	**0.015**	2.14	0.120	1.66	0.193	4.26	**0.015**	2060
	Climate Model	19.79	**<0.001**	15.13	**<0.001**	33.37	**<0.001**	13.48	**<0.001**	2060
	Provenance	7.32	**0.001**	6.06	**0.003**	5.60	**0.004**	4.12	**0.018**	2100
	Climate Model	2.45	0.089	7.22	**0.001**	17.76	**<0.001**	2.24	0.109	2100
Respiration	Provenance	4.28	**0.015**	3.44	**0.034**	7.78	**0.001**	31.22	**<0.001**	2060
	Climate Model	19.79	**<0.001**	18.85	**<0.001**	51.27	**<0.001**	13.87	**<0.001**	2060
	Provenance	7.32	**0.001**	6.06	**0.003**	5.60	**0.004**	4.12	**0.018**	2100
	Climate Model	2.45	0.089	7.22	**0.001**	17.76	**<0.001**	2.24	0.109	2100

Table S_7. Pure Provenance (PP) simulations Tukey post-hoc results. *Basal area, Biomass, NPP and Respiration results of the Tukey post-hoc test. Means and significant differences for each provenance are shown for each climate scenario (historic, RCP 2.6, 4.5, 8.5) and time steps (2060, 2100). Different letters indicate significant differences (e.g., a-b) between provenances, while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab). Significant differences are also marked in bold.*

Var	**Provenance**	**historic**		**2.6**		**4.5**		**8.5**		**Year**
		mean	**p**	**mean**	**p**	**mean**	**p**	**mean**	**p**	
Basal Area	Western Alps	8.82	**c**	8.79	**c**	8.82	**c**	8.75	**c**	2060
	Northern Apennines	12.79	**b**	13.53	**b**	13.17	**b**	13.58	**b**	2060
	Southern Apennine	17.79	**a**	17.95	**a**	18.05	**a**	18.11	**a**	2060
	Western Alps	13.41	**c**	13.50	**c**	13.81	**c**	13.48	**c**	2100
	Northern Apennines	15.25	**b**	15.60	**b**	16.06	**b**	16.70	**b**	2100
	Southern Apennine	20.67	**a**	20.67	**a**	21.05	**a**	21.30	**a**	2100
Biomass	Western Alps	316.09	**b**	327.57	**b**	320.75	**b**	313.47	**b**	2060
	Northern Apennines	340.79	**a**	355.81	**a**	348.80	**a**	339.55	**a**	2060
	Southern Apennine	315.32	**b**	336.36	**b**	330.52	**b**	320.90	**b**	2060
	Western Alps	418.35	**b**	454.78	**b**	462.86	**b**	489.11	**b**	2100
	Northern Apennines	468.15	**a**	510.42	**a**	520.88	**a**	542.89	**a**	2100
	Southern Apennine	421.53	**b**	472.26	**b**	482.76	**b**	512.85	ab	2100
NPP	Western Alps	2.88	ab	3.26	a	3.02	a	3.18	**b**	2060
	Northern Apennines	2.95	**a**	3.40	a	3.15	a	3.32	ab	2060
	Southern Apennine	2.77	**b**	3.28	a	3.09	a	3.38	**a**	2060
	Western Alps	2.10	**b**	2.37	**b**	2.53	**b**	2.89	**b**	2100
	Northern Apennines	2.29	**a**	2.58	**a**	2.77	**a**	3.12	**a**	2100
	Southern Apennine	2.09	**b**	2.41	**b**	2.60	ab	2.97	ab	2100
Respiration	Western Alps	0.96	ab	1.12	ab	1.09	**a**	1.29	**a**	2060
	Northern Apennines	0.98	**a**	1.15	**a**	1.13	**a**	1.34	**a**	2060
	Southern Apennine	0.92	**b**	1.09	**b**	1.03	**b**	1.13	**b**	2060
	Western Alps	0.70	**b**	0.79	**b**	0.84	**b**	0.96	**b**	2100
	Northern Apennines	0.76	**a**	0.86	**a**	0.92	**a**	1.04	**a**	2100
	Southern Apennine	0.70	**b**	0.80	**b**	0.87	ab	0.99	ab	2100

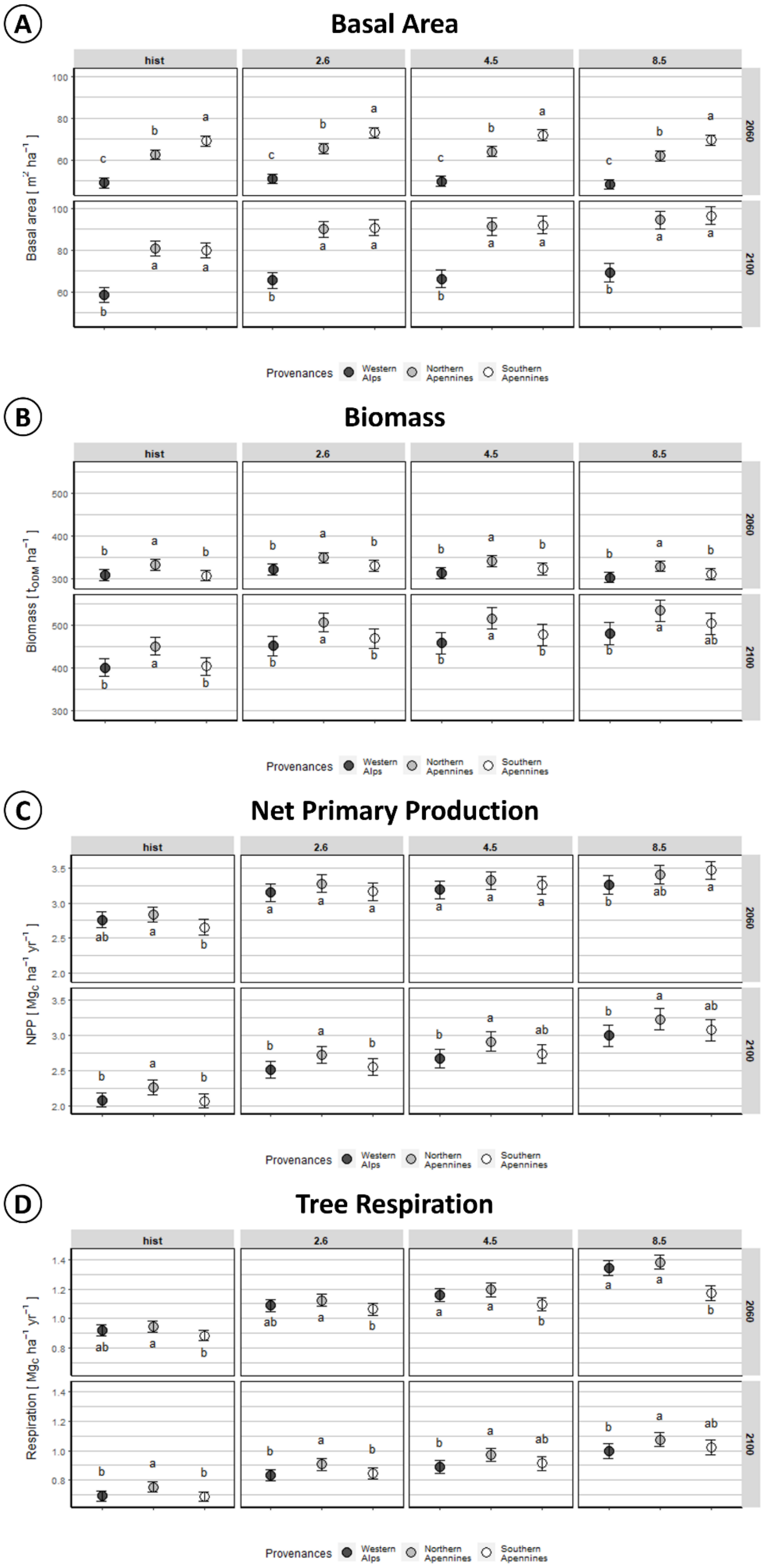

Figure S_4. Pure Provenance (PP) simulations results. *Different letters above the boxes indicate significant differences between provenances (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

Table S_8. Mixed Provenances (MP) simulations results. *Basal area, Biomass, NPP and Respiration ANCOVA results. F-statistics and p-value for each model predictor are shown for each climate scenario (historic, RCP 2.6, 4.5, 8.5) and time steps (2060, 2100).*

Var	Factor	historic		2.6		4.5		8.5		Year
		F_statistic	p	F_statistic	p	F_statistic	p	F_statistic	p	
Basal Area	Provenance	741.29	**<0.001**	586.15	**<0.001**	739.13	**<0.001**	704.24	**<0.001**	2060
	Climate Model	0.13	0.875	0.96	0.382	1.84	0.160	0.48	0.617	2060
	Seedlings Density	2.89	0.056	3.89	**0.021**	3.89	**0.021**	1.17	0.311	2060
	Provenance : Density	2.26	0.061	3.19	**0.013**	1.74	0.139	3.34	**0.010**	2060
	Provenance	247.29	**<0.001**	201.66	**<0.001**	222.18	**<0.001**	214.48	**<0.001**	2100
	Climate Model	0.99	0.373	2.76	0.064	0.86	0.424	2.83	0.060	2100
	Seedlings Density	2.50	0.083	0.44	0.643	0.07	0.930	0.31	0.735	2100
	Provenance : Density	3.49	**0.008**	4.40	**0.002**	1.33	0.258	6.57	**<0.001**	2100
Biomass	Provenance	155.16	**<0.001**	152.84	**<0.001**	171.99	**<0.001**	186.91	**<0.001**	2060
	Climate Model	0.22	0.802	1.18	0.307	0.97	0.379	0.08	0.921	2060
	Seedlings Density	2.48	0.085	4.05	**0.018**	4.11	**0.017**	0.68	0.508	2060
	Provenance : Density	1.63	0.165	3.23	**0.012**	1.96	0.099	2.65	**0.032**	2060
	Provenance	4.80	**0.008**	3.07	**0.047**	2.34	0.097	9.70	**<0.001**	2100
	Climate Model	1.35	0.261	2.22	0.109	0.69	0.504	3.08	**0.047**	2100
	Seedlings Density	0.89	0.412	**0.01**	0.985	0.18	0.833	0.20	0.817	2100
	Provenance : Density	4.53	**0.001**	5.04	**0.001**	1.64	0.163	6.25	**<0.001**	2100
NPP	Provenance	132.19	**<0.001**	150.84	**<0.001**	183.05	**<0.001**	219.68	**<0.001**	2060
	Climate Model	16.58	**<0.001**	51.55	**<0.001**	84.46	**<0.001**	40.42	**<0.001**	2060
	Seedlings Density	0.08	0.928	7.40	**0.001**	0.80	0.450	1.25	0.287	2060
	Provenance : Density	3.83	**0.004**	2.99	**0.018**	1.63	0.165	2.50	**0.042**	2060
	Provenance	42.36	**<0.001**	40.21	**<0.001**	54.52	**<0.001**	44.37	**<0.001**	2100
	Climate Model	10.32	**<0.001**	0.19	0.824	34.99	**<0.001**	2.56	0.078	2100
	Seedlings Density	42.38	**<0.001**	24.34	**<0.001**	18.62	**<0.001**	11.84	**<0.001**	2100
	Provenance : Density	0.51	0.727	1.57	0.181	0.63	0.641	5.59	**<0.001**	2100
Respiration	Provenance	52.02	**<0.001**	55.91	**<0.001**	73.57	**<0.001**	99.12	**<0.001**	2060
	Climate Model	26.75	**<0.001**	7.49	**0.001**	62.32	**<0.001**	63.90	**<0.001**	2060
	Seedlings Density	0.16	0.849	16.85	**<0.001**	0.74	0.477	1.56	0.212	2060
	Provenance : Density	6.78	**<0.001**	2.63	**0.034**	2.87	**0.022**	3.13	**0.014**	2060
	Provenance	71.36	**<0.001**	72.95	**<0.001**	80.60	**<0.001**	58.91	**<0.001**	2100
	Climate Model	1.17	0.311	3.52	**0.030**	14.23	**<0.001**	4.44	**0.012**	2100
	Seedlings Density	88.56	**<0.001**	88.86	**<0.001**	67.38	**<0.001**	49.08	**<0.001**	2100
	Provenance : Density	1.89	0.110	2.47	**0.044**	2.76	**0.027**	0.45	0.771	2100

Table S_9. Mixed Provenances (MP) simulations Tukey post-hoc results. *Basal area, Biomass, NPP and Respiration results of the Tukey post-hoc test. Means and significant differences for each provenance are shown for each climate scenario (historic, RCP 2.6, 4.5, 8.5) and time steps (2060, 2100). Different letters indicate significant differences (e.g., a-b) between provenances, while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab). Significant differences are also marked in bold.*

Var	Provenance	historic		2.6		4.5		8.5		Year
		mean	p	mean	p	mean	p	mean	p	
Basal Area	Western Alps	8.82	**c**	8.79	**c**	8.82	**c**	8.75	**c**	2060
	Northern Apennines	12.79	**b**	13.53	**b**	13.17	**b**	13.58	**b**	2060
	Southern Apennine	17.79	**a**	17.95	**a**	18.05	**a**	18.11	**a**	2060
	Western Alps	13.41	**c**	13.50	**c**	13.81	**c**	13.48	**c**	2100
	Northern Apennines	15.25	**b**	15.60	**b**	16.06	**b**	16.70	**b**	2100
	Southern Apennine	20.67	**a**	20.67	**a**	21.05	**a**	21.30	**a**	2100
Biomass	Western Alps	47.15	**c**	47.03	**b**	47.26	**b**	46.53	**b**	2060
	Northern Apennines	63.17	**b**	67.04	**a**	65.08	**a**	66.99	**a**	2060
	Southern Apennine	66.35	**a**	67.54	**a**	67.65	**a**	67.39	**a**	2060
	Western Alps	77.73	**b**	78.64	a	81.12	a	79.08	b	2100
	Northern Apennines	77.44	**b**	79.55	a	82.02	a	85.76	a	2100
	Southern Apennine	82.59	**a**	83.36	a	85.17	a	87.96	a	2100
NPP	Western Alps	0.99	**c**	1.05	**c**	0.96	**c**	0.98	**c**	2060
	Northern Apennines	1.22	**b**	1.37	**b**	1.25	**b**	1.34	**b**	2060
	Southern Apennine	1.30	**a**	1.44	**a**	1.34	**a**	1.42	**a**	2060
	Western Alps	1.13	**c**	1.16	**c**	1.19	**c**	1.22	**b**	2100
	Northern Apennines	1.26	**b**	1.29	**b**	1.35	**b**	1.40	**a**	2100
	Southern Apennine	1.34	**a**	1.37	**a**	1.44	**a**	1.44	**a**	2100
Respiration	Western Alps	0.72	**c**	0.90	**c**	0.88	**c**	1.03	**c**	2060
	Northern Apennines	0.82	**b**	1.07	**b**	1.07	**b**	1.32	**b**	2060
	Southern Apennine	0.89	**a**	1.13	**a**	1.14	**a**	1.41	**a**	2060
	Western Alps	0.75	**c**	0.89	**c**	0.97	**c**	1.14	**b**	2100
	Northern Apennines	0.91	**b**	1.08	**b**	1.21	**b**	1.41	**a**	2100
	Southern Apennine	0.99	**a**	1.18	**a**	1.31	**a**	1.49	**a**	2100

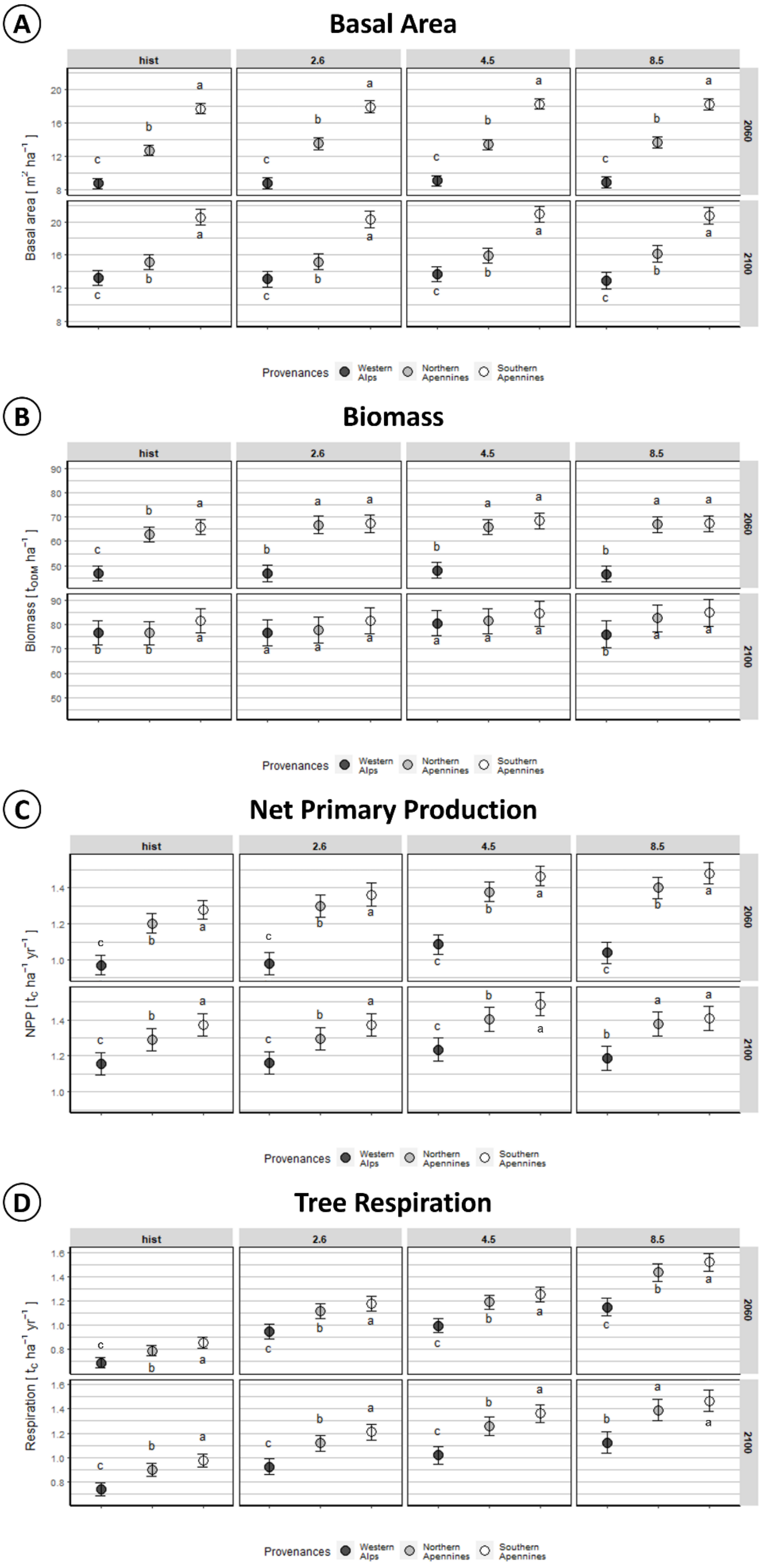

Figure S_5. Mixed Provenances (MP) simulations results. *Different letters above the boxes indicate significant differences between provenances (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

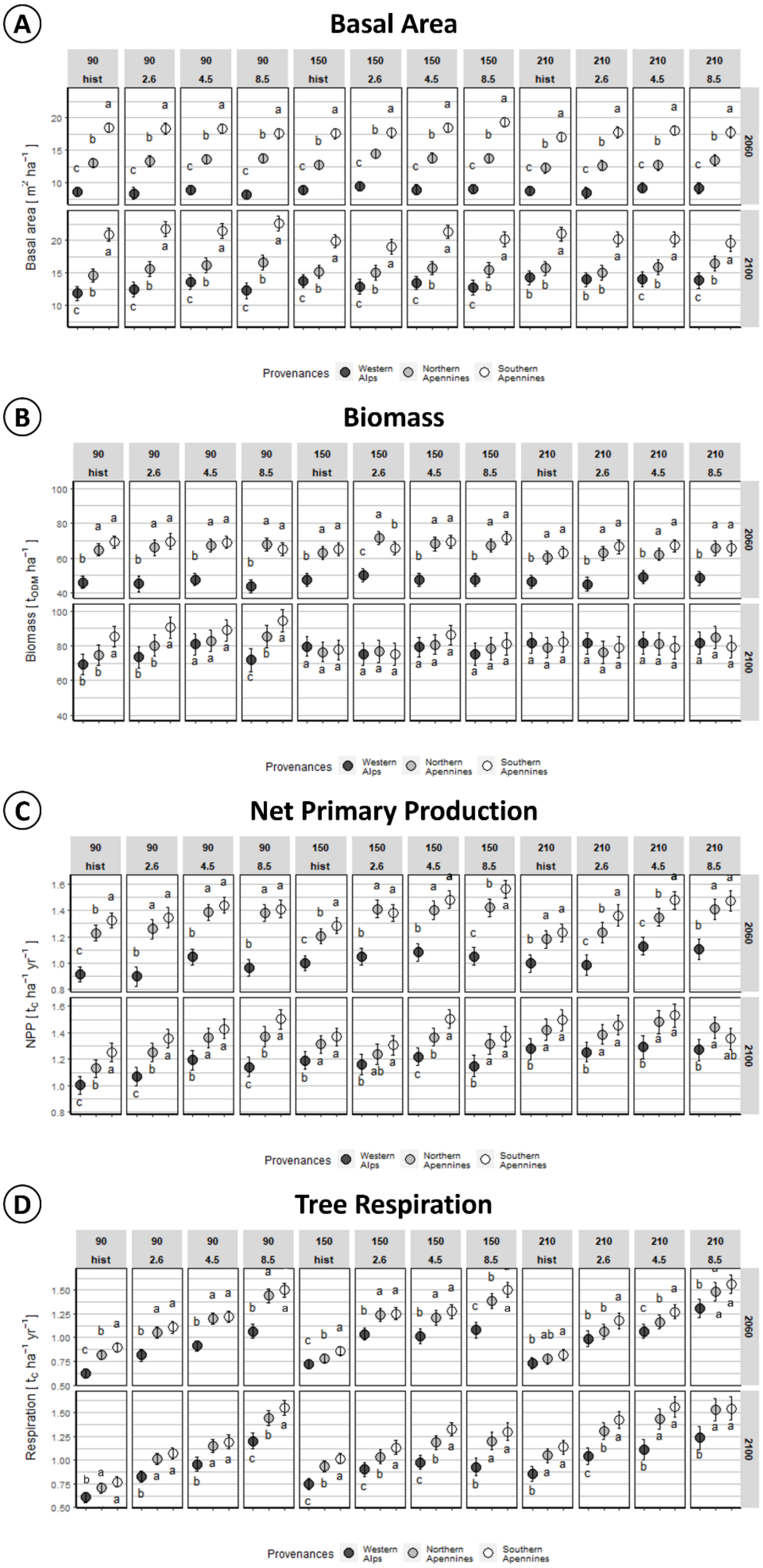

Figure S_6. Mixed Provenances (MP) simulations results analysing the 'provenance : seedling density' interaction. *Different letters above the boxes indicate significant differences between provenances (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

Interplay of Species Mixture, Climate Change, and Management Regimes on Carbon Stocks and Sinks in a Mediterranean Beech Forest

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Abstract

Beech (*Fagus sylvatica* L.) is the most widespread species in the Apennines, but at the same time it is susceptible to climatic stress. Therefore, forestry should strive to increase the adaptability of beech forests to climate variations, and thus maintain or improve the ecosystem services they provide. Here we analyzed the role of forest management and climate on the potential of beech forests for climate change mitigation. In the Tuscan-Emilian Apennine National Park (PNATE), we compared five different management types (coppice, stored coppice, high forest, mix with broadleaves, mix with silver fir) in their ability to store carbon under different climate change scenarios and management intensities. We collected tree and stand data in 57 forest plots, estimated the current carbon stocks and sinks, assessed expected changes in the species distribution under climate change scenarios by environmental niche modelling, and projected the future growth of forests using the 3-PGmix forest growth model. Carbon sinks are higher in beech forests mixed with broadleaves than in pure beech coppice or stored coppice (+25% and +40%, respectively), suggesting a positive effect of biodiversity on the forest's ability to mitigate climate change. Distribution models showed a drastic reduction in the species' distribution range in the future, highlighting PNATE as a possible site for climate refugia. Growth simulations revealed that species complementarity (mix with broadleaf or fir) greatly increases carbon stocks and sinks, as long as harvest stays at intermediate intensities. Beech in mix with fir showed higher average delta carbon stocks (> 98 - 317%) and carbon sink (> 38 - 330%) compared to pure beech managements in the different climate scenarios simulations. Climate change scenario SSP 1 - 2.6 results in an average increase of carbon stocks and sink across management and intensities, while SSP 3- 7.0 implies a decrease for all treatments, except for the mix with silver fir that shows a remarkable increase. Active coppice is the management that is less sensitive to an increase of management intensity on biomass carbon sink (-0.5% and 7.8%). Our findings underline the crucial role of beech forest management in locally optimizing carbon uptake, underlying the positive effect of mix with fir and other broadleaves. We therefore recommend an informed and adaptive forest management approach that considers harvest intensity, species mixture, and ongoing climate change to effectively maintain resilient and functional forests through a mosaic of different forest management approaches.

Keywords: beech management, species distribution models, forest modelling, 3-PG, dendrochronology

Introduction

Forests play an important role in the global carbon cycle as they remove carbon dioxide from the atmosphere, sequester and store it within biomass and soil. In Europe it is estimated that forest biomass contains 9.8 Gt of carbon, offsetting nearly 7-12 % of yearly emissions of the EU27 countries (Janssens et al., 2003). At the same time forest ecosystems are increasingly threatened by higher temperatures and erratic precipitation patterns, especially in southern Europe, a region particularly vulnerable to climatic fluctuations. The Mediterranean basin is expected to suffer worse drought periods than the rest of Europe due to temperature rise, decrease in precipitation and changing atmospheric circulation patterns leading to a more arid climate(Dorado-Liñán et al., 2019). Additionally, the Mediterranean presents a complex topography with many species highly adapted to specific environments, making them more vulnerable to rapidly changing conditions (Dorado-Liñán et al., 2019). Since pre-industrial times annual mean temperatures across the Mediterranean have risen about 1.5°C, a trend that is expected to continue and intensify; should global temperatures be held below 2°C until 2100 temperatures are expected to rise between 0.5-2°C whereas a high warming scenario foresees 3.8-6.5°C warming (RCP8.5), which would be disastrous for the majority of mediterranean species (Cramer et al., 2020). Summer precipitation is expected to keep decreasing between 10-30% with strong regional differences but a clear trend of increasing drought periods during summer months (Cramer et al., 2020, Vacchiano et al., 2017). Many forest species in the country, from sea level to the upper treeline, are expected to experience a northwards and upwards shift (Mauri et al., 2022).

Beech (*Fagus sylvatica* L.) forests are integral to most mountain ecosystems and cover 10.1% of Italian forests extending across over 1000 ha (Gasparini et al., 2022). This species is one of the most important forest types in Europe, serving as biodiversity hotspot, contributing to wood production, and regulating the climate. However, beech is experiencing climate-change driven growth reduction and increased mortality due to drought, especially in the Mediterranean areas (Martinez del Castillo et al., 2022, Piovesan et al., 2008). Understanding climate responses of beech at the trailing edge of its distribution is particularly useful to support ecosystem functioning, resilience and adaptation in suboptimal conditions.

Beech forests in the Italian Apennines area have been heavily manipulated and harvested for centuries. Most were managed as coppices for fuelwood, an important source of income for mountainous areas. Recent societal changes have left many of these forests in a state of abandonment, determining the overageing of coppices beyond traditional rotations, or were directly converted to high forest (Nocentini, 2009; D'Amato et al., 2011). The different configurations of beech forests, from coppice to stored coppice to high forest, affect soil available water, microclimate, competition and light availability, eventually influencing tree growth and vitality in ways that have not been unequivocally ascertained. On one hand, active and climate-smart forest management may enhance carbon uptake and drought resilience (D'Amato et al., 2011, Roig et al., 2005, Blanco et al., 2011), especially at trailing edges of species distributions (D'Amato et al., 2011). In high forests, thinning can improve drought resilience and increase soil water availability (Garcia-Gonzalo et al., 2007, D'Amato et al., 2013). On the other hand, mature forests represent a stable long-term carbon pool, although they generate slower economic returns compared to coppice systems. Most of these findings are however highly site specific, and depend on species mixture, site characteristics, local climate and other factors (Forrester, 2014).

Additionally, across the Apennines, Beech mixes with other broadleaf species at its lower elevational limit, and with silver fir (*Abies alba* Mill.) at its upper limit, at approx. 1200 m asl. The extent of beech forests warrants a huge carbon storage potential within the forest and in wood products, including material and energy substitution effects, but also other ecosystem services such as soil protection in mountainous regions and regulation of the water cycle (Chianucci et al., 2016). However, beech is expected to shrink its geographical distribution across the whole mountain range under climate change, due to increasingly frequent and prolonged drought periods, and a strong drought sensitivity of the tree (Gazol et al., 2019). Along elevational gradients, higher temperatures can push the species into the habitat of silver fir, whilst increasing the competitiveness of other broadleaves at lower elevations. Beech mixtures have been found to be more productive and healthier than pure beech stands thanks to overyielding and niche complementarity (Pretzsch et al., 2013), and also more resilient to extreme weather events and carbon loss due to disturbances (Forrester, 2014). However, the true effect of mixture can strongly depend on management type and intensity and on local site conditions. More studies are needed to understand the effect of beech mixing with other broadleaves or conifers on carbon stocks and sinks, and to model the influence of climate change on expected ecosystem and carbon resilience, in order to identify the most appropriate management strategies for climate change mitigation.

To unravel the multifaceted dynamics of how climate variations and silvicultural strategies impact carbon stock and carbon sinks (defined as the carbon uptake in Mg of carbon per hectare per year in the forest biomass) in Apennine beech forests, we integrated field measurement of tree, litter, and soil carbon with Ecological Niche Modelling (MaxEnt) and process-based modelling (3-PG). Different management types, harvest intensity, rotation lengths and mixtures, and climate scenarios (SSP1-2.6 and SSP 3-7.0) were simulated to identify the management option conducive to the highest carbon stock and sink. Our specific objectives were: (i) modelling the climatic niche and future habitat extent of beech across our study area, (ii) modelling the effect of mixing on carbon stock and sink, and (iii) modelling the effect of different silvicultural approaches on carbon stock and sink. The results of all three objectives provide a better understanding of the interplay between forest management, species composition, and climate change. This knowledge can guide forest management decisions to optimize carbon sequestration and enhance the resilience of beech forests in the face of climate change.

Materials and methods

Study area

PNATE lies between the regions of Tuscany and Emilia Romagna on an area of 228 km2 encompassing peaks of just about 2.100 masl. Being in central-north Italy the mountain ridge also marks the boundary between continental and Mediterranean climate which results in a large heterogeneity of habitats and species. It is a temperate broadleaf and mixed forest ecoregion with relatively high rainfall and a mostly temperate climate, drought conditions are not present currently above 1000 masl. Until 900 masl the main tree species is chestnut mixed with oak and hornbeam, above 900 masl beech becomes dominant at times mixed with silver fir, most conifers are plantations from the 60s with a few natural populations (Ferrarini, 1983). The upper tree limit is around 1700 masl, meadow highlands which were often used for pasture are found above. More than 1.500 species find their habitat here with about 10-20% being endemic highlighting the importance of this area (Sillo et al., 2012).

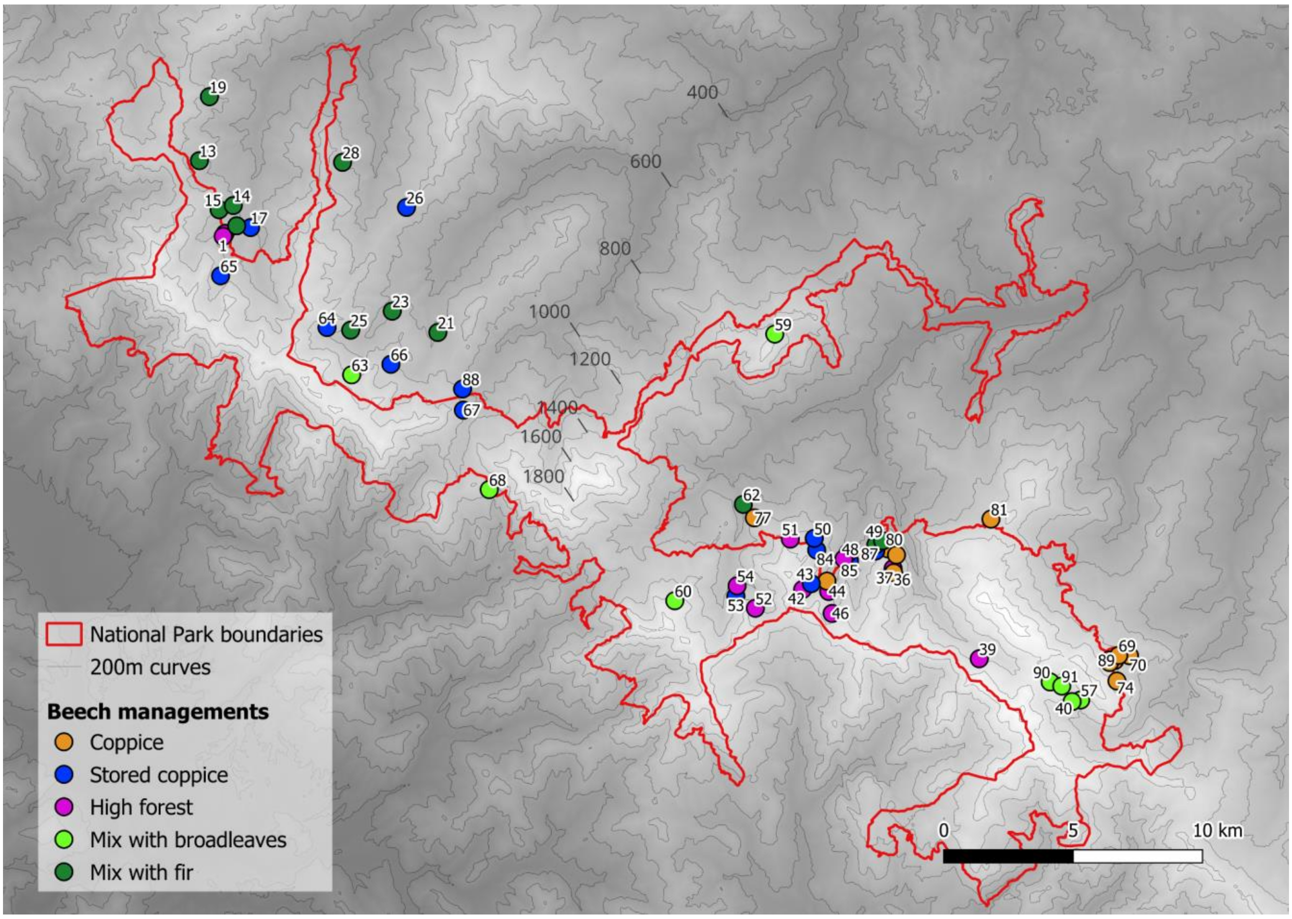


Figure 1. *Map of the 57 stands sampled in the National Park of the Tuscan-Emilian Apennine. Colors represent the management of each stand (orange: 'Coppice'; blue: 'Stored coppice'; purple: 'High forest'; light green: 'Mix with broadleaves'; dark green: 'Mix with silver fir';).*

Sampling Design

We identified five main management types of beech forests in the area, via i) forest maps from the online page (Geoportale) of the Regione Emilia-Romagna (2020) and ii) online meetings with local forest managers. Through these beech management systems, it was possible to identify 57 study areas (Fig. 1) throughout the PNATE area, classified as follows:

- Pure beech - coppice: Forests near the end of the rotation period. In PNATE, coppice is managed with a rotation of. 40 years, although this limit is often exceeded. (12 study areas)
- Pure beech - stored coppice: These unmanaged areas represent a significant portion of the park where beech coppice management has been abandoned. They cover a broad range of elevations and environmental conditions in the whole national park area. (13 study areas)
- Pure beech - converted to high forest: former coppices that have been converted to high forest for at least 20 years. (12 study areas)

At the upper and lower limits of the beech forests, in unmanaged beech stands, the abandonment of management (or lack of timber harvesting) was a crucial factor for the colonization of other tree species:

- Mixed beech-broadleaves forests - Unmanaged forest areas, mixed with hardwoods at elevations <1200 m asl. (12 study areas in mix with *Castanea sativa, Quercus cerris, Malus sylvestris, Ostrya carpinifolia, prunus avium, Alnus incana*).
- Mixed beech-fir forests - Unmanaged forest areas, mixed with silver fir at elevations >1200 m asl. (8 study areas)

For each of the 57 identified study areas (Fig. 1), a circular plot (radius: 13m) was established for data collection. Plots were selected to represent the species composition, slope, exposition, and average density of the surrounding areas, avoiding elements of the surrounding environment that may affect the representativeness of the area (forest roads, streams, sudden bumps, etc.).

Data collection

In each of the sampling areas dendrometric data were collected at individual tree level, and edaphic and topographic data at forest plot level. In each area we collected 5 40x40 cm litter samples, 5 soil cores (0-20cm depth) for carbon (C) and nitrogen (N) analysis, and 5 soil samples each consisting of three 5-cm diameter soil sampling rings to estimate soil bulk density (0-5 cm depth). Litter and soil samples and soil cores were collected from the same points, at increasing distances (1, 2, 3, 4, 5 m) from 5 model trees in each plot to capture soil variability within the area. In each plot we measured the diameter at 130 cm height (DBH) of all trees; collected tree height, crown diameter, crown depth and two tree-ring samples from 10 model trees; healthy trees were chosen as model trees representing the average diameter classes and height classes of the sampling area.

Litter and soil analysis

The 5 soil samples collected in each plot were combined to create a composite sample representing the intrinsic variability of the soil in the specific location. After air-drying and sieving at 2mm, the composite samples were analyzed for: Bulk density, Inorganic C content, Organic C content, and total N. Inorganic carbon content was analyzed using the Bernard's calcimeter methodology (Lamas et al., 2005), total carbon and nitrogen using an elemental analyzer (Carlo Erba, Milano). Soil texture was obtained by means of the "Pipette Method'' (Paturno et al., 1997). For bulk density, three replicates sampled at 0-5 cm depth were oven-dried at 105 °C for 48 hours and weighed. The weight was divided by the volume of the 5cm diameter sampling ring to get the bulk density of the sample. For the 5-20cm depth, we used a pedotransfer function from Ferré et al. (2023) calibrated in the Italian Alpine to estimate the soil bulk density. The 5 litter samples were combined, oven-dried at 105 °C for 48 hours, and weighed.

Similar to the C stock and sink analyses in tree biomass, statistical differences between SOC stock values were analyzed using GLM. The model included management type (factor), elevation, slope, aspect, tree density, mean tree age and total soil nitrogen as predictors. Model selection (based on AIC), collinearity test (VIF) and statistical comparisons (Tukey post-hoc test) followed the same methods applied to the GLMs of C stock and sink in tree biomass.

Tree data processing

We fitted height-diameter curves for each plot (10 measurements) and used them to estimate the height of all measured trees. Consequently, we calculated above-ground total biomass of each tree using allometric relationships already available for major Italian forest species (Tabacchi et al., 2011), and scaled it to a per-hectare basis. Root biomass was estimated as 24% of total aboveground biomass (Easdale et al., 2019; Mokany et al., 2006). Carbon stocked in above- and below-ground tree biomass was calculated by applying a carbon density coefficient of 0.47 (IPCC, 2006).

Via dendrochronological analysis, the tree carbon sink was assessed. Tree-ring samples collected from the 10 model trees (57 plots * 10 trees * 2 cores = 1140 cores) were manually sanded and scanned (EPSON Perfection v850 Pro scanner at 2400 dpi resolution); we measured tree-ring width, crossdated all samples and calculated average individual tree chronologies (CooRecorder and CDendro v. 9.3.1 – Cybis, 2022; Maxwell and Larsson, 2021). The crossdating was carried out both at the individual level and at the plot level among the 10 sample trees in each plot. We converted tree-ring widths into diameter and tree height chronologies, using the height-diameter curves previously estimated. We finally entered the diameter and height of each past year into allometric equations to calculate and create biomass and carbon stock time series. By subtraction, it was possible to estimate the annual carbon sink for each of the 10 model trees, thus deriving the average C sink per tree. A diameter-sink regression was then applied to estimate the C sink of all trees measured in each plot, whence the carbon sink per hectare could finally be estimated.

We analyzed statistical differences in C stock and sink between management types using generalized linear models (GLM) with Gamma distribution. The models have several environmental covariates, such as elevation, slope, aspect (linearize by cosine transformation), tree density, mean tree age, soil organic carbon (SOC), and total soil nitrogen. Model selection was carried out by backward removal of non-influential predictors based on Akaike's Information Criterion (AIC). The final model was finally tested for collinearity between predictors by calculating the Variance Inflation Factor (VIF); if collinearity was detected (VIF > 10 – Dormann et al., 2013) one of the two collinear variables was excluded from the model, based on the highest p-value. The VIF was calculated using the VIF function of the car R package (Fox et al., 2023). All statistical analyses were carried out using the R software (version 4.2.3) (R Core Team, 2022). GLMs were run using the stats package and McFadden's R-squared was used to estimate the model fit. Tukey post-hoc tests were used to analyze differences in carbon stocks and sinks pairwise between management types.

Species distribution models (SDM)

In order to forecast changes in the realized niche of beech, we modelled current and future species distribution using MaxEnt, one of the most common SDM algorithms that requires presence only data (Hernandez et al., 2006). The maximum entropy principle assumes that the probability to find a species in space is equal everywhere, and then constrains the distribution with all that is known based on the set of presence points and environmental predictors at all locations (Franklin, 2010). It is a correlative approach in that a cell with environmental variables similar to those found in cells with presence points will have a high probability to be a suitable habitat, represented on a scale from 0 (low) to 1 (high) (Merow et al., 2013) (Pearce and Boyce, 2006) (Stanton et al., 2012). The presence points for Italy were retrieved from the EU-forest dataset(Mauri, 2017) (Marchi and Ducci, 2018).

We retrieved climate predictors describing mean annual and seasonal temperatures, precipitation, evapotranspiration and more from CHELSA climatologies on a 1km^2 grid (Table S2) for both historic (averaged over the period from 1979-2013) and future climates (projected to mid- and end of century), under the SSP1-2.6 and SSP3-7.0 scenarios (Karger et al., 2016). To take into consideration the amount of variability inherent in climate scenarios, we used the GCMeval tool (Parding et al., 2020) to visualize the 15 best performing GCM's, based on their representation of the current climate, for southern Europe. From this selection, the four most dissimilar GCMs based on their climate projections were chosen based on an evaluation by Sanderson et al (2015) and occurrence probabilities calculated under each of the four GCMs were averaged for each pixel (Goberville et al., 2015). Finally, model choice was driven by MaxEnt intern AUC scores ranging from 0-1 with 0.5 indicating a model no better than random distribution and >0.9 excellent (Merow et al., 2013). Further, the threshold dependent true skill statistic was calculated (TSS) which sums sensitivity (observed presences) and specificity (observed absences) minus 1 (Allouche, 2006). Further, the threshold dependent true skill statistic was calculated (TSS) which sums sensitivity (observed presences predicted as such) and specificity (observed absences predicted as such) minus 1 (Allouche, 2006). The threshold to identify sensitivity and specificity within the data was the maximum test sensitivity and specificity for PNATE which equally predicts where the species is present as well as absent and thus as similar as possible to the realized distribution. For the whole of Italy, the 10-percentile training presence was chosen which omits all pixels with habitat values lower than the lowest 10% allowing a 10% sampling error or occurrence outside of suitable habitat (Liu et al., 2009).

Forest growth modelling

We modelled forest dynamics using the process-based model 3-PGmix via the r3PG R package (Trotsiuk et al. 2020). The model comprises five sub-modules that simulate metabolic processes (GPP, NPP, respiration), carbon allocation, density-dependent mortality, soil water balance and biomass variables at monthly resolution (Forrester and Tang, 2016). 3-PGmix models forest dynamics taking into account climate variables (temperature, precipitation, solar radiation, frost days) and atmospheric CO_2 concentration, and is therefore able to simulate the effects of climate change on forest stands (Forrester et al., 2021). The model provides monthly output on biomass in different carbon pools (stems, foliage and roots), metabolic variables (GPP, NPP), and variables useful for forest management such as mean tree diameter, height and basal area. While

3PG was originally developed for pure even-aged stands, 3PG-mix allows to simulate mixed and multi-layered stands thanks to some adjustment in light absorption, vertical climatic gradients and dendrometric variables (Forrester et al., 2015).

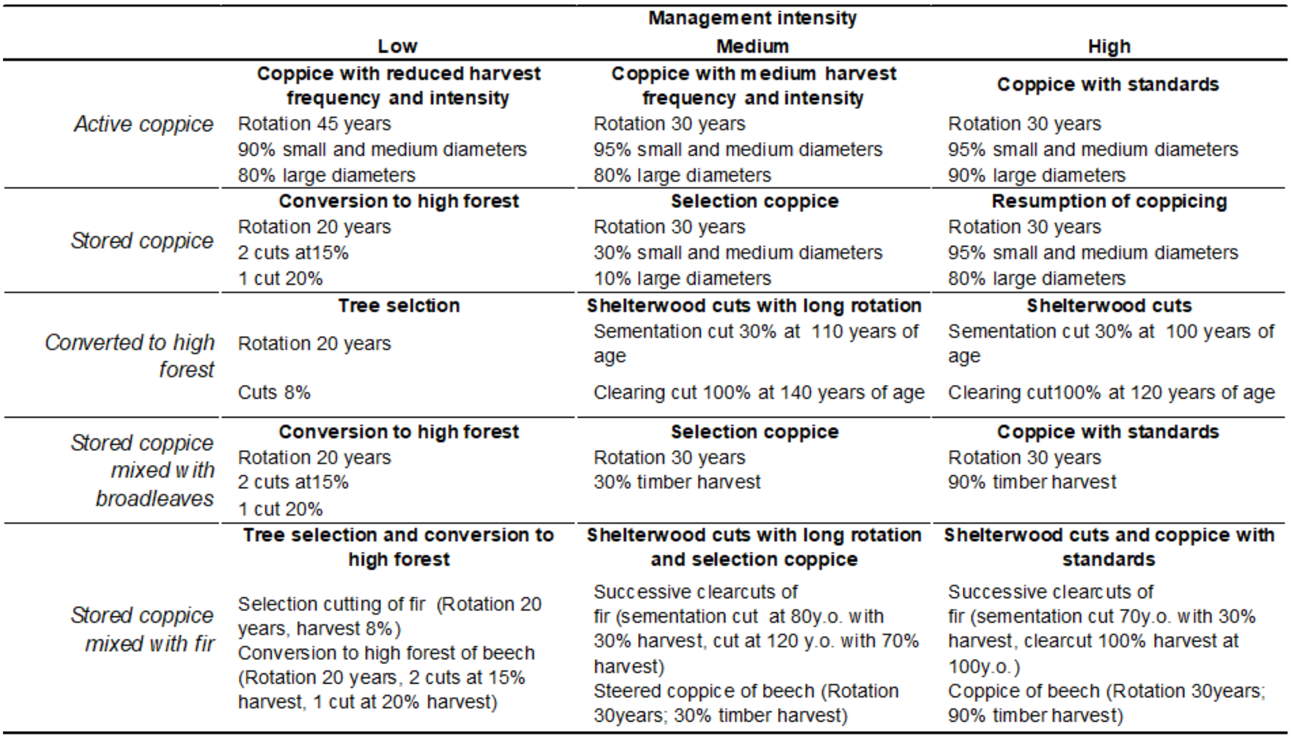
In this study, we refined the representation of beech and silver fir forests in our area by tuning species-specific model's allometric parameters by employing the methodology outlined in Trotsiuk et al. (2020), consisting in fitting field data with different allometric equations that link height and diameter with stem volume, crown stem diameter and live-crown length. For the 'Stored coppice of beech – mix with broadleaves', as it was not possible to parameterize all tree species observed in the field, we decided to simplify the composition of the mix in the following way: i) we initialized the model with dendrometric parameters (DBH, stand density, height) averaged over all the species measured in the field sampling areas; ii) we parameterized all broadleaves using ecophysiological parameters for chestnut, i.e., the most abundant species in mix with the beech, representing 41% of all stems belonging to other broadleaves. Model parameters for chestnut, which was not included in the original set of 3PG species, were mutated from studies using other process-based models, notably iLand and 3D-CMCC-FEM (Seidl et al., 2012; Collalti et al., 2014). To calibrate the model, we used the carbon sink data observed in the field, and adjusted the quantum photosynthetic efficiency of beech, chestnut, and silver fir until the carbon sink modelled in the first 15 years of simulation was consistent (+/- 10%) to the average sink observed in each management type.

We downloaded climate predictors for 3PG runs from the ESGF CORDEX database, using the MPI-EMS1.2-HR GCM with a monthly scale and 0.1 deg resolution (Müller et al., 2018). First, we preprocessed with Climate Data Operators (Schulzweida 2020): merged NetCDFs of the same climate model and scenario, rotated from EUR-11 latitude-longitude grid to regular coordinates, and cropped smaller surfaces to restrict the size of climate files. Then we downscaled climate data using the CSTools R package (Pérez-Zanón et al., 2021). All the input related to site and stand characteristics, such as soil texture, stem biomass, and stand density, were gathered during fieldwork. We ran simulations for the period 2020-2100 using data from climate scenarios SSP 1-2.6, SSP 3-7.0 and a historic climate, which was obtained by randomly shuffling historical climate data (1970-2000).

To understand the effect of management on carbon stocks and sinks in beech forests we simulated three different levels of harvest intensity:

- Low: forest management with close-to-nature approaches and reduced harvest frequency and intensity, i.e., promoting conversion of coppices to high forest, and applying single tree or group selection in high forests
- Medium: sustainable management with medium harvest intensity and frequency, i.e., selection coppicing (uneven-aged coppice stools with two or three age classes on the same stool), and shelterwood cuts with long rotation for high forests
- High: Management aimed at increasing wood production, with resumption of coppicing in abandoned coppice forests, coppicing with release of standards in active coppice, and shelterwood cuts for high forest.

Table 1. Management specifics for the different modelled management intensity scenarios in 3-PGmix. *For each management intensity scenario values are given for the rotation time and the harvest intensity in percentage.*



	Management intensity		
	Low	**Medium**	**High**
Active coppice	**Coppice with reduced harvest frequency and intensity** Rotation 45 years 90% small and medium diameters 80% large diameters	**Coppice with medium harvest frequency and intensity** Rotation 30 years 95% small and medium diameters 80% large diameters	**Coppice with standards** Rotation 30 years 95% small and medium diameters 90% large diameters
Stored coppice	**Conversion to high forest** Rotation 20 years 2 cuts at15% 1 cut 20%	**Selection coppice** Rotation 30 years 30% small and medium diameters 10% large diameters	**Resumption of coppicing** Rotation 30 years 95% small and medium diameters 80% large diameters
Converted to high forest	**Tree selction** Rotation 20 years Cuts 8%	**Shelterwood cuts with long rotation** Sementation cut 30% at 110 years of age Clearing cut 100% at 140 years of age	**Shelterwood cuts** Sementation cut 30% at 100 years of age Clearing cut100% at 120 years of age
Stored coppice mixed with broadleaves	**Conversion to high forest** Rotation 20 years 2 cuts at15% 1 cut 20%	**Selection coppice** Rotation 30 years 30% timber harvest	**Coppice with standards** Rotation 30 years 90% timber harvest
Stored coppice mixed with fir	**Tree selection and conversion to high forest** Selection cutting of fir (Rotation 20 years, harvest 8%) Conversion to high forest of beech (Rotation 20 years, 2 cuts at 15% harvest, 1 cut at 20% harvest)	**Shelterwood cuts with long rotation and selection coppice** Successive clearcuts of fir (sementation cut at 80y.o. with 30% harvest, cut at 120 y.o. with 70% harvest) Steered coppice of beech (Rotation 30years; 30% timber harvest)	**Shelterwood cuts and coppice with standards** Successive clearcuts of fir (sementation cut 70y.o. with 30% harvest, clearcut 100% harvest at 100y.o.) Coppice of beech (Rotation 30years; 90% timber harvest)

Results

Carbon stocks in soil and biomass

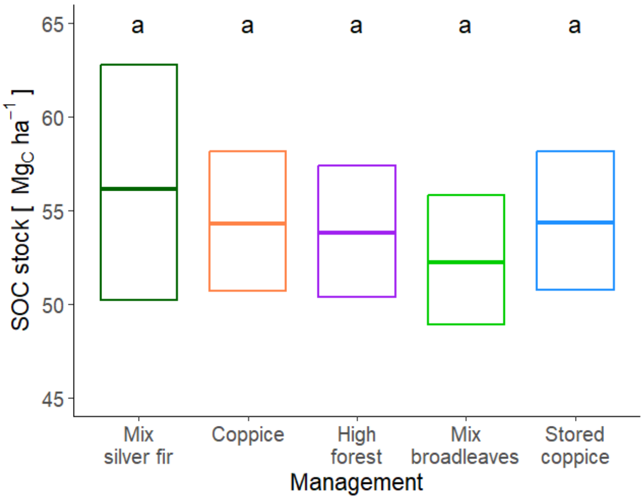


Figure 2. Carbon stocks in MgC * ha^{-1} in the first 0-20 cm of soil. *The results are derived from GLM holding constant the effects of significant variables, enabling a clearer understanding of the relationship between management and C stock results. The boxplot shows the mean value +/- the standard deviation. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

The final GLM for SOC stock included only management (factor) and total soil Nitrogen as predictors. Results show an absence of effect of management on carbon stocks in soil (Fig. 2). Soil carbon stocks in the first 20 cm of soil vary from a minimum of 52.2 ± 3.5 Mg C ha^{-1} in the Mix broadleaves and 56.1 ± 6.3 Mg C ha^{-1} in the mix with silver fir. Coppice, converted to high forest and stored coppice amount soil carbon stocks respectively at 54.3 ± 3.7, 53.8 ± 3.5 and 54.3 ± 3.7 MgC ha^{-1}.

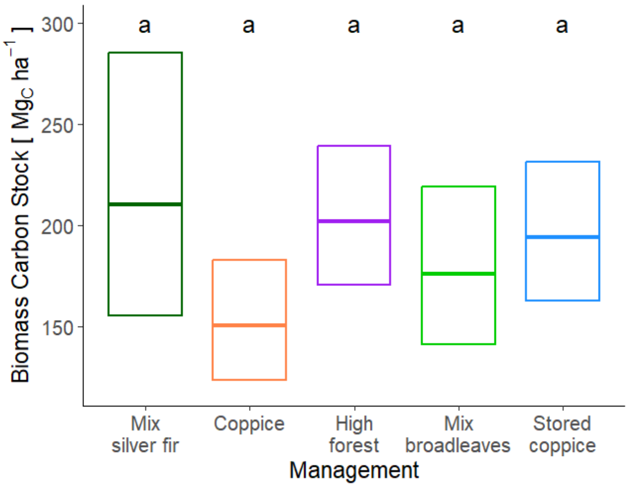


Figure 3. Biomass carbon stocks in MgC * ha^{-1} in the biomass of trees. *The results are derived from GLM holding constant the effects of significant variables, enabling a clearer understanding of the relationship between management and C stock results. The boxplot shows the mean value +/- the standard deviation. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

The final GLM for C stock in biomass included the following predictors: management (factor), elevation, tree density, mean tree age and soil organic carbon (SOC). Total soil nitrogen was excluded as it was showing high collinearity with soil organic carbon (SOC). Carbon stocks in biomass (Fig. 3) do not statistically differ among management but show more heterogeneous values with a minimum of 150 ± 30 MgC ha^{-1} in coppice and a maximum of 211 ± 65 MgC ha^{-1} in mix with silver fir. Coppice converted to high forest stock 202 ± 34 MgC ha^{-1}, mix with broadleaves 176 ± 40 MgC ha^{-1} and abandoned coppice 194 ± 34 MgC ha^{-1}.

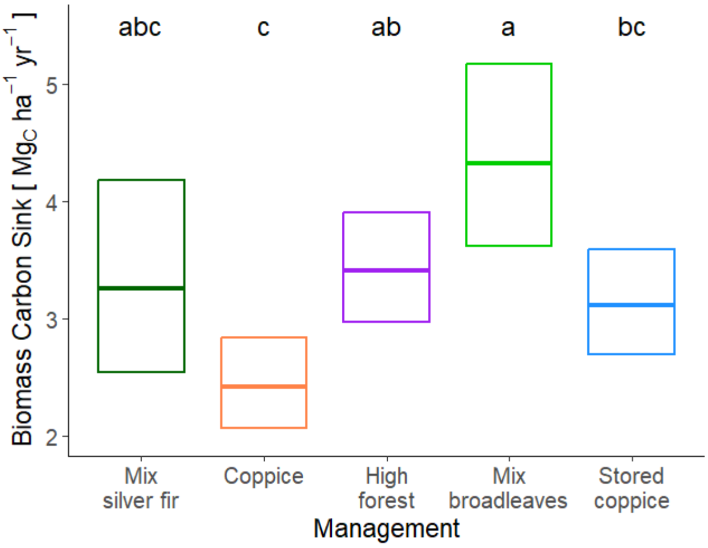


***Figure 4. Biomass carbon sinks** in MgC * ha^{-1} * yr^{-1}. The results are derived from GLM holding constant the effects of significant variables, enabling a clearer understanding of the relationship between management and C stock results. The boxplot shows the mean value +/- the standard deviation. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

The final GLM for C sink in biomass included the same predictors as C stock GLM in biomass: management (factor), elevation, tree density, mean tree age and soil organic carbon (SOC). Total soil nitrogen was excluded as showing high collinearity with soil organic carbon (SOC). Carbon sinks in biomass (Fig. 4) are significantly influenced by management. Highest carbon sink can be found in the mix with broadleaves, with an uptake equal to 4.3 ± 0.8 MgC ha^{-1} yr^{-1}, stati. These results are followed by intermediate values of high forest and mix with silver fir with 3.4 ± 0.5 and 3.3 ± 0.8 MgC ha^{-1} yr^{-1}, respectively. Finally, stored coppice and active coppice uptake yearly respectively 3.1 ± 0.4 and 2.4 ± 0.4 MgC ha^{-1} yr^{-1}. C sink in mix with broadleaves forests is significantly higher than coppice and store coppice, and high forests show higher C sink mean values than traditional coppice.

Species distribution model MaxEnt

The model for the current potential distribution of beech for the northern Apennines has an AUC of 0.9 and a TSS of 0.72 both considered good/very good. For the study area, mean daily maximum temperature of warmest month (bio5) gained significance with a permutation importance of 82%. Habitat suitability drops to low values with a max. mean summer temp above 22/23°C. Otherwise, low annual heat moisture levels are ideal as well as lower levels of precipitation seasonality. The whole of the park area is currently suitable habitat.

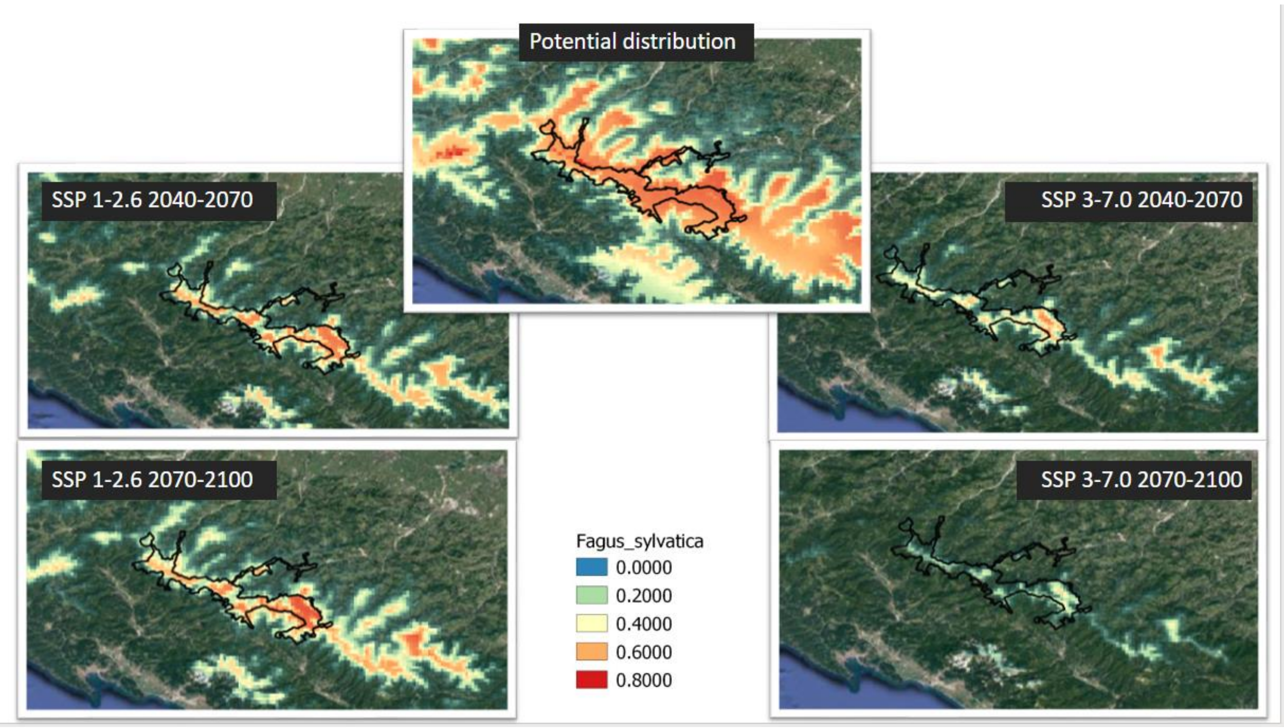


Figure 5. Results of the species distribution models. *Actual potential distribution of F. sylvatica in the area of the Tuscan Emilian National Park and potential future distribution under two climate change scenarios (0 - 0.2 very unsuitable, 0.2 - 0.4 less suitable, 0.4 - 0.6 moderately suitable, 0.6 - 0.8 very suitable, 0.8 - 1 highly suitable). Model performance high with an AUC of 0.95 and TSS of 0.85.*

The final GCM used for the future projections were: GFDL-ESM4, IPSL-C;6A-LR and MPI-ESM1-2-HR. The habitat remains relatively unchanged across SSP 1-2.6 but starts to decrease with the SSP 3-7.0 scenario both towards the middle and especially end of the century. Within PNATE the variable which is likely to be the most constraining within the model is Bio5 (max.temp of warmest month) which reaches temperatures higher than 4°C than the ideal range (Table S3). Precipitation seasonality does not exceed the ideal range, but temperature seasonality does as well as annual heat moisture, used as a drought index and calculated with the following formula: (bio1 + 10) ÷ (bio12 × 0.001) in which higher values indicate drier conditions and lower values wetter conditions. with values laying outside suitability range. Within the park the habitat shift's habitat towards the highest elevations of PNATE (Fig. 5).

Table S3. *Variable contribution, average historic value and changes under climate change scenarios*

	Mean max.temp of Warmest month (Bio5)	*Precipitation seasonality (Bio15)*	*Temperature seasonality (Bio4)*	*Annual heat moisture (AHM)*
% contribution	*90.5*	*5.1*	*2.7*	*1.7*
mean baseline	*21.58*	*31.65*	*615.9*	*15.8*
SSP1.26 2100	*24.6*	*33.33*	*660*	*17.6*
SSP3.70 2100	*28.8*	*33.85*	*697*	*20.6*

3-PGmix modelling - C stocks

3-PGmix simulations show a higher delta carbon stock (as difference between C stocks in 2020 and C stock in 2100) in climate scenarios SSP 1-2.6 compared to historical and SSP 3-7.0 climate scenarios (Fig. 6, S1; Tab. S3).

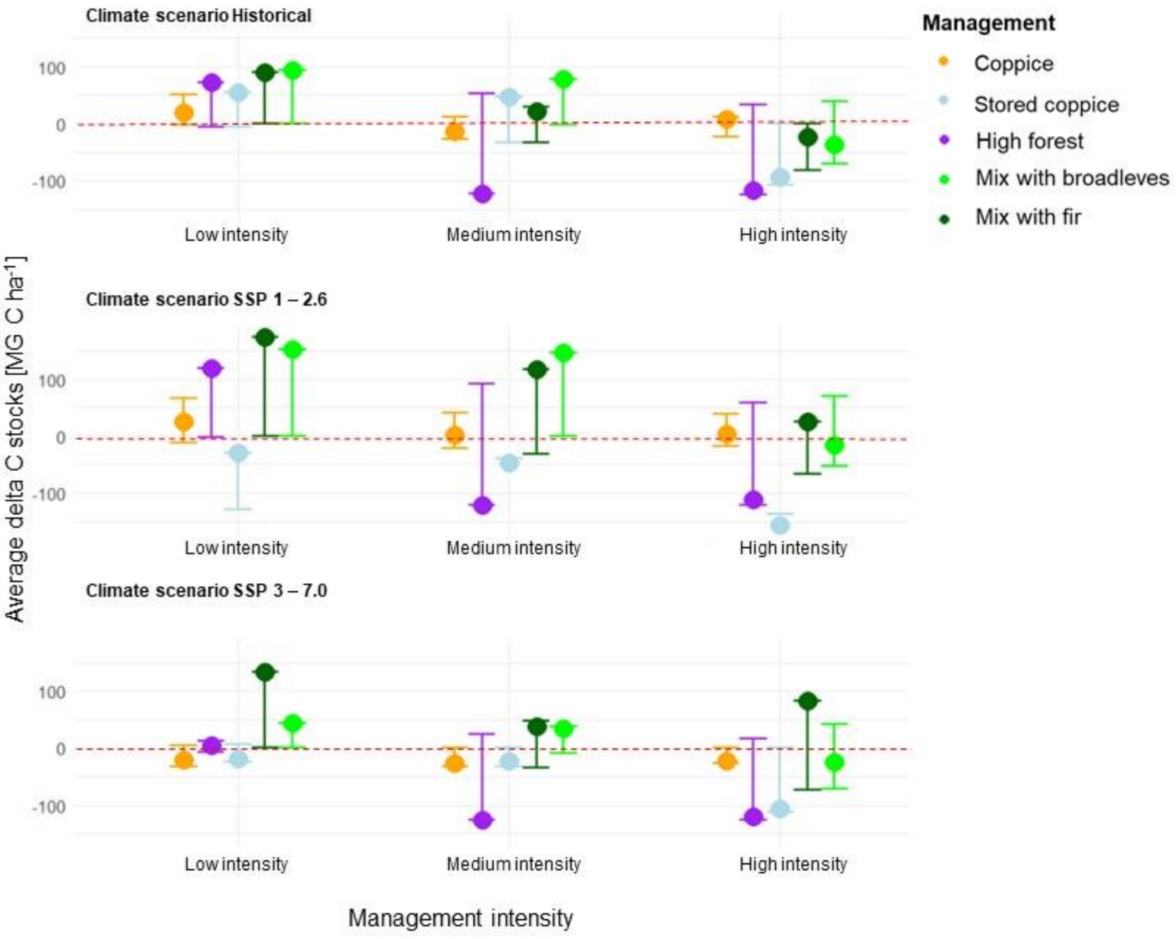


Figure 6. Delta carbon stocks over the period 2020 - 2100 *simulated with 3-PGmix for pure beech coppice (red dot), pure beech stored coppice (orange dot), pure beech high forest (light blue dot), stored beech coppice mixed with broadleaves (light green) and stored beech coppice mixed with fir (dark green). Positive error bars represent the difference between the maximum stock reached during the modelled period and the initial carbon stock (delta carbon stock max) and the negative error bars the difference between the minimum stock reached during the modelled period and the initial carbon stock (delta carbon stock min).*

Simulations with historical climate

For the historical climate change scenario, coppice shows a similar carbon balance throughout the different managements and is the only treatment with a positive net carbon increase with high intensity management (+8.7 MgC * ha^{-1}, Table S3). Stored coppice has positive delta carbon with low and medium intensity, while showing a delta C loss in high intensity management scenario. High forest has a positive carbon balance only with low intensity management, while medium and high intensity have the highest net C losses compared to other managements and intensities (respectively -123.1 MgC * ha^{-1}, -116.9 MgC * ha^{-1}; Table S3). *F. sylvatica* in mix with silver fir shows a decreasing delta C stock over the period 2020-2100 with increasing management intensity, resulting in a negative delta carbon loss only with high intensity (-23.4 MgC * ha^{-1}). The best performances in terms of delta C stock are observed with *F. sylvatica* mixed with broadleaves with low and medium intensity management (respectively + 96.2 and 77.6 MgC * ha^{-1}). The mix with broadleaves with high intensity management has a net C loss.

Simulations with climate scenario SSP 1 - 2.6

Compared to the historical scenario, the trend of different management with increased management intensity remains the same, however the positive delta C stock increase. Coppice do not significantly differ from historical scenarios, with low variation in delta C stock with increased intensity, however all the delta carbon values are positive with the lower delta C stocks with medium intensity management (+0.6 MgC * ha^{-1}). Stored coppice shows the highest positive delta carbon across management and intensities with low and medium intensity (+203.1MgC * ha^{-1} and +190.8 MgC * ha^{-1} respectively) but also the highest decrease of delta C stocks with high intensity management (-157 MgC * ha^{-1}). High forest has the same trend of the historical climate, with a positive delta C only with low intensity management, and important delta C losses with medium and high intensity management. Mix with broadleaves and silver fir has similar trends with important positive C stocks increase with low and medium intensity management (Table S3) and C losses with high intensity for mix with broadleaves, while the mix with silver fir has a positive delta C also with high intensity management (+24.5 MgC * ha^{-1}, Table S3).

Simulations with climate scenario SSP 3 - 7.0

With the most severe climate change scenario the overall carbon balance drastically changes, and the only positive delta carbon are observed with *F. sylvatica* mixed with broadleaf and silver fir. With SSP 3 -7.0 *F. sylvatica* mixed with silver fir has a better performance than historical climate, with highest delta carbon increase with low intensity management (+133 MgC * ha^{-1}). Mix with broadleaves have a negative delta C with high intensity management, and a positive balance with medium and low intensity management (+34.2 and +44 MgC * ha^{-1} respectively). Active coppice has the same constant trend of the other climate scenarios, but the delta is always negative, independently of the management intensity (Table S3). Stored coppice with low and medium intensity management shows low negative carbon delta (Fig YY, Figure 3), while with high management the delta C losses increase (-106 MgC * ha^{-1}). Finally, high forest has the highest losses with medium and low intensity management (- 125.6 and 121.3 MgC * ha^{-1} respectively) while has low positive C delta with low intensity management.

3-PGmix modelling - C sinks

Average carbon sink over the period 2020 - 2100 is highly sensitive to climate change, while less sensitive to management intensity. C sink is higher with climate scenario SSP 1 - 2.6 and lower with climate scenario SSP 3 - 7.0, with the exception of mix with silver fir, where the lowest average C sink can be observed for the historical climate scenario (Fig. 7, S2; table S4).

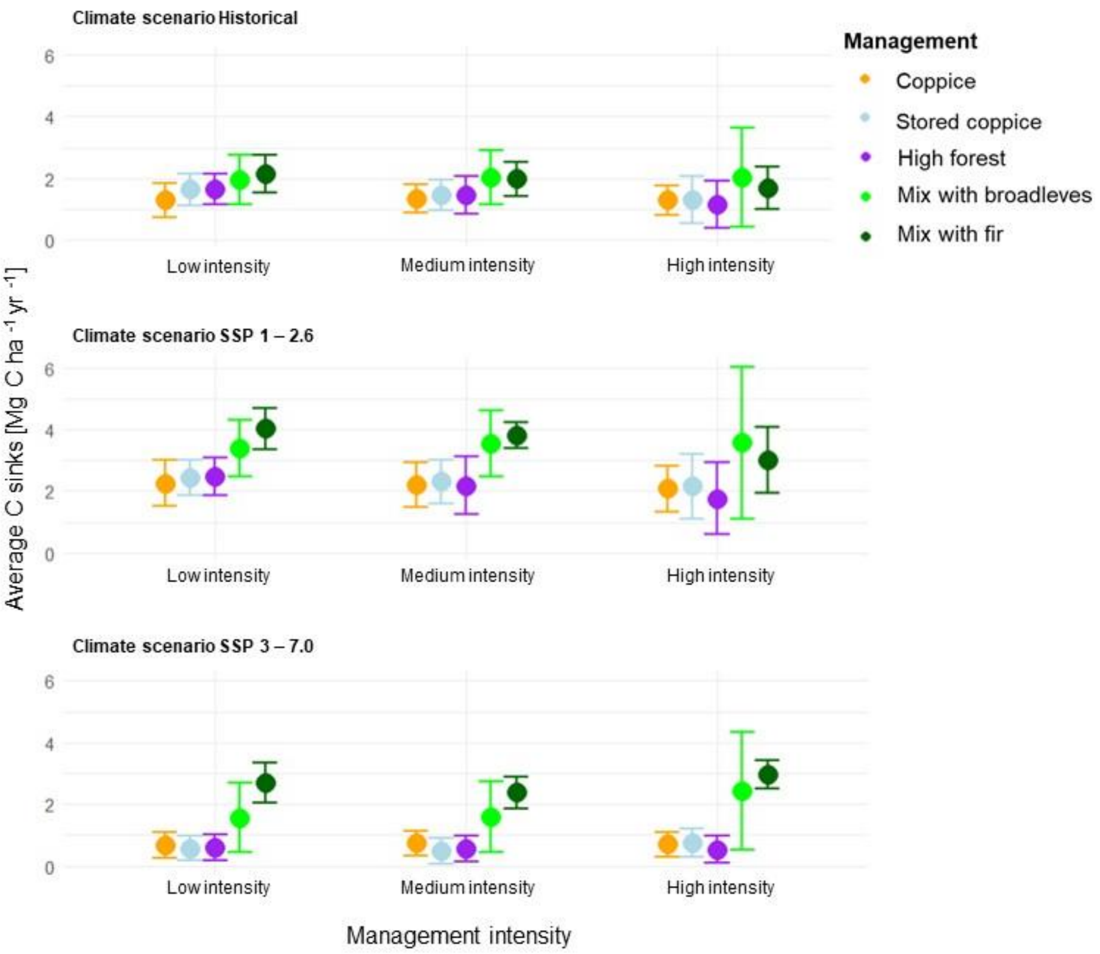


Figure 7. Average carbon sink over the period 2020 - 2100 *simulated with 3-PGmix for pure beech coppice (red dot), pure beech stored coppice (orange dot), pure beech high forest (light blue dot), stored beech coppice mixed with broadleaves (light green) and stored beech coppice mixed with fir (dark green). Error bars represent the standard deviation of the carbon sink over the modelled time period.*

Simulations with historical climate

Active coppice does not respond to increased intensity of management and have a constant C sink of 1.3 MgC * ha^{-1} * yr^{-1}. Stored coppice and high forest decrease the C sink with increasing intensity, passing from 1.6 MgC * ha^{-1} * yr with low intensity management to 1.3 and 1.1 MgC * ha^{-1} * yr^{-1} respectively. Stored coppice mixed with broadleaves has a constant carbon sink of 2 MgC * ha^{-1} * yr^{-1} independently of the management intensity. Stored coppice mixed with silver fir present the highest C sink of 2.2 MgC * ha^{-1} * yr^{-1} with low intensity management, that decrease with increasing intensity to 2 and 1.7 MgC * ha^{-1} * yr^{-1} with medium and low intensity management respectively.

Simulations with climate scenario 1 - 2.6

In Climate scenario 1 - 2.6 Active coppice shows an increased C sink potential that decrease with intensity from 2.3 to 2.1 MgC * ha^{-1} * yr^{-1} with low and high intensity respectively (Fig YY, Table S4). Similar average C sink values and response to management are modelled for stored coppice (Fig YY, Table S4). High forest has a higher C sink variability but similar trend, with 2.5 MgC * ha^{-1} * yr^{-1} with low intensity management and 1.8 MgC * ha^{-1} * yr^{-1} with high intensity management. Higher and more constant are the C sink average values of stored coppice mixed with broadleaves (3.4 MgC * ha^{-1} * yr^{-1} for low intensity and 3.6 MgC * ha^{-1} * y^{-1} for medium and high intensity). Again, mix with silver fir shows the highest C sink potential with low intensity management (4 MgC * ha^{-1} * yr^{-1}) decreasing with increasing management intensity (3.8 and 3 MgC * ha^{-1} * yr^{-1} for medium and high intensity).

Simulations with climate scenario 3 - 7.0

The climate change scenario 3 - 7.0 has the lowest modelled carbon sinks. Active coppice has a constant C sink of 0.7 MgC * ha^{-1} * yr^{-1} independently of the management intensity. Stored coppice, interestingly, shows increasing carbon sinks with increasing management intensity (0.6 MgC * ha^{-1} * yr^{-1} with low intensity, 0.7 MgC * ha^{-1} * yr^{-1} with high intensity management). High forest shows rather constant C sink with increasing management intensity (0.6 MgC * ha^{-1} * yr^{-1} for low and medium intensity, 0.5 MgC * ha^{-1} * yr^{-1} for high intensity). Mix with broadleaves and mix with silver fir are the management that perform the best and they increase the C sink with increasing management intensity. Stored coppice in mix with broadleaves pass from 1.6 MgC * ha^{-1} * yr^{-1} with medium and low intensity management to 2.4 MgC * ha^{-1} * yr^{-1} with high intensity management. Mix with silver fir from 2.7 MgC * ha^{-1} * yr^{-1} with low intensity to 3 MgC * ha^{-1} * yr^{-1} with high intensity management, the highest value for this climate scenario.

Discussion

Analyzing the effect of beech forest management on their carbon storage capacity is a key issue in understanding their response to different contexts. In the context of climate change this becomes increasingly crucial, providing important insights about the mitigative potential of forest management. The results of this study offer a comprehensive perspective on carbon dynamics in the forests of the Tuscan-Emilian Apennines National Park, and may be of practical significance for forest managers, especially when in need to address climate change challenges. Furthermore, this study explores the impacts of different management intensities and their interaction with climate scenarios, providing a detailed overview of how future climate conditions might influence the carbon dynamics of these forests. The results show an interesting variability of response when crossing climatic and management intensity scenarios, showing higher growth under more promising climatic scenarios and lower productivity under high management intensities. However, results are variable with varying forest management, paving the way for interesting considerations regarding the future of beech forests in the Tuscan-Emilian Apennines. Knowledge of these forest dynamics is crucial in developing targeted management guidelines that balance carbon sequestration with other ecosystem services, such as biodiversity conservation and wood production. This understanding can help forest managers, policymakers and administrators develop management practices that ensure the long-term sustainability and functionality of forest ecosystems in the face of climate change.

Effect of mixture and management on soil organic carbon stocks

Beech-fir mixed forests had more heterogeneous SOC stock and higher soil carbon concentration than pure forests. However, forest management types had no effect on total SOC stock (Fig. 2). Both evidence can be due to site morphology and soil depth. Beech and fir mixed forests on the Tuscan-Emilian Apennines generally grow at higher elevations than pure beech or other broadleaf forests (Tab. S1), occurring on more impervious and rocky soils of shallow depth. The presence of outcropping rocks often creates a highly heterogeneous soil, with some bare patches and others where the spaces between outcropping rocks result in pockets of litter accumulation. The litter accumulation and the fact that deeper mineral horizons were often absent have resulted in a carbon percentage that is on average higher in forests mixed with fir than in the other managements analyzed (Fig. S3). The lower bulk density of this type of horizon means, however, that there is no difference between the mix with silver fir and the other treatments after conversion to carbon stock. The same dynamics are reflected by the pedotransfer function, that follows an inverse correlation between SOC% and bulk density, determining a lower bulk density for mix with silver fir management as the carbon content in % was relatively high (Fig. S3) An important step to determine the carbon stock in these areas would be to map the emergent rocks and correct the carbon stock amounts for the presence of soilless areas. The higher SOC concentration, however, is confirmed by other studies (Rehschuh et al., 2021, 2019). The authors also observed a higher SOC stock in beech mixed with fir than in pure beech forests, possibly due to a higher crown density or different root system conformation (Rehschuh et al., 2021, 2019). However, the increased SOC stocks from the study do not discuss the slope, rockiness, and organic horizon depth, making a comparison with our situation difficult. At the same time, Rehschuh et al. (2021) found no differences between the SOC of pure beech forests and beech forests mixed with other broadleaves, confirming our results. Finally, the absence of differences between pure beech management shows a good resilience of soil carbon content to changing forest utilization, confirming that silvicultural practices have relatively little influence in the C edaphic stocks of beech forests (Tejedor et al., 2017; Wäldchen et al., 2013).

Biomass stocks and sinks

In the case of total carbon stocks in biomass, the results also show no significant differences when varying forest management, although forests mixed with fir again show greater biomass data variability. These results are unexpected, as recent studies have often shown how species or management diversity can influence the amount of carbon stored in forests (Antonucci et al., 2021; Bouriaud et al., 2019; Kaipainen et al., 2004; Kasper et al., 2021). The absence of differences may in part be due to the low intensity of forest use by forest managers in the Tuscan-Emilian Apennines. Local management, in fact, is carried out with long rotations, producing forests where thinning or cutting frequency and intensity is sufficiently low to allow a reconstitution of the stocks (Bouriaud et al., 2019). In particular, the beech coppice forests we analyzed in this study had an average age generally higher than the canonical silvicultural turn, producing sufficiently high C stock values to show no significant differences ($p > 0.237$). In our study, both forests that had been under forest management in the past and unmanaged forests were included in the "beech-fir mix" category, including rather diverse forest contexts. In addition, in a recently published study, the genetic composition of silver fir stands across the PNATE territories was analyzed, demonstrating a high genetic variability of the species and a different growth response to climate (Oggioni et al., submitted). These two evidences may explain the high variability of carbon stock data of forests mixed with silver fir, highlighting the benefits of this specific composition in the most productive forest plots (Schwarz and Bauhus, 2019).

The results on C sink, i.e. the amount of carbon stored annually by forests (MgC * ha^{-1} * yr^{-1}), reveal significant differences according to forest management strategies. On average, beech mixed with other broadleaves uptake more carbon than coppice in rotation or stored coppice, both of which are considered pure beech forests. High forests composed of pure beech and the mix with silver fir reveal intermediate values. The distribution of C sink values in the two types of mix (deciduous or fir) shows a higher C data variability than in pure forests, possibly due to the variability of growth responses of the different species considered in the mixes. Indeed, it is often shown how beech mixed with other broadleaf trees improves its ability to store carbon and resilience to external stresses, due to functional diversity and complementarity between species, maintaining a more constant growth over time and improving the ecosystem service supply (Antonucci et al., 2021; Leuschner and Ellenberg, 2017; Zimmermann, 2016). Our results also highlight how the beech-fir mix can sometimes be highly productive in terms of C sinks, with several studies highlighting the importance of the complementarity between beech and fir with changing climatic conditions (Baumbach et al., 2019; Schwarz and Bauhus, 2019). Finally, our results show a general increase in the carbon sink with forests managed with longer rotations and higher average age as already found by other authors (Kaipainen et al., 2004). Coppice and stored coppice result in significantly lower C sink values than the mix with broadleaves, which may be due to the fact that local managers cut the coppice forests abundantly over the age prescribed by law of 30 years. In fact, C sink in forests rapidly increases with age in the first 20-30 years and then rapidly decreases (Zhou et al., 2015).

Potential and future distribution of beech forests

Under the selected scenarios, end-of-century climate will become less hospitable for beech forests. Mean maximum temperature of warmest months will exceed the ideal range by 2-5 °C in SSP1-2.6 and SSP3-7.0, respectively. Annual heat moisture and seasonality will also exceed ideal values for beech. Such changes may determine a decline in vitality and distribution of beech, a species characterized by a high drought sensitivity, as also reported by other studies at least at the lowest elevations (Fang and Lechowitz 2006; Piovesan et al., 2008). Consequently, within the projections, it is predominantly summer heat and likely drought conditions restricting the beech range across the park but also nation- wide (Innangi et al., 2015). Whilst overall SSP1.26 does project a significant habitat decrease, SSP3.70 is a truly critical scenario in which survival of the species across the park may not be guaranteed and dynamics like population connectivity and gene flow will likely be lost. Our own, as well as various other models, agree that towards the end of the century beech could have lost all connectivity between populations and be restricted to some national parks in southern Italy, the Abruzzi region as well as the Park and the alps. As such the Park emerges as a refuge should the climatic scenarios hold true (Valentini et al., 2000; Nocentini, 2009). However, a variety of factors may be adversely at play at higher elevations such as a high irradiation regime detrimental to regeneration and seedling survival. Similarly, it could be related with spring frost, for which forest cover and litter plays a protective role (Aussenac et al., 2002; Pignatti, 2011). This being said, MaxEnt only allows for an assessment of suitable climatic and topographic conditions however does not allow to model the influence of silviculture and forest management on microhabitat conditions. As discussed, thinning may be a practice to alleviate drought stress, mixed forest may allow beech to recover faster from drought and forest cover tends to lower the overall temperature below the canopy cover as well as maintain better soil conditions and moisture (Lebergeois et al., 2013; Schwarz and Bauhus, 2019; Montagnoli et al., 2021).

Future scenarios for beech in the Apennines

Modelling the effect of management and mixture is a key step to better understand the ideal management options for climate change adaptation and mitigation (Antonucci et al. 2021). However, only 15% of studies regarding management effect on C stocks and sink in beech forests were conducted on coppice management, and few modelling work was implemented on the subject (Antonucci et al. 2021). This study is therefore an important starting point to unravel the effect of management of coppice in different climate change scenarios, and the possibilities of using a process-based model to investigate them. It must be underlined, however, that a calibration was made on photosynthetic efficiency to return a modelled value of C sink of the first 10 years of modelling similar to the one observed in the field (+/- 10%). Data collected in the field regarding density, diameter, height, crown geometry, and growth rate were used to model the different managements. However, no further adaptation of the model was implemented to better simulate coppice physiology in 3-PGmix. Further studies should focus on implementing a specific set of parameters for coppice management. This is one of the reasons why 3-PGmix thinning module is still considered not completely accurate, since it can under- or overestimate biomass after thinning (Lopéz Serrano et al., 2015). An important factor that needs to be considered is the time of the cut, especially for shelterwood systems. Considering the delta C stocks (Fig. 6, S1) the timing of the cut deeply influences the final carbon stock, which in turn influences the delta carbon stock. The timing of the cut was decided to mimic realistic first management options starting in 2020, and the final year 2100 was decided arbitrarily. A different time period would result in different delta C stock results. This is not true, however, for the average C sink, that consider the entire lifespan of the forest during the modelled 80 years.

Climate change scenario SSP 1 - 2.6 favor forest carbon sink and, with low management, also conservation of forest carbon stocks. This behavior has been observed by previous modelling work, that shows the increase of CO_2 concentration being positively related with photosynthetic efficiency and biomass production, the so-called CO_2 fertilization (Reyer et al. 2014). However, this dynamic is lost in the scenario SSP 3 - 7.0. Different authors underline how in southern Europe a more intense climate change effect can impact the productivity of beech forests due to changes in environmental drivers (Schelhaas et al. 2015; Zimmermann et al., 2016). It is interesting to note that, with increasing climate change intensity, the effects of management are less pronounced (as difference between low intensity and high intensity management on delta carbon stocks and average carbon sinks). The stress related growth decreases in the SSP 3 - 7.0 scenario is therefore more prominent than the one caused by management intensity and reduces the possibility of increasing forest carbon sinks with less intense management options.

Active coppice management shows the lowest variability of carbon stocks and average carbon sinks with increasing climate change effects. This effect could be due to the short rotation times of beech coppice (30 - 45 years) that sensibly decrease the impact of competition, improving recovery to drought stress and to climate change growth reduction. Meta analysis shows that density reduction can alleviate growth declines during drought, however the effects on growth after stress are uncertain as local-scale processes play a pivotal role in influencing these responses (Castagneri et al., 2022). Active coppice is also less sensitive to an increase of management intensity. Lengthening the rotation does not seem to significantly increase the carbon storage in active coppice forest. However, the maximum rotation increase that can be considered is 45 years, as an older coppice would have to be converted in high forest under Italian law (Regione Emilia Romagna, 2018). For this reason, under the ‘active coppice management’, it might be preferable to increase the high intensity management and prioritize other ecosystem services (e.g. productivity) than carbon storage, as in the legislation limits active coppice do not seem to show high margins of carbon storage increase.

Stored coppices show pretty consistent biomass carbon sinks over the modelled period, although delta carbon stocks drastically change between low/medium intensity and high intensity management. Return to active coppice management has a dramatic effect on delta carbon stocks, however it does only marginally influence the carbon sinks. It is interesting to notice how the medium management (e.g. stored coppice) has values for delta C stock and average carbon sink close to the one of low intensity (conversion to high forest). This result underlines the possibility of a resumption of management with medium intensity, to preserve carbon sink and accumulated stocks without losing the cultural and economic value of the coppice management. As expected, conversion to high forest has the highest sensitivity to management: single tree selection has better performances in terms of sinks and delta carbon stocks compared with shelterwood systems, as confirmed by the majority of literature (e.g. Gusti 2020; Ameray et al., 2021, 2023). Increased rotation length contributes to augment the carbon stocks in the forests (Kaipainen et al., 2004; . Couture and Reynaud, 2011; Yan, 2018). However, it is interesting to notice that, in SSP 3 - 7.0, so in more extreme climate change scenarios, the effect of management is less intense, probably due to stresses related to environmental factors that overshadow the effect of management. It is important to underline, once again, that to better evaluate the role of managed forests as carbon stocks also products and their fate should be considered. In addition, natural regeneration processes are hindered by climate change, making renovation in high forest stands particularly difficult (Cullotta et al., 2016).

Mixtures of beech with silver fir and broadleaves have proven to have the best performance in terms of average carbon sink and delta carbon stocks, across managements and climate change scenarios. The better performance of mixed forest stands in terms of sinks and stocks and in face of climate change is supported by a large body of literature (e.g. Zimmermann, 2016; Paul et al., 2019a, 2019b; Pretzsch, 2020) with fir specimens showing larger diameters compared to F. sylvatica (Thurm & Pretzsch, 2016). Modelling the effect of beech coppice mixed with broadleaves, however, is a needed step to better understand possible scenarios of beech forest facing climate change (Antonucci et al., 2021). Due to the sensitivity of beech to droughts (Zimmermann, 2016), silver fir tends to replace beech specimens in the mix, with a future dominance of conifer species in the beech mixture. At lower elevations, in mix with broadleaves, F. sylvatica is expected to lose competitive strength in the large dominant trees (as they struggle to face droughts), however smaller trees might still be strong competitors, maintaining the forest composition unaltered (Zimmermann, 2016).

When in mix with broadleaves, conversion to high forest has the best performance in terms of delta carbon stocks, but similar average carbon sink, with the exception of the high management option in SSP 3 - 7.0 having higher average carbon sink compared to low and medium management. This result underlines that increasing management intensity has lower (and sometimes positive) effects on biomass carbon sinks, as observed by other studies (e.g. Krug 2019; Ameray et al., 2021). This effect is probably due to lower competition, a more proportional contribution of all sizes of trees to carbon sinks, improved resource use efficiency (Krug 2019). However, a higher management intensity means a higher biomass removal, therefore a decrease in the carbon stocks. It is necessary to consider the fate of the wood-derived products, their life cycle and the substitution effect to really understand the effect of an increase of management on carbon stocks and climate change mitigation (Profft et al., 2009; Iordan et al., 2018). The overall C sink of mix with broadleaves shows a higher variability, probably due to the differential responses of beech and chestnut to climate. This higher C sink results variability might be due to the parameterization of chestnut. Parametrization of forest species is still an important bottleneck for process-based models like 3PG, and should be better investigated in the field, creating a large database of parametrized species (van Oijen 2017; Forrester et al., 2021). It is important to underline that in our modelling the occurrence of disturbances was not included. Disturbances are likely to become an important driver for carbon storage dynamics, especially under a climate change perspective and the effect of management and mixture on their return time should be considered to better understand the climate mitigation potential of these forests (Seidl et al., 2014; Müller et al., 2019).

The 3-PG model has gained broad acceptance due to its successful performance in forest management and practical research applications (Gupta et al., 2019). It shows good predictive abilities in different climate conditions and for a variety of species. Of the several model variants that have been developed, the r3-PG package for R represents one of the fastest, allowing to perform complex computational experiments within the R environment (Trotsiuk et al., 2020). A key feature of the model is its sensitivity to different climate conditions: the growth of trees accounts for variations in temperature, precipitations, vapor pressure deficit (VPD) and CO_2 concentration. The overall effect of climate change is thus a complex interplay between CO_2 fertilization effect, optimal temperature ranges and potential reduction in photosynthesis rate due to extreme temperatures and precipitation scarcity (Almeida et al., 2016, Gupta et al., 2021). Despite its wide use, 3-PG still has some limitations. Bibliography provides parameters for the most common species from Central Europe and tropical areas. Nevertheless, different provenances can lead to different values of several parameters, due to the high plasticity of some species (Forrester et al., 2021): since parametrization demands a high effort in data collection, it is common to use species-specific (and not provenance-specific) parameters. Moreover, a wide number of species is still not parameterized, as for chestnuts in our study area. It is worth noting that models are a simplification of reality, and parameters may not exactly represent their real-world counterpart. Thus, it appears legit to fine-tune some parameters in order to make the model more representative of reality (van Oijen 2017; Forrester et al., 2021). Finally, several studies have documented the limitations of the model to accurately reproduce soil and plant water balance (Almeida et al. 2016), and to simulate the interactive effects of CO_2 fertilization with water and nutrient availability (Almeida et al., 2009). In summary, while the 3-PG model is a powerful tool in forest management and research, understanding its limitations, especially in parameterization and sensitivity to climatic factors, is crucial for accurate application and interpretation of its results.

Management guidelines for beech forests in the Apennine region

The main guidelines that derive from this study are:

- Increase mixture of beech forests with broadleaves at lower elevation and with silver fir on the upper tree limits to increase climate mitigation potential and carbon stock.
- Active coppice can be preserved as it is the management that shows the lower variability due to climate change in terms of average carbon sink and delta carbon stock. Moreover, it provides important provision and cultural services.
- High forest should be protected, and management should be reduced to the minimum, to provide biodiversity services and protect carbon stocks, and a shelterwood system is suggested.
- For abandoned coppice, a conversion to high forest or a management with medium intensity (e.g. steered coppice) is suggested and can be adapted to the local needs.

Landscape heterogeneity is essential for enhancing ecosystem services (Catullo et al., 2017), as patches of different species mixtures and different aged forests. We add that also different management can provide an important benefit to ecosystem services provisions, where conserving different management can increase sustainable use of forest and resources and, ultimately, climate change resilience, introducing the concept of ‘forest management mosaic’.

Conclusions

This study offers valuable results on the interaction between climate change, forest management and carbon sink capacity in beech forests of the Tuscan-Emilian Apennines. Our results underline the role of beech forests as carbon sinks in a changing climate and highlight how different management strategies, including mixing with other species or different silvicultural approaches, influence their ability to respond to climate.

Modelling of the beech's climatic niche under different climate scenarios predicts significant reductions in its distribution range over the next century, underlining the role of the Tuscan-Emilian Apennine National Park as a potential last refuge for the species under more extreme scenarios. This evidence is essential when defining conservation and management strategies, suggesting the need for enhanced climate resilience to ensure the survival of beech forests under changing environmental conditions. The analysis of carbon stocks and sinks highlights how the mixing of beech with other species can significantly increase carbon stocks and sinks in the Apennines. This underlines the importance of promoting a certain degree of biodiversity in local forest management practices, not only for ecological resilience but also to increase the supply of ecosystem services. Future growth simulations emphasize this result once again, highlighting how the mix with fir or other broadleaf trees shows significant differences in carbon storage and sequestration capacities compared to pure beech forests. Simulation of different beech managements also reminds us how the transition from traditional coppice to high coppice could lead to increased carbon uptake, offering a strategic pathway for climate change mitigation. The evidence mentioned here are generally valid for low and medium intensity silvicultural treatments, while with high intensity utilizations the differences between management types are difficult to quantify.

These results may have direct implications for forest management policies in the Tuscan-Emilian Apennines and similar ecosystems. We therefore emphasize the need for an integrated approach that considers both ecological and climatic factors in forest management to optimize carbon sequestration and sustain ecosystem services at the local scale. Our study contributes to the broader understanding of the role of forest ecosystems in climate change mitigation by providing a set of replicable analyses in other contexts to shed light on the response of forest species to climate change.

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Supplementary Materials

Table S1. *Average structural and topographic data collected in the field for each of the five identified beech managements. The mean data refer to the sample trees used for the parameterization of the 3-PGmix model. The following are shown: diameter, height, age, elevation, slope, and forest density.*

Management	**Species**	**Diameter** [cm]	**Height** [m]	**Age** [years]	**Elevation** [masl]	**Slope** [%]	**Forest density** [plant * ha^{-1}]
Coppice	*F. sylvatica*	20.2±8.2	15.1±3.6	60.4±16.7	1386.7±93.5	30.4±13.8	2087.2±691.3
Stored Coppice	*F. sylvatica*	23.7±7.7	17.1±3.9	67±9.6	1250±114.8	30.7±17.5	1966.1±469.5
High forest	*F. sylvatica*	26.5±8.5	19.2±3.1	71.8±15.4	1352.9±173.9	30.7±11.6	1276.1±518.5
Stored coppice mix with broadleaves	*F. sylvatica*	24.2±7.8	16.2±4.6	55.5±15.8	1073.9±54.3	34.4±15.9	1205.4±491.5
Stored coppice mix with broadleaves	*Broadleves*	25.4±10.4	13.6±3.1	47.4±16.3			
Stored coppice mix with fir	*F. sylvatica*	41.1±14.9	18.4±5.9	90±36.5	1512.1±140.2	37.9±26	1540.1±236.4
Stored coppice mix with fir	*A. alba*	22.2±6.8	16.3±4.3	77.7±21.7			

Table S2. *Parameters used in MaxEnt simulations to set up species distribution models (SDMs).*

variable	*explanation*	*scale*
AHM	Annual heat moisture	
Bio1	Mean annual air temperature	°C
Bio2	Mean diurnal air temperature range	°C
Bio3	Isothermality	°C
Bio4	Temperature seasonality	°C
Bio5	Mean daily maximum air temp of warmest month	°C
Bio6	Mean daily minimum air temp of coldest month	°C
Bio7	Annual range of air temperature	°C
Bio8	Mean daily air temp of wettest quarter	°C
Bio9	Mean daily air temp of driest quarter	°C
Bio10	Mean daily air temp of warmest quarter	°C
Bio11	Mean daily air temp of coldest quarter	°C
Bio12	Annual precipitation amount	kg m-2 year-1
Bio13	Precipitation of wettest month	kg m-2 month-1
Bio14	Precipitation of driest month	kg m-2 month-1
Bio15	Precipitation seasonality	kg m-2
Bio16	Mean monthly precipitation of wettest quarter	kg m-2 month-1
Bio17	Mean monthly precipitation of driest quarter	kg m-2 month-1
Bio18	Mean monthly precipitation of warmest quarter	kg m-2 month-1
Bio19	Mean monthly precipitation of coldest quarter	kg m-2 month-1

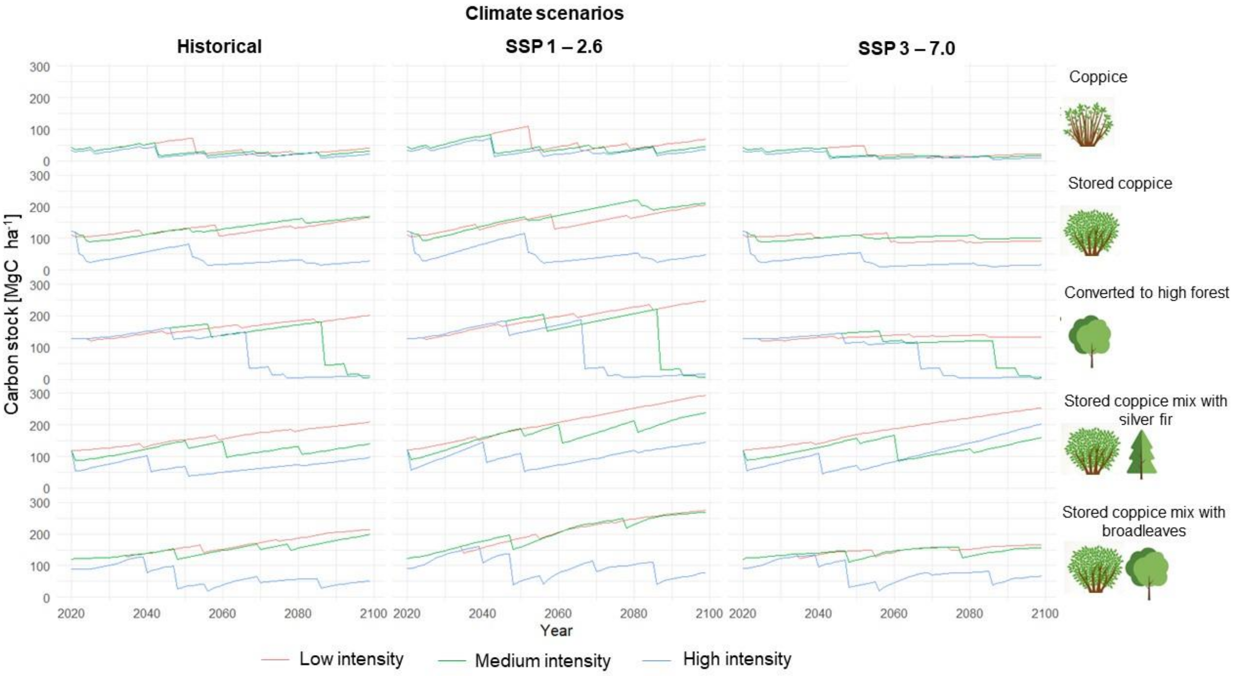


Figure S1. *Carbon stock results (Mg C * ha^{-1}) of the 3-PGmix simulations for each climate scenario (historical., SSP 1-2.6, SSP 3-7.0) and forest management type (coppice, store coppice, high forest, stored coppice mixed with broadleaves and stored coppice mixed with fir). The three colored lines shown in each graph represent the forest management intensity applied to the simulation (red = low, green = medium and blue = high intensity) according to the parameters shown in Tab. 1.*

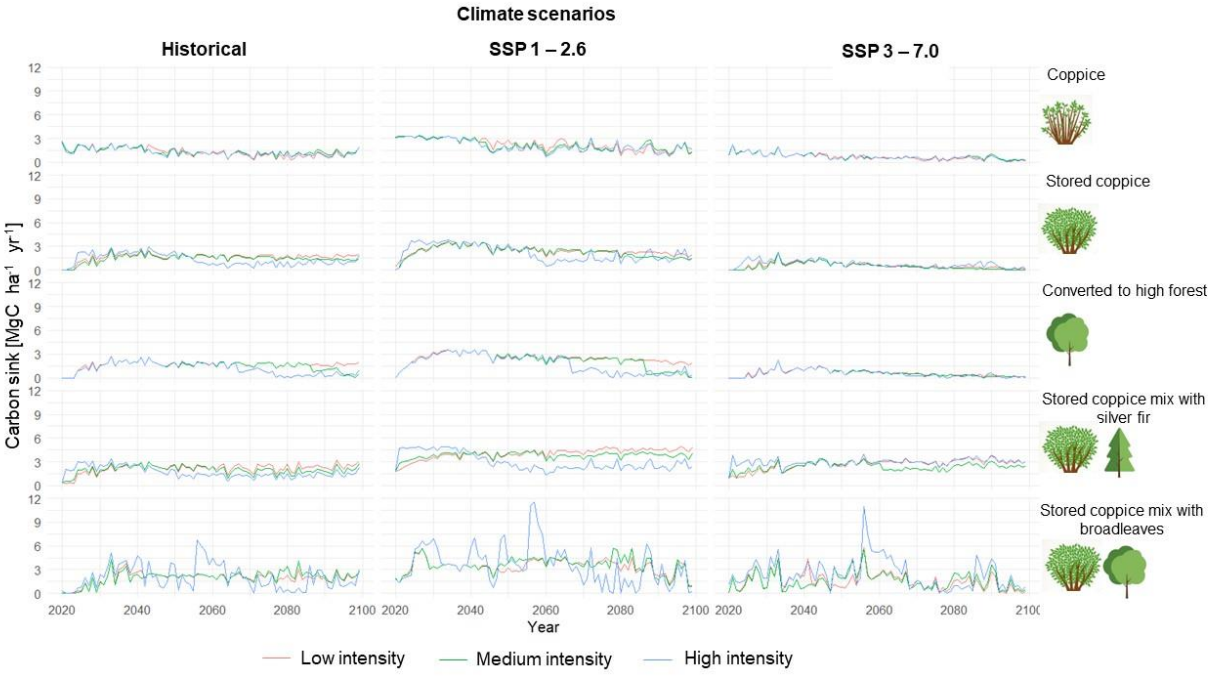
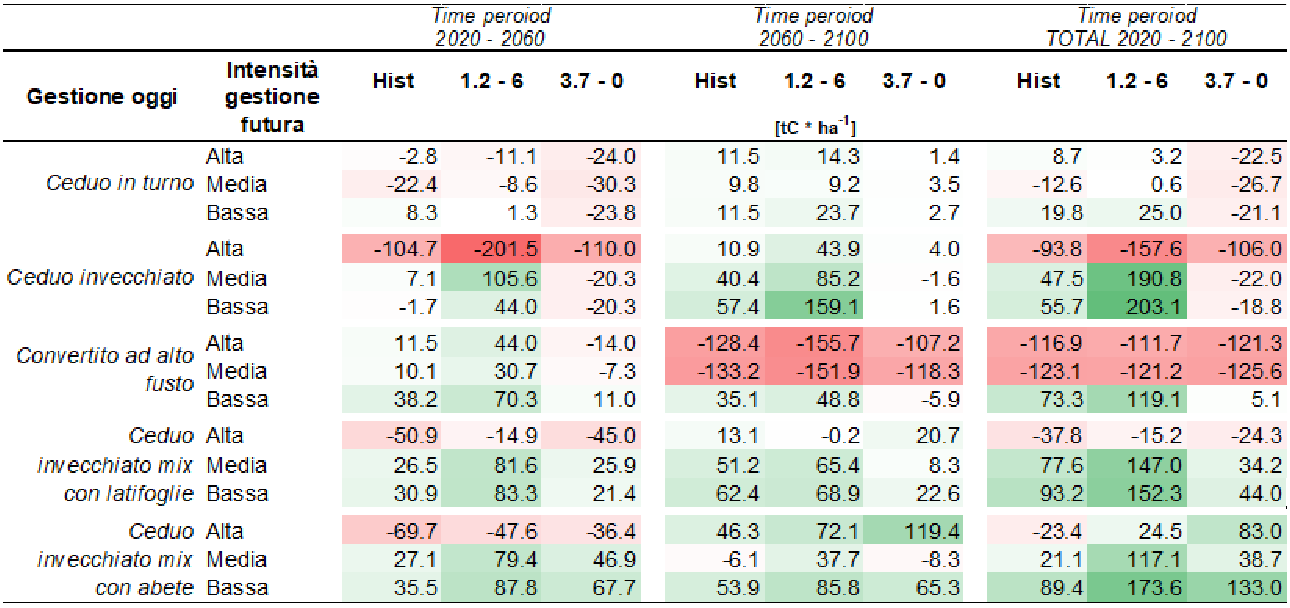


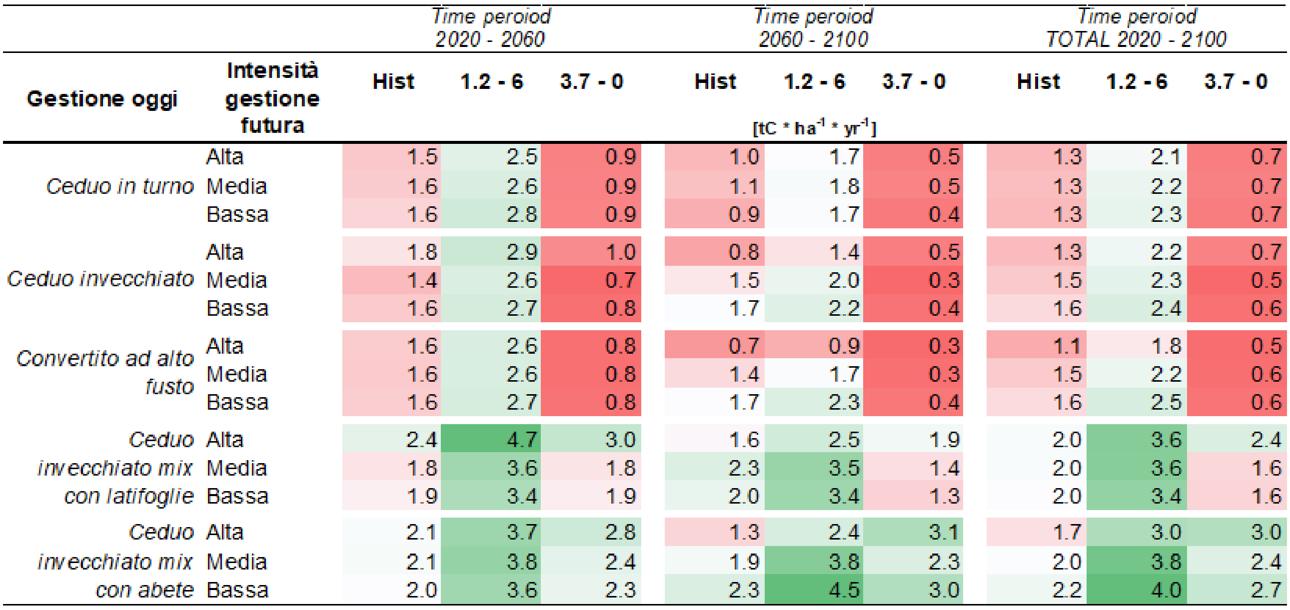
Figure S2. *Carbon sink results (Mg C * ha^{-1} * yr^{-1}) of the 3-PGmix simulations for each climate scenario (historical., SSP 1-2.6, SSP 3-7.0) and forest management type (coppice, store coppice, high forest, stored coppice mixed with broadleaves and stored coppice mixed with fir). The three colored lines shown in each graph represent the forest management intensity applied to the simulation (red = low, green = medium and blue = high intensity) according to the parameters shown in Tab. 1.*

Table S3*. *Delta carbon stocks *over three different periods of time i) 2020 - 2060, ii) 2060 - 2100, and iii) 2020 - 2100. Red or green cells indicate negative or positive deltas, respectively, and their color intensity reveals the difference from delta=0.*



		Time peroiod 2020 - 2060			*Time peroiod 2060 - 2100*			*Time peroiod TOTAL 2020 - 2100*		
Gestione oggi	**Intensità gestione futura**	**Hist**	**1.2 - 6**	**3.7 - 0**	**Hist**	**1.2 - 6**	**3.7 - 0**	**Hist**	**1.2 - 6**	**3.7 - 0**
						[tC * ha^{-1}]				
Ceduo in turno	Alta	-2.8	-11.1	-24.0	11.5	14.3	1.4	8.7	3.2	-22.5
	Media	-22.4	-8.6	-30.3	9.8	9.2	3.5	-12.6	0.6	-26.7
	Bassa	8.3	1.3	-23.8	11.5	23.7	2.7	19.8	25.0	-21.1
Ceduo invecchiato	Alta	-104.7	-201.5	-110.0	10.9	43.9	4.0	-93.8	-157.6	-106.0
	Media	7.1	105.6	-20.3	40.4	85.2	-1.6	47.5	190.8	-22.0
	Bassa	-1.7	44.0	-20.3	57.4	159.1	1.6	55.7	203.1	-18.8
Convertito ad alto fusto	Alta	11.5	44.0	-14.0	-128.4	-155.7	-107.2	-116.9	-111.7	-121.3
	Media	10.1	30.7	-7.3	-133.2	-151.9	-118.3	-123.1	-121.2	-125.6
	Bassa	38.2	70.3	11.0	35.1	48.8	-5.9	73.3	119.1	5.1
Ceduo invecchiato mix con latifoglie	Alta	-50.9	-14.9	-45.0	13.1	-0.2	20.7	-37.8	-15.2	-24.3
	Media	26.5	81.6	25.9	51.2	65.4	8.3	77.6	147.0	34.2
	Bassa	30.9	83.3	21.4	62.4	68.9	22.6	93.2	152.3	44.0
Ceduo invecchiato mix con abete	Alta	-69.7	-47.6	-36.4	46.3	72.1	119.4	-23.4	24.5	83.0
	Media	27.1	79.4	46.9	-6.1	37.7	-8.3	21.1	117.1	38.7
	Bassa	35.5	87.8	67.7	53.9	85.8	65.3	89.4	173.6	133.0

Table S4:* *Average Carbon sink *over three different periods of time i) 2020 - 2060, ii) 2060 - 2100, and iii) 2020 - 2100. To better confront the different management options, red or green cells and their color intensity indicates the difference from the 50th percentile of the average data.*



		Time peroiod 2020 - 2060			*Time peroiod 2060 - 2100*			*Time peroiod TOTAL 2020 - 2100*		
Gestione oggi	**Intensità gestione futura**	**Hist**	**1.2 - 6**	**3.7 - 0**	**Hist**	**1.2 - 6**	**3.7 - 0**	**Hist**	**1.2 - 6**	**3.7 - 0**
						[tC * ha^{-1} * yr^{-1}]				
Ceduo in turno	Alta	1.5	2.5	0.9	1.0	1.7	0.5	1.3	2.1	0.7
	Media	1.6	2.6	0.9	1.1	1.8	0.5	1.3	2.2	0.7
	Bassa	1.6	2.8	0.9	0.9	1.7	0.4	1.3	2.3	0.7
Ceduo invecchiato	Alta	1.8	2.9	1.0	0.8	1.4	0.5	1.3	2.2	0.7
	Media	1.4	2.6	0.7	1.5	2.0	0.3	1.5	2.3	0.5
	Bassa	1.6	2.7	0.8	1.7	2.2	0.4	1.6	2.4	0.6
Convertito ad alto fusto	Alta	1.6	2.6	0.8	0.7	0.9	0.3	1.1	1.8	0.5
	Media	1.6	2.6	0.8	1.4	1.7	0.3	1.5	2.2	0.6
	Bassa	1.6	2.7	0.8	1.7	2.3	0.4	1.6	2.5	0.6
Ceduo invecchiato mix con latifoglie	Alta	2.4	4.7	3.0	1.6	2.5	1.9	2.0	3.6	2.4
	Media	1.8	3.6	1.8	2.3	3.5	1.4	2.0	3.6	1.6
	Bassa	1.9	3.4	1.9	2.0	3.4	1.3	2.0	3.4	1.6
Ceduo invecchiato mix con abete	Alta	2.1	3.7	2.8	1.3	2.4	3.1	1.7	3.0	3.0
	Media	2.1	3.8	2.4	1.9	3.8	2.3	2.0	3.8	2.4
	Bassa	2.0	3.6	2.3	2.3	4.5	3.0	2.2	4.0	2.7

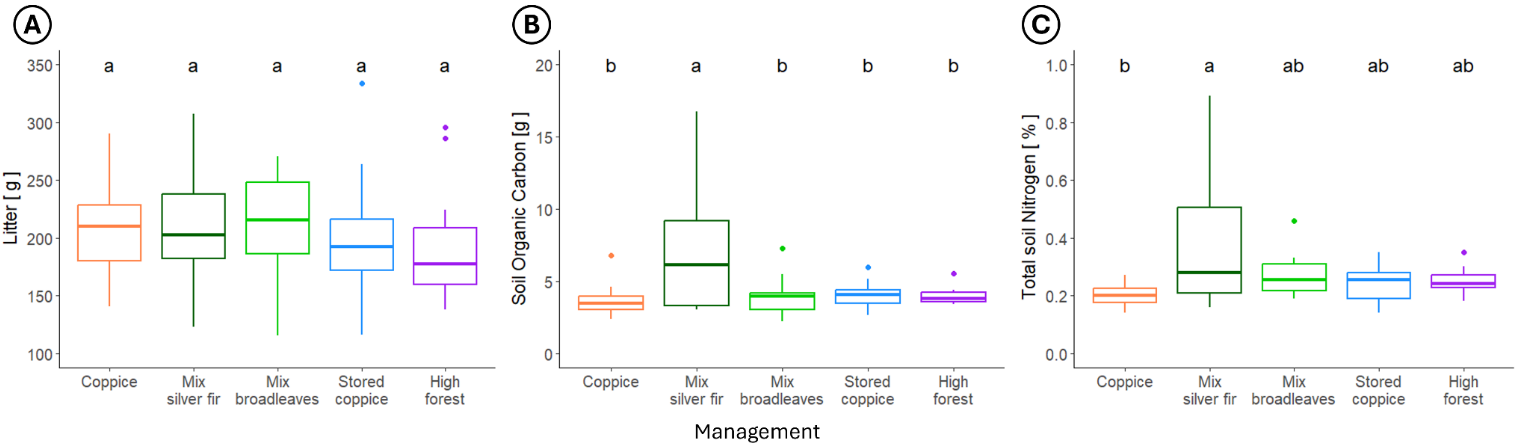
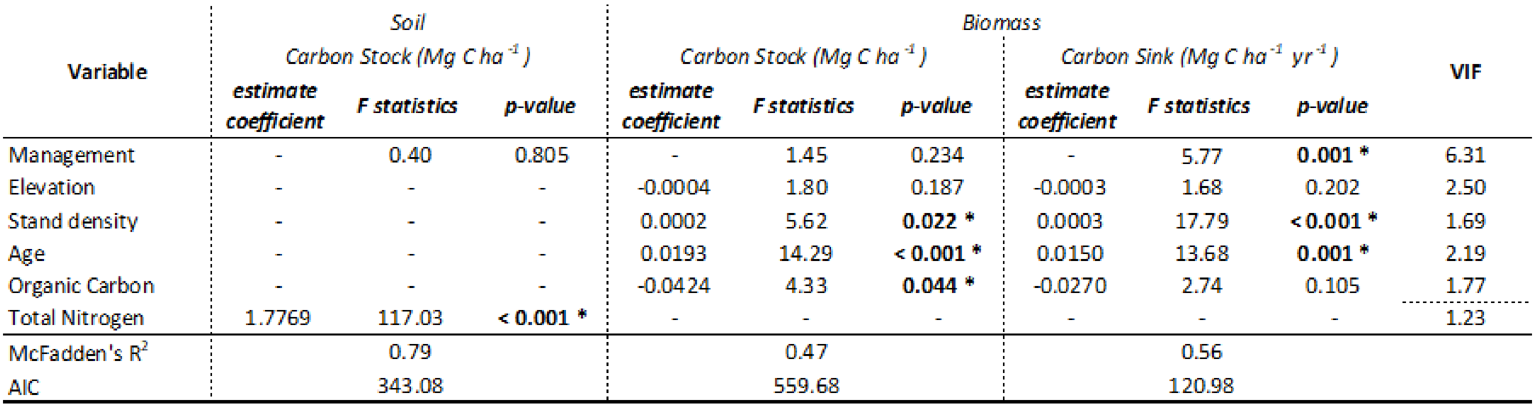


***Figure S3. Field soil parameters**: Litter (g) percentage of soil Carbon and percentage of soil Nitrogen. The boxplot shows the median value +/- the standard deviation. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicates no significant differences (e.g., a-a; a-ab; b-ab).*

***Table S5.** Statistics of the three GLMs: SOC stock, Biomass C stock, and Biomass C sink. Estimate coefficients indicate if the relationship between BAI and the predictor is positive or negative. F statistics and p-value indicate GLM summary results. VIF is the Variance Inflation Factor*



Variable	*Soil*			*Biomass*						VIF
	Carbon Stock (Mg C ha $^{-1}$)			*Carbon Stock (Mg C ha $^{-1}$)*			*Carbon Sink (Mg C ha $^{-1}$ yr $^{-1}$)*			
	estimate coefficient	***F statistics***	***p-value***	***estimate coefficient***	***F statistics***	***p-value***	***estimate coefficient***	***F statistics***	***p-value***	
Management	-	0.40	0.805	-	1.45	0.234	-	5.77	**0.001 ***	6.31
Elevation	-	-	-	-0.0004	1.80	0.187	-0.0003	1.68	0.202	2.50
Stand density	-	-	-	0.0002	5.62	**0.022 ***	0.0003	17.79	**< 0.001 ***	1.69
Age	-	-	-	0.0193	14.29	**< 0.001 ***	0.0150	13.68	**0.001 ***	2.19
Organic Carbon	-	-	-	-0.0424	4.33	**0.044 ***	-0.0270	2.74	0.105	1.77
Total Nitrogen	1.7769	117.03	**< 0.001 ***	-	-	-	-	-	-	1.23
McFadden's R^2		0.79			0.47			0.56		
AIC		343.08			559.68			120.98		

Table S6. FORMIND Model parametrization: *Parametrization coefficients reported by management type. Coefficients have been derived from field data, literature review and other model parametrization files.*

Parameter	**Meaning**	**Fagus sylvatica**				**Castanea sativa**	**Abies alba**	**Source**
		High forest	Coppice	Stored coppice	Stored coppice mix	Mix with beech	Mix with beech	
pFS2	foliage:stem partitioning ratios diam2cm	0.7	0.7	0.7	0.7	0.42	0.3745	Forrester et al. 2021; 3D-CMCC-FEM;
pFS20	foliage:stem partitioning ratios diam20cm	0.06	0.06	0.06	0.06	0.095	0.1084	Forrester et al. 2021;
aWS	Constant of the stem mass VS diam relationship	0.155848	0.086827	0.200006	0.014273	0.1205	0.082	Forrester et al. 2021;
nWS	exponent of the stem mass VS diam relationship	2.341514	2.45348	2.163928	2.955099	2.25436	2.459	Forrester et al. 2021;
pRx	Maximum fraction of NPP to roots	0.7	0.7	0.7	0.7	0.31	0.3714	Forrester et al. 2021; Chiesi et al. 2010;
pRn	Minimum fraction of NPP to roots	0.3	0.3	0.3	0.3	0.1	0.0946	Forrester et al. 2021;
gammaF1	maximum litterfall rate	0.02	0.02	0.02	0.02	0	0.0041	Forrester et al. 2021;
gammaF0	litterfall rate at t = 0	0.001	0.001	0.001	0.001	0	0.001	Forrester et al. 2021;
tgammaF	Age at which litterfall rate has median value	60	60	60	60	36.735	60	Forrester et al. 2021;
gammaR	Average monthly root turnover rate	0.015	0.015	0.015	0.015	0.083	0	Forrester et al. 2021; iLand;
leafgrow	If deciduous, leaves are produced at end of this month	5	5	5	5	4	0	Forrester et al. 2021;
leaffall	If deciduous, leaves all fall at start of this month	11	11	11	11	11	0	Forrester et al. 2021;
Tmin	Minimum temperature for growth	-5	-5	-5	-5	5	2.3251	Forrester et al. 2021; iLand;
Topt	Optimum temperature for growth	20	20	20	20	25	22.178	Forrester et al. 2021; iLand;
Tmax	Maximum temperature for growth	25	25	25	25	38	36.8918	Forrester et al. 2021;
kF	Days production lost per frost day	1	1	1	1	1	1	Forrester et al. 2021;
SWconst	Moisture ratio deficit for fq = 0.5	0.7	0.7	0.7	0.7	0.7	0.7	Forrester et al. 2021;
SWpower	Power of moisture ratio deficit	9	9	9	9	9	9	Forrester et al. 2021;
fCalpha700	Assimilation enhancement factor at 700ppm	1	1	1	1	1.2	1.1877	Forrester et al. 2021;
fCg700	Canopy conductance enhancement factor at 700ppm	1	1	1	1	1	0.7116	Forrester et al. 2021;
m0	Effect of soil fertility on biomass partitioning to roots	0	0	0	0	0	0	Forrester et al. 2021;
fN0	Lowest value the fertility modifier can take	0.5	0.5	0.5	0.5	0.6	0.6	Forrester et al. 2021;
fNn	Power of (1-FR) in 'fNutr'	1	1	1	1	1	1	Forrester et al. 2021;
MaxAge	Maximum stand age used in age modifier	300	300	300	300	800	550	Forrester et al. 2021; iLand;
nAge	Power of relative age in function for fAge	4	4	4	4	4	4	Forrester et al. 2021;
rAge	Relative age to give fAge = 0.5	0.95	0.95	0.95	0.95	0.95	0.95	Forrester et al. 2021;
gammaN1	Mortality rate for large t	0	0	0	0	0	0	Forrester et al. 2021; Davelos et al. 2004
gammaN0	Seedling mortality rate (t = 0)	0	0	0	0	0.44	0	Forrester et al. 2021; Davelos et al. 2004
tgammaN	Age at which mortality rate has median value	0	0	0	0	0	0	Forrester et al. 2021;
ngammaN	Shape of mortality response	1	1	1	1	1	1	Forrester et al. 2021;
wSx1000	Max stem mass per tree with 1000 trees/ha	400	400	400	400	317.157	316.1296	Forrester et al. 2021; 3-PGmix manual
thinPower	Power in self-thinning rule (nm)	1.5	1.5	1.5	1.5	-1.88501	1.9833	Forrester et al. 2021; 3-Pgmix manual
mF	Fraction mean single-tree foliage biomass lost per dead tree	0	0	0	0	0.3615	0.492	Forrester et al. 2021;
mR	Fraction mean single-tree root biomass lost per dead tree	0.2	0.2	0.2	0.2	0.3488	0.446	Forrester et al. 2021;
mS	Fraction mean single-tree stem biomass lost per dead tree	0.4	0.4	0.4	0.4	0.3802	0.444	Forrester et al. 2021;
SLA0	Specific leaf area at age 0	24.719	24.719	24.719	24.719	14	12.32	Forrester et al. 2021; 3D-CMCC-FEM;
SLA1	Specific leaf area for mature leaves	19.40205	19.40205	19.40205	19.40205	8.5	5.85	Forrester et al. 2021; iLand;
tSLA	Age at which specific leaf area = (SLA0+SLA1)/2	35	35	35	35	70	18.1	Forrester et al. 2021;
k	Extinction coefficient for absorption of PAR by canopy	0.417818	0.417818	0.417818	0.417818	0.65	0.6024	Forrester et al. 2021; Gomes-Laranjo et al. 1998;
fullCanAge	Age at canopy closure	10	10	10	10	5	3	Forrester et al. 2021; Covone et al. 2006;
MaxIntcptn	Maximum proportion of rainfall evaporated from canopy	0.237333	0.237333	0.237333	0.237333	0.3275	0.3381	Forrester et al. 2021;
LAImaxIntcptn	LAI for maximum rainfall interception	3	3	3	3	3	3	Forrester et al. 2021;
cVPD	LAI for 50% reduction of VPD in canopy	5	5	5	5	5	5	Forrester et al. 2021;
alphaCx	Canopy quantum efficiency	0.029886	0.027396	0.029886	0.024905	0.0741	0.02023	Forrester et al. 2021; fine-tuned to regulate the sink
Y	Ratio NPP/GPP	0.47	0.47	0.47	0.47	0.47	0.47	Forrester et al. 2021;
MinCond	Minimum canopy conductance	0	0	0	0	0	0	Forrester et al. 2021;
MaxCond	Maximum canopy conductance	0.02	0.02	0.02	0.02	0.017	0.0137	Forrester et al. 2021; iLand;
LAIgcx	LAI for maximum canopy conductance	3.33	3.33	3.33	3.33	3.33	3.33	Forrester et al. 2021;
CoeffCond	Stomatal response to VPD	0.057	0.057	0.057	0.057	0.05	0.0889	Forrester et al. 2021; 3D-CMCC-FEM;
BLcond	Canopy boundary layer conductance	0.2	0.2	0.2	0.2	0.2	0.2	Forrester et al. 2021;
RGcGw	The ratio of diffusivities of CO2 and water vapour in air	0.66	0.66	0.66	0.66	0.66	0.66	Forrester et al. 2021;
D13CTissueDif	d13C difference of modelled tissue and new photosynthate	2	2	2	2	2	2	Forrester et al. 2021;
aFracDiffu	Fractionation against 13C in diffusion	4.4	4.4	4.4	4.4	4.4	4.4	Forrester et al. 2021;
bFracRubi	Enzymatic fractionation by Rubisco	27	27	27	27	27	27	Forrester et al. 2021;
fracBB0	Branch and bark fraction at age 0	0.75	0.75	0.75	0.75	0.2	0	Forrester et al. 2021; 3D-CMCC-FEM;
fracBB1	Branch and bark fraction for mature stands	0.15	0.15	0.15	0.15	0.2	0	Forrester et al. 2021; Álvarez-Álvarez et al. 2018;
tBB	Age at which fracBB = (fracBB0+fracBB1)/2	2	2	2	2	10	0	Forrester et al. 2021; 3D-CMCC-FEM;
rhoMin	Minimum basic density - for young trees	0.567	0.567	0.567	0.567	0.49	0.37	Forrester et al. 2021; Koukos et al. 1997;
rhoMax	Maximum basic density - for older trees	0.567	0.567	0.567	0.567	0.49	0.37	Forrester et al. 2021;
tRho	Age at which rho = (rhoMin+rhoMax)/2	1	1	1	1	1	1	Forrester et al. 2021;
crownshape	Crown shape	3	3	3	3	4	3	Forrester et al. 2021; 3D-CMCC-FEM;
aH	Height equations parameters	2.509388	2.619692	0.988831	1.007927	5.9885	30.91	Calculated as indicated by Trotsiuk et al. 2020;
nHB	Height equations parameters	0.620573	0.582638	0.887877	0.537535	0.27705	16.78	Calculated as indicated by Trotsiuk et al. 2020;
nHC	Height equations parameters	0.211673	0.870162	0.05726	0.449848	0.083	0.00925	Calculated as indicated by Trotsiuk et al. 2020;
aV	Volume equations parameters	0.12897	0.144603	0.050191	0.039876	0.00027	0.000128	Calculated as indicated by Trotsiuk et al. 2020;
nVB	Volume equations parameters	2.573705	2.543169	2.844079	2.92443	2.21827	1.92	Calculated as indicated by Trotsiuk et al. 2020;
nVH	Volume equations parameters	0.865296	0.267116	0.870162	0	0.754	0.75	Calculated as indicated by Trotsiuk et al. 2020;
nVBH	Volume equations parameters	0	0	0	0	0	0	Calculated as indicated by Trotsiuk et al. 2020;
aK	Crown diameter equations parameters	49.89444	171.7607	62.99794	1075.681	0.77373	0.83	Calculated as indicated by Trotsiuk et al. 2020;
nKB	Crown diameter equations parameters	0.734764	0.367124	0.713875	-0.22365	0.68718	0.53	Calculated as indicated by Trotsiuk et al. 2020;
nKH	Crown diameter equations parameters	0	0	0	0	0	0	Calculated as indicated by Trotsiuk et al. 2020;
nKC	Crown diameter equations parameters	-0.63164	0.01327	-0.09732	0.01327	-0.09264	0	Calculated as indicated by Trotsiuk et al. 2020;
nKrh	Crown diameter equations parameters	-0.79705	-0.14542	0.027332	0.244425	0.00927	0	Calculated as indicated by Trotsiuk et al. 2020;
aHL	Live-crown length equations parameters	1.365082	8.311811	0.444113	0.368746	17.53427	24.93	Calculated as indicated by Trotsiuk et al. 2020;
nHLB	Live-crown length equations parameters	0.189164	0.189164	0.189164	0.189164	15.20864	25.09	Calculated as indicated by Trotsiuk et al. 2020;
nHLL	Live-crown length equations parameters	0	0	0	0	0	0	Calculated as indicated by Trotsiuk et al. 2020;
nHLC	Live-crown length equations parameters	0	0.001358	0.024114	0.001358	-0.04945	-0.002	Calculated as indicated by Trotsiuk et al. 2020;
nHLrh	Live-crown length equations parameters	0.655128	0.002996	0.363927	0.392933	0.18282	0	Calculated as indicated by Trotsiuk et al. 2020;
Qa	Intercept of net v. solar radiation relationship	-90	-90	-90	-90	-90	-90	Forrester et al. 2021;
Qb	Slope of net v. solar radiation relationship	0.8	0.8	0.8	0.8	0.8	0.8	Forrester et al. 2021;
gDM_mol	Conversion of molC to DryMatter	24	24	24	24	24	24	Forrester et al. 2021;
molPAR_MJ	Conversion of Net Radiation to PAR	2.3	2.3	2.3	2.3	2.3	2.3	Forrester et al. 2021;

Calabrian silver fir provenances show higher growth in lower altitudes and warmer climates of Upper Austria.

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Abstract

Assisted migration can be a valid silvicultural tool to improve the adaptation of forest species to climate change but the species-specific scientific evidence is still weak and with little local applicability. Silver fir (*Abies alba*) is one of the most widely used conifers in European forestry, with a high adaptive potential in the context of global warming, and with a high genetic variability that includes provenances with a highly diversified environmental response. In this study, we compare the growth of Calabrian (southern Italy) and Austrian (local) silver fir provenances in two provenance trials in upper Austria with different elevations and climates. We analyze productivity (height, volume, and carbon stock), stability (height/diameter ratio), and annual growth (basal area increment) as an indication of adaptive performance, in addition we analyze the effect of competition in comparative analyses. Our results show that one Austrian provenance shows higher values in terms of productivity and annual growth at the highest location, while the two Calabrian provenances are more productive and faster growing at the warmer and lower elevation site. The two Calabrian provenances show lower H/D values than the Austrian provenances at both study sites, index of higher stability. These results show different growing performances within silver fir to changing environmental conditions, revealing how southern provenances could grow better in warmer and lower elevation climates in Austria. It is important to carefully select forest reproductive material for future forestation projects, and in the context of climate change it is crucial to consider the diversified response of different genetic groups to improve productivity, health, and resilience. Competition also plays a key role in the analyses, explaining at least 40% of the models' variance. Competition often plays a marginal role in the analysis of forest data; with this result we show how important it is to include it in the analyses in order not to risk overlooking its effect.

Keywords: Abies alba, genetic diversity, provenance trial, climate adaptation, competition index

Introduction

Silver fir (*Abies alba*) is one of the most important conifers in Europe both in terms of ecology and timber production, occupying a large part of central and southern Europe with its distribution area (Fig. 1) (Chakraborty et al., 2021; Dyderski et al., 2018; Mauri et al., 2022). Silver fir is a fundamental species for maintaining high biodiversity in forest ecosystems because of its shade tolerance, plasticity to environmental conditions and ability to coexist with many tree species (Dobrowolska et al., 2017). Its wood is widely used as construction timber, furniture, plywood, and pulpwood; in addition, because of its good physical properties of elasticity and durability, it is also used in hydraulic engineering works (Wolf, 2003).

Silver fir suffers from the effects of climate change like many European forest tree species, showing declining volume of the forest stand (Ficko et al., 2011), especially at the southern limits of the species distribution (Gazol et al., 2015; Peguero-Pina et al., 2007). In addition to ongoing climate change, the current distribution and abundance of the species (Fig. 1) have strongly been shaped by human activities: silver fir wood was used extensively during the 19th century, mainly through overexploitation and improper forest management, which has significantly reduced the distribution range of this species in Europe (Wolf, 2003). This is compounded by air pollution and damage caused by wildlife (Dobrowolska et al., 2017; Klopčič et al., 2017). However, silver fir shows high adaptive potential with respect to the environmental conditions in which it grows, historically showing high survival in warmer and drier climates than those in which it is currently distributed (Walder et al., 2021). This ranks silver fir as a conifer potentially suited to cope with the effects of climate change, showing greater resistance and resilience to drought than other more widespread conifers such as Norway spruce (Vitasse et al., 2019). In Central Europe, silver fir is actually more drought-resistant than other widely distributed conifers, especially during extreme drought events (Dobrowolska et al., 2017; Schueler et al., 2021; Vitali et al., 2017). In addition, silver fir is significantly more wind-stable than other conifers, an important characteristic for building resilient forests to the effects of climate change (Hanewinkel et al., 2013; Sharma et al., 2021). In fact, several activities already aim at the progressive replacement of spruce by silver fir in many contexts, given also its greater ability to germinate and survive from the earliest stages of growth (Huth et al., 2017).

Although the future of silver fir is uncertain under climate change, especially at the southern limit of its distribution range, (Schueler et al., 2014), its high plasticity and genetic diversity (Piotti et al., 2017; Vendramin et al., 1999) make it an essential tree species in mitigation and adaptation actions across Europe given that its genetic diversity is sufficiently understood and conserved within in situ and ex situ conservation measures. The high genetic diversity of silver fir results mainly from its distribution during the last glaciation and subsequent post-glacial recolonization dynamics. Three main refugia have been identified in southern Europe: the Pyrenees, the Apennines, and the Balkan Peninsula. However, the postglacial (11,000-6000 years ago) migration of large parts of Central Europe started only from the Balkans and the northernmost stands in the central Apennines of Italy, leaving the southern Italian stands genetically isolated from the rest of the species (Liepelt et al., 2009). Southern Italian silver fir (i.e., from the Calabria region) shows important differences from populations in central and northern Italy, both in anatomical (Larsen & Mekic, 1991; Rinallo & Gellini, 1988) and genetic traits (Konnert & Bergmann, 1995; Longauer et al., 2003; Piotti et al., 2017).

To increase forest adaptation and resilience to climate change effects, "assisted migration" has been proposed as silvicultural adaptation strategy (Aitken & Bemmels, 2016), intended as the use of forest reproductive material of non-local provenances better adapted to future climate conditions (Breed et al., 2013; Mihai et al., 2020; Millar et al., 2007). In fact, there is ample evidence that different seed provenances can exhibit an adaptive eco-physiological and growth response dependent on environmental conditions (Chakraborty et al., 2015; Correia et al., 2018; Kapeller et al., 2012) and that some provenances are more resilient in the face of extreme drought events (George et al., 2015; Zas et al., 2020). The use of non-local species and provenances is a difficult task that should not be underestimated due to the potential environmental risks involved: assisted species migration could lead to the introduction of pests and diseases from other ecosystems while assisted population migration, without adequate production and growth performance evaluation, could result in use of provenances or genotypes that are not adapted to local conditions (Alfaro et al., 2014). In addition, forest policies at the local or national scale often limit the transfer of forest reproductive material across borders, encouraging only the use of local FRM in afforestation and reforestation programs (Gömöry et al., 2020; Konnert et al., 2015). Empirical studies on the species' adaptation are crucial to inform policies and sensitize forest owners on the risks and benefits of using non-local forest reproductive materials (Vinceti et al., 2020). To study in depth the growth performance of different silver fir provenances several studies have been done, mainly in provenance trials. The results highlight the large heterogeneity in climate response of different provenances (Martínez-Sancho et al., 2021; Mihai et al., 2021) and higher growth performance of southern Italian provenances (Calabria) compared with central European provenances in both juvenile (Hansen & Larsen, 2004) and adult stages of plants (Kerr et al., 2015). However, manifold studies of silver fir provenances have been made outside of the species' current range ((Hansen & Larsen, 2004) (Kerr et al., 2015) and comparably few studies evaluate southern Italian provenances within its current distribution tackling local adaptation to different climates and topographic conditions as a basis for local forest management decisions.

When analyzing results from mature provenance trials (>15/20 years old), where trees could start to compete for light, space and resources, the effect of competition among individual trees is frequently overlooked, potentially leaving out a significant effect on radial growth due to silvicultural measures used on the trial (Gömöry et al., 2021). Competition has a direct effect on individual tree growth, influencing the diameter increment especially in juvenile ages (Dobrowolska et al., 2017). When analyzing individual-tree data, the competition from neighboring trees plays an important role in plant growth, and including this information in statistical models can greatly improve growth predictions (Ledermann, 2010). Competition is usually included in models through an individual-tree-based competition index, calculated from the morphology of the subject tree (i.e., diameter, height, crown shape, etc.) and that of its competitors. More precise competition indices also include the position of individuals in space, often defined as the distance between the subject tree and its competitors (distance-dependent indices) (Burkhart & Tomé, 2012). Distance is inversely proportional to the competition intensity, varying its weight according to the index used (Ledermann & Stage, 2001). These indices easily find application in permanent plots with long-term monitoring, such as provenance trials, where measurement effort is low and data collection continuous over time (McTague & Weiskittel, 2016).

This study aims at (i) comparing production, growth and stability of silver fir provenances, of Austrian (local) and Calabrian origin, to understand the adaptive response to different climatic conditions. In addition, (ii) we examine the relative influence of competition in predictive models developed from provenance trials data.

Materials and Methods

Provenances and testing sites

In this study, we tested 4 silver fir (*Abies alba*) provenances: 2 from Austria and 2 from Italy. The Austrian provenances originate from the region of Upper Austria and are named according to local names Hausruck and Gosau, while the Italian provenances originate from the region Calabria in southern Italy, specifically from the Monte Gariglione (C120) and Monte Pecoraio (C39) (Fig. 1). The provenance origin of the Calabrian provenances differs from the Austrian origins in terms of its climatic conditions, revealing that the Calabrian stands are associated with lower precipitations, higher temperatures and likely more frequent and stronger drought conditions especially during the growing season (Tab. 1, Fig. A3a-d).

Figure 1. *Silver fir current distribution (source: EUFORGEN), provenance trials under study and tested provenances from Austria and Italy*

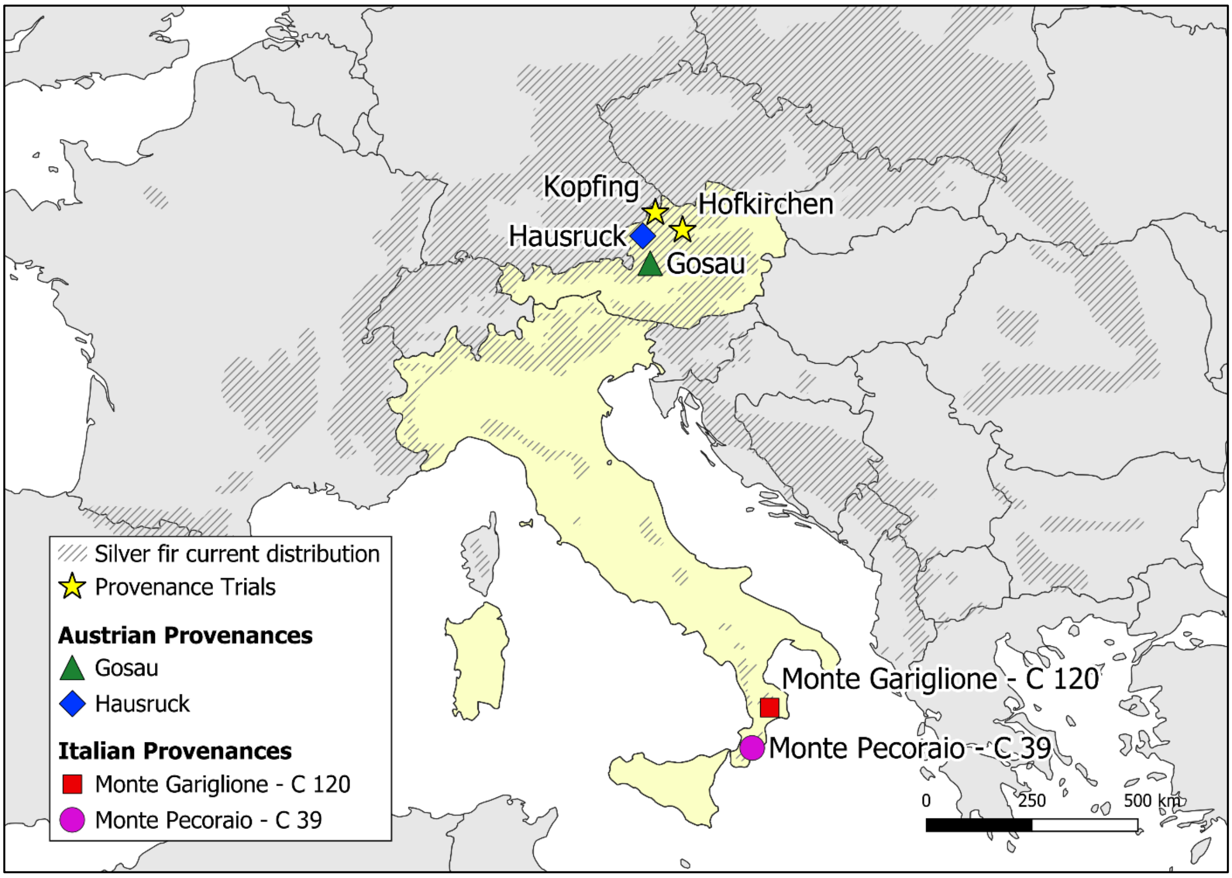

Table 1. *Climatic conditions of the 4 provenances origin location. Reference period 1960-1990.*

	Country	Altitude [m a.s.l.]	Precipitation [mm]		Temperature [°C]	
			Annual	Growing season	Annual	Growing season
Provenances origin location						
Hausruck	*Austria*	≈ 700	1212	802	7.9	12.2
Gosau	*Austria*	≈ 800	1624	1111	4.8	8.3
Monte Pecoraio (C39)	*Italy*	≈ 400	1084	361	16.1	19.1
Monte Gariglione (C120)	*Italy*	≈ 1600	992	350	8.0	11.1
Provenance Trials						
Kopfing	*Austria*	730	915	515	8.9	15.1
Hofkirchen	*Austria*	345	868	525	10.4	17

The silver fir provenances under study were tested in two different provenance trials in Upper Austria, comparing the performance of the local silver fir provenances with the Calabrian provenances. The two study sites are named Kopfing (48.47097; 13.66383) and Hofkirchen (48.16741; 14.37640) (Fig. 1), both established and managed by the Austrian Chamber of Agriculture in cooperation with local forest owners and scientifically maintained by the Austrian Research Centre for Forests BFW, Vienna. The trial Kopfing is located at 730 m a.s.l. and is characterized by typical Bohemian Massif rock substrate (gneiss and granite). The annual precipitation in the period 1990-21 was 915 mm (515 mm in April-September growing season) and mean annual temperatures were 8.9 °C (15.1 °C in April-September growing season) (Fig. A2b, Tab. A1). The provenance trial has been established in 1991 by planting 4-year-old seedlings previously grown in the nursery, adopting an 11-block scheme, with areas between 390 and 810 m², with three replicates of 3 fir tree provenances and two replicates for the Hausruck provenance (Fig. A4a). The trial Hofkirchen is located at 345 m a.s.l. and is characterized by a loess/clay-rich substrate. Annual precipitation is 868 mm (525 mm in April-September growing season) and the mean annual temperature is 10.4 °C (17 °C in April-September growing season) (Fig. A2a, Tab. A1). Thus, Hofkirchen is located at lower altitudes and characterized by drier and warmer climate compared to Kopfing. The provenance trial has been established in 1990 by planting 4-year-old seedlings previously grown in the nursery, adopting a 12-block scheme, with areas of 400 m², with three replicates of each provenance (Fig. A4b).

All climate data were obtained from the E-OBS database (Cornes et al., 2018) (version 26.0e) with a spatial resolution of 0.1 deg. regular grid. To compare the provenance origin location, average data from 1960 to 1990 are shown; to analyze provenance trials climate data have been collected for the period 1990-2021 (trees life span).

Data collection

All the diameters at breast height (DBH) and heights (H) of the trees inside the stands have been sampled. Data were collected at the Hofkirchen site in 2010, 2015 and 2018; the spatial positions of all trees were recorded in 2015 and 2018. The stand was thinned once in 2011. The Kopfing site was sampled in 2018 and 2021, recording both the morphological traits and the spatial positions. The stand was not thinned between the sampling dates.

From this data it was possible to derive the response variables dominant height (H_{dom} - m), individual stem Volume (V - m^3) and the related carbon stock (CO_2 eq. - kg) as proxies of tree productivity. The mean annual basal area increment (BAI – cm^2/y), calculated from the DBH difference for each tree, was considered as an estimate of annual growth performance. Finally, the individual H/D ratio was calculated to estimate tree stability. We defined dominant height as all tree height values greater than the 75th percentile of height distribution of each provenance (Chakraborty et al., 2015; Kapeller et al., 2012), while the stem volume was calculated from Austrian-fitted form factor equations (Pollanschütz, 1974) according to the following equation:

$$V = BA * H * f$$

Where *BA* is the basal area of the tree, *H* its height and *f* a form factor depending on tree DBH according to these equations:

$$If\ \mathrm{DBH}_i < 1.05\ \mathrm{dm} \quad f = a + b * \log(DBH)^2 + c\frac{1}{H} + d\frac{1}{DBH}$$

$$If\ \mathrm{DBH}_i > 1.05\ \mathrm{dm} \quad f = a + b * \log(DBH)^2 + c\frac{1}{H} + d\frac{1}{DBH} + e\frac{1}{DBH^2} + f\frac{1}{DBH * H} + g\frac{1}{DBH^2 * H}$$

Where a, b, c, d, e, f and g are specific coefficients based on the tree DBH (Tab. 2). DBH and H must be used in dm.

Table 2. *Equation coefficients for the Volume form factor formulas*

	a	b	c	d	e	f	g
If DBH < 1.05 dm	0.560673	0.15468	-0.65583	0.033210	-	-	-
If DBH > 1.05 dm	0.580223	-0.0307373	-17.15070	0.089869	-0.080557	19.6610	-2.45844

The individual tree carbon stock was calculated based on the stem (Önorm, 2003) and branch (Ledermann & Neumann, 2006) biomass, and then transformed into kg of CO_2eq (Weiss et al., 2000). The following equations have been implemented:

$$C = Biomass_{stem} * 0.497 + Biomass_{braches} * 0.473$$

Where:

$$Biomass_{stem} = V * \left(1 - \frac{10.85}{100}\right) * 410$$

$$Biomass_{branches} = e^{(-2.96496 + 2.20663 * \ln(\mathrm{DBH}) + 0.43844 * \ln(\mathrm{CH})) * 1.07)}$$

Where CH is the Crown / Height ratio of each tree. Volume is expressed in m^3 and Biomass in Kg. Response variables of this study (Hdom, V, H/D ratio and BAI) were all calculated at individual tree level.

Competition index

To better understand the differences in production, growth, and stability between the silver fir provenances we include in our analysis the competition to which the individual trees were subjected. We used the distance-dependent competition index TB of Tome & Burkhart (1989) as shown by Ledermann (2010), which is based on the DBH of the subject tree, the DBH of its competitors and the distance between them. TB was calculated according to the following equations:

$$If\ \mathrm{DBH}_j < \mathrm{DBH}_i \qquad \mathrm{TB} = \sum_{i=1}^{k} \frac{DBH_i}{DBH_j}\left(\frac{1}{Dist_{ij}}\right)$$

$$If\ \mathrm{DBH}_j > \mathrm{DBH}_i \qquad \mathrm{TB} = -\sum_{i=1}^{l} \frac{DBH_j}{DBH_i}\left(\frac{1}{Dist_{ij}}\right)$$

Here DBH_j and DBH_i are the diameter at breast height (DBH) of subject tree *j* and competitor *i*, respectively; Dist_{ij} is the distance between subject tree *j* and competitor *I*, *k* is the number of competitors that have a larger DBH than subject tree *j*; *l* is the number of competitors that have a smaller DBH than subject tree *j*. The TB index was applied to all test trees and their competitors within 10 m around each subject tree, based on the index's sensitivity to the competitors' distance (Ledermann & Stage, 2001). To avoid the edge effect of trees placed at the outer edge of the trial, the diameter and spatial position of all real competitors outside the trial were sampled at Hofkirchen. At the Kopfing site, the competition from individuals outside the trial was estimated by replicating the external blocks of the trial beyond the trial boundary, either by horizontal or vertical translation, in order to replicate the internal competition conditions. The estimation of external Kopfing competition follows the methodology described by Monserud & Ek (1974).

Statistical analysis

All statistical analyses were performed using the R software (version 4.2.1)(R Core Team, 2022). Generalized linear models (GLM) with Gamma distribution including the TB competition index as a predictor were used to evaluate differences in volume, higher trees, BAI, and H/D ratio of the provenances under investigation:

$$\text{Response variable} = \alpha + \beta_1 * (\text{Provenance})_i + \beta_2 * (\text{TB competition index})_i + \varepsilon_i$$

GLM models were run through the *stats* package using the glm() function. To estimate the model fit, McFadden's R-squared was used. F-statistics and p-value for each GLM predictor were estimated through the Anova() function of the *car* package. The contribution of individual predictors to the model was quantified by importance plots through the *tornado* package and the importance() function, quantifying the relative impact of each variable on the model fit and expressing it as a percentage of total deviance explained by each predictor based on McFadden's R-squared values. Significant differences between provenances were quantified by Tukey post-hoc tests using the *multcomp* package. Besides testing for differences in mean distributions, we also aimed to compare the shape of the density distribution for volume data by plotting distributions and testing differences using a two-sample Kolmogorov-Smirnov test through the *stats* package and the ks.test() function. This analysis has been restricted to volume data of the latest measurements within the respective site (2018 at the Hofkirchen site, 2021 at the Kopfing site).

Results

Tree height

The results show a clear difference in the dominant height trends (H_{dom}) between the two study sites. At the lower elevation trial Hofkirchen significant differences among provenances were observed for dominant height in 2015 and 2018 (Table 2, Fig. 2a). The Calabrian provenance C120 were in both years significantly taller than any of the local provenances and better than the Calabrian provenance C39. At the higher elevation site Kopfing, the Austrian provenance Gosau revealed significantly higher trees in 2018 and 2021, while the provenance C39 is the analysis group with the significantly lower values (Fig. 2a).

Table 2. *Statistics of the GLMs for each variable, study site and year under study.*

Variable	Site	Year	***Provenance effect***		***Competition Effect***		McFadden's R^2
			F statistic	*p-value*	*F statistic*	*p-value*	
Dominant Height (H_{dom})	*Hofkirchen*	2015	27.6	2.5e-16	924.3	< 2.2e-16	0.71
		2018	20.8	1.5e-12	1070.6	< 2.2e-16	0.70
	Kopfing	2018	63.1	< 2.2e-16	766	< 2.2e-16	0.50
		2021	48.0	< 2.2e-16	760.3	< 2.2e-16	0.45
Tree Volume and individual C stocks (V)	*Hofkirchen*	2015	22.4	1.8e-13	952.3	< 2.2e-16	0.75
		2018	32.3	< 2.2e-16	2306.8	< 2.2e-16	0.84
	Kopfing	2018	25.2	3.2e-15	1304.6	< 2.2e-16	0.74
		2021	16.6	2.6e-10	965	< 2.2e-16	0.69
Height/Diameter Ratio (H/D)	*Hofkirchen*	2015	26.5	1.1e-15	646.7	< 2.2e-16	0.66
		2018	32.6	< 2.2e-16	1059.6	< 2.2e-16	0.75
	Kopfing	2018	44.8	< 2.2e-16	903.4	< 2.2e-16	0.66
		2021	29.4	< 2.2e-16	647.8	< 2.2e-16	0.59
Basal Area Increment (BAI)	*Hofkirchen*	2010-2015	10.3	1.5e-06	1068.9	< 2.2e-16	0.74
		2015-2018	8.0	3.2e-05	1188.2	< 2.2e-16	0.73
	Kopfing	2018-2021	10.6	8.7e-07	371.8	< 2.2e-16	0.45

Tree volume and individual C stock

The two Calabrian provenances show significantly higher single tree volumes and carbon stock at Hofkirchen compared to the Austrian ones (Tab. 2). These differences between the two provenances groups are significant in 2015, but in 2018 only for the provenance C120 (Fig. 2b). At Kopfing, the local provenance Gosau reveals higher volume compared to the other three provenances at both measurements 2018 and 2021 (Fig. 2b). Differences in volume can also be expressed in carbon stock (kg of CO_2 eq.) as summarized and shown in Supplementary materials (Tab. A5).

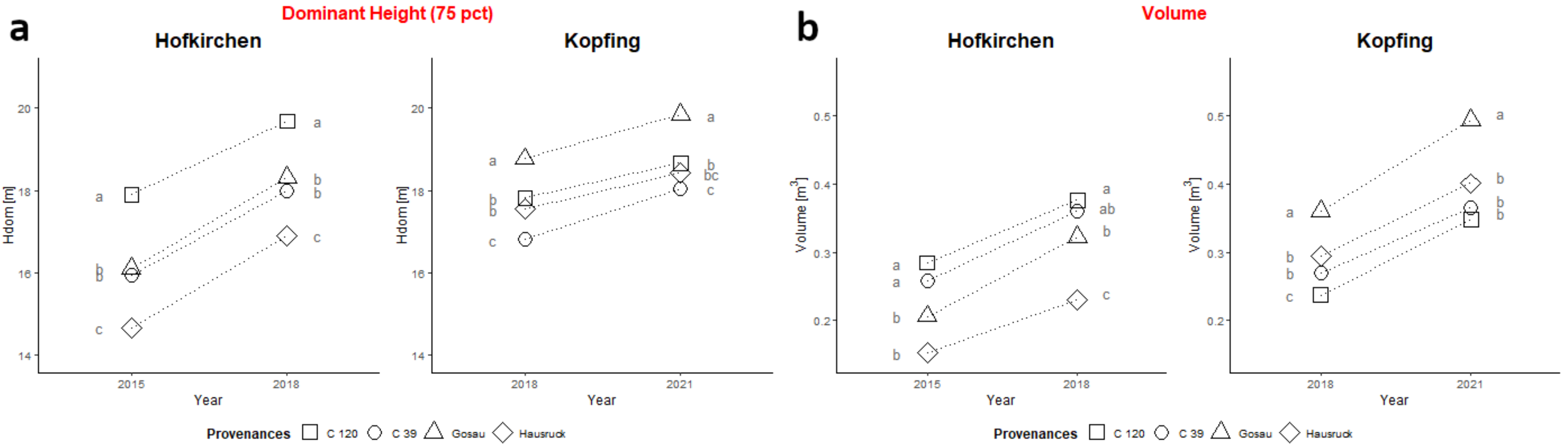

Figure 2. *Dominant height (a) and Volume (b) predicted data of the different provenances resulting from the GLM analysis of the two trials under study. Different letters show significant differences between provenances, while same letters show no significant differences.*

The analysis of the volume data distribution in trial Hofkirchen in 2018 revealed significant differences between the Calabrian and the Austrian provenances (D>0.20, p<0.02). The Austrian provenances show a remarkably stronger left-shaped volume distribution with few trees showing high volumes and a large number showing low volumes. In contrast, the density distribution of both Calabrian provenances shows a more homogenous distribution of size classes. No differences were found between the data distribution of the Calabrian provenances C120 and C39 (D=0.14, p=0.28) and between the Austrian provenances Gosau and Hausruck (D=0.16, p=0.13) (Fig. 3a). At the colder trial Kopfing, similar differences between the two provenance groups are visually appearing (Fig. 3b), but here the Austrian provenances revealed the highest number of trees at intermediate volumes, while the Calabrian provenances are more homogeneously distributed. However, the statistical comparison with the Kolmogorov–Smirnov test showed that significant differences exist only between the Austrian Gosau provenance and the two Calabrian provenances C120 (D=0.25, p<0.01) and C39 (D=0.16, p=0.13) (Fig. 3b).

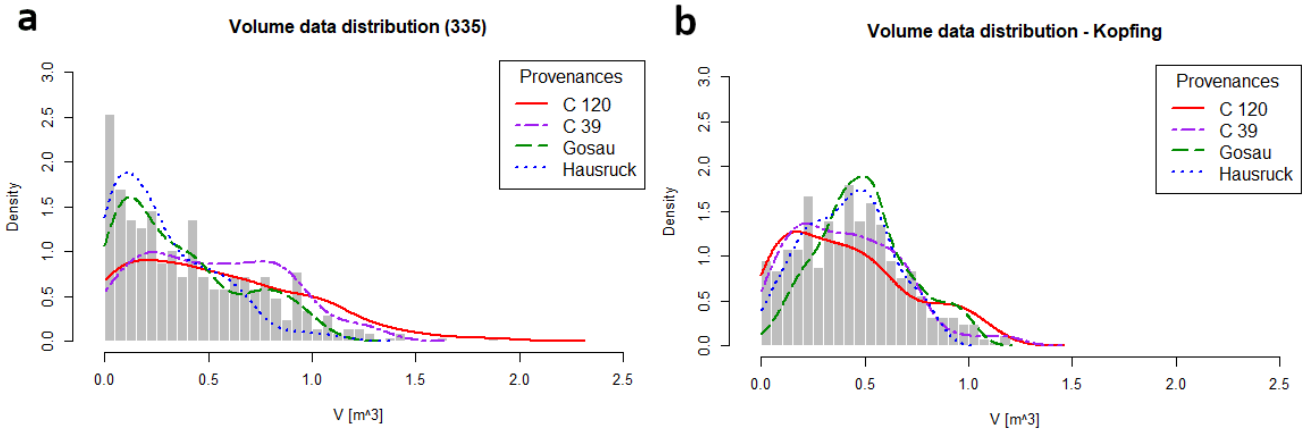

Figure 3. *Volume data distribution of the different provenances. Grey bars represent the data distribution of the whole provenance trial. 2018 data are shown for the Hofkirchen site (a), 2021 data are shown for the Kopfing site (b).*

Height/Diameter Ratio

The H/D ratio of the Calabrian provenances at both sites was lower than the ratio of the Austrian provenances (Fig. 4). At Hofkirchen, H/D ratio values were significantly lower for the Calabrian provenance C39 than for all provenances under investigation in 2015 and 2018. The Calabrian provenance C120 also showed significantly lower H/D values than provenance Gosau in 2018 (Fig. 4a). At Kopfing, provenance C39 showed significantly lower H/D values than all provenances in 2018 and lower values than the Austrian provenances in 2021. Also, the Calabrian C120 provenance showed significantly lower H/D values than both Austrian provenances in 2021, but no significant difference to the Austrian provenance Hausruck in 2018 (Fig. 4b).

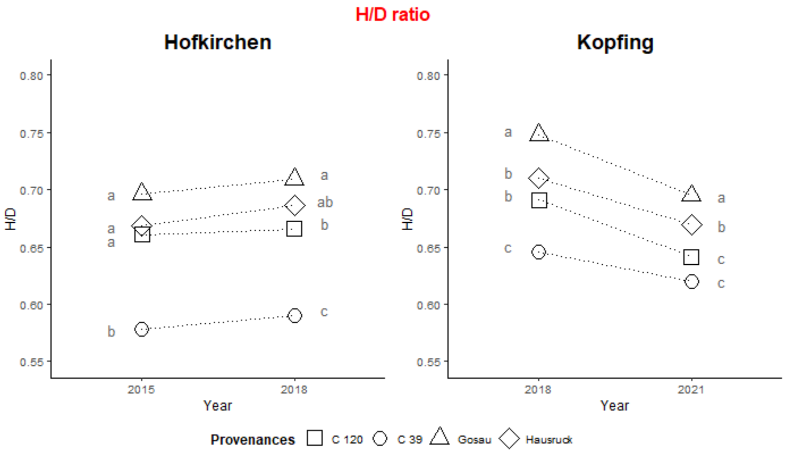

Figure 4. *H/D ratio predicted data of the different provenances resulting from the GLM analysis of the two trials under study. Different letters show significant differences between provenances, while same letters show no significant differences.*

Basal Area Increment

The Basal Area Increment (BAI) within past assessment periods confirms the significant differences between the provenances under study (Tab. 2). At Hofkirchen, the Calabrian provenances show higher BAI compared to the Austrian ones in the period 2010-2015. However, in the years 2015-2018 the BAI difference between Gosau and C120 is no longer significant even if C39 shows higher values than Gosau and both Calabrian provenances higher BAI than provenance Hausruck (Fig. 5a). At the Kopfing site, instead, the Austrian provenance Gosau and the Calabrian provenance C120 show higher BAI compared to the two other provenances (Fig. 5b).

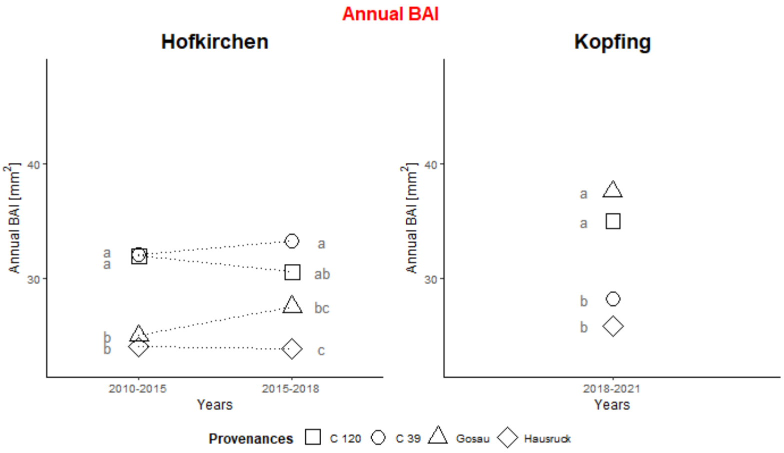

Figure 5. *Annual BAI predicted data of the different provenances resulting from the GLM analysis of the two trials under study. Different letters show significant differences between provenances, while same letters show no significant differences.*

Impact of competition

Competition shows relatively high importance within the models; the rest is explained by differences between the provenances under consideration. In the analysis of H_{dom} at Hofkirchen, the TB competition index explains 63% of the model variability from the data measured in 2015 and 64% from the data measured in 2018. Similarly, at Kopfing, the competition explains 41% of model variability from 2018 and 39% from 2021. The parameters volume and carbon revealed an even higher impact of competition, with relative importance on the GLM of 68% in 2015 and 77% in 2018 at Hofkirchen, while at Kopfing its importance is 73% in 2018 and 68% in 2021. The TB competition index explained 55% and 64% of the H/D ratio model predictions in the Hofkirchen site in 2015 and 2018 respectively, while in the Kopfing site the competition explained 59% and 53% for the 2018 and 2021 H/D model data. The TB competition index explains both in the periods 2010-2015 and 2015-2018 (Hofkirchen site) 69% of the BAI data model variability and in the period 2018-2021 (Kopfing site) 42% (Fig. 6).

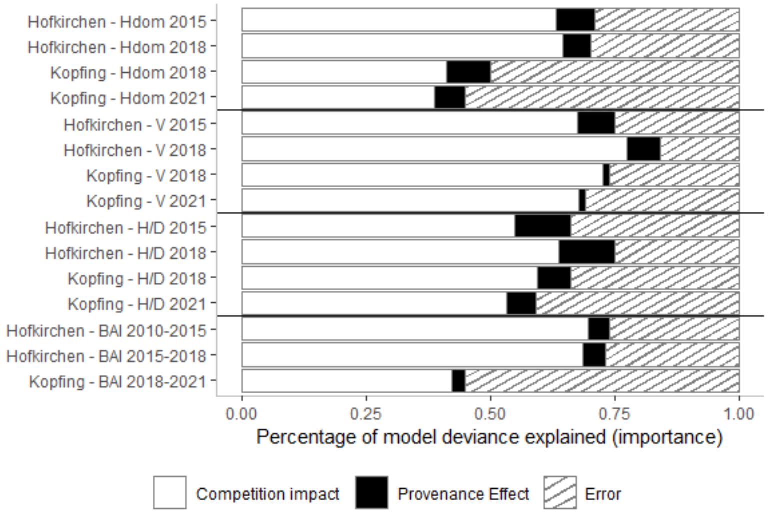

Figure 6. *Importance of model predictors as a percentage of the explained model deviance.*

Discussion

The provenances under examination show a clear difference in the productivity, growth and stability of the trees at the two sites under analysis, providing clear indications of how silver fir response to the local climate is highly related to the origin of the FRM. At the site with the higher elevation (Kopfing - 730m a.s.l), the local (Austrian) provenance Gosau shows higher volume, carbon stock and dominant height than the other three provenances, making it the most competitive provenance. At these altitudes, silver fir is one of the conifers most commonly found in Austria (Eckhart, 1970; Mauri et al., 2022) and the local provenance most accustomed to the mountain climate is in fact the most productive, showing a good adaptive capacity of Austrian silver fir in mountainous regions. Also, the increase in diameter over the three years analyzed underlines the excellent growth capacity of the local Gosau provenance under these climate conditions. The diameter increase is similarly high for the Calabrian origin C120, which, despite not showing a higher volume, reveals high annual growth capacity in the three years 2018-2021, an indication of good adaptation in the analyzed period. The lower productivity may be due to a lower ability of the Calabrian silver fir to cope with harsh winters compared to populations in Central Europe, although this response may also vary greatly among Calabrian provenances (Hansen & Larsen, 2004).

Moving to locations with a warmer climate (Hofkirchen site - 345m a.s.l) the volume and the annual diameter growth are significantly higher for the two Calabrian provenances, as it is for the height for the Calabrian provenance C120 than for the two Austrian provenances. At these altitudes, silver fir occurs at the edge of its natural distribution range in Austria, which is mainly limited by high temperatures (Eckhart, 1970; Mauri et al., 2016). The high productivity of Calabrian silver fir provenances at this altitude shows the ability of these genetics to survive and growth also at warmer conditions, which is useful information for both local forest management and forest adaptation management in climate change. Current estimates of climate change in Austria predict a rise in temperatures and a slight increase in drought conditions (Kronberger-Kießwetter et al., 2013), especially in the northern and eastern parts of the country (Strauss et al., 2012) and during the summer period (Loibl et al., 2011). Changing climatic conditions lead to shifts in the distribution range of forest species, to changes in the regional species composition as well as to modifications in the provision of important ecosystem services (Chakraborty et al., 2021; Ledermann et al., 2022; Schueler et al., 2014). Other authors have confirmed particularly high growth performance for Calabrian silver fir provenances compared with other European genetics (Hansen & Larsen, 2004; Larsen & Mekic, 1991) and how the growth of Italian genetics is particularly linked to the temperature regime (Bosela et al., 2016). In a climate change context, it is therefore crucial to consider the provenance origin of forest reproductive material to create high climate resilience forests (Gömöry et al., 2020; Konnert et al., 2015).

Finally, in both locations, H/D ratio analyses reveal high stability of the Calabrian provenances, with significantly lower H/D values, especially for the C39 provenance. The H/D ratio is a measure directly related to the taper of a tree (Hanewinkel et al., 2013) which is considered an index of individual tree stability with respect to snow accumulation or high-intensity wind events (Ledermann, 2017). Low H/D values, in fact, are characteristic of more stable trees and in conifers generally values below 80 are an indication of good resistance and resilience to wind and snow (Wonn & O'Hara, 2001). The four provenances under study respect this condition (Fig. 4), with Calabrian provenances showing values even below 70. In the context of climate change, this trait is considered crucial, coupled with the study of dominant height (Hanewinkel et al., 2013), to define ecosystems resilient to increasingly frequent extreme wind events (Sharma et al., 2021). Austrian forests have shown an increase in wind damage in recent decades, and windstorms are expected to increase throughout central Europe, risking an increase in crashes and insect and pest attacks as a consequence (Spathelf et al., 2014). In particular, forests in central and northern Austria prove to be the most susceptible to wind (Ledermann, 2017; Thom et al., 2013), revealing the importance of our results in this context and underlining the usefulness of choosing appropriate provenances in the context of climate change.

The relative importance of the variables within the models shows how competition plays a key role in the correct interpretation of the data. In all analyses, competition explains at least 40% of the variation in the data included in the model, underlining the importance of including it in the analyses of individual tree growth (Ledermann, 2010). The importance of competition is lower in plant height analyses, confirming that height is less affected by competition and thus by management practices (Hansen & Larsen, 2004). Provenance trials, or common gardens, are forest plots normally subjected to repeated management interventions over time (i.e. thinning, removal of dead plants or pruning), which could directly influence competition between individuals. Although the initial planting design of a provenance trial is normally geometric, silvicultural interventions may open up gaps or spacing trees unevenly, creating discontinuities that may favor the growth of some individuals over others, thus compromising the comparability of growth performance (Gömöry et al., 2020). Our results confirm that even if environmental variability is minimized in a provenance trial, the use of models that include individual-tree competition as a predictor is preferable to the simple comparison of raw morphological data, increasing the accuracy and reliability of comparative results (Burkhart & Tomé, 2012; Ledermann, 2010).

Finally, the distribution of the most recent volume data at the two study sites reveals a consistency in the production and growth of the provenances under examination, especially at the lower elevation site. At the Kopfing site (730m a.s.l.), the distribution of tree volumes of the Austrian Gosau provenance differs statistically from the data of the Calabrian genetics, confirming that the productive performance of this provenance at higher altitudes is reflected throughout the stand and that its growth response is uniform and characteristic, especially compared to provenances belonging to different genetic clusters. Similarly, at the Hofkirchen site (345m a.s.l), the volumetric data show a clear morphological consistency between the groups of provenances: the volumetric distribution of the Calabrian provenances is statistically different from that of the Austrian ones but does not differ within the regional macro-groups. As the limit of the ideal climatic conditions for the species' establishment approaches, the differences between the genetic clusters become more pronounced and the similarities between regional groups of provenances become more pronounced. These latter analyses are only a first approximation to the study of morphological similarities between genetic clusters, which can be further investigated through additional morphological comparison variables (Kerr et al., 2015; Mihai et al., 2021) or in ecophysiological performance (Konôpková et al., 2020; Robakowski et al., 2022). We emphasize the possibility that the distribution of tree volumes may be partly affected by silvicultural interventions that occurred at the two study sites. Specifically, the results for the Hofkirchen site could be influenced by the thinning that occurred in 2011, while no significant thinning is recorded for the Kopfing site. In any case, the thinning practices were made at similar intensity at each provenance plot. Silvicultural interventions before 2011 are not recorded although slight thinning in the early stages of trial management cannot be excluded.

The results of this study gather scientific evidence to support differentiated climate adaptation according to the origin of forest reproductive material, which are very important considerations from the perspective of forest conservation and management. Austrian forests will locally tend to change their species composition as climatic conditions change (Kronberger-Kießwetter et al., 2013), and consequently the ecosystem services provided at the local scale will be modified (Jandl et al., 2021; Ledermann et al., 2022). To support the natural climate adaptations of forests but at the same time maintain the provision of ecosystem services, it is important to consider the productive and adaptive performance of the various genetics of species of interest, especially those from the distribution range boundaries (Gömöry et al., 2020). Indeed, the use of forest reproductive material with greater climate adaptability allows forestation projects to create healthy and stable ecosystems for the future, resulting in greater resilience and resistance to the direct and indirect effects of climate change (Aitken & Bemmels, 2016). Assisted migration thus emerges as an essential tool for actively acting on sustainable forest management, enabling improved local forest adaptation. In the specific case discussed here, we recommend that the use of forest reproductive material of silver fir in Austria at low to medium altitudes should include provenances from the southern edge of the distribution range, possibly from Monte Gariglione. New plantings should include these provenances to ensure promising yields, also allowing further study of their performances locally. This study suffers from few limitations with respect to data availability, mainly concerning the limited number of provenances under investigation and study sites, and thus climatic conditions to be compared. The choice of the two available trials was forced by the availability of comparable data, as no other trials with the same provenance were available. We assume these shortcomings and hope that this study can be an input for further specific analyses, assessing both growth as well as physiological response to climate.

Conclusions

The study of the adaptation of different provenances is crucial for enhancing forest adaptation to climate change and creating resilient forests, which can be achieved through sustainable management of forest genetic resources and practical application of assisted migration techniques. The migration of provenances within the distribution range of a species requires a solid background on the growth performance of individual genetic groups, which is necessary to truly understand and assist the natural ecological dynamics of tree migration. It is evident from this study that some Austrian fir provenances are well suited to Austrian mountainous contexts, revealing, however, that Calabrian provenances tend to be better suited to conditions with higher temperatures and lower rainfall. This confirms the need for a careful eye in the choice of forest reproductive material in afforestation and reforestation processes on Austrian territory, the outcome of which can depend greatly on the provenances used. This study defines a framework for the application of the results that are not very extensive due to the narrow range of climatic conditions of comparison. However, this study shows a clear difference in growth response, productivity and stability characteristics useful for defining guidelines on the use of silver fir forest reproductive material in Austria. We encourage that the study of the response of different provenances to climate change is more widely addressed in the forestry literature and that the evidence produced is used locally for a broad sustainable use of forest reproductive material and forest genetic resources.

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Supplementary Materials

Table A1. *Stand characteristics of the two silver fir provenance trials under study in upper Austria.*

Provenances trial	**Altitude** *[m a.s.l.]*	**Temperature** *[°C]*	**Precipitation** *[mm]*	**Stems / ha**	**H_{dom}** *[m]*	**Basal area / ha** *[m^2]*	**Volume / ha** *[m^3]*	**Quadratic mean diameter**
Kopfing	730	8.9	915	856	18.2	42.6	357	25
Hofkirchen	345	10.4	868	791	18.7	39.7	343	25

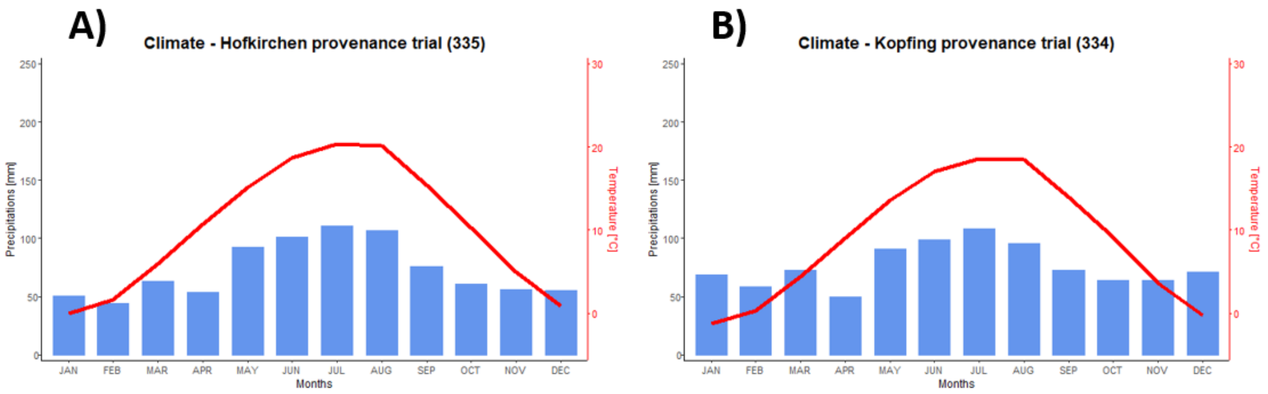


Figure A2. *Thermopluviometric charts of the average climate (average temperature and cumulative precipitation) of the 2 provenance trials: (A) Hofkirchen site and in the (B) Kopfing site. Average climate data are calculated over the period 1990-2021.*

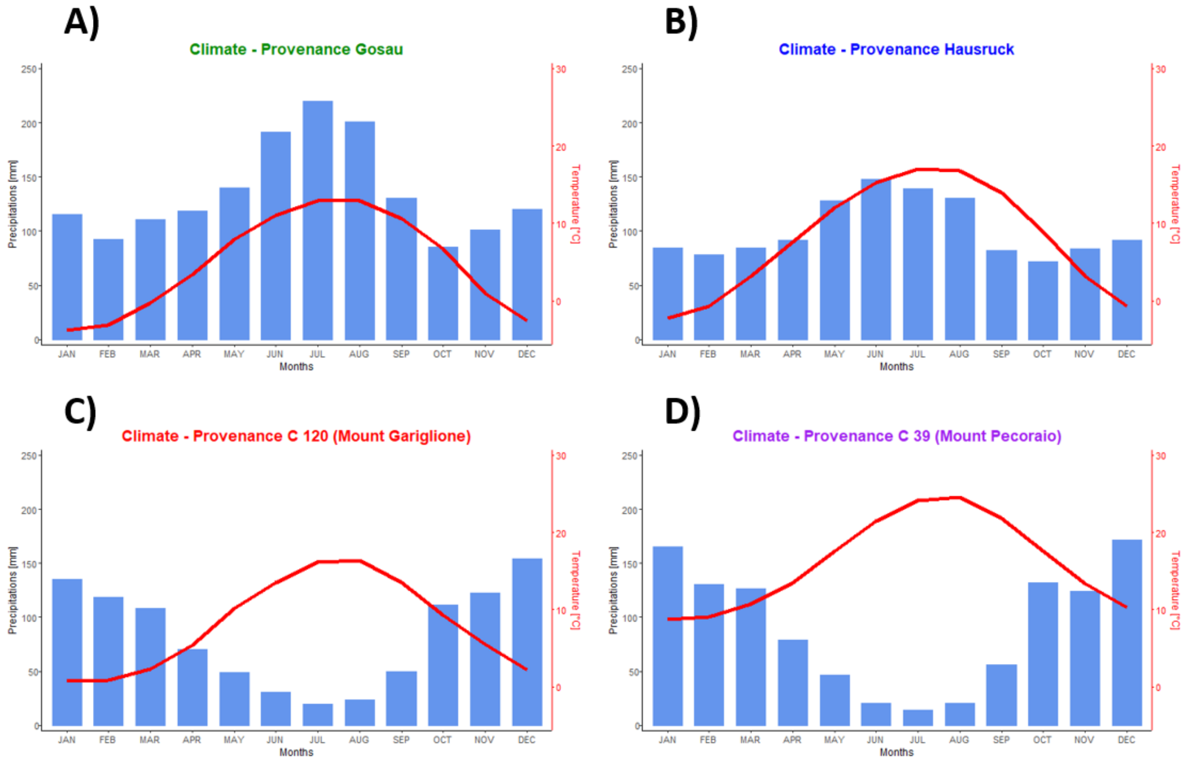
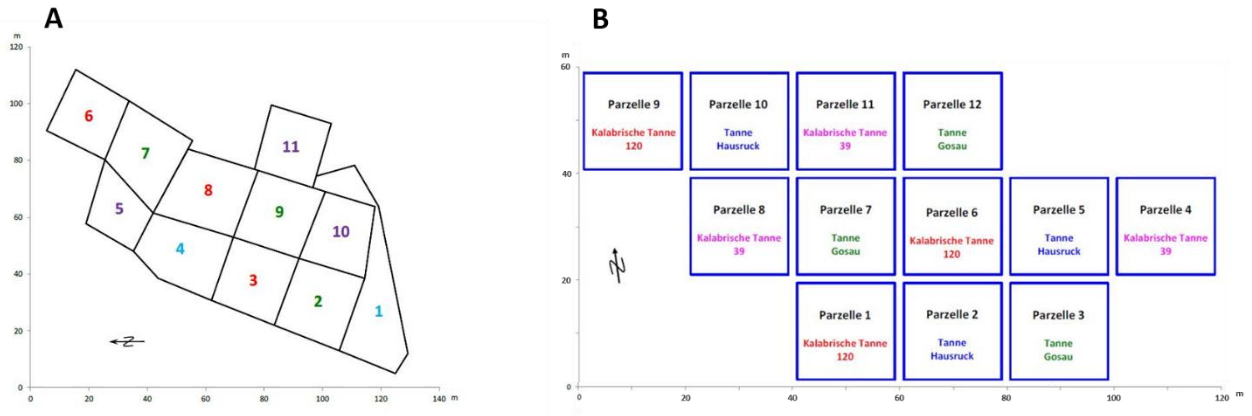


Figure A3. *Thermopluviometric charts of the average climate (average temperature and cumulative precipitation) of the 4 provenance origin sites: (A) Gosau, (B) Hausruck, (C) Mount Gariglione and (D) Mount Pecoraio. Average climate data are calculated over the period 1960-1990.*

Figure A4. *Provenance trials setup in the (A) Kopfing site and in the (B) Hofkirchen site.*



Conclusions

The conclusions of the four studies presented here provide a comprehensive view of the importance of genetic diversity and resilience of silver fir (*Abies alba* Mill.) in the context of climate change. Resilience to changing climate and drought emerges as a recurrent theme, where concepts of genetic diversity, environmental adaptability and sustainable forest management strategies are combined. Indeed, the ability of silver fir to withstand variable environmental conditions is highlighted by its high resilience to drought under multiple climate scenarios. Indeed, the silver fir emerges as a particularly resilient species to climate change, distinguishing itself from other tree species such as spruce and beech by its high adaptability to climatic variations. The resilience of the silver fir is based on several factors, including its high genetic variability and evolutionary and palaeoecological history. The considerable genetic variability of this species is indeed a key aspect of its climate resilience, allowing it to adapt to a wide range of environmental conditions. This genetic diversity has been favored by both its evolutionary history and its geographical spread. The palaeoecological history of the species talks about multiple glacial and interglacial phases, prospering and resisting in different environments, effectively adapting to environmental changes or changing its distribution in response to climatic variations. In our study, silver fir showed a positive response to increasingly severe climatic scenario in all simulations and was also extremely competitive with beech under all climatic scenarios and intensities of forest use, making it a promising resource in forestry. In this sense, the initial hypotheses were confirmed, underlining the potential of the silver fir in the Tuscan-Emilian Apennines. The resilience of forest species in the edge of their geographical distribution is influenced by several factors, such as greater evolutionary pressure and more intense natural selection. This can potentially result in smaller stands subject to more severe climates, but also in greater specialization and adaptability to specific environmental conditions. In the Apennines, silver fir is positioned at the southern edge of its European distribution, showing drought resilience despite the physical and genetic limitations associated with its marginal position. The resilience of silver fir to climate change at the edge of its distribution not only underlines its ecological importance, but also offers valuable insights for the development of forest management strategies that are resilient, adaptable, and sustainable, thus contributing to biodiversity conservation and climate change mitigation. The choice of forest reproductive material emerges as a key factor in planning healthy and productive forests, as the choice of silver fir provenances can optimize the resilience and adaptation of forests to changing climate conditions, as long as provenance performance is tested from different perspectives. Our hypotheses concerning the effect of genetic diversity on tree growth characteristics were generally supported by the results obtained. Fir trees from southern Italy have shown excellent growth performance and adaptation to drought both in Italy and abroad, found to be better able to withstand higher temperatures and drought conditions, possibly due to the more extreme conditions of the origin sites and the resulting adaptation. Local provenance is also often markedly productive, highlighting the importance of supplementing eventual assisted migration strategies with locally sourced material. Provenances used to colder and mountainous climates struggled to compete and were less adaptable to future climatic scenarios. Genetic variability within fir populations allows for greater flexibility and adaptability, suggesting that forest management should be oriented towards preserving and enhancing the genetic diversity of this species. These aspects highlight the importance of integrating knowledge about the performance of different forest provenances into forest management strategies, with the aim of supporting assisted forest migration and optimizing the provision of ecosystem services.

Finally, our results emphasize the importance of integrating forest provenance data into growth models, addressing the challenges of parameterizing multiple morphological, physiological and environmental variables. Our results reveal that parametrization of different forest provenances can be an important step to include in forest models, increasing their accuracy and ability to capture hidden nuances. Working with forest genetic diversity can be an important tool to sustainably manage forests in the context of climate change.

This need must be reflected in multidisciplinary approaches that include forest science, ecology, modelling and forest management. The next steps in climate change adaptation and mitigation research must necessarily focus on forest genetic diversity, which is increasingly playing a major role in management and adaptation strategies at both local and global scales. Incorporating this diversity into modelling is an important step in ecological research, increasing the effectiveness of forest management decisions and involving modelers, ecologists, and foresters through a multidisciplinary and integrated approach. Furthermore, by studying the performance of different forest provenances, researchers will have to produce an increasing number of studies that address multiple components of climate response, focusing on both growth processes and physiological response, so as to provide a complete picture of the role of genetic diversity. Finally, I believe it is important to work towards clear regulations for the movement of forest reproductive material, with the aim of facilitating the movement of seeds and seedlings internationally between countries, encouraging international agreements on climate-smart forestry like assisted migration programmes. Trees do not recognize borders. In conclusion, the resilience and adaptability of silver fir to climate change are significantly influenced by genetic diversity and understanding these dynamics is important for sustainable and resilient forest management.

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Declaration of originality and certificate of ownership

I, Silvio Daniele Oggioni, hereby declare that I am the sole author of this dissertation entitled ‘Silver fir and its provenances in a climate change perspective’. All references and data sources that were used in the dissertation have been appropriately acknowledged. I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure.

Milan, 19/04/2024

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