Stand age diversity affects forests' resilience and stability, although unevenly

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Running Head: Forest age and resilience and stability.

Abstract

Stand age significantly influences the functioning of forest ecosystems by shaping structural and physiological plant traits, affecting water and carbon budgets. Forest age distribution is determined by the interplay of tree mortality and regeneration, influenced by both natural and anthropogenic disturbances. Thus, human-driven alteration of tree age distribution presents an underexplored avenue for enhancing forest stability and resilience. In our study, we investigated how age distribution impacts the stability and resilience of the forest carbon budget under both current and future climate conditions. We employed a biogeochemical model on three historically managed forest stands and projecting their future as undisturbed systems, i.e. leaved at their natural evolution with no management interventions. The model, driven by climate data from five Earth System Models under four representative climate scenarios and one baseline scenario, spanned 11 age classes for each stand. Our findings indicate that Net Primary Production (NPP) peaks in the young and middle-aged classes (16- to 50-year-old), aligning with ecological theories, regardless of the climate scenario. Under climate change, the beech forest exhibited an increase in NPP and maintained stability across all age classes, while resilience remained constant with rising atmospheric CO_2 and temperatures. However, NPP declined under

climate change scenarios for the Norway spruce and Scots pine sites. In these coniferous forests, stability and resilience were more influenced. These results underscore the necessity of accounting for age classes and species-specific reactions in evaluating the impacts of climate change on forest stability and resilience. We, therefore, advocate for customized management strategies that enhance the adaptability of forests to changing climatic conditions, taking into account the diverse responses of different species and age groups to climate.

Keywords: carbon cycle, climate change, forest resilience, forest age, forest management, modeling.

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Introduction

Over the last decade, the European forest policies (Cerulo et al., 2023) have geared towards
sustainable and climate-resilient forests to ensure ecosystem functioning under future climate
conditions and the sustained provision of services (e.g., regulation, supply, cultural services), including
carbon sequestration for forest-based mitigation strategies (Yousefpour & Hanewinkel, 2016; Nabuurs
et al., 2018; Churkina et al., 2020; Favero et al., 2021). The contribution of forests to land-based
mitigation actions is shaped by external and internal drivers that influence the ecosystem's net carbon
accumulation. This dependency is uncertain under future changing environmental conditions
(Yousefpour & Hanewinkel, 2016). Carbon assimilation and wood production are affected by
environmental drivers like precipitation and temperature, light availability, atmospheric CO_2
concentration (CO_2), and nitrogen deposition (Barford et al., 2001; D'Andrea et al., 2020, 2021; He et
al., 2023). In the temperate biome, the effects of increasing temperature on wood production are
ambiguous, with studies reporting both positive and negative impacts (Jump et al., 2006; Potočić et al.,
2021). As reported in several studies, the positive synergistic effect of elevated atmospheric CO_2 levels
and climate dynamics has likely accelerated European forest growth in recent decades (Bellasen et al.,
2011; Pretzsch et al., 2014; He et al., 2023). Other studies, however, question the strength and future
persistence of the CO_2 fertilization effect on the forest carbon sink due to the emergence of other
limiting factors, like water and nutrient availability (Nabuurs et al., 2013; Wang et al., 2020; Duffy et
al., 2021). Climatic models have predicted that the impacts of future climate change will likely alter
temperature and precipitation patterns, subsequently influencing atmospheric vapor pressure deficit and
soil water availability (IPCC, 2021). These changes could affect the rates of photosynthesis and plant
respiration and, ultimately, plant productivity (Reyer et al., 2014; Yuan et al., 2019; He et al., 2023). In
addition, significant impacts on forest structural and biological diversity are anticipated (IPCC 2021).
These changes will interact with environmental factors, influencing ecosystem productivity, resilience,
and stability. Therefore, evaluating forest ecosystems' stability is critical for understanding their
resistance to environmental pressures and human-induced disturbances. The sensitivity of forests to
climate change underscores the importance of comprehensive conservation strategies to protect these
fragile ecosystems. Forest stand heterogeneity in landscapes (Bohn and Huth, 2017), variations in leaf
area index (LAI, Vilà et al., 2013), and species compositions (Asner et al., 2003) are all factors
influencing forest productivity. Climate change is expected to accelerate tree growth, induce earlier

maturation, and shorten tree lifespan (Collalti et al., 2019; Brienen et al., 2020), potentially affecting

forests of various age structures differently (Anderson-Teixeira et al., 2013; Colangelo et al., 2021).

The traditional view of forest dynamics in undisturbed ecosystems describes an initial stepwise

increase in productivity, followed by stabilization and a slight decline (Kira and Shidei, 1967; Odum,

1969). While this view has been found robust under current climate conditions, this concept has been

scarcely re-evaluated under climate change scenarios. Notably, future environmental shifts (e.g.,

climate, nutrients, atmospheric CO_2 levels) might impact forest stands, or 'cohorts' of different ages

differently, as both gross primary production (GPP) and plant respiration —key components of the

autotrophic carbon budget— vary with stand development (Drake et al., 2011; Goulden et al., 2011;

Collalti et al., 2020a). The net balance between photosynthesis and respiration, i.e. net primary

production (NPP), being climate- and age-dependent, is likely to respond differently across age spectra

under future climatic conditions because these two processes respond differently (Goulden et al., 2011;

Collalti 2020a, 2020b).

Given the significant role of silvicultural practices in shaping the current age distribution of managed

forests (Wulder et al., 2009; Latterini et al., 2023), understanding the tree-level age-sensitivity to

climate change in the forest carbon budget is fundamental for developing future climate-smart forest

management schemes. A deep understanding of the processes affecting the age dependency of CO_2

uptake and wood production is essential for devising strategies to enhance forest resilience and stability

under climate change.

Despite the potential impact of climate change on forests of all ages, there is a lack of prospective

understanding of its interaction with forest age. Unfortunately, only a few models have examined age

and the ecosystem carbon budget interplay in a climate change context (Anderson-Teixeira et al.,

2013). Process-based models (PBMs) enable investigations into the effects of climate change and

atmospheric CO_2 on different age cohorts within the same geographic location, a task challenging with

field measurements. Using a validated biogeochemical, biophysical PBM, this study aims to quantify

controls on carbon assimilation in undisturbed forests, considering the effects of climate change and

stand age. We also evaluated the sensitivity of NPP, a crucial flux representing the annual net carbon

sequestration capacity, to key variables such as mean annual temperature (MAT), atmospheric CO_2

concentration, and vapor pressure deficit (VPD) across different stand ages under five climate

scenarios, including a no-change climate scenario.

The specific objectives are: (i) to explore the direct impact of climate change on forest productivity

across various stands, species, and age cohorts in different European regions; (ii) to investigate how

forest age might modulate dynamics in response to future climate change; (iii) to assess whether age

diversity influences the stability and resilience of future forests under changing climatic conditions.

Materials and Methods

Study sites and virtual stands

The study was conducted in three even-aged, previously managed European forest stands: i) the Boreal

Scots pine (*Pinus sylvestris* L.) forest of Hyytiälä, Finland (FI-Hyy); ii) the wet temperate continental

Norway spruce (*Picea abies* (L.) H. Karst) forest of Bílý Krìz in the Czech Republic (CZ-BK1); and

iii) the temperate oceanic European beech (*Fagus sylvatica* L.) forest of Sorø, Denmark (DK-Sor). For

each site, daily bias-adjusted downscaled climate data from five Earth System Models (i.e., HadGEM2-

ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, GFDL-ESM2M, and NorESM1-M) driven by four

Representative Concentration Pathways, namely RCP 2.6, 4.5, 6.0, and 8.5 were available (Fig. SX).

For more detailed information on the study sites characteristics and climate data, see Collalti et al.

(2018, 2019), Reyer et al. (2020), Mahnken et al. (2022), and Dalmonech et al. (2022). The chosen

sites have been selected due to their long monitoring history and the availability of a wide range of data

sources for both carbon fluxes and biometric data for model evaluation, as well as bias-corrected

climate scenarios for simulations under climate change scenarios. In addition, these stands: i) cover a

wide climatic gradient, ii) their current state is the result of the legacy of past forest management, iii)

they are mainly mono-specific and therefore represent interesting «living labs» to study the effects of

climate change on single-species and their productivity, reducing confounding effects which otherwise

make models struggle to predict forest growth and carbon dynamics (e.g., Vacchiano et al., 2012;

Marèchaux et al., 2021), and they have already been in-depth investigated in the context of climate-

smart-forestry silvicultural scenarios (Dalmonech et al., 2022).

The model was forced with the modeled climate under different emission scenarios, corresponding to

the RCP atmospheric CO_2 concentration values for the period 1997 to 2100, ranging from 421.4 µmol

mol-1 in the "best-case scenario" (RCP 2.6) to 926.6 µmol mol^{-1} of the 'worst-case scenario' (RCP

8.5). For comparison purposes, the forest model was forced with a detrended and repeated meteorology

and atmospheric CO_2 concentration from 1996-2006, i.e., the current climate scenario (CCS),

considered the current climate's baseline.

At the beginning of the simulations, we created a Composite Forest Matrix (CFM) following the

approach described in Dalmonech et al. (2022) to simulate the potential effect of climate stressors on

stands of different ages. The 3D-CMCC-FEM v.5.6 has been run at each site to cover the rotation

period of each species (from 1997 to 2099) amid the current climate scenario (fixed atmospheric CO_2

concentration at the year 2000 of 368.8 µmol mol^{-1}) consisting of detrended and repeated cycles of the

present-day observed meteorology from 1996 to 2006 and the BAU management practices observed at

the site. Data required to re-initialize the model at every tenth of the rotation length were retrieved from

each simulation. Hence, ten additional stands were chosen for each age in the composite matrix and

added to the CFM. This collection of virtual forest stands was used to set different starting ages at the

present day (age_{t0}) due, ideally, to the past silvicultural practice and climate. These new stands were

used to assess the impact of climate forcing on a full range of age_{t0}, as the model has already been

shown to be sensitive to forest stand development and the relative standing biomass (Collalti et al.,

2018, 2019, 2020a).

The model, model runs, and results evaluation

The 3D-CMCC-FEM (*Three Dimensional - Coupled Model Carbon Cycle - Forest Ecosystem Module*; Collalti et al., 2014, 2016; Marconi et al., 2017; Mahnken et al., 2022; Dalmonech et al., 2022, 2024; Testolin et al., 2023) was initialized with the structural attributes of the newly created stands from 1997, which was consequently the starting year of all simulations. Modeled climate change simulations under different RCP-emissions scenarios started to differentiate in 2006 (up to 2100). The simulation runs from the different stand initial conditions, corresponding to different age_{t0} classes, were carried out without management as we are interested in the direct climate impact on undisturbed forest stand response, avoiding the confounding effects of forest management on the responses (for forest management effects, see Dalmonech et al., 2022). A total of 825 different simulations were performed as they are the combination of 5 ESM*5 RCP (4 RCPs + 1 present-day climate scenario) * 11 age_{t0} classes * 3 sites. Results were reported for NPP as it is considered one of the most representative and fundamental variables in the carbon cycle. The 3D-CMCC-FEM model underwent initial assessment against observed climate conditions based on field data availability for GPP and NPP ($gC \ m^{-2} \ year^{-1}$) as well as the diameter at breast height (DBH) following the methodology reported by Dalmonech et al. (2022; see "Model validation" in Supplementary Material). We compared GPP and NPP against eddy covariance estimates and ancillary data for the years 1997-2005 for DK-Sor and FI-Hyy and 2000-2005 for CZ-BK1. We also compared the diameter at breast height (DBH) in all sites with field measures.

Sensitivity, resilience, and stability analysis

To assess the impact of climate drivers on the NPP of different age_{t0} classes, i.e., initial conditions, we performed a sensitivity analysis under all climate change scenarios considered. In this sense, sensitivity refers to the extent to which a system is either negatively or positively impacted. We tested the dependence of NPP on MAT, atmospheric CO_2 concentrations, and VPD. These variables constitute three pivotal environmental factors that influence crucial growth processes, including the rates of photosynthesis, carbon and water use efficiency, and stomatal regulation. We calculate the slope associated with each forcing variable by fitting a multivariate linear model to account for multi-collinearity among climate drivers. We use NPP as the dependent variable and MAT, atmospheric CO_2, and VPD as independent variables. The higher the slope in absolute terms, the higher the sensitivity to that forcing variable.

Theoretical research has shown that when systems approach a point of no return, where a significant and irreversible change is likely to occur, they become less capable of handling disruptions and

preventing significant shifts in their behavior (Zampieri et al., 2021). This capacity to deal with

perturbations is often called resilience. It has been suggested that this reduced ability to bounce back

can be observed through the increased temporal autocorrelation (TAC) in the system's behavior over

time (Scheffer et al., 2015; Forzieri et al., 2022), reflecting a slower recovery process caused by critical

changes at these tipping points, a process also called Critical Slowing Down (CSD)(Smith & Boers,

2023). Another suggested predictor of approaching a tipping point is the temporal variability

(Carpenter and Brock, 2006; Hewitt and Thrush, 2010; Drake and Griffen, 2010; Smith & Boers,

2023), which can be expressed as the variance or standard deviation of the state variable (i.e., NPP)

along time. An increase in temporal variance can foreshadow a regime shift and a loss in stability.

In this study, we calculated the long-term resilience and stability for each scenario and age_{t0} as the 1-lag

TAC and standard deviation (SD) of the whole time series, respectively. We also computed the 1-lag

TAC and standard deviation of detrended NPP time series within a 20-year moving window for each

age_{t0} and scenario to assess the interaction between resilience and stability during the simulation

period.

Results

Effect of age_{t0} classes and climate change on productivity

At the CZ-BK1, NPP values vary under CCS from ~350 to ~225 gC m^{-2} year^{-1}, while from ~370 to

~210 gC m^{-2} year^{-1} similarly across all RCPs (Figure 1A). Also, at CZ-BK1, NPP peaks in the younger

age_{t0} classes, independently of the climate scenarios considered (i.e., 12- to 36-year-old class). At CZ-

BK1, any of the combinations of age_{t0} x RCPs shows a reduction of NPP compared to CCS. At FI-Hyy,

younger age_{t0} classes started with very low NPP values (~120 gC m^{-2} year^{-1}), step wisely increasing

and then stabilizing at the middle of the century at ~420 gC m^{-2} year^{-1} and then declining, more in the

oldest age_{t0} classes, from ~250 gC m^{-2} year^{-1} under RCP 2.6 to ~230 gC m^{-2} year^{-1} under RCP 8.5

(Figure 1B). At FI-Hyy, the more productive cohorts are clustered around the first third of the age_{t0}

classes (i.e., 28- to 56-year-old). Similar to CZ-BK1, at FI-Hyy NPP shows a reduction under RCPs

when compared to CCS, except for RCP 6.0 (see Table S3 in Supplementary Material). Last, at DK-

Sor, results show different patterns concerning other sites, with NPP at the end of the century varying

from ~800 gC m m^{-2} year^{-1} (under RCP 8.5) to ~560 gC m^{-2} year^{-1} (under CCS) and then smoothly

increase toward the end of the century as the severity of the scenario increase in all age_{t0} classes (Figure

1C). Mean annual NPP has the maximum values for the younger age_{t0} classes, with the peak for the 14-

year-old. Different from the other sites, at DK-Sor, in all age_{t0} classes, higher RCPs show

proportionally increased NPP compared to the CCS scenario (see Table S3 in Supplementary Material).

Overall, in all sites and climate conditions, the model effectively captures the typical age-dependent

patterns of NPP with relatively stable productivity at young and intermediate ages and a more

pronounced decline in older forests. The two conifer stands show a sharper growth decline toward the

end of the century across all climate scenarios. This trend was not observed in broadleaf stands.

Climate sensitivity

The results of the sensitivity analysis are shown in Figure 2 for each site and the three forcing variables

considered (MAT, atmospheric CO_2 concentration, and VPD). At the CZ-BK1 site, under all climate

change scenarios, the relationship between productivity and temperature MAT was always negative,

with the least sensitive age_{t0} classes being the oldest ones (108-120 years old) in all scenarios except

for RCP 2.6, where all classes exhibit a similar sensitivity to MAT. On the contrary, Norway spruce

showed a positive relationship with the atmospheric CO_2 except under RCP 2.6 (i.e. the less enriched

CO_2 scenario), and the least sensitive age_{t0} classes were the middle ones (60-86 years old).

Furthermore, as the climate scenario intensified, Norway spruce exhibited an increased sensitivity to

elevated temperature and CO_2 levels. Similar to MAT, the relationship between NPP and VPD was

negative under all scenarios for most age_{t0} classes (only the youngest classes showed a positive

relationship with VPD under RCP 4.5-8.5). However, the sensitivity increased almost linearly with

age_{t0}.

Scot pine at FI-Hyy showed similar behavior to Norway spruce but with opposite trends, exhibiting a

positive relationship between NPP and MAT only for the youngest age_{t0} (14-28 years-old). The same

holds for the atmospheric CO_2 concentration, but the sensitivity decreases with the severity of the

scenario. Similarly to Norway spruce, the sensitivity to VPD generally increases with the age_{t0} but with

the highest value for the youngest classes.

At DK-Sor, the beech forest exhibits different patterns with respect to the other sites, featuring a

consistently positive correlation between NPP and MAT (but with no clear patterns across age_{t0} and

scenarios). On the contrary, a negative relationship was observed against the atmospheric CO_2 for most

age_{t0} classes under all climate change scenarios, except for RCP 6.0 (where the beech exhibited the

least sensitivity). The sensitivity to VPD did not exhibit a clear pattern when comparing different age_{t0}.

However, the highest sensitivity was reached under RCP 4.5.

The findings from the sensitivity analysis indicate that younger age_{t0} classes in the coniferous forests
are more vulnerable to variations in climate variables and atmospheric CO_2 concentration compared to
beech forests. Specifically, NPP in conifers demonstrates an inverse correlation with elevated
temperature and VPD, whereas in beech forests, the relationship is characterized by a direct
proportionality. Overall, NPP sensitivity to forcing variables mildly increases with the severity of
climate change in coniferous stands, while the beech forest reaches the highest sensitivity (in particular
to MAT and VPD) under RCP 4.5.

Resilience and stability

The resilience and stability analysis results for each site are reported in Figures 3 and 4, respectively.
Figure 5 shows the temporal variation of stability and resilience calculated within a moving window of
20 years. At the CZ-BK1 site, Norway spruce shows increased NPP resilience and stability,
progressing from younger to older stands. This observed trend is consistent across all climate scenarios,
but as the severity of the scenario increases, resilience tends to increase while stability decreases. In
CZ-BK1, younger stands exhibited an initial phase characterized by higher instability and lower
resilience, converging over time to conditions comparable to those observed in older stands.

In contrast, older stands demonstrated minimal stability and resilience metrics fluctuations throughout
the simulation. The Scot pine at FI-Hyy exhibited a more stable trend in stability, unaffected by the
different climate scenarios, with the youngest age_{t0} class showing slightly more stability, although the
difference is minimal. Conversely, the younger classes demonstrated the highest long-term
autocorrelation, regardless of the climate scenario. As for Norway spruce, the Scots pine showed a
similar trend in the temporal variation of stability and resilience. In this pattern, the older classes
exhibited remarkable stability and resilience during the simulation period and the tightening of climate
scenarios.

Meanwhile, age_{t0} younger than 60 years reach a stable and resilient state at the end of the simulation
period. The beech stands at DK-Sor showed an opposite trend concerning the coniferous strands,
showing low stability that slightly but steadily increases with the escalation of climate scenarios and
high resilience, with minimum differences among age_{t0} classes and scenarios. Throughout the
simulation, slight variation in stability and resilience was observed, with only minor variations among
the different age_{t0} classes. The results indicate that the most 'favorable' climate scenarios were RCP
6.0, characterized by higher stability, and RCP 8.5, in which resilience is highest.

Discussions

Stand age and climate effects on productivity.

The emerging pattern from the modeling simulation framework shows that regardless of the climate scenarios and in the absence of human intervention, productivity in coniferous stands will decline in the foreseeable future, more likely in the older age_{t0} classes. On the contrary, the future productivity of beech forests at DK-Sor will be expected to increase under most RCP scenarios. These results align with current observations indicating that conifers are suffering from a climate-related decline in NPP (likely due to the greater hydraulic limitation and, therefore, higher sensitivity to the increased soil and atmospheric aridity)(Krezjka et al., 2021). The decline was pronounced in conifers compared to broadleaf, especially beech forests, in the most northern species distribution (De Castillo et al., 2022). Recent studies confirm our results, finding lower relative increment gains for the conifer species Norway spruce and Scots pine (18 and 35%) compared to the deciduous species as European beech and sessile/common oak (75 and 46%)(Pretzsch et al., 2023). Many model simulations have failed to replicate this phenomenon. For example, Reyer (2015) observed that 87% of the simulations run with changing climate and CO_2 concentration (757 out of 870 simulations) performed with 55 different process-based stand-scale models in Europe predict positive responses in NPP under climate change scenarios and increasing atmospheric CO_2 concentrations. Reyer (2015) found that only 13% of the simulations show decreasing forest productivity and declining biomass carbon pools, which is opposite to our study. However, in many of the models investigated, as also in other studies considered (e.g., Vitale et al., 2003; Jansson et al., 2008), factors such as photosynthetic acclimation (saturation) to increasing atmospheric CO_2 concentration, acclimation to rising temperature in autotrophic respiration and drought were not fully and always accounted for, and, often, NPP is considered a fixed fraction of the GPP (see Collalti & Prentice, 2019) or empirically constrained based on current climate conditions (e.g., de Wergifosse et al., 2022). The main consequence of considering NPP as a fixed fraction of GPP instead of prognostically simulating it under climate change scenarios is the increases in NPP *via* increasing GPP, thanks to the CO_2 fertilization effect (Keenan et al., 2023) and the lengthening of the growing season (Peano et al., 2019). On the other hand, the negative feedback on NPP due to increased autotrophic respiration (for maintenance respiration at tree and stand level) is not considered. As other researchers found (e.g., Musavi et al., 2017), the evidence that the main fluxes of the carbon cycle (i.e., GPP and NPP) are mainly controlled by age suggests that the effects of climate change on forest cohorts could be generally less significant than the effect of age, in particular in coniferous

forests, where climate change affects evenly all age_{t0} investigated in this study. These findings align with Foster et al. (2016), who stated in their study that growth variation (in biomass) could be explained mainly by age and size rather than climate variables. In our case, the influence of age_{t0} (that is, the age at the start of the simulation but that increases its effects throughout the model runs) is not a standalone "effect" but rather the result of multiple age-dependent factors. These factors encompass the size of living biomass pools, forest structural traits (e.g., canopy closure, changes in LAI, and alterations in the sapwood volume and mass per unit leaf area), reduction in stomatal conductance (and its effect on photosynthesis), and changes in Non-Structural Carbon usage and allocation. This carbon pool buffers any asynchrony between assimilation, allocation, and plant respiration induced by environmental variability (Collalti et al., 2016, 2020a; Guillemot et al., 2017), thus leading to higher resilience in times of stress (Richardson et al., 2013). The reduction in NPP becomes more prominent with forest aging, probably because of increased maintenance respiration costs due to higher substrate amount and higher enzymatic activity with rising temperatures, although all these mechanisms are yet to be understood (see Collalti et al., 2020a and 2020b). Productivity peaked in the young-intermediate age classes, as also found by Goulden et al. (2011), while in older stands, NPP was drastically reduced. However, it appears that the decline in NPP is not necessarily attributed to the decrease in GPP (thus excluding the fact that NPP is a fixed fraction of GPP), as some suggest (see Drake et al., 2011). Instead, the reduction in NPP is associated with increased autotrophic respiration rate (see DeLucia et al., 2007; Goulden et al., 2011; Drake et al., 2011; Collalti & Prentice, 2019; Collati et al., 2020b) driven by the high maintenance costs for the living, and thus respiring, biomass as identified in this study. The underlying hypothesis is that photosynthesis and dry matter production increase as leaf area increases until the canopy is completely closed. After that, an indirect decrease in soil nutrient availability (Goulden et al., 2011; but not accounted for here), water resources, and an increase in stomatal limitation led to reduced photosynthetic rates; thus, carbon allocation shifts from leaves and roots to aboveground wood production (Litton et al., 2007; Guillemot et al., 2017; Meng et al., 2023) but at the expense of increasing respiratory costs. At the stand-level, such a hypothesis is also strengthened by the age-related reductions in population tree density.

Age and climate-dependent effects of climate change on forest resilience and stability

A growing number of studies have used temporal variance and 1-lag TAC as indicators of CSD (Feng et al., 2021; Smith et al., 2022; Forzieri et al., 2022), also referred to as early-warning signals, primarily through remote sensing-based vegetation indices. However, long-term monitoring and prediction of

CSD are challenging and not wholly reliable based on satellite time series data. Firstly, remote sensing-based vegetation indices are constrained to the past-present temporal window, are time-delayed, and are often unavailable as suitable long time series. Secondly, remote sensing time series data are often constructed by aggregating multiple data sources with different spatiotemporal and spectral characteristics. This could lead to spurious variations in CSD being misinterpreted as changes in system resilience (Smith & Boers, 2023). Also, satellite data does not yet have a standardized and commonly accepted pre-processing routine to monitor resilience (Smith et al., 2023). Finally, in high biomass density regions, optical sensors have a well-known tendency to saturate (Chirici et al., 2020; Vangi et al., 2021; Smith & Boers, 2023). On the contrary, PBMs can provide long and consistent time series of different key state variables (such as GPP, NPP, carbon stocks, and other structural variables), which can also be extended into the future by simulating the responses of the forest ecosystem to changing environmental conditions, under the most accepted scenarios of climate change. Furthermore, PBMs can be applied to a wide variety of forest ecosystems, assessing the mechanisms of resilience and stability not only in the long-term time dimension but also from the local to continental spatial spectrum.

At the same time, however, the effects of climate change on the carbon budget are highly uncertain and largely debated with models that simulate an overall increase in NPP, possibly due, among other things, to the fixed relation between NPP and GPP (e.g., Reyer 2015) and those models that return an increase in tree and stand respiratory costs over, e.g., the positive effects on GPP because of CO_2 fertilization and prolonging vegetative seasons (Peano et al., 2019; Keenan et al., 2023). Forest stability and resilience under climate change are even more uncertain.

However, while these two effects, i.e., age and climate change, at different levels, are primarily discussed and reported in the literature, their interaction and effects on forest stability and resilience are not fully investigated. In this regard, it is worth remembering that, as Smith and Boers (2023) pointed out, CSD indicators are not a direct measure of resilience and stability but proxies for state changes. Increasing variance or 1-lag TAC can be caused not only by a resilience loss. This is why it is important to at least investigate the 1-lag TAC and temporal variance together and test whether their behavior is consistent (Ditlevsen & Johnsen, 2010).

In beech stands, the main driver of CSD was the climate. The direct fertilization effect of CO_2 and the lengthening of the growing season outweigh other limiting factors, which might cause the beech forest to respond more positively to the different climate change scenarios, with productivity increasing up to

RCP 8.5 in all age classes. For instance, during the simulation period, under RCP 8.5, there will be an average of 21 more days with MAT>0 °C compared to the CCS scenario. The substantial variability in NPP (as shown in the shaded area of Figure 1C) is emphasized under climate change scenarios in which the growing season of the European beech at this latitude is likely to be short, even shorter than in coniferous stands.

The negative 1-lag TAC under the less warm scenarios (CCS and RCP 2.6) can be caused by the "memory effect" (Harris et al., 2014; Simonello et al., 2008): the whole leaf biomass is replaced at the start of each new growing season, losing the "memory" of the precedent year climate and causing significant differences in productivity from one year to another. Also, the stability was not affected by age at the start of the simulation (age$_{t0}$), while it increased evenly up to RCP 6.0 and then stabilized. The relationship between resilience and stability indicators (e.g., 1-lag TAC and temporal variance, Figure 5C) in the beech stands are not clustered by age$_{t0}$, suggesting a prominent role of climate in resilience and stability patterns.

Coniferous stands, on the contrary, have a more extended "memory" given to longer leaf turnover rates, preserving the biomass leaf the whole year and for more than one year (about four years for both Scots pine and Norway spruce, Mäkelä et al., 1997 and Pietsch et al., 2005), resulting in a prolonged vegetative phase and less variability in productivity. However, despite this longer "memory" with respect to deciduous species, young needle-leaf stands are generally characterized by a lower LAI (and higher leaf mass per unit leaf area), a shallower root system that brings in less efficient water management, exposing them to drought-induced stress, ultimately causing a loss in stability and resilience (Figure 4A).This evidence is confirmed by the highly clustered resilience-stability scatterplot (Figure 5A-B), suggesting that age$_{t0}$ is the primary driver of resilience and stability in coniferous stands.

In particular, at CZ-BK1, where Norway spruce grows at the edge of its ranges, the effects of environmental changes are amplified, making it the most climate-sensitive species. NPP showed a negative trend under all scenarios, suggesting that the species was already at its optimum and that even slight climatic variations would affect the resistance and resilience of the species. Indeed, several studies highlight the lower stability of the species to water shortage and subsequent drought conditions (Vital et al., 2017; Bosela et al., 2021; Mensah et al., 2021; Marchand et al., 2023). Generally, differences among the analyzed species are in line with meta-analyses showing, for instance, how coniferous tend to show greater drought-legacy, which could be mirrored by a higher TAC-1, compared to angiosperms such as beech (see Anderegg et al., 2015)

However, it is interesting that the decrease in stability was compensated by the increase in resilience in the most severe scenarios (RCP 6.0 and 8.5), which could result from dying trees toward the end of the simulation, making perhaps the remaining trees more resilient because of less competition.

Scots pine, despite a similar resilience-stability relationship to Norway spruce, had an intermediate pattern compared to the other two species. The species showed a steady decline in productivity for the older age classes compared to the younger ones, corresponding to lower values of 1-lag TAC (higher resilience), reflecting the instability of young, small trees. Uri et al. (2022), studying the dynamics of carbon storage and fluxes in a Scots pine forest, found that the maximum levels of NPP are observed during the pole and middle-aged developmental stages. Forest stability and resilience are the legacy of past ecosystem states, shaped mainly by species-climate relationships, climate adaptation, and the history of the disturbance regimes (Johnstone et al., 2016). Older forest stands exhibit a higher stability and resilience, probably due to higher robust and stable interaction with climate stressors and better coping with changing environmental factors and conditions than younger stands. Older trees generally have larger carbon pools in sapwood and reserves, which might help buffer the impact of the year-to-year climate variability on tree growth and lead to higher long-term resilience than younger trees (Zweifel et al., 2023). The same argument would hold for beech versus pinus spp, the former characterized by larger carbon pools. In this sense, forest ages could be seen as a "memory" pool of adaptation strategies inherited from past climate and disturbance regimes, dampening the effect of climate change on stability and resilience. Old forests are characterized by species-specific traits perfectly aligned with the climate and disturbance conditions in which they grow, making them more stable and resilient to changes (Reyer et al., 2015).

Consequences on and for forest management

The diverse behavior exhibited by forests of varying ages, in terms of productivity, stability, and resilience, underscores the potential of utilizing structural heterogeneity at the landscape level to counter climate change impacts while preserving resilience. Heterogeneous and un-even aged forests profit from increased structural complexity, as evidenced by Jandl et al. (2019), de Wergifosse et al. (2022), and Asbeck et al. (2023). A forest of different age groups integrates young, middle-aged, and mature trees, leading to vertical stratification that augments ecosystem complexity and stability. This stratification fosters gradients in biomass (both deadwood and living aboveground biomass), diverse carbon allocation methods (Merganičová et al., 2019), and ecological niches for flora and fauna,

thereby enhancing biodiversity and the capacity to adaptively respond to environmental disturbances
(Lafond et al., 2014; Pardos et al., 2021).

Our research, intentionally designed to isolate the effects of management strategies, reveals significant
implications for climate-adaptive silviculture, even under scenarios where 'active' forest management
ceases. Functionally, age-diverse forests display a range of physiological and lifecycle traits, enhancing
their ability to absorb and store carbon, and mitigating climate change impacts. Present-day young trees
absorb more CO_2 than their historical counterparts, contributing significantly to carbon capture and
efficient biomass production (DeLucia et al., 2007; Campioli et al., 2015; Collalti et al., 2020b), albeit
potentially at the expense of a shorter lifespan. Conversely, older trees bolster ecosystem stability and
resilience, acting as long-term carbon sinks and regeneration shelters. Thus, maintaining age-diverse
forests, facilitated through proactive management, is vital for maximizing the ecological and climatic
benefits of structural and functional diversity, balancing each age group's advantages and drawbacks,
as supported by Ehbrecht et al. (2021), Zampieri et al. (2021), and Kauppi et al. (2022). These insights
on the interplay between age, climate, resilience, and system stability should be integrated into the
functional network approach (Messier et al., 2019), which combines functional traits and landscape
connectivity to evaluate functional diversity and its dispersal potential, aiding in recognizing stability
and resilience in proactive forest management.

Contrastingly, several studies, including Drake et al. (2011), Jandl et al. (2019), and Dalmonech et al.
(2022), argue that unmanaged, aging forests may become less effective against climate change. Forests
mainly composed of old-age classes often experience reduced growth and carbon absorption due to
competition, nutrient scarcity, and increased disease and pest risks, leading to higher mortality rates.
This diminishes their role as carbon sinks (Zhu et al., 2019). Peng et al. (2023) suggest that reducing
forest harvesting could be an effective mitigation strategy, though other issues contribute to the debate,
such as the 'higher value' of short-term mitigation strategies or the unlikely scenario of "no shift" in
other emission sources. Arguing for the superior value of near-term emissions and mitigation is
questionable, especially considering the short analysis period (2010 – 2050) relative to the lifespan of
forest and wood products, which calls for care in interpreting simulation results.

Moreover, the assumption that harvesting cessation will not lead to a shift in emission activities is
overly simplistic. Forests have multiple functions, including protection, particularly in Alpine areas. In
order to maintain forest functionality and protection against natural hazards (e.g., rockfalls, avalanches,
landslides), silvicultural interventions must be applied according to very strict regulations (Moos et al.,
2023). Therefore, diversifying forest ages through management not only leverages the rapid growth of

younger trees but also balances the benefits and disadvantages of different age classes. A mosaic of
varied age patches enhances biodiversity, stability, and resilience to stressors.

Moreover, management prevents forest abandonment, reducing wildfire risks, especially in
Mediterranean areas where accumulated combustible material is a concern (Llovet et al., 2009; Ursino
& Romano, 2014). Adopting proactive management practices, including selective cutting and
promoting natural regeneration and diversity, is crucial. This approach maintains forests of different
ages, reflecting varied climate responses, thus ensuring their continued role in climate change
mitigation, carbon sequestration, and biodiversity conservation under uncertain climatic futures.

Limitations

In this study, we did not account for the indirect effects of climate change like altered disturbance
regimes and potential extreme events (e.g., fires, insect outbreaks, storms), unless these are already
incorporated in the climate scenarios used. This approach intentionally avoids confounding influences
on productivity and carbon accumulation estimates. Our focus is on the direct impacts of climate
change, specifically increased atmospheric CO_2 levels, while excluding other environmental drivers
such as Nitrogen (N), Phosphorus (P), or Ozone (O_3). These elements have been recognized as
significant influences on forest productivity and vary across different age classes (De Marco et al.,
2022a, 2022b; Ye et al., 2023). Notably, N deposition rates, which are predicted to double before
stabilizing (LeBauer and Treseder, 2008), could enhance fertilization in temperate forests.
Additionally, P limitation, rather than N, is more likely to restrict the growth of smaller trees (Ye et al.,
2023). The increase in N availability might also mitigate the observed decline in NPP in our
simulations, as suggested by LeBauer and Treseder (2008).

Another significant limitation is the exclusion of heterotrophic and soil responses to avoid additional
complexity. This study focuses exclusively on tree-level physiological responses across different age
classes, considering the combined effects of altered CO_2 concentration, temperature, and precipitation.
This specific focus is chosen for its direct relevance to forestry management and its potential for short-
and long-term mitigation.

Furthermore, we did not include natural regeneration and the possible migration of new species into the
study areas. The capacity of tree species change as a climate change mitigation strategy in unmanaged
forests might be limited. This is due to the potential discrepancy between species migration or
replacement rates and the projected rates of climate change, particularly under more severe RCP
scenarios (Settele et al., 2014; Noce et al., 2016).

Conclusions

In light of growing uncertainty about future climate conditions, forests' long-term functionality and their consistent delivery of diverse ecosystem services will be unevenly impacted. This impact hinges on several factors: tree species, the geographical position of the forest within the species' distribution range, the structural attributes at the stand level, and the stage of stand development. Anticipating climate change, younger forests are expected to experience accelerated growth and earlier maturity but may also have a reduced lifespan. A range of stressors intensified by climate change, including higher temperatures, shifting precipitation patterns, and more frequent extreme weather events, pose significant threats to the stability and resilience of European forests. Grasping the interplay of stability and resilience across different forest age classes is vital for devising strategies to effectively preserve and manage forests in an era of climate change. Adaptive forest management practices that enhance species diversity, support a range of forest ages, and encourage natural regeneration can bolster the resilience of European forests in the face of climate change. Our research underscores the necessity of factoring in both age class and species-specific responses to fully understand the impact of climate change on forest productivity and carbon storage. The varied reactions of tree species to changing climate conditions emphasize the urgent need for customized management and conservation approaches to strengthen forest resilience, stability and adaptability.

Credit authorship contribution statement

E. Vangi: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing; **D. Dalmonech**: Investigation, Writing – original draft, Writing – review & editing, Software and Model curation; **E. Cioccolo**: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing; **G. Marano**: Writing – original draft, Writing – review & editing; **L. Bianchini**: Data curation, Formal analysis, Writing – review & editing; **P. Puchi**: Writing – original draft, Writing – review & editing; **E. Grieco**: Writing – original draft, Writing – review & editing; **A. Cescatti**: Conceptualization, Writing – review & editing; **A. Colantoni**: Writing – original draft, Writing – review & editing, **G. Chririci**: Writing – original draft, Writing – review & editing; **A. Collalti**: Conceptualization, Formal analysis, Investigation, Funding acquisition, Resources, Software, Supervision, Project administration, Writing – review & editing.

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Figure 1 | NPP (gC m^{-2} year^{-1}) for age classes at the three sites in all scenarios along the simulation
period (2006-2099). Lines represent the moving average of 10 years. The solid line corresponds to the
real stand, while the dotted line to the virtual one. The shaded area represents two standard deviations

from the mean predictions of the five ESMs models. In the legend– for CZ-BK1, FI-Hyy and DK-Sor,

respectively – the age_{t0} classes represented by 1) are 12, 14, 14 years-old classes and so on until 11) are

120, 140, 140 years-old classes.

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Figure 2 | Sensitivity of NPP to three forcing variables (mean temperature, atmospheric CO_2
concentration, and vapor pressure deficit) in terms of the slope of the regression line resulting from a
multivariate linear model. In the legend– for CZ-BK1, FI-Hyy and DK-Sor, respectively – the age_{t0}

classes represented by 1) are 12, 14, 14 years old classes and so on until 11) are 120, 140, 140 years-old classes.

Figure 3 | stability (standard deviation of NPP) of each age_{t0} class at the three sites in the five climate scenarios. In the legend– for CZ-BK1, FI-Hyy and DK-Sor, respectively – the age_{t0} classes represented by 1) are 12, 14, 14 years-old classes and so on until 11) are 120, 140, 140 years-old classes.

Figure 4 | resilience (1-lag TAC of NPP) of each age$_{t0}$ class at the three sites in the five climate scenarios. In the legend– for CZ-BK1, FI-Hyy and DK-Sor, respectively – the age$_{t0}$ classes represented by 1) are 12, 14, 14 years-old classes and so on until 11) are 120, 140, 140 years-old classes.

Figure 5 | Scatterplot of stability (x-axis) vs. resilience (y-axis) in terms of standard deviation and 1-lag TAC of NPP, respectively. In the legend– for CZ-BK1, FI-Hyy and DK-Sor, respectively – the age$_{t0}$ classes represented by 1) are 12, 14, 14 years-old classes and so on until 11) are 120, 140, 140 years-old classes.

References

Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D., Delucia, E.H., (2013). Altered dynamics of forest recovery under a changing climate. Global Change Biology 19, 2001–2021.. https://doi.org/10.1111/gcb.12194

Asbeck, T., Benneter, A., Huber, A., Margaritis, D., Buse, J., Popa, F., Pyttel, P., Förschler, M., Gärtner, S., & Bauhus, J. (2023). Enhancing structural complexity: An experiment conducted in the Black Forest National Park, Germany. *Ecology and Evolution*, 13, e9732. https://doi.org/10.1002/ece3.9732

Asner, G. P., Scurlock, J. M. O., Hicke, J. A. (2003). Global Synthesis Of Leaf Area Index Observations: Implications For Ecological and Remote Sensing Studies. Global Ecology and Biogeography, 3(12), 191-205. https://doi.org/10.1046/j.1466-822x.2003.00026.x

Barford C., Wofsy S.C., Goulden M., Munger J.W., Hammond Pyle E., Urbanski S.P., Hutyra L., Saleska S., R. Fitzjarrald D., Moore K. (2001). Factors Controlling Long- and Short-Term Sequestration of Atmospheric CO_2 in a Mid-latitude Forest. DOI:10.1126/science.1062962

Batista, G. E. A. P. A.; Keogh, E.J.; Tataw, O.M.; De Souza, V.M.A. CID (2013). An efficient complexity-invariant distance for time series. Data Min. Knowl. Discov., 28, 634–669. https://doi.org/10.1007/s10618-013-0312-3

Bohn FJ, Huth A. (2017). The importance of forest structure to biodiversity-productivity relationships. R Soc Open Sci. Jan 4;4(1):160521. doi: 10.1098/rsos.160521. PMID: 28280550; PMCID: PMC5319316.

Bosela, M., Tumajer, J., Cienciala, E., Dobor, L., Kulla, L., Marčiš, P., Popa, I., (...), Büntgen, U. (2021). Climate warming induced synchronous growth decline in Norway spruce populations across biogeographical gradients since 2000. Science of the Total Environment, 752, art. no. 141794. https://doi.org/10.1016/j.scitotenv.2020.141794

Brienen, R.J.W., Caldwell, L., Duchesne, L. et al. (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. Nat Commun 11, 4241. https://doi.org/10.1038/s41467-020-17966-z

Campioli, M., Vicca, S., Luyssaert, S. et al. (2015). Biomass production efficiency controlled by management in temperate and boreal ecosystems. Nature Geosci 8, 843–846. https://doi.org/10.1038/ngeo2553

Churkina G., Organschi A., Reyer C. P. O., Ruff A., Vinke K., Liu Z., Reck B. K., T. E. Graedel & Hans Joachim Schellnhuber (2020). Buildings as a global carbon sink Nature Sustainability volume 3, 269–276
https://doi.org/10.1038/s41893-019-0462-4

Colangelo M., Camarero J.J., Gazol A., Piovesan G., Borghetti M., Baliva M., Gentilesca T., Rita A., Schettino A., Ripullone F. (2021). Mediterranean old-growth forests exhibit resistance to climate warming, Science of The Total Environment, Volume 801, 149684, ISSN 0048-9697, https://doi.org/10.1016/j.scitotenv.2021.149684.

Collalti A., Perugini L., Santini M., Chiti T., Nolè A., Matteucci G., Valentini R. (2014). A process-based model to simulate growth in forests with complex structure: Evaluation and use of 3D-CMCC Forest Ecosystem Model in a deciduous forest in Central Italy. Ecological Modelling, 272, 362– 378, https://doi.org/10.1016/j.ecolmodel.2013.09.016

Collalti A., Marconi S., Ibrom A., Trotta C., Anav A., D'Andrea E., Matteucci G., Montagnani L., Gielen B., Mammarella I., Grünwald T., Knohl A., Berninger F., ZhaoY., Valentini R., Santini M. (2016). Validation of 3D-CMCC Forest Ecosystem Model (v.5.1) against eddy covariance data for ten European forest sites, Geoscientific Model Development, 9, 1-26, https://doi.org/10.5194/gmd-9-479-2016

Collalti, A., Trotta, C., Keenan, T.F., Ibrom, A., Bond-Lamberty, B., Grote, R., Vicca, S., Reyer, C.P.O., Migliavacca, M., Veroustraete, F., Anav, A., Campioli, M., Scoccimarro, E., ˇSigut, L., Grieco, E., Cescatti, A., Matteucci, G., 2018. Thinning can reduce losses in carbon use efficiency and carbon stocks in managed forests under warmer climate. J. Adv. Model. Earth Syst. 10 (10), 2427–2452. https://doi.org/10.1029/2018MS001275

Collalti A., Thornton P. E., Cescatti A., Rita A., Nolè A., Borghetti M., Trotta C., Ciais P., Matteucci G. (2019). The sensitivity of the forest carbon budget shifts between different parameters and processes along stand development and climate change. Ecological Applications, 29(2): 1-18, https://doi.org/10.1002/eap.1837

Collalti A. & Prentice I.C., (2019). Is NPP proportional to GPP? Waring's hypothesis twenty years on. Tree Physiology, 39(8): 1473-1483 https://doi.org/10.1093/treephys/tpz034

Collalti A., Tjoelker M.G., Hoch G., Mäkelä A., Guidolotti G., Heskel M., Petit G., Ryan M.G., Battipaglia G., Prentice I.C., (2020a). Plant respiration: Controlled by photosynthesis or biomass?. Global Change Biology, 26(3): 1739–1753 https://doi.org/10.1111/gcb.14857

Collalti, A., Ibrom, A., Stockmarr, A., Cescatti, A., Alkama, R., Fernandez-Martínez, M., Matteucci, G., Sitch, S., Friedlingstein, P., Ciais, P., Goll, D. S., Nabel, J. E. M. S., Pongratz, J., Arneth, A., Haverd, V., & Prentice, I. C. (2020b). Forest production efficiency increases with growth temperature. Nature Communications, Nature Communications, 11: 5322, https://doi.org/10.1038/s41467-020-19187-w

Daigneault A., Favero A. (2021). Global forest management, carbon sequestration and bioenergy supply under alternative shared socioeconomic pathways. Land Use Policy Volume 103, 105302 https://doi.org/10.1016/j.landusepol.2021.105302

Dalmonech D., Marano G. , Amthor J., Cescatti A., Lindner M., Trotta C., Collalti A. (2022). Feasibility of enhancing carbon sequestration and stock capacity in temperate and boreal European forests via changes to forest management, Agricultural and Forest Meteorology, 327(109203), https://doi.org/10.1016/j.agrformet.2022.109203

Dalmonech D., Vangi E., Chiesi M., Chirici G., Fibbi L., Giannetti F., Marano G., Massari C., Nolè A., Xiao J., Collalti A. (2024). Regional estimates of gross primary production applying the Process-Based Model 3D-CMCC-FEM vs. Remote-Sensing multiple datasets. European Journal of Remote Sensing, 57:1, 2301657, https://doi.org/10.1080/22797254.2023.2301657

D'Andrea A., Rezaie N., Prislan P., Gričar J., Collalti A., Muhr J., Matteucci G. (2020). Frost and drought: effects of extreme weather events on Stem Carbon Dynamic in a Mediterranean beech forest. Plant Cell & Environment, 43(10):2365–2379, https://doi.org/10.1002/PCE.13858

D'Andrea E., Scartazza A., Battistelli A., Collalti A., Proietti S., Rezaie N., Matteucci G., Moscatello S. (2021). Unraveling resilience mechanisms in forests: role of non-structural carbohydrates in responding to extreme weather events. Tree Physiology, 41:1808- 1818, https://doi.org/10.1093/treephys/tpab044

DeLucia, E. H., Drake, J. E., Thomas, R. B. & Gonzalez-meler, M. A. (2007). Forest carbon use efficiency: is respiration a constant fraction of gross primary production? Glob. Chang. Biol. 13, 1157–1167.

De Marco A., Garcia-Gomez H., Collalti A., Khaniabadi Y.O., Feng Z., Proietti C., Sicard P., Vitale M., Anav A., Paoletti E. (2022b). Ozone modelling and mapping for risk assessment: an overview of different approaches for human and ecosystem health, Environmental Research, 211, 113048,https://doi.org/10.1016/j.envres.2022.113048,

De Marco A, Sicard P, Feng Z, Agathokleous E, Alonso R, Araminiene V, Augustatis A, Badea O, Beasley JC, Branquinho C, Bruckman VJ, Collalti A, David-Schwartz R, Domingos M, Du E, Garcia Gomez H, Hashimoto S, Hoshika Y, Jakovljevic T, McNulty S, Oksanen E, Omidi Khaniabadi Y, Prescher AK, Saitanis CJ, Sase H, Schmitz A, Voigt G, Watanabe M, Wood MD, Kozlov MV, Paoletti E. (2022). Strategic roadmap to assess forest vulnerability under air pollution and climate change. Glob Chang Biol; 28(17):5062-5085. doi: 10.1111/gcb.16278.

De Wergifosse L., Andrè F., Goosse H., Boczon A., Cecchini S., Ciceu A., Collalti A., Cools N., D'Andrea E., De Vos B., Hamdi R., Ingerslev M., Knudsen M.A., Kowalska A., Leca S., Matteucci G., Nord-Larsen T., Sanders T., Schmitz A., Termonia P., Vanguelova E., Van Schaeybroeck B., Verstraeten A., Vesterdal L., Jonard M. (2022). Simulating tree growth response to climate change in structurally diverse oak and beech forests, Science of The Total Environment, Volume 806, Part 2, 150422, https://doi.org/10.1016/j.scitotenv.2021.150422.

Diers, M., Weigel, R. & Leuschner, C. (2023). Both climate sensitivity and growth trend of European beech decrease in the North German Lowlands, while Scots pine still thrives, despite growing sensitivity. Trees 37, 523–543. https://doi.org/10.1007/s00468-022-02369-y

Drake J.E., Davis S.C., Raetz L.M., DeLucia E.H. (2011). Mechanisms of age related changes in forest production: the influence of physiological and successional changes. Glob. Chang. Biol. 17, 1522–1535.

Duffy KA, Schwalm CR, Arcus VL, Koch GW, Liang LL, Schipper LA. (2021). How close are we to the temperature tipping point of the terrestrial biosphere? Sci Adv. 2021 Jan 13;7(3):eaay1052. doi: 10.1126/sciadv.aay1052.

Dunkl, I., Lovenduski, N., Collalti, A., Arora, V. K., Ilyina, T., and Brovkin, V. (2023). Gross primary productivity and the predictability of CO2: more uncertainty in what we predict than how well we predict it. Biogeosciences, 20, 3523–3538, https://doi.org/10.5194/bg-20-3523-2023

Ehbrecht M., Seidel D., Annighöfer P. (2021). Global patterns and climatic controls of forest structural complexity. Nat Commun 12, 519. https://doi.org/10.1038/s41467-020-20767-z

Fang, J., Lechowicz M.J. (2006). Climatic limits for the present distribution of beech (Fagus L.) species in the world J. Biogeogr., 33, pp. 1804-1819, 10.1111/j.1365-2699.2006.01533.x

Favero A., Mendelsohn R., Sohngen B., Stocker B. (2021). Assessing the long-term interactions of climate change and timber markets on forest land and carbon storage. Environ. Res. Lett. 16 014051 https://doi.org/10.1088/1748-9326/abd589

Felzer B., Kicklighter D., Melillo J., Wang C., Zhuang Q., Prinn R. (2002). Effects of ozone on net primary production and carbon sequestration in the conterminous United States using a biogeochemistry model. Tellus B. 2004;56:230–48.

Förster A., Culmsee H., Leuschner C. (2021). Thinned northern German Scots pine forests have a low carbon storage and uptake potential in comparison to naturally developing beech forests. Forest Ecology and Management, 479, art. no. 118575.

Nabuurs GJ., Verkerk P.J., Schelhaas MJ., González Olabarria J.R., Trasobares A., Cienciala E. (2018). Climate-Smart Forestry: mitigation impacts in three European regions. From Science to Policy 6. European Forest Institute.

Glienke, S., Irvine, P. J., and Lawrence, M. G. (2015). The impact of geoengineering on vegetation in experiment G1 of the GeoMIP, J. Geophys. Res. Atmos., 120, 10,196– 10,213, doi:10.1002/2015JD024202

Goulden, M.L., McMillan, A.M., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W., Bond-Lamberty, B.P. (2011). Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Global Change Biology, 17(2), 855–871. https://doi.org/10.1111/j.1365-2486.2010. 02274.x

Guillemot J., Francois C., Hmimina G., Dufrêne E., Martin- StPaul N.K., Soudani K. et al. (2017). Environmental control of carbon allocation matters for modelling forest growth. New Phytologist, 214, 180–193.

He Y., Liu Y., Lei L., Terrer C., Huntingford C., Peñuelas J., Xu H., Piao, S. (2023). CO_2 fertilization contributed more than half of the observed forest biomass increase in northern extra-tropical land. Global Change Biology, 00, 1– 14. https://doi.org/10.1111/gcb.16806

James H. Speer. (2010). Fundamentals of Tree Ring Research. University of Arizona Press. ISBN: B00GA42F4O

Jandl, R., Spathelf, P., Bolte, A. *et al.* (2019). Forest adaptation to climate change—is non-management an option?. *Annals of Forest Science* 76, 48 https://doi.org/10.1007/s13595-019-0827-x

Jansson, P. E., Svensson, M., Kleja, D. B., & Gustafsson, D. (2008). Simulated climate change impacts on fluxes of carbon in Norway spruce ecosystems along a climatic transect in Sweden. Biogeochemistry, 89, 81-94.

Jump Alistair S., Hunt J.M., Peñuelas J. (2006). Rapid climate change-related growth decline at thesouthern range edge ofFagus sylvatica. Global Change Biology 12,2163–2174, doi: 10.1111/j.1365-2486.2006.01250.xr2006.

Kauppi P.E., Stål G., Arnesson-Ceder L., Hallberg Sramek I., Hoen H.F., Svensson A., Wernick I.K., Högberg P., Lundmark T., Nordin A., (2022). Managing existing forests can mitigate climate change, Forest Ecology and Management, Volume 513, 120186, ISSN 0378-1127, https://doi.org/10.1016/j.foreco.2022.120186

Keith H., Mackey B. G., Lindenmayer D. B. (2009). Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proc. Natl. Acad. Sci. U.S.A.106, 11635–11640.

Kira T., Shidei T. (1967). Primary Production And Turnover Of Organic Matter In Different Forest Ecosystems Of The Western Pacific. Japanese Journal Of Ecology 17: 70-87.

Kolb T.E., Matyssek R. (2001). Limitations and perspectives about scaling ozone impacts in trees Environmental Pollution, 115 (3) , pp. 373-393.

Lafond, V., Lagarrigues, G., Cordonnier, T. *et al.* (2014). Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. *Annals of Forest Science* 71, 173–186 https://doi.org/10.1007/s13595-013-0291-y

Latterini F., Jagodziński A.M., Horodecki P., Stefanoni W., Venanzi R., Picchio R. (2023). The State of the Art of Forest Operations in Beech Stands of Europe and Western Asia. https://doi.org/10.3390/fl4020318

LeBauer, D.S., Treseder, K.K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology, 89: 371-379. https://doi.org/10.1890/06-2057.1

Lehman, A., O'Rourke, N., Hatcher, L., Stepanski, E.J. (2013). JMP® for Basic Univariate and Multivariate Statistics (S. I. I. 2013 (ed.)).

Lingua E., Garbarino M., Borgogno Mondino E., Motta R. (2011) Natural disturbance dynamics in an old-growth forest: from tree to landscape, Procedia Environmental Sciences, Volume 7, 2011, Pages 365-370, ISSN 1878-0296,https://doi.org/10.1016/j.proenv.2011.07.063.

Llovet J., Ruiz-Valera M., Josa R., Vallejo V.R. (2009). Soil responses to fire in Mediterranean forest landscapes in relation to the previous stage of land abandonment. International Journal of Wildland Fire 18, 222-232. https://doi.org/10.1071/WF07089

Luterbacher J., Dietrich D., Xoplaki E., Grosjean M., Wanner H. (2004). European seasonal and annual temperature variability, trends, and extremes since 1500. Science303, 1499–1503

Ma J., Hu Y., Bu R., Chang Y., Deng H., Qin Q. (2014). Predicting impacts of climate change on the aboveground carbon sequestration rate of a temperate forest in northeastern China. PLoS ONE 9(4):e96157. https://doi.org/10.1371/journal.pone.0096157

Mahnken, M., Cailleret,M., Collalti A., Trotta C., Biondo C., D'Andrea E., Dalmonech D., Marano G., Mäkelä A., Minunno F., Peltoniemi M., Trotsiuk V., Nadal-Sala D., Sabate S., Vallet P., Aussenac R., Cameron D.R., Bohn F.J., Grote R., Reyer C.P.O. (2022). Accuracy, realism and general applicability of European forest models. Glob. Change Biol. 00, 1–23. https://doi.org/10.1111/gcb.16384.

Marchand W.A., Buechling M., Rydval V., Čada A.I., Stegehuis A., Fruleux M., Poláček J., Hofmeister J., Pavlin D., Ralhan M., Dušátko P., Janda M., Mikoláš O., Vostarek R., Bače M., Frankovič D., Kozák C.C., Roibu O., Chaskovskyy S., Mikac T., Zlatanov M., Panayotov A., Diku E., Toromani M., Svoboda. (2022). Accelerated growth rates of Norway spruce and European beech saplings from Europe's temperate primary forests are related to warmer conditions. Agric. For. Met., 329, Article 109208, 10.1016/j.agrformet.2022.109280

Marconi S., Chiti T., Nolè A., Valentini R., Collalti A. (2017). The role of respiration in estimation of the net Carbon cycle: coupling soil Carbon dynamics and canopy turnover in a novel version of 3D-CMCC Forest Ecosystem Model, Forests, 8: 220, https://doi.org/10.3390/f8060220

Maréchaux I., Langerwisch F., Huth A., Bugmann H., Morin X., Reyer C., Collalti A. De Paula M., Fischer R., Gutsch M., Lexer M., Rammig A., Roedig E., Sakschewski B., Taubert F., Thonicke, K., Vacchiano G., Bohn F.. (2021). Tackling unresolved questions in forest ecology: The past and future role of simulation models. Ecology and Evolution. 1-25 10.1002/ece3.7391.

McCarthy HR., Oren R., Johnsen KH. et al. (2010). Re-assessment of plant carbon dynamics at the Duke free-air CO2 enrichment site: interactions of atmospheric [CO_2] with nitrogen and water availability over stand development. New Phytologist, 185, 514– 528.

Meng, F., Hong, S., Wang, J., Chen, A., Zhang, Y., Zhang, Y. et al. (2023). Climate change increases carbon allocation to leaves in early leaf green-up. Ecology Letters, 26, 816– 826. Available from: https://doi.org/10.1111/ele.14205

Merganičová K., Merganič J., Lehtonen A., Vacchiano G., Sever Maša Z.O, Augustynczik A., L.D. Grote R., Kyselová I., Mäkelä A., Yousefpour R., Krejza J., Collalti A., Reyer, C.P.O. (2019). Forest carbon allocation modelling under climate change. Tree Physiology Volume 39, Issue 12, Pages 1937– 1960, https://doi.org/10.1093/treephys/tpz10.

Molina-Valero, J.A., Camarero, J.J., Álvarez-González, J.G., Cerioni, M., Hevia, A., Sánchez-Salguero, R., Martin-Benito, D., (...), Pérez-Cruzado, C. (2021). Mature forests hold maximum live biomass stocks. (2021) Forest Ecology and Management, 480, art. no. 118635

Mori U., Mendiburu A., Lozano J.A. (2016). Distance Measures for Time Series in R: The TSdist Package R journal, 8(2), 451--459. URL https://journal.r-project.org/archive/2016/RJ-2016-058/index.html

Motta R., Garbarino M., Berretti R. *et al.* (2015). Development of old-growth characteristics in uneven-aged forests of the Italian Alps. *Eur J Forest Res* 134, 19–31. https://doi.org/10.1007/s10342-014-0830-6

Noce S., Collalti A., Valentini R., Santini M., (2016). Hot Spot maps of forest presence in the Mediterranean Basin. iForest – Biogeoscience and Forestry, https://doi.org/10.3832/ifor1802-009

Norby RJ., Warren JM., Iversen CM., Medlyn BE., McMurtrie RE. (2010). CO_2 enhancement of forest productivity constrained by limited nitrogen availability. Proceedings of the National Academy of Sciences, 107, 19368– 19373.

Nord-Larsen T., Vesterdal L., Bentsen N.S., Larsen J.B. (2019). Ecosystem carbon stocks and their temporal resilience in a semi-natural beech-dominated forest For. Ecol. Manag., 447 (2019), pp. 67-76, 10.1016/j.foreco.2019.05.038

Odum E.P. (1969). The Strategy of Ecosystem Development. Science, 164, 262-270. http://dx.doi.org/10.1126/science.164.3877.262

Ortiz N., Armada E., Duque E., Roldan A., Azcon R. (2015). Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: Effectiveness of autochthonous or allochthonous strains. Journal of Plant Physiology, 174 , pp. 87-96.

Pardos M., del Río M., Pretzsch H., Jactel H., Bielak K., Bravo F., Brazaitis G., Defossez E., Engel M., Godvod K., Jacobs K., Jansone L., Jansons A., Morin X., Nothdurft A., Oreti L., Ponette Q., Pach M., Riofrío J., Ruíz-Peinado R., Tomao A., Uhl E., Calama R (2021). The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe, Forest Ecology and Management, Volume 481, 118687, ISSN 0378-1127, https://doi.org/10.1016/j.foreco.2020.118687.

Pastorello G., Trotta C., Canfora E., Chu H., Christianson D., Cheah Y.W., Poindexter C., Chen J., Elbashandy A., Humphrey M., Isaac P., Polidori D., Ribeca A., van Ingen C., Zhang L., Amiro B., Ammann C., Arain M.A., et al., Papale D. (2020). The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data. Sci. Data 7 (1), 225. https://doi.org/10.1038/s41597-020-0534-3

Patacca M., Lindner M., Lucas-Borja ME., Cordonnier T, Fidej G., Gardiner B., Hauf Y., Jasinevičius G., Labonne S., Linkevičius E., Mahnken M., Milanovic S., Nabuurs GJ., Nagel T., Nikinmaa L., Panyatov M., Bercak R., Seidl R., Ostrogović Sever MZ., Socha J., Thom D., Vuletic D., Zudin S., Schelhaas MJ. (2022). Significant increase in natural disturbance impacts on European forests since 1950. https://doi.org/10.1111/gcb.16531

Peano D., Materia S., Collalti A., Alessandri A., Anav A., Bombelli A., Gualdi S. (2019). Global variability of simulated and observed vegetation growing season. Journal of Geophysical Research, Biogeosciences, 124, 3569-3587, https://doi.org/10.1029/2018JG004881

Peng, L., Searchinger, T.D., Zionts, J. et al. (2023). The carbon costs of global wood harvests. Nature 620, 110–115 (2023). https://doi.org/10.1038/s41586-023-06187-1

Potočić N., Timmermann V., Ognjenović M., Kirchner T., Prescher AK., Ferretti M., Michel AK. (2021). Tree health is deteriorating in the European forests (ICP Forests Brief No. 5) DOI:10.3220/ICP1638780772000

Poudel BC., Sathre R., Gustavsson L., Bergh J., Lundström A., Hyvönen R. (2011). Effects of climate change on biomass production and substitution in north-central Sweden. Biomass BioenergyFigure S1 | 35:4340–4355. https://doi.org/10.1016/j.biombioe.2011.08.005

Yousefpour R., Hanewinkel M. (2016). Climate Change and Decision-Making Under Uncertainty. Current Forestry Reports volume 2, pages143–149 https://doi.org/10.1007/s40725-016-0035-y

Reay D.S., Dentener F., Smith P., Grace J., Feely RA. (2008). Global nitrogen deposition and carbon sinks. Nat Geosci. 2008;1:430–7.

Reyer C.P.O. (2015). Forest Productivity Under Environmental Change—a Review of Stand-Scale Modeling Studies. Current Forestry Reports, 1, 53-68, https://doi.org/10.1007/s40725-015-0009-5

Reyer C.P.O., Brouwers N., Rammig A., W. Brook B., Epila J., Grant R., Holmgren M., Langerwisch F., Leuzinger S., Lucht W., Medlyn B., Pfeifer M., Steinkamp J., Vanderwel M., Verbeeck H., Villela D. (2014). Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. Journal of ecology https://doi.org/10.1111/1365-2745.12337

Reyer C.P.O., Silveyra Gonzalez R., Dolos K., Hartig F., Hauf Y., Noack M., Lasch-Born P., Rötzer T., Pretzsch H., Meesenburg H., Fleck S., Wagner M., Bolte A., Sanders T.G.M., Kolari P., Mäkelä A., Vesala T., Mammarella I., Pumpanen J., Frieler K. (2020). The PROFOUND Database for evaluating vegetation models and simulating climate impacts on European forests. Earth Syst. Sci. Data 12 (2), 1295–1320. https://doi.org/10.5194/essd-12-1295-2020.

Roebroek CTJ., Duveiller G., Seneviratne SI., Davin EL., Cescatti A. (2023). Releasing global forests from human management: How much more carbon could be stored? Science; 380(6646):749-753. doi: 10.1126/science.add5878. Epub 2023 May 18. PMID: 37200428.

Senf C., Seidl R. (2021). Post-disturbance canopy recovery and the resilience of Europe's forests Global Ecology and Biogeography pages: 822-825 https://doi.org/10.1111/geb.13406

Settele J., Scholes R., Betts R., Bunn S., Leadley P.,Nepstad D., Overpeck J.T., Taboada M.A. (2019). Terrestrial and inland water systems. In H. O.Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai,M. Tignor, E. Poloczanska, K. Mintenbeck, A.Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama,N. Weyer (Eds.), IPCC special report on the oceanand cryosphere in a changing climate (435-523).Cambridge University Press.

Testolin R., Dalmonech D., Marano G., D'Andrea E., Matteucci G., Noce S., Collalti A. (2023). Simulating diverse forest management in a changing climate on a Pinus nigra subsp. Laricio plantation in Southern Italy, Science of the Total Environment, 857: 159361, https://doi.org/10.1016/j.scitotenv.2022.159361

Thom D., Rammer W., Dirnböck T., Müller J., Kobler J., Katzensteiner K., Helm N., Seidl R. (2016). The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. Forest Biodiversity and Ecosystem Services https://doi.org/10.1111/1365-2664.12644

Ursino, N., Romano, N. (2015), Wild forest fire regime following land abandonment in the Mediterranean region, Geophys. Res. Lett., 41, 8359– 8368,doi:10.1002/2014GL061560.

Vacchiano G., Magnani F., Collalti A. (2012). Modeling Italian forests: state of the art and future challenges. iForest 5: 113-120. - doi: 10.3832/ifor0614-005

Vilà M., Carrillo-Gavilán A., Vayreda J., Bugmann H., Fridman J., Grodzki W., Haase J., Kunstler G., Schelhaas M., Trasobares, A. (2013). Disentangling biodiversity and climatic determinants of wood production. PloS one, 8(2), p.e53530.

Vitale, M., Scimone, M., Feoli, E., & Manes, F. (2003). Modelling leaf gas exchanges to predict functional trends in Mediterranean Quercus ilex forest under climatic changes in temperature. Ecological Modelling, 166(1-2), 123-134.

843 Yang, Y., Ren, L., Li, H., Wang, H., Wang, P., Chen, L., et al. (2020). Fast climate responses to aerosol
844 emission reductions during the COVID-19 pandemic. Geophysical Research Letters, 47,
845 e2020GL089788. https://doi.org/10.1029/2020GL089788

846 Yousefpour, R., Hanewinkel, M. (2016). Climate Change and Decision-Making Under Uncertainty.
847 Curr Forestry Rep 2, 143–149. https://doi.org/10.1007/s40725-016-0035-y
848
849 Zampieri M., Grizzetti B., Toreti A., De Palma P., Collalti A. (2021). Rise and fall of vegetation annual
850 primary production resilience to climate variability projected by a large ensemble of Earth System
851 Models' simulations, Environmental Research Letter, 16, 105001, https://doi.org/10.1088/1748-
852 9326/ac2407
853
854 Zhu K., Song Y., Qin C. (2019). Forest age improves understanding of the global carbon sink.
855 https://doi.org/10.1073/pnas.1900797116

Supplementary materials

Model evaluation

Daily model outputs were evaluated against eddy-covariance and measured structural data at the site level, in terms of percentage root mean squared error (RMSE%) and Pearson correlation coefficient (r). The GPP simulations forced with observed site-specific daily weather data (1997-2005 for FI-Hyy, and DK-Sor, and 2000-2005 for CZ-BK1) resulted in a RMSE% of 1.05, 1.52 and 1.43, with r values of 0.92, 0.87 and 0.94 for FI-Hyy, CZ-BK1 and DK-Sor, respectively (Table 1). Similar results were obtained for NPP_{woody} in the site of DK-Sor and CZ-BK1 (351 ±61 gC m^{-2} year^{-1} vs. 346 ±36 gC m^{-2} year^{-1} measured, and 442 ±79 gC m^{-2} year^{-1} vs. 380 ± 38 gC m^{-2} year^{-1} measured, respectively). At FI-Hyy, modeled NPP_{woody} data was overestimated in respect to the measured values (317 ±21 gC m^{-2} year^{-1} vs. 228 ±23 gC m^{-2} year^{-1} measured).

Table S1 | Performance statistics (coefficient of determination R^2 , relative root mean square error RMSE (gC m^{-2} day^{-1}) and Fractional Mean Bias, FMB) computed from monthly seasonal values and annual series of model gross primary productivity, GPP, against eddy covariance estimated and diametric annual increment data, DBH increment, against measured data. Results are reported for simulations forced with local and modeled climate (i.e., EMS).

		GPP SEASONAL		GPP ANNUAL			DBH increment	
	CLIMATE	FMB	RMSE	R^2	FMB	RMSE	FMB	RMSE
CZ-BK1	Local	-0.06	17.92	0.95	-0.06	180.96	-0.17	0.26

	ESM1	-0.22	28.68	0.38	-0.07	161.16	-0.29	0.24
	ESM2	-0.22	25.56	0.65	-0.07	150.29	-0.31	0.25
	ESM3	-0.16	21.78	0.009	-0.01	180.68	-0.22	0.2
	ESM4	-0.23	28.33	0.06	-0.08	187.55	-0.33	0.22
	ESM5	-0.17	24.15	0.97	-0.02	131.99	-0.28	0.23
FI-Hyy	Local	-0.02	34056	0.74	-0.03	99.62	0.02	0.23
	ESM1	-0.2	44051	0.23	-0.16	166046	-0.02	0.26
	ESM2	-0.22	39023	0.13	-0.17	182.23	-0.05	0.26
	ESM3	-0.13	35053	0.06	-0.09	124.75	0.09	0.26
	ESM4	-0.23	43.76	0.18	-0.19	191.98	-0.03	0.26
	ESM5	-0.24	43.66	0.18	-0.2	199.04	-0.1	0.25
DK-Sor	Local	0.01	24.56	0.75	0.009	122.61	-0.47	0.77
	ESM1	-0.12	19.01	0.22	-0.07	210.27	-0.8	0.62
	ESM2	-0.7	23.63	0.21	-0.02	173.82	-0.61	0.57
	ESM3	-0.7	33.46	0.46	-0.02	150.62	-0.6	0.6
	ESM4	-0.12	26.55	0.55	-0.07	195.54	-0.7	0.61
	ESM5	-0.09	27.69	0.41	-0.05	168.62	-0.65	0.59

Figure S1| Evaluation of monthly seasonal GPP (gC m^{-2} day^{-1}) fluxes (left column) and annual values (central column) for the sites of Sorø, Bily Kriz and Hyytiala (rows). Quality-checked and -filtered GPP values evaluated at the sites by the eddy covariance technique are reported as black dots. The shaded area for seasonal values reports maximum and minimum monthly value recorded in the time

series. Grey shaded area for annual data represents the relative uncertainty bounds. In the third column, comparison of the predicted annual DBH increment (cm y^{-1}) with site observations at the three sites is reported. Measured data are shown as black dots. Simulated data are reported as continuous line.

Table S2 | Differences in NPP (in %) for each age class scenario to the youngest one (the benchmark) within the same climate scenarios. Values are reported for each site and scenario. For CZ-BK1, FI-Hyy and DK-Sor respectively - the age classes represented by 1) are 12, 14, 14-year-old and so on until 11) are 120, 140, 140-year-old classes.

Site	Scenario	1	2	3	4	5	6	7	8	9	10	11
						Age class						
CZ-BK1	CCS	0	0.79	–0.24	–1.00	–2.93	–4.46	–9.21	–14.34	–20.11	–29.59	–33.26
	2.6	0	0.84	–0.16	–0.86	–2.77	–4.24	–9.27	–14.54	–20.33	–31.55	**–40.31**
	4.5	0	**7.13**	6.22	5.47	3.50	2.07	–3.71	–9.41	–15.30	–26.46	–31.19
	6.0	0	1.04	0.09	–0.31	–10.64	–11.88	–8.31	–13.38	–18.55	–31.21	–34.70
	8.5	0	3.54	2.73	2.25	1.46	–0.63	–6.56	–11.93	–16.82	–31.91	–35.19
FI-Hyy	CCS	0	23.20	50.84	37.95	**53.47**	49.66	46.01	41.75	36.97	31.01	28.34
	2.6	0	**21.75**	48.04	35.90	50.44	46.84	43.09	38.64	33.76	27.63	24.82
	4.5	0	21.89	48.46	36.29	51.12	47.88	44.03	39.64	34.76	28.73	26.22
	6.0	0	22.07	48.88	36.64	51.74	48.64	44.83	40.54	35.78	29.90	27.57
	8.5	0	22.17	48.97	36.81	51.83	48.84	44.78	40.39	35.55	29.63	27.40
DK-Sor	CCS	0	–1.49	–1.27	–1.42	–0.87	–2.74	–3.29	–5.88	–10.83	–13.49	–13.96
	2.6	0	–1.31	–1.09	–1.25	–0.62	–3.09	–3.37	–6.09	–11.59	–14.05	**–14.54**
	4.5	0	–1.34	–1.14	–1.30	–0.63	–3.21	–3.40	–6.18	–11.52	–13.85	–14.37
	6.0	0	–1.38	–1.18	–1.35	–0.70	–3.13	–3.39	–6.18	–11.27	–13.59	–14.12
	8.5	0	–1.35	–1.15	–1.33	**–0.60**	–3.47	–3.48	–6.40	–11.62	–13.80	–14.34

Table S3 | Differences in NPP (in %) within the same age class between climate different climate change scenarios to the CCs scenarios (the benchmark). Values are reported for each site and scenario. For CZ-BK1, FI-Hyy and DK-Sor respectively - the age classes represented by 1) are 12, 14, 14-year-old and so on until 11) are 120, 140, 140-year-old classes.

Site	Age class	CCS	RCP scenario			
			2.6	4.5	6.0	8.5
CZ-BK1	1	0	−3.28	−9.54	−3.32	−10.13
	2	0	−3.31	−4.60	−3.14	−8.12
	3	0	−3.29	−4.53	−3.10	−7.97
	4	0	−3.28	−4.43	−2.79	−7.71
	5	0	−3.29	−4.32	−11.12	−6.74
	6	0	−3.24	−4.18	−10.88	−7.15
	7	0	−3.51	−4.50	−2.46	−7.78
	8	0	−3.69	−4.57	−2.29	−7.75
	9	0	−3.74	−4.25	−1.40	−6.59
	10	0	−6.69	−5.38	−6.16	−12.98
	11	0	−14.01	−6.55	−5.84	−12.56
FI-HYY	1	0	−0.31	0.44	2.66	−1.43
	2	0	−1.40	−0.57	1.83	−2.23
	3	0	−2.13	−1.12	1.49	−2.65
	4	0	−1.69	−0.65	1.93	−2.13
	5	0	−2.22	−0.92	1.92	−2.26
	6	0	−2.01	−0.27	2.79	−1.31
	7	0	−2.17	−0.50	2.60	−1.73
	8	0	−2.43	−0.65	2.62	−1.85
	9	0	−2.67	−0.81	2.68	−1.93
	10	0	−3.00	−0.92	2.89	−1.81
	11	0	−3.06	−0.44	3.76	−0.87
DK-Sor	1	0	7.20	10.87	11.84	14.25
	2	0	7.38	11.02	11.95	14.40
	3	0	7.38	11.01	11.94	14.38
	4	0	7.37	10.99	11.91	14.34
	5	0	7.45	11.12	12.02	14.54
	6	0	6.85	10.35	11.38	13.37
	7	0	7.14	10.77	11.74	14.04
	8	0	7.03	10.58	11.52	13.66
	9	0	6.43	10.17	11.39	13.34
	10	0	6.71	10.62	11.88	14.05

| 11 | 0 | 6.70 | 10.57 | 11.80 | 13.95 |

Table S4 | Differences in tCWS (in %) for each age class scenario to the youngest one (the benchmark) within the same climate scenarios. Values are reported for each site and scenario. For CZ-BK1, FI-Hyy and DK-Sor respectively - the age classes represented by 1) are 12, 14, 14-year-old and so on until 11) are 120, 140, 140-year-old classes.

Site	Scenario	Age class										
		1	2	**3**	4	**5**	6	**7**	8	**9**	10	**11**
CZ-BK1	CCS	0	4.08	24.63	41.12	46.53	62.07	71.11	74.65	72.84	77.79	106.38
	RCP 2.6	0	4.52	25.52	42.44	48.08	63.99	73.19	76.93	75.20	76.64	85.86
	RCP 4.5	0	11.45	32.97	50.87	56.98	73.22	83.80	88.17	86.20	93.28	123.33
	RCP 6.0	0	4.46	25.46	42.52	36.88	52.53	73.44	77.32	76.02	71.14	98.81
	RCP 8.5	0	8.28	29.56	47.25	55.48	69.99	80.20	83.89	82.53	74.28	100.38
FI-Hyy	CCS	0	49.17	173.44	100.35	272.10	301.23	328.66	349.26	367.72	379.03	456.88
	RCP 2.6	0	47.10	168.98	97.22	267.17	296.60	324.01	344.10	362.36	372.95	450.93
	RCP 4.5	0	46.95	168.79	97.11	267.19	296.91	324.38	344.39	362.42	373.04	451.23
	RCP 6.0	0	47.05	168.81	97.21	266.95	296.60	323.95	343.98	361.96	372.49	450.58
	RCP 8.5	0	47.16	169.40	97.56	268.08	298.06	325.66	345.71	363.89	374.60	453.03
DK-Sor	CCS	0	16.51	19.91	22.84	23.47	23.87	30.88	42.32	57.70	71.11	75.41
	RCP 2.6	0	15.64	18.90	21.67	22.25	22.59	29.13	39.89	54.09	66.02	70.17
	RCP 4.5	0	15.62	18.88	21.65	22.27	22.29	28.92	39.47	52.84	64.53	68.38
	RCP 6.0	0	15.73	19.01	21.79	22.44	22.32	29.10	39.64	52.84	64.72	68.72
	RCP 8.5	0	15.57	18.82	21.56	22.21	21.95	28.66	39.00	51.41	62.83	66.83

Table S5 | Differences in tCWS (in %) within the same age class between climate different climate change scenarios to the CCs scenarios (the benchmark). Values are reported for each site and scenario. For CZ-BK1, FI-Hyy and DK-Sor respectively - the age classes represented by 1) are 12, 14, 14-year-old and so on until 11) are 120, 140, 140-year-old classes.

Site	Age class	RCP scenario				
		CCS	**2.6**	**4.5**	**6.0**	**8.5**
CZ–BK1	1	0	–2.94	–8.44	–2.28	–7.24
	2	0	–2.54	–2.95	–1.93	–4.14
	3	0	–2.23	–2.62	–1.62	–3.83
	4	0	–2.00	–2.32	–1.27	–3.41
	5	0	–1.88	–2.18	–9.19	–1.89
	6	0	–1.73	–1.96	–9.00	–2.67
	7	0	–1.71	–1.96	–0.89	–2.61

	8	0	−1.62	−1.85	−0.74	−2.71
	9	0	−1.57	−1.67	−0.41	−2.31
	10	0	−3.33	−1.64	−5.53	−8.39
	11	0	−12.63	−1.77	−5.69	−9.40
FI–HYY	1	0	0.68	1.51	2.80	1.01
	2	0	−0.83	−0.16	1.21	−0.50
	3	0	−1.68	−1.07	0.26	−1.32
	4	0	−1.25	−0.55	0.82	−0.78
	5	0	−1.68	−0.98	0.28	−1.13
	6	0	−1.49	−0.58	0.69	−0.55
	7	0	−1.50	−0.60	0.61	−0.53
	8	0	−1.61	−0.78	0.49	−0.74
	9	0	−1.61	−0.89	0.36	−0.77
	10	0	−1.78	−1.01	0.20	−0.88
	11	0	−1.64	−0.80	0.44	−0.63
DK–Sor	1	0	8.43	10.50	9.92	12.83
	2	0	7.57	9.60	9.12	11.83
	3	0	7.46	9.47	9.01	11.69
	4	0	7.32	9.33	8.87	11.51
	5	0	7.28	9.33	8.91	11.55
	6	0	7.26	9.01	8.45	10.94
	7	0	6.86	8.68	8.24	10.67
	8	0	6.43	8.07	7.61	9.87
	9	0	5.85	6.96	6.38	8.08
	10	0	5.07	6.03	5.58	6.99
	11	0	5.03	5.81	5.46	6.89