



Simulating silver fir provenance responses to climate change: A forest modelling approach in the Northern Apennines

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ABSTRACT

Understanding how genetic variation within forest species influences growth responses under climate change is essential for improving the accuracy of forest models and guiding adaptive management strategies. 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 (RCPs). The individual-based model FORMIND was parameterized 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 $>10\% \pm 1\%$) and carbon uptake (net primary productivity, NPP $>8\% \pm 1\%$) at the end of the century compared to the Western Alps provenance in the pure provenance (PP) and no regeneration scenario. Conversely, the Southern Apennines provenance showed higher biomass (biomass $>5\%–10\%$) and NPP ($>15\%–18\%$) in mixed provenance (MP) and regeneration scenarios. These results show that genetic diversity strongly affects forest growth and resilience to environmental changes. Hence, it should be included as a predictor variable in forest models. 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 in forest management and conservation strategies, in support of assisted migration strategies aiming to enhance the resilience of forest ecosystems in a changing climate.

1. Introduction

Predicting how forest ecosystems will respond to climate change is a critical challenge for forest science and management, especially in regions where tree species exhibit high genetic diversity and ecological plasticity. 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 general decline in productivity is observed in the Mediterranean area, where the effects of climate change are particularly evident (Peñuelas et al., 2017; Vitasse et al., 2019a). This trend poses a serious problem for the range of ecosystem services provided by forests, such as timber production, carbon sequestration, biodiversity conservation, and water cycle regulation, which are

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essential for environmental stability and human well-being (Lindner et al., 2010). In this context, understanding the dynamics of forests under future climate change pressure becomes crucial.

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 option 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. However, the response of tree populations to climate change is not only species-specific but also influenced by intraspecific genetic variation, a dimension often overlooked in forest management and modelling. In fact, the genetic diversity of the silver fir 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, has 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), an essential skill in the context of global warming (Vitasse et al., 2019b). To optimize 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). To functionally test the growth and adaptation performance of forest species in a context of climate change, a great opportunity is offered by forest modelling, which can include and simulate climatic, environmental, and even genetic variability (Aitken and Bemmels, 2016; Bohn et al., 2014).

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 (Bohn et al., 2014, 2018; Fischer et al., 2016). The effectiveness of forest growth models in simulating and predicting 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, like inventory data, are essential to calibrate and validate model performance to accurately reflect real-world conditions. Given the complex topography and the sensitivity of mountain forests to climatic variability, accurate and fine-resolution climate data are crucial for the development of effective management and conservation strategies (Charru et al., 2017; Gentilucci and D'aprile, 2021; Pepin et al., 2015). In this context, spatial downscaling methods can help refine climate data to a more relevant scale (Terzago et al., 2018).

To effectively model forest growth under different climate scenarios, we would need not only reliable climate inputs but also information on intraspecific variation to develop robust management strategies. However, we still know little about the climatic adaptability potential of different forest provenances and how provenances can be effectively represented in forest growth models. 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 individual-based 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 investigate 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 simulated the growth of three Italian silver fir provenances (Western Alps, Northern Apennines, and Southern Apennines) under three climate change scenarios (representative concentration pathways, RCP 2.6, 4.5, and 8.5) in comparison with the historical climate. To include different growth conditions, forests composed of a single forest provenance among those under consideration (pure provenance (PP) forests) and forests with a mix of the three silver fir provenances considered in this study (mixed provenance (MP) forests) were simulated. The growth simulations were carried out using the individual-based forest growth model FORMIND (Bohn et al., 2014) 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.

2. 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 parameterized within the model thanks to the collection of tree morphological data in the field, making it possible to achieve a realistic representation of silver fir forest growth and dynamics in the national park and the surrounding territory.

2.1. 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 (20 m × 20 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 gross primary production (GPP), respiration, and specific

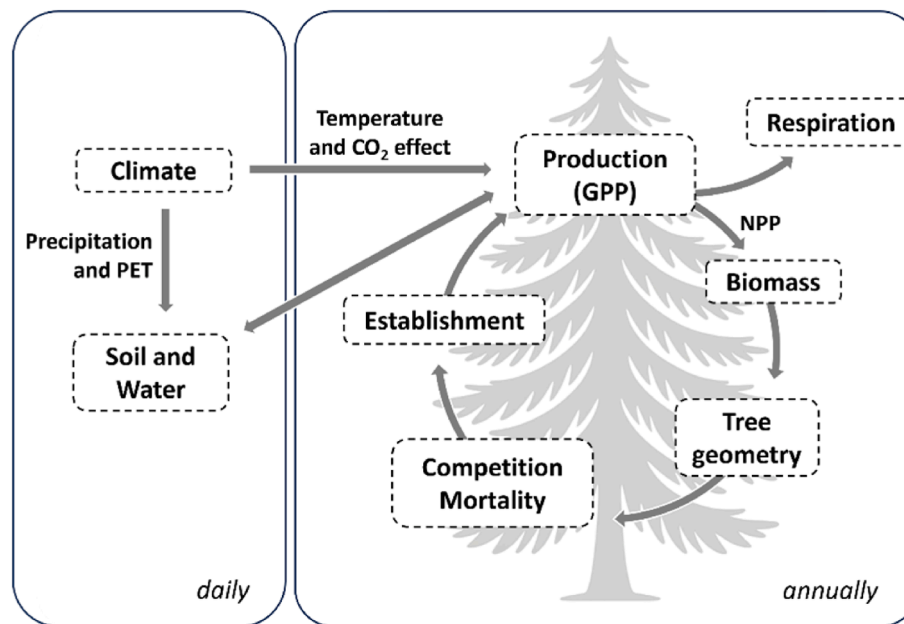


Fig. 1. General working scheme of FORMIND and main connections between modules. All input climatic and edaphic variables are the same for the entire simulated area. Precipitation and PET are used to limit GPP through the soil, while temperature and CO₂ are used to regulate photosynthesis. GPP is divided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

physiological parameters), mortality (described by specific mortality rates and crowding in dense forest stands), and competition (e.g., calculation of light conditions and species-specific GPP depending on environmental conditions for each individual tree). The model calculates GPP, growth, respiration, and net primary productivity (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. Individual and process-based modelling, such as that offered by FORMIND, is fundamental to informing sustainable forest management. Such models provide 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).

2.2. Input data

2.2.1. 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 1,000 to 1,650 m above sea level (a.s.l.), on a diatomite marl substrate. The study area experiences a Mediterranean Apennine climate, characterized by dry summers and rainy autumns, with an average annual rainfall of 2,100 mm, an average annual temperature of 7.5 °C, and an average daily temperature range of 6 °C.

2.2.2. Field data

In a previous work (Oggioni et al., 2024), we analyzed 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_Al—local), and Southern Apennines (S_Al) (Oggioni et al., 2024; 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., 2024). 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 parameterize 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). The spatial extent of the forest stands considered in this study varied considerably, ranging approximately between 1 and 8 ha (Table S1). Each tree was assigned to a specific provenance based on the genetic analyses of Oggioni et al. (2024). Only individuals that had been genetically characterized, and for which provenance was known, were sampled for model parametrization. The trees chosen for genetic analysis met the following selection criteria: in each stand, 24 trees had been sampled at ≥ 20 m spacing and genotyped with 16 SSR markers, and only individuals assigned to a genetic cluster with $>80\%$ probability were retained. Trees close to stand borders were excluded a priori in order to minimize edge effects. For the present study, stratified systematic sampling has been applied, where strata are defined by genetic provenance and the systematic component derives from the original spacing of the genetic survey. Within each stand, for every provenance represented, we selected up to ten individuals with the highest assignment probability to that provenance; when fewer than ten such individuals were available, all were included. The resulting number of sampled trees per stand and provenance is reported in Table S1. This procedure has been applied to ensure that sampled individuals were both genetically robust and spatially representative within each stand, important elements to consider when defining sampling criteria (Cudjoe et al., 2024;

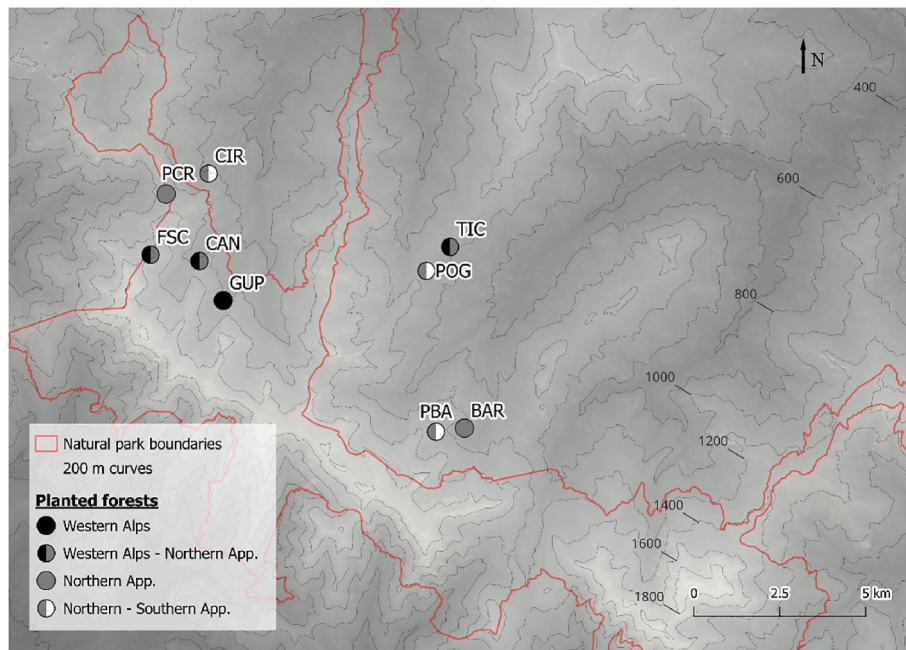


Fig. 2. Map of the 9 stands sampled in the National Park of the Tuscan-Emilian Apennine for FORMIND model parametrization. Circles represent silver fir planted stands. Colors represent the provenance of each stand, as reconstructed by means of molecular markers (black: “Western Alps”; dark grey: “Northern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

Trautenmüller et al., 2021). Trees were identified in the forest through the previously affixed tags. The following morphological data were collected for each tree: diameter, height, crown diameter, and crown height. Diameters at breast height (DBH) were measured using a tree calliper, while crown diameters were assessed with a laser distance meter (Leica). For each tree, crown measurements were taken from four directions (north, south, east, and west) by standing under the edge of the crown and measuring the distance to the trunk; the average of these four measurements was then used as the crown diameter. Tree and crown base heights were recorded using an electronic hypsometer (VERTEX IV, Haglöf, Sweden). Additionally, two increment cores were extracted from each sampled tree using an increment borer (Pressler), in order to assess the diameter increment of the examined individuals. On sloping sites, tree cores were extracted perpendicularly to the slope to avoid growth anomalies related to stem inclination (Martínez-Sancho et al., 2020). Samples were manually prepared and scanned at 2,400 dpi using an EPSON Perfection v850 Pro. Ring-widths were measured with CooRecorder and CDendro (v. 9.3.1; Cybis, 2022; Maxwell and Larsson, 2021). In Oggioni et al. (2024), individual tree competition was assessed by establishing 10 m radius circular subplots centered on each sampled tree and recording the diameter of all neighboring trees within those plots. Tree density per hectare was calculated separately for each subplot and then averaged to obtain a stand-level estimate. Although some of the subplots may overlap due to spatial proximity between sample trees (i.e., <20 m apart), this does not affect the calculation, as the final density is derived from the mean of individual subplot densities. Soil depth was sampled at 3 random points around each sampled tree within 2 m from the tree stem, using a hammer and a sharp stick/pike till 90 cm 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 1 m 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 mean reference values from Rawls et al. (1993): permanent wilting point, field capacity, soil porosity, fully saturated conductivity, pore size distribution index, and residual soil water content.

2.2.3. Climate data and downscaling

To generate future projections of forest growth that cover a range of climate change scenarios, CMIP5-driven regional climate models (RCMs) from the ESGF CORDEX database (ESGF, 2023) were considered. The RCMs were chosen based on the following characteristics: (i) availability of simulations at the finest spatial resolution (0.11°) for the domain of study (EUR-11); (ii) availability of historical data and climate change projections under three RCP scenarios (2.6, 4.5, and 8.5); (iii) availability of an ensemble of simulations driven by different global climate models (GCMs). These criteria lead us to choose the Rossby Centre Regional Atmospheric Climate Model (RCA4, Strandberg et al., 2014), providing an ensemble of 3 GCM-RCM complete datasets over the three RCP scenarios, at the finest spatial resolution available. The driving GCMs are 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), and MPI-ESM1 (Max Planck Institute Earth System Model, Müller et al., 2018). 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 coordinates), 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 a finer resolution to better represent the local climate conditions in which silver fir is currently distributed. The CSTools R package (Pérez-Zanón et al., 2023) has been used for downscaling temperature and precipitation data (Pérez-Zanón et al., 2022; Terzago et al., 2018). Temperature downscaling takes into account the mismatch between the coarse RCM topography and a fine-scale digital elevation model (DEM), and it applies an orographic correction assuming a constant orographic lapse rate. For temperature downscaling, the CST RFTemp function has been employed, using the SRTM30+ Global 1-km DEM (Sandwell et al., 2021) and a constant lapse rate of $-6.5^\circ\text{C}\cdot\text{km}^{-1}$ (International Civil Aviation Organization, 1993). To downscale precipitation data, the RainFARM

stochastic downscaling method (D'Onofrio et al., 2014), optimized for complex topography (Terzago et al., 2018), has been used. The method is implemented in CSTools through the CST_RainFARM function, and it has been demonstrated in Pérez-Zanón et al. (2022). Precipitation downscaling was performed using a refinement factor of 10 (the output resolution is increased from 0.11° to 0.011°). To take into account orographic enhancement of precipitation, WorldClim 2.1 at 30" resolution (Fick and Hijmans, 2017) has been used as a fine-scale reference precipitation climatology to derive orographic weights (Terzago et al., 2018). Weights have been calculated through the CST_RFWeights function for each month of the year separately (i.e., 12 spatial maps in total) in order to take into account the annual cycle of precipitation, and then applied to downscale precipitation data on a monthly basis. For precipitation downscaling, the CST_RainFARM function requires a spectral slope value, which describes how precipitation changes with spatial scale (Pérez-Zanón et al., 2023). We employed 12 monthly spectral slopes, calculated with the CST_RFSlope function.

The downscaling methodology described here was applied to all climate model simulations (HadGEM2-RCA4, NorESM1-RCA4, and MPI-ESM1-RCA4) and all climate scenarios (historic, RCP 2.6, 4.5, and 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 historical climate datasets over future time horizons. Specifically, temperature and precipitation data over the period 1970–2005 were used to simulate the historical climate patterns up to 2100. This was achieved through a randomization process, where annual climate datasets (datasets of the past years' climate) were randomly selected and replicated over the period 2006–2100. In this way, the past 35 years of climate data (1970–2005) were replicated randomly in the future to cover 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 (Kittel et al., 2004; Thorndahl et al., 2017). 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 ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$), potential evapotranspiration (PET, mm), day length (daylight hours), and the concentration of CO₂ in the air (CO₂, ppm) as additional climate inputs. Daily irradiance values (1951–2100) for the Italian territory in all climate scenarios (historical, RCP 2.6, 4.5, and 8.5) based on the CMIP5 model experiments were obtained from the Copernicus database (C3S, 2023). Daylength values were derived using the daylength (a) function of the R package geosphere (Hijmans et al., 2022). The PET values were obtained on a monthly scale using the thornthwaite (a) function of the SPEI package of R (Beguería and Vicente-Serrano, 2023), then scaled to a daily level by 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 GCMs.

2.2.4. 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 parameterize the three provenances as part of the model inputs. The three provenances were differentiated according to the following geometric and morphological characteristics: ratio of tree height: stem diameter, crown diameter: stem diameter, crown length: tree height, aboveground biomass: stem diameter, and diameter increment: diameter. Table S2 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 S3 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 parameterization of D - and ΔD -dependent background mortality are given in Table S4.

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 parameterize 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, hypothesizing a diversified adaptation according to the geographical origin of the forest material. In order to define these values, historical temperature data were extracted based on the distribution range of the species in the native areas of the three forest provenances used in this study (western Alps, northern Apennines, and southern Apennines). Historical temperatures were obtained from the 3 GCM-RCM under consideration (HadGEM2-RCA4, NorESM1-RCA4, and MPI-ESM1-RCA4). The distribution of silver fir has been derived from the European forest species distribution maps database (Caudullo et al., 2023), using the exact location of the data used for the genetic analysis as a proxy of the native areas of the three forest provenances (Oggioni et al., 2024; Piotti et al., 2017). The 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 summarized in Table S5, together with the coefficients identified by FORMIND used to define photosynthesis limitations.

2.3. Model simulations

2.3.1. Model 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; Jagiello 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 crucial 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 parameterization of the FORMIND model, the growth of the nine forest plots in the national park, which were originally used to parameterize the provenances in use, was simulated, attempting to replicate their productivity (volume and biomass). In this work, we used the same dataset for the model parametrization and validation since the silver fir distribution in the area is confined to those forest plots. For this purpose, nine simulations were carried out with the aim of replicating the conditions of the original plots retrospectively. The simulations were initialized 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 1,100 to 1,500 plants·ha⁻¹), choosing for the final run the value that resulted in the closest approximation of the 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 a pure N_Ap provenance stand, while the CAN plot was simulated as a mix 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., 2024), 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).

2.3.2. Pure and mixed provenances simulation

To simulate growth and dynamics of different provenances, we initialized FORMIND with two different types of virtual stands: managed single-provenance forests (without regeneration) and MP 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 climate model datasets (HadGEM2, NorESM1, and MPI-ESM1) and for each considered climate scenario (historical, RCP 2.6, 4.5, and 8.5). The simulations were initialized 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, 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 1,500 plants·ha⁻¹, 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 MP, three arbitrary densities of established seedlings (seedling density, SD) were used in the simulation: 90, 150, and 210 plants·ha⁻¹. These numbers define the number of plants actually established each year, initialized 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, m²·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, NPP (MgC·ha⁻¹) as a proxy for annual net carbon storage, and tree respiration (R , MgC·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 climate model simulations were included to express the range of possible outputs of the model. In the PP runs, the climate model was used as a covariate in the ANCOVA tests, while in the MP runs, both the climate model and established regeneration density were used as covariates. The interaction between provenance and established regeneration density was also analyzed in the MP runs. Differences between the climate model simulations are considered as an expected uncertainty range of simulation outputs. The ANCOVA analyses were performed in two-time steps, analyzing model outputs at the years 2060 and 2100.

3. Results

3.1. Model validation

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 lower values than those observed in the field (<14%–40%), while the PCR and FSC plots showed higher simulated volumes and biomass per hectare than those observed (>12%–36%) (Figs. 3a and S2, and Table S6). The simulated forest volume per hectare data showed no significant differences with the observed values (F -statistic = 1.175, p -value = 0.294) (Fig. S3a), with a bias of $-77 \text{ m}^3\cdot\text{ha}^{-1}$, corresponding to -11% . This resulted in an RMSE of 147.0 m^3 , corresponding to 23.5% of the mean observed value (RRMSE), indicating a moderate deviation between simulated and observed volumes (Analytics Vidhya, 2021). Similarly, the biomass per hectare data showed no significant differences between simulated and observed values (F -statistic = 0.751, p -value = 0.399) (Figs. 3b and S3b), with a bias of $-30 \text{ t}_{\text{ODM}}\cdot\text{ha}^{-1}$, corresponding to -8% . This resulted in an RMSE of $67.7 \text{ t}_{\text{ODM}}$, corresponding to a RRMSE of 21.3%. As expected, the data on the number of stems per hectare at the end of the simulation did not differ statistically between the simulated and observed data (F -statistic = 0.491, p -value = 0.494) (Fig. S3c), with a bias of $+25$ plants per hectare, corresponding to $+5\%$, which resulted in an RMSE of 25.3 and RRMSE of 5.2%.

3.2. 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 BA values showed differences depending on the tree provenance (Table S7), 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 ($p < 0.001$) (Table S8). In 2100, the differences between the S_Ap and N_Ap provenance disappeared ($0.9 \geq p \geq 0.6$), while both showed higher BA values than the W_Al provenance ($p \leq 0.001$). These trends were similar in the historical run and the three climate scenarios, and BA values do not change significantly among the different simulations (Fig. S4a and Table S8). Biomass values (B) also showed differences according to forest provenance (Table S7), 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 model runs (historical climate and RCP scenarios) and time steps (2060 and 2100). As for BA, biomass projections were also consistent among the climate scenarios, showing higher biomass than the historical scenario and rather consistent between them (Fig. S4b and Table S8). The NPP values also showed differences between the provenances under investigation in some of the analysis levels (Table S7). Fig. 4 shows the NPP values for each provenance under the different climate scenarios and time steps in PP simulations. The local provenance (N_Ap) displayed higher NPP values than the other two provenances in several scenarios, particularly under RCP 8.5 in both 2060 and 2100. The figure also illustrated a general increase in NPP values with the severity of the climate scenario. In 2060, we found higher NPP values for the local provenance than for the S_Ap provenance in the historical run ($2.95 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1} > 2.77 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $p = 0.011$), and higher NPP values for the local provenance than the W_Al provenance in the RCP 8.5 scenario ($3.38 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1} > 3.18 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $p = 0.013$). In 2100, for the historical run and for the RCP 2.6 scenario, the NPP of the N_Ap provenance was higher than the S_Ap ($0.02 \geq p \geq 0.002$) and W_Al ($0.004 \geq p \geq 0.003$) provenances, while no differences between N_Ap and S_Ap were found in the RCP 4.5 and 8.5 scenarios (Fig. S4c and Table S8). NPP increased with more severe climate scenarios, especially in 2100, resulting in increasing values towards sce-

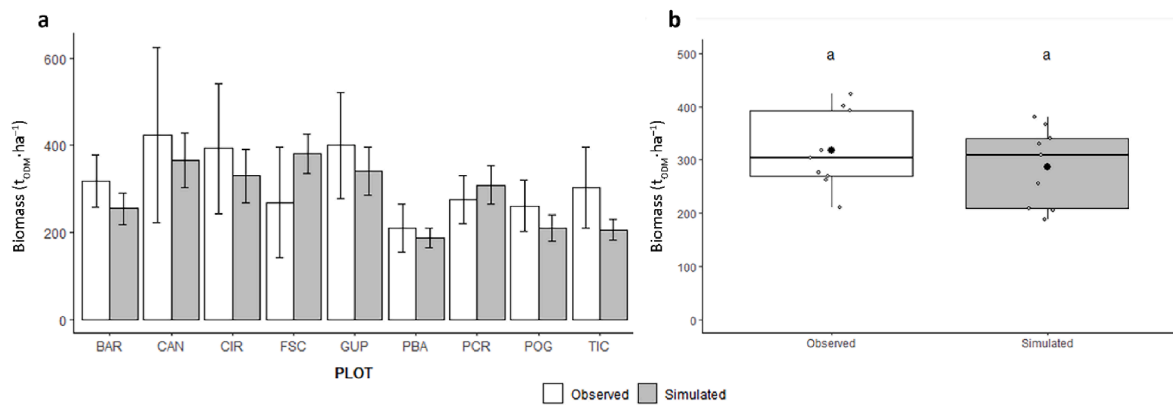


Fig. 3. Validation of biomass results at plot level and for the whole study area. **(a)** Observed (white) vs. simulated (grey) biomass values per hectare for each plot used for model parametrization and **(b)** mean biomass values per hectare. Common letters above the boxes (i.e., a-a) indicate no significant differences between observed and simulated data.

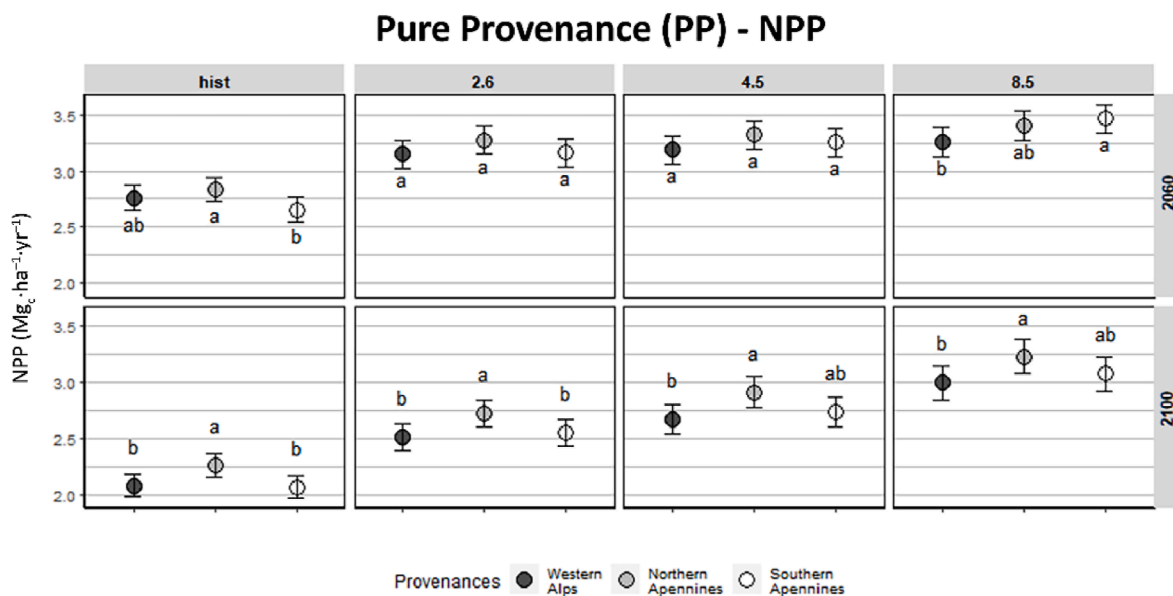


Fig. 4. PP simulations NPP results. Comparison between NPP values of W_Al (black), N_Ap (grey), and S_Ap (white) silver fir provenances, under historical climate and three climate scenarios (RCP 2.6, 4.5, and 8.5) and in two different timesteps (2060 and 2100). Different letters indicate significant differences between provenances.

nario 8.5 compared to the historical run (Figs. 4 and S4c). Finally, the respiration results showed significantly different values between the provenances too (Table S7), favoring the N_Ap provenance over the S_Ap ($p \leq 0.02$) and W_Al ($p \leq 0.01$) provenances. In 2060, local provenance always showed higher R with respect to the S_Ap provenance, while no statistical differences were found between the local and W_Al provenance. On the contrary, in 2100, N_Ap provenance showed significantly higher R values compared to the W_Al provenance in all model runs, and higher R values than the S_Ap provenance in the historical and RCP 2.6 runs (Fig. S4d).

3.3. MP simulations

The results of the MP simulations showed 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 (Table S9), revealing higher values for the S_Ap provenance than for the other two provenances ($p < 0.001$), in all climatic scenarios and time horizons. Similarly, the N_Ap (local)

provenance showed higher BA values than the W_Al provenance in all MP simulations ($p < 0.001$) (Fig. S5a and Table S10). The model results indicated a significant interaction between BA and SD in 2060 and 2100 for RCP 2.6 ($p = 0.01$ and $p = 0.001$, respectively) and RCP 8.5 runs ($p = 0.01$ and $p < 0.001$, respectively), and in 2100 for the historical run ($p = 0.008$). Analyses of the unbundled results of the three SD levels revealed that the previously observed trend for the RCP 2.6 scenario repeats in all SDs and time horizons, except for $\text{SD} = 210 \text{ plants} \cdot \text{ha}^{-1}$ in 2100, where the difference in BA between N_Ap and W_Al disappears. The same happened for the historical run at 2100, where no differences were found in BA between N_Ap and W_Al for $\text{SD} = 210$. For RCP 8.5 simulations, on the other hand, the observed trend (i.e., $\text{BA}_{\text{S_Ap}} > \text{N_Ap}} > \text{W_A}$) remained unchanged for all levels of SD (Fig. S5a). Biomass (B) generally shows 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. S5b). Again, the results indicated 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 historical run ($p = 0.001$)

(Table S9). In 2060, the common trend (S_Ap and N_Ap biomass > W_Al biomass) was changed only in RCP 2.6 scenario with SD = 150, showing higher B values for the N_Ap than for the S_Ap provenance ($70.5 \text{ Mg ODM}\cdot\text{ha}^{-1} > 64.9 \text{ Mg ODM}\cdot\text{ha}^{-1}$, $p = 0.018$), which in turn resulted in higher B than the W_Al ($64.9 \text{ Mg ODM}\cdot\text{ha}^{-1} > 49.2 \text{ Mg ODM}\cdot\text{ha}^{-1}$, $p < 0.001$). In 2100, the trend varies considerably according to SD: with SD = 90 significant differences between the provenances appeared, with biomass greater in S_Ap than the other two provenances in the historical run, 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 increased with more extreme climate scenarios, while this trend disappeared at higher seed densities (Fig. S6b). The results for the NPP values showed differences according to provenance (Table S9), following the trend S_Ap > N_Ap > W_Al in all scenarios and time horizons except for RCP 8.5 in 2100, in which the NPP difference between S_Ap and N_Ap disappeared (Figs. 5 and S5c). Fig. 5 reports the NPP values for the three provenances under MP simulations across different climate scenarios and time horizons. The S_Ap provenance showed higher NPP values compared to the others in most scenarios and both reference years (2060 and 2100). Differences among provenances remained visible across climate scenarios, with generally higher NPP values observed under more severe climate conditions. Specifically, in 2060, the NPP increased as climate scenarios became more intense, while by 2100, the differences in NPP between climate scenarios were less pronounced. In the NPP ANCOVA results, the interaction between provenance and SD was significant for the historical run ($p = 0.004$) and RCP 2.6 ($p = 0.018$) scenario in 2060, while in both 2060 and 2100 for the RCP 8.5 scenario ($p = 0.042$ and $p < 0.001$, respectively) (Table S9). Analyzing the decoupled NPP values for each SD, we see that the difference in NPP between S_Ap and N_Ap only remained at SD = 90 in the historic scenario in 2060, at SD = 150 in the historical run and RCP 8.5 scenario, and RCP 2.6 and 4.5 for SD = 210. In 2100, instead, the trend (S_Ap NPP > N_Ap NPP) was respected in all SD = 90 (except for RCP 4.5) and in RCP 4.5 for SD = 150 (Fig. S6c). Finally, the R results followed the same trend as the NPP results, showing a progressive increase as the severity of climate scenarios intensifies at both 2060 and 2100 time horizons (Fig. S5d). The interactions between provenance and SD were 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) (Table S9). This significant interaction can be explained by non-significant differences between the R values of the S_Ap and N_Ap provenances in several cases when analyzing the model results divided by seedling density levels (Fig. S6d).

4. Discussion

Our study provides evidence of significant differences in the growth patterns, productivity, and carbon storage capacities of the three silver fir provenances under various climate change scenarios. The Northern Apennines provenance consistently showed higher biomass production and carbon uptake in pure stands (Fig. S4), suggesting its robustness and adaptability in managed forest conditions. The Southern Apennines provenance excelled in mixed stands with active regeneration (Fig. S5), indicating high resilience and productivity under more competitive and dynamic forest environments. Additionally, the simulations underscored the resilience of silver fir to climatic stressors, revealing consistent basal area and biomass values across different RCP scenarios. These results highlight the role of genetic diversity in enhancing forest resilience and productivity in a climate change context, supporting the incorporation of provenance-specific data into forest models for more accurate and reliable predictions. The observed growth patterns show the potential of silver fir to adapt and thrive under varying climatic conditions, underlying the importance of this species for future forest management and conservation strategies that address the impacts of climate change.

4.1. Model validation

The successful validation of the FORMIND model is evident by its performance across the different forest plots (Fig. 3). 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, demonstrating the model's robustness in capturing forest dynamics across heterogeneous environments, important for subsequent simulations. By confirming its accuracy, FORMIND can be applied with greater confidence in subsequent PP

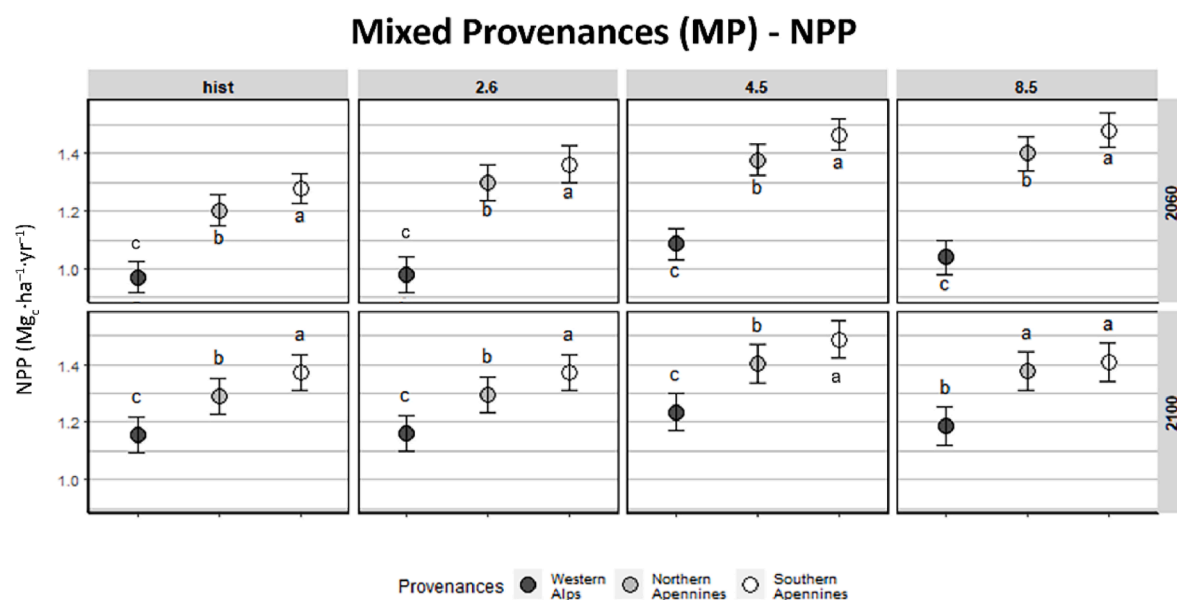


Fig. 5. MP simulations NPP results. Comparison between NPP values of W_Al (black), N_Ap (grey) and S_Ap (white) silver fir provenances, under historical climate and three climate scenarios (RCP 2.6, 4.5, and 8.5), and in two different timesteps (2060 and 2100). Different letters indicate significant differences between provenances.

and MP runs, simulating different forest contexts under various scenarios, including climate change impacts and forest management strategies. Finally, 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, which require localized attention to understand the relationships between forest growth and climate. Spatial downscaling enables the development of high-resolution climate projections that are crucial to address the specific needs (Terzago et al., 2018). Thus, downscaling serves as a critical methodology for providing detailed, area-specific climate projections, which are essential for the sustainable management and preservation of mountain ecosystems under changing climatic conditions. In subsequent PP and MP simulations, while biomass and other forest metrics differ between sites due to local environmental conditions, the observed patterns and trends between PP and MP simulations remain consistent, also between climate scenarios. This consistency suggests that although the specific magnitudes may vary, the relative differences and overall dynamics captured by the model are applicable across different forest contexts. This robustness is crucial for making generalized conclusions about forest dynamics under varying climatic conditions.

4.2. Performance of silver fir provenances

The results of our study show significant differences in the growth patterns, productivity, and metabolism. The carbon storage capacity of the silver fir provenances considered in this study confirms how silver fir forest material of different origins is associated with a diverse environmental response (Hansen and Larsen, 2004; Kerr et al., 2015; Konôpková et al., 2020; Oggioni et al., 2024). Further, the study underlines 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 (Fig. S5) are in line with other works that have found high performance in drought response and productivity for southern Italian provenances (Hansen and Larsen, 2004; Kerr et al., 2015; Mihai et al., 2021; Oggioni et al., 2024). Basal area values were statistically higher for the Southern Apennine provenance than for the other two provenances, also in PP simulations (Fig. S4a), identifying it as the provenance that exhibited larger diameters and greater space occupation in the horizontal plane. Despite the significant differences in basal area between the Southern Apennines and Western Alps provenances across climate scenarios, aboveground biomass values are not equally divergent, particularly under PP simulations. Although basal area and biomass are typically positively correlated (Jagodźiński et al., 2019), several factors may explain this decoupling. First, biomass estimates account for wood density, while basal area reflects only stem cross-sectional area. If one provenance exhibited lower wood density than the other, as might occur given intraspecific variation linked to climatic origin and growth rates, this could result in reduced biomass despite higher basal area. Furthermore, differences in tree architecture, such as height-to-diameter or biomass-to-diameter ratios, may lead to divergent growth allocation strategies, with S.Alp favouring radial expansion and W.Alp allocating more biomass to height or crown development. Additionally, the use of general allometric equations, which do not capture provenance-specific variation in stem shape, crown mass, or taper, may contribute to the mismatch: Trees with thicker stems but lighter crowns, as potentially observed in S.Alp, may be underrepresented in biomass estimates. Finally, differences in stand structure, such as a more uneven size distribution or a stronger influence of dominant individuals, could disproportionately increase basal area without a corresponding rise in total biomass. These findings underscore the limitations of relying exclusively on morphological traits for provenance parameterization and highlight the need for future model improvements incorporating provenance-specific wood density and structural traits. In parallel, our simulations in PP plots indicate a superior production and carbon sink of

the Northern Apennines provenance (local), particularly when compared to the W.Alp provenance (Fig. S4b and S4c). In the PP simulations, the higher biomass and NPP values of the local provenance are often consistent with the performance 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 (Figs. S4b, S4c, S5b, and S5c). 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, favoring continental climates such as the Czech Republic over rapidly changing Mediterranean climates (Lionello and Scarascia, 2018). The different trends between pure and MP 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 the genetic composition of 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 provenances respond better during forest growth simulations, marking these two provenances as valuable resources for forest management in the Tuscan-Emilian Apennine National Park area. This confirms the results of previous studies on the performance of these same provenances in the same study area (Oggioni et al., 2024) and clearly highlights the potential of silver fir genetic diversity in adapting to a changing climate (George et al., 2015; Vitasse et al., 2019b). These results provide valuable insights for forest managers in the Tuscan-Emilian Apennines, where reforestation and afforestation programs can benefit from selecting local or Southern Apennines provenances. In particular, the superior growth performance of these provenances under different climate scenarios suggests their suitability for seed sourcing initiatives aimed at increasing forest resilience and carbon sequestration potential. Provenance selection based on modelled productivity and stability across climate scenarios represents a proactive strategy to enhance adaptive forest management under climate change. 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 programs 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).

4.3. Climate change effects

The resilience of silver fir growth to varying climatic conditions, as indicated by the consistent BA and biomass values across different RCP scenarios (Fig. S4a and S4b and S5a and S5b), is evidence for silver fir's remarkable adaptability and resilience to drought conditions (Gazol et al., 2015; Gazol and Camarero, 2016; Oggioni et al., 2024). Silver fir response to warmer and drier climates revealed high resilience, 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 PP simulations (Fig. 4), 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 run in the next decades in the territories studied, assuming a good response of silver fir to a rise in temperatures and aridity in the areas 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 annually (Zhu et al., 2019). Our results reveal that while maintaining a good regeneration rate (MP simulations), NPP does not vary between 2060 and 2100 (Fig. 5), while it decreases in PP simulations without regeneration (Fig. 4), underlining a possible effect of forest age. The reduced capacity of mature forests to store carbon annually in our simulations could also be due to the general underestimation of forest growth models (Carey et al., 2001). Even if productivity (NPP) tends to decrease with forest age beyond a variable threshold, the conservation of old-growth forests remains fundamental. The role of old-growth forests should not be underestimated, as they represent a significant storage of biomass and provide critical habitats for various species that depend on the unique conditions of old-growth ecosystems (Carey et al., 2001; Desai et al., 2005). Our results also show an increase in plant respiration as a function of the severity of the climate scenario (Figs. S4d and S5d), emphasizing 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 processes (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 with rising temperatures in the climate scenarios is accompanied by higher NPP. This implies that GPP increases more than respiration. This pattern is found, 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 its ability to ensure the carbon sequestration of the forest (Oggioni et al., 2024; Vitasse et al., 2019a), and should therefore be promoted on suitable sites to ensure healthy forests that provide multiple ecosystem services (Vitasse et al., 2019b).

The inclusion of forest provenance data is a fundamental aspect of forest modelling. Genetic diversity, often overlooked in traditional modelling, emerged in this study 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 under different climate scenarios, suggesting that climate change may not alter the distinctive patterns between provenances in the simulated areas. It is therefore clear that forest modelling can greatly benefit from the integration of provenance-specific parameters, providing more reliable projections under different climate change scenarios and informing more sustainable and resilient forest management. Integrating forest provenance data into forest models can present significant challenges. Parametrizing 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 and serves 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 and analyze the role of climate-smart forestry practices on the response of species to climate. From an operational perspective, incorporating the results of provenance-specific modelling into forest policy and seed transfer guidelines may enhance the adaptive potential of reforestation programs. Our findings suggest that current seed sourcing protocols should consider not only local adaptation but also the demonstrated performance of Southern provenances, especially in mixed stand contexts with active regeneration. These insights can inform regional/national seed transfer rules and assisted migration frameworks, making forest stands more robust to expected climatic shifts.

Despite the robustness of our approach, several limitations should be acknowledged. One important aspect concerns the simplification of regeneration dynamics, which were parameterized uniformly across provenances and scenarios. This assumption likely underrepresents the ecological variability of natural regeneration, which may differ in timing, intensity, and sensitivity to climate conditions. Another relevant limitation relates to the uncertainty inherent in climate projections. Although three GCMs and three RCPs (2.6, 4.5, and 8.5) were used to account for a range of possible future climates, climate projections inherently carry uncertainty. Our simulations should therefore be interpreted as possible trajectories rather than deterministic forecasts. Incorporating additional model ensembles or regionally downscaled projections could further improve the robustness of future scenarios. A further limitation concerns the parameterization of genetic provenances, which, although innovative, relied on limited individual sampling and morphological traits only. While this approach allowed for a relatively straightforward implementation of provenances in the model, it does not fully account for the physiological or genomic variability within each provenance, which may affect growth and responses to stress. Finally, only a limited number of silver fir provenances could be parameterized in this study. Although silver fir is one of the few species in Italy with available genetic characterization, data are still limited to a small number of provenances. Extending this approach to include additional provenances or to apply it to other species is currently difficult, mainly due to the lack of provenance trials and the limited availability of genetic data. This limits the broader application of provenance-based modelling approaches and highlights the need for greater investment in long-term genetic monitoring across forest species.

5. Conclusions

In this study, we investigated the dynamics of Italian silver fir forests and three of their provenances under climate change, using the individual-based forest model FORMIND. By accurately reproducing forest dynamics, the model proves to be a valuable tool for ecological simulation and a solid basis for developing long-term forest

management strategies. Silver fir showed resilience across climate scenarios, with consistent basal area and biomass values suggesting potential robustness in diverse environmental contexts. Its increasing carbon sequestration capacity under warmer scenarios also highlights its relevance for climate mitigation. However, this potential is influenced by forest age, as younger stands tend to sequester more carbon than older ones, as shown in our simulations without regeneration.

Provenance-specific analyses revealed marked differences in growth, productivity, metabolism, and carbon storage, with local (Northern Apennines) and Southern Apennines provenances outperforming the Western Alps in the study area. These consistent differences across scenarios underline the importance of genetic diversity in shaping forest adaptability and resilience. Our results support the integration of provenance data into forest models to better represent morphological and environmental variability. Including genetic diversity is essential for predicting forest responses to climate change and for informing adaptive management, assisted migration strategies, and conservation planning. In fact, these findings provide valuable insights for future forest planning, particularly in selecting appropriate provenances for afforestation or assisted migration under climate change. The approach also offers a framework for incorporating genetic considerations into forest policy, promoting resilience-based management strategies. Further research integrating physiological traits and broader genetic datasets could enhance model precision and support evidence-based decision-making in both forestry and conservation contexts. We hope this work will encourage further research and model development that combines genetic and ecological information to improve the accuracy and applicability of forest projections in a changing climate.

CRedit authorship contribution statement

Silvio Daniele Oggioni: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lorenzo Matteo Walter Rossi:** Writing – review & editing, Supervision, Investigation. **Silvia Terzago:** Writing – review & editing, Visualization, Software, Methodology. **Friedrich J. Bohn:** Writing – review & editing, Software, Resources, Methodology, Investigation, Conceptualization. **Giorgio Vacchiano:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Giorgio Vacchiano reports financial support was provided by Tuscan-Emilian Apennine National Park. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2025.100389>.

Data availability

Data will be made available on request.

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