Stand age diversity weakens forests' sensitivity to climate change

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Abstract

Forest age results from population dynamics, disturbance regimes, and silviculture playing an important role in the global Carbon (C) cycle. To examine the shaping effects of forest age on the forest productivity under current and future climate conditions, we used a biogeochemical-based model in three managed forest stands and then modeled their development as undisturbed systems. The model was forced with climate outputs of five Earth System Models under four representative climate scenarios plus one baseline scenario, over a matrix of 11 age classes for each stand. We find that the Net Primary Production (NPP) peak was reached in the young and middle-aged class (16- to-50-year-old) regardless of the climate scenario, while total C-woody stocks (tCWS) increased with age with different trajectories in the three sites, but not linearly as expected. Under climate change scenarios, the beech forest shows an expected increasing NPP with increasing atmospheric CO_2 and temperature as much for younger age classes as for older ones. Conversely, in the spruce and Scots pine-dominated

sites NPP and tCWS decrease under climate change scenarios. A factorial ANOVA and Tukey's *Post hoc* test (p = 0.05) were performed to verify if differences between age groups, climate scenarios, and their interactions during the simulation period were statistically significant and not just the result of different forcing in the model configuration. The ANOVA test showed that both age and, only for some sites, climate scenarios have effects with differences on the forest carbon balance only when taken individually, while when analyzed in combination, the analysis showed no effects due to the interaction of the two factors showing, then, a pervasive buffering effect of age on climate but also vice–versa. The consistent influence of age remains the primary determining factor across all sites for both NPP and tCWS. This calls for tailored management strategies to enhance the resilience and adaptability of forests in the face of changing climatic conditions, reflecting the different species and age-dependent response to climate.

Keywords: carbon cycle, climate change, fluxes, forest age, forest management, stocks.

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Introduction

Over the last decade, policies at the European level have geared towards sustainable and climate-resilient forests to ensure ecosystem services functioning and provision (e.g., regulation, supply, cultural services) including carbon sequestration in face of climate change in form of mitigation strategies (Yousefpour & Hanewinkel, 2016; Nabuurs et al., 2018; Churkina et al., 2020; Favero et al., 2021). By removing atmospheric carbon dioxide (hereafter CO_2), trees hold onto carbon (C) mainly in the form of wood, as long as they are alive. Once trees die, part of the C is released back into the atmosphere. However projected changes in global climate have a substantial impact on forest productivity, biological diversity and natural areas management: as the climate changes and scientists try to predict its future course, great uncertainty surrounds the response of forests (IPCC 2021). The contribution of trees to climate change carbon-based mitigation is shaped by both external and internal drivers influencing the forest net growth balance, and thus is labile and very uncertain under future climate change impacts (Yousefpour & Hanewinkel, 2016). Indeed carbon assimilation and wood production is influenced by several environmental factors, such as precipitation and temperature, and climate extremes, light availability, atmospheric CO_2 and nitrogen deposition (Barford et al., 2001; D'Andrea et al., 2020, 2021, He et al.2023). Some studies report a boost in European forest growth, likely driven by rising atmospheric CO_2 and combined with the climate effect (e.g. Bellasen et al. 2011, Pretzsch et al.2014, He et al.2023). Others however question the strength and the persistence of the CO_2 fertilization effect and the forest carbon sink (Duffy et al., 2021, Nabuurs et al. 2013, Wang et al.2020, Duffy et al.2021). In the temperate biome, positive effects of temperature on wood production, (i.e. biomass stock as wood, tCWS) as well as negative ones, have been found (Jump et al., 2006, Potočić et al., 2021). The effects of future climate change, with changes in temperature and precipitation regimes, with in turns affects atmospheric vapor pressure deficit and soil water availability, and the accompanying increasing atmospheric CO_2 concentration, is therefore expected to alter wood production by modifying in first instance the rates of photosynthesis and respiration rates of trees (Reyer et al., 2014; Yuan et al.2019, He et al., 2023). Many existing modeling studies show that higher CO_2 concentration and higher temperature would increase global mean forests' net primary production (NPP) and vegetation carbon stocks compared to present day climate, mainly because of CO_2 fertilization on photosynthesis (Friend et al.2013, Reyer et al., 2015, Glienke et al., 2015). However, the magnitude of the increase is uncertain as it depends on the extent to which CO_2 fertilization of land plants is limited by nutrient and water availability (e.g. Dunkl et al., 2023) and

others environmental constrain (Peñuelas et al. 2017). Yet, warmer temperatures are expected to accelerate tree growth at the northern latitudes and mountain areas, indirectly prolonging vegetation periods (Pretzsch et al.2014). Under climate change, forests are, thus, expected to grow faster, mature earlier, but also potentially have their lifespan shortened (Collalti et al., 2019, Brienen et al. 2020), implying that forests of different ages will respond differently (Anderson-Teixeira et al., 2013, Colangelo et al.2021). Some authors have also found that a positive effect of rising temperature on carbon assimilation and wood production fades with forest aging in temperate deciduous forests (West et al.2020), hampering thus our ability to depict a clear and coherent picture of the forest response to temperature changes Indeed, along the direct influence of climate drivers, carbon assimilation and wood production are also affected by stand dynamics and structural features. The heterogeneity of forest stands in the landscape (Bohn and Huth, 2017), changes in the leaf area index (LAI, Vilà et al., 2013) or species compositions (Asner et al., 2003) were shown to affect forest productivity. The traditional view of forest dynamics, as described in textbooks, reports that after an initial stepwise increase, forest productivity stabilizes and then even slightly declines (Kira and Shidei, 1967; Odum, 1969). But despite the validity of this ecological cornerstone, which has a solid foundation under past/present-day climate, this has been scarcely questioned under climate change conditions.

Particularly, future climate change may affect forest stands of different age groups, namely ‘cohorts’, differently, as forest gross primary production (GPP) and plant respiration change during stand development and younger forests are naturally more productive and more efficient than older ones (Drake et al., 2011; Goulden et al., 2011; Collalti et al., 2020a). The dynamic balance between growth (in terms of both GPP and NPP) and respiration is climate-dependent but expected thus to responds differently across the stand age spectrum under future scenarios (Goulden et al., 2011; Collalti 2020a, 2020b). As, through past silvicultural practices, human intervention shaped the distribution, structural features and age of forests (Wulder et al. 2009, Latterini et al., 2023), it is important to quantify carbon storage and flux sensitivity to climate change at different developmental stages and vegetation types to analyze the C cycle's mechanisms to better monitor the processes that control CO_2 uptake and wood production

Although climate change will potentially affect forests of all ages, we lack a prospective understanding of how future climate change will interact with forest age, particularly given that few models studied the interplay of age and C-cycle under a climate change perspective (Anderson-Teixeira et al., 2013).

Process-based forest models make it possible to investigate the effects of climate change and atmospheric CO_2 impact on different age cohorts growing in the same location, which would be challenging with direct field measurements of both fluxes and stocks and would require decades or even more. To this respect, this study questions the role of different forest age classes in maintaining high productivity under future climate conditions and to this aim, we used a validated biogeochemical process-based forest model to quantify the controls on carbon uptake and storage in forests left to develop undisturbed, considering how combinations of climate change and stand age might affect these controls.

In this context, assessing stock and fluxes via NPP and tCWS offer the possibility to analyze stand dynamics through two aspects of the same phenomenon, as NPP (i.e. the annual carbon sequestration capacity), depends on the GPP (mainly dependent on the incoming solar radiation, soil moisture and temperature) and the autotrophic respiration, while tCWS (i.e. the standing woody biomass *in situ*), depends mainly on age and long-term processes and climate trends.
We investigated thus: (i) how climate change directly impacts overall forest productivity and C-storage capacity across different stands, species and age-cohorts located in different regions of Europe; and, shed light on (ii) how and if forest age can modulate stand dynamics in response to future climate change. To this aims a factorial ANOVA and Tukey's Post hoc test ($p = 0.05$) were performed on model results to verify statistically significant differences between age groups, climate scenarios, and their interactions during the simulation period and showing as differences are not only the results of different forcing and model setting.

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 site characteristics and climate data, see also 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, and 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 results of the legacy of 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. Marèchaux et al., 2021,Vacchiano et al.2012 iv) they have already been investigated in the context of climate-smart-forestry silvicultural scenarios (Dalmonech et al., 2022). The 3D-CMCC-FEM model was first evaluated under observed climate, and based on field data availability, for GPP and NPP_{woody} (gC m^{-2} $year^{-1}$) and the diameter at breast height (DBH) (see 'Model validation' in Supplementary Material; Mahnken et al., 2022; Dalmonech et al., 2022) and then 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 umol mol^{-1} in the 'best-case scenario' (RCP2.6) to 926.6 umol mol^{-1} of the 'worst-case scenario' (RCP 8.5). For comparison purposes, we forced the forest model with a detrended and repeated meteorology and atmospheric CO_2 concentration from 1996-2006, i.e. the current climate scenario (CCS), which is considered the baseline for the current climate scenario. To simulate the potential effect of climate stressors on the whole range of age classes over an entire rotation period, we created a Composite Forest Matrix (CFM) following the approach described in Dalmonech et al. (2022). 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 class in the composite matrix and added to the CFM. This collection of virtual forest stands was used to set different initial conditions in the present day as due, ideally, to the past silvicultural practice and climate. These new stands were used to assess the impact of climate forcing on the full range of age classes, as the model has already been shown to be sensitive to forest stand development, and the relative standing biomass, and climate change (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 Model*; Collalti et al., 2014, 2016; Marconi et al., 2017; Mahnken et al., 2022; Dalmonech et al., 2022; 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. Modelled Ccimate 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 classes, were carried out without management as we are interested in the direct climate impact on undisturbed forest stand response and to avoid confounding responses of forest management (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 current climate scenario) * 11 age classes * 3 sites. Results are reported for NPP and tCWS for fluxes and stocks, respectively, as they are considered some of the most representative and fundamental variables in the carbon cycle. We evaluate the model forced with the modeled climate following the methodology reported by Dalmonech et al. (2022; see Table S1 in Supplementary Materials). We compare GPP andNPP_{woody} against eddy covariance estimates and ancillary data for the years 1997-2005 for DK-Sor and FI-Hyy and 2000-2005 for CZ-BK1. In all sites, we also compared the diameter at breast height (DBH) with field measures. After 2006 the different CO_2 concentration scenarios in the ESMs made the model evaluation inconsistent.

Statistical analysis

Statistical tests were performed to check for significant differences between the age classes, taken singularly; the different climate scenarios, taken singularly; and including their combination, during the simulation period to test the probability that one factor (ages or climate scenarios) rather than another or the combination of these has an effect on the variable under consideration. For this purpose, the factorial ANOVA test (p = 0.05) was used to assess the effect of two factors (age class and scenario), singularly taken, and their interaction on the subject on the continuous outcome variable NPP and tCWS. Significance between means was determined using the Tukey *post hoc* multiple comparisons of means test at the 95% family-wise confidence level (p = 0.05). Before proceeding, normality, and homogeneity of variance were checked via the Shapiro-Wilk and Levene's tests, respectively (for both p = 0.05). All analyses were performed for each site (CZ-BK1, DK-Sor, FI-Hyy) with the JMP PRO 17 (Trial Version ©SAS Institute Inc.; Cary, NC, USA)(Lehman et al., 2013). Statistical significance analysis is useful for assessing the differences among various simulations and understanding the factors that drive the investigated variables.

Results

Statistical analysis

The results of the factorial ANOVA show significant differences in all sites for the age factors for the NPP and tCWS variables. The climate scenario factor is highly significant at the CZ-BK1 and DK-Sor sites but not for FI-Hyy (Table 1, *p-value* <0.001). While the interaction of these two factors yields a non-significant effect.

In FI-Hyy site, the only highly significant effect is exhibited by the age factor. Neither the climatic scenario effect nor the interaction between the two factors yielded significant results. The post hoc analysis exhibits markedly different behaviors for the two variables, NPP and tCWS. In the former case, there are significant differences between groups, with a notable distinction for the younger age classes (except for class 14), the middle-aged group, and finally, the older ones. In the latter case, all age classes show significant differences, except for classes 70 and 56, which do not display significant distinctions (see Table S7 in 'Statistical analysis' in Supplementary Material).

While in CZ-BK1 for tCWS and NPP both the effect of the age variable and the climatic scenario show significant different statistical differences, even for tCWS there is a well-defined effect even in the interaction between the two factors. In tCWS variable, the only scenario with an effect is the CCS one which shows significant statistical differences from all others (*post hoc* Table S6 in Supplementary Material). In DK-Sor's site, highly significant differences are shown for the CCS scenario, which has a different behavior to all others. The most productive age groups, in terms of NPPs, are the youngest (42, 14 and 28), while a totally different behavior is shown by the oldest classes (112, 126 and 140).

On the other hand, regarding the effect of the climate scenario on the tCWS factor, a different behavior from all others is shown under the effect of RCP 8.5 (see Table S8 in 'Statistical analysis' in Supplementary Material).

In all three sites, a different pattern was observed for the CCS scenario. In Tukey's post hoc analyses (differences in least-squares means) the scenario under consideration was represented as a settling block with respect to climate forcing (see Tables S6-8 in 'Statistical analysis' in Supplementary Material).

To summarize, all statistical indexes show that, both for NPP and for tCWS, differences between age classes within the same climate scenario are similarly important and statistically significant, if taken singularly, as those within the same age class but between different climate scenarios, while their interaction (age classes X climate scenarios) taken together tends to reduce, if not cancelling off, both effects (Table 1).

Table 1 | Factorial ANOVA for NPP and tCWS analyzing the age class and climate scenario factors and the interaction between the two, for the CZ-BK1, DK-Sor and FI-Hyy sites. Asterisks in superscript indicate different levels of significance (conventionally * $p < .05$, ** $p < .01$, *** $p < .001$).

	NPP			**tCWS**		
Site	**Age class**	**Scenario**	**Age class X scenario**	**Age class**	**Scenario**	**Age class X scenario**
CZ-BK1	<0.001***	<0.001***	0.5496	<0.001***	<0.001***	<0.001***
FI-Hyy	<0.001***	0.0723	0.9975	<0.001***	0.1602	1.0000
DK-Sor	<0.001***	<0.001***	0.9223	<0.001***	<0.001***	1.0000

Effect of age 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} $year^{-1}$ in a similar way across all RCPs (Figure 1B). Also, at CZ-BK1, NPP shows a peak, independently of the climate scenarios considered in the younger age classes (i.e. 12- to 36-year-old class), but with higher values under CCS of ~330 gC m^{-2} $year^{-1}$ and ~300 gC m^{-2} $year^{-1}$ in the worst case scenario, with percentages varying from –40% (120-year-old age class under RCP 2.6) to +7% (16-year-old class under RCP 4.5) when compared to the youngest age class and lowest values at ~220 gC m^{-2} $year^{-1}$ for the oldest age class (120-year-old class) independently of the climate scenario considered (Figure 3B and Table S2 in Supplementary Material). At CZ-BK1, emerges that in any of the combinations of age x RCPs, NPP shows a reduction compared to CCS (see Table S3 in Supplementary Material). At FI-Hyy, younger age classes showed characteristic behavior with NPP, independently of the climate scenario, starting 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 classes, from ~250 gC m^{-2} $year^{-1}$ under RCP 2.6 to ~230 gC m^{-2} $year^{-1}$ under RCP 8.5 (Figure 1C). Slightly differently from CZ-BK1 at FI-Hyy the more productive cohorts are clustered around the first third of the age classes (i.e. 28- to 56-year-old) and higher NPP values of ~430 gC m^{-2} $year^{-1}$ under CCS and ~410 gC m^{-2} $year^{-1}$ for all other RCPs, with percentages +51% (56-year-old class under RCP 6.0) and lowest values at ~340 gC m^{-2} $year^{-1}$ for the oldest age class and under RCP 8.5 (Figure 2C and Table S2 in Supplementary Material). Similar to CZ-BK1, at FI-Hyy there is no clear pattern within the same class and across all RCPs, although in any of the combinations, 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 with respect to other sites, with NPP at the end of the century varying from ~800 gC m^{-2} $year^{-1}$ (under RCP 8.5) to ~560 gC m^{-2} $year^{-1}$ (under CCS) and then with NPP that smoothly increase toward the end of the century as the severity of the scenario increase in all age classes (Figure 1D). Mean annual NPP has the maximum values for the younger-age classes, with the peak for the 14-year-old one. A reduction of around –14% in annual NPP under all scenarios was seen in the oldest class when compared to the youngest age class (Figure 2D and Table S2 in Supplementary Material). The lowest values were reported for the oldest age classes (112- to 140-year-old) corresponding to ~620 gC m^{-2} $year^{-1}$. At DK-Sor, differently from the other sites, in all age classes higher RCPs show proportionally increased NPP compared to the CCS scenario (see Table S3 in Supplementary Material).

Effect of age classes and climate change on total carbon woody stock

Norway spruce at CZ-BK1 shows mean tCWS values for the youngest and oldest classes ranging between ~72 to ~145 tC ha^{-1} under CCS over the century, while from ~75 to ~150 tC ha^{-1} until mid-century, then decreasing to ~90 to ~200 tC ha^{-1} at the end of the century, with the same pattern across all RCPs (Figure 3B). In the older classes (84 to 120 years old) repeated cycle of sharp decrease in tCWS was observed along the simulation period. Under RCP 8.5 the younger classes also began to show signs of decay at the end of the century. The peak of tCWS was reached in the oldest class (120-year-old class) in all climate scenarios, but with the highest values under CCS (~145 tC ha^{-1}) and the lowest under RCP 8.5 (~127 tC ha^{-1})(Figure 4B), with percentages differences compared to the youngest age class varying between +4% (16-year-old age class under CCS) and 123% (120-year-old class under RCP 4.5)(Table S4 in Supplementary Material). The reduction of tCWS in the same age class but in the different RCPs scenarios (compared to the CCS) was of similar magnitude among scenarios but ranged between –0.5% (for the 120-year-old class) and –12% (for the 12-year-old class) with a mean of –3% among age classes (Table S5 in Supplementary Material). At FI-Hyy, younger age classes (14- to 56-year-old) showed the fastest increase in tCWS culminating around 2080 (between 100 and 140 tC ha^{-1} under all scenarios), while the older classes showed a more stable trend all over the century (Figure 3C), culminating at ~150 tC ha^{-1}. The Scot pine reached the peak in tCWS at 126 years old (~174 tC ha^{-1} under RCP 6.0 versus ~160 tC ha^{-1} under all other scenarios) but with a logarithmic trend over the age classes, in all scenarios, with differences compared to the youngest classes ranged between 47% (for the 16-year-old class under RCP 4.5) and 456% (for the 140-year-old class under CCS)(Figure 4C and Table S4 in Supplementary Material). Minor differences were found in mean tCWS between CCS and other RCP scenarios, ranging from –1.6% (140-year-old class under RCP 2.6) to +2.8% (14-year-old class under RCP 6.0). Interestingly, the only positive differences were found in RCP 6.0 (Table S5 in Supplementary Material). At DK-Sor, results for tCWS show similar patterns to the NPP, with values ranging between ~240 tC ha^{-1} (under CCS) to ~255 tC ha^{-1} (under RCP 8.5) at the end of the century with the least tCWS under CCS. The younger classes showed a shallow increase in tCWS during the simulation period, declining at the end of the century while stands older than 76 years (except for the 98-year-old class) kept growing (Figure 3D). Mean annual tCWS reached the maximum for the oldest classes (140-years-old), showing a sharp increase for age classes older than 84 years (Figure 4D). Comparing the mean tCWS of each age class against the youngest one led to an increase between 16% and 75% (from the 28- to the 140-year-old class, respectively, under

the CCS), with similar values in the other scenarios (Table S4 in Supplementary Material). At DK-Sor, in the age classes, higher RCPs show an increase in tCWS when compared to the CCS scenario, higher for stands younger than 76 years, with absolute values comparable to Fi-Hyy (see Table S5 in Supplementary Material).

Discussions

Stand age effects on productivity and C-stocks

The emerging pattern from the modeling simulation framework shows that regardless of the climate scenarios and in the absence of human intervention, both productivity and C storage capacity decline with forest aging, with differences being greater among different age groups under the same scenario than in different climate scenarios under the same age class. The evidence that the stand carbon budget is controlled by age suggests that the effects of climate change on forest cohorts are generally less significant than the effect of age, mainly in terms of the amount of standing biomass rather than because of age. In our case, age is not a *per se* effect but rather the result of factors, such as biomass accumulation, changes in forest structure (closing canopies), reduction in stomatal conductance (and its effect on photosynthesis), and changes in Non-Structural Carbon usage, as this pool buffer any asynchrony between assimilation, allocation and respiration induced by environmental variability (Collalti et al., 2016, 2020, Guillemot et al.2017). All these processes control mainly photosynthesis and autotrophic respiration, which are forest trees' main inflow and outflow fluxes. The reduction in NPP becomes more pronounced as forest aging because of increased maintenance respiration costs due to higher enzymatic activity and substrate and as the severity of the climate scenario increases. The peak of productivity was reached in the young-intermediate classes, as also found by Goulden et al. (2011), while in older stands, NPP was drastically reduced. This mechanism is yet to be understood and much discussed. However, it appears that the reduction in NPP is not necessarily due to the decrease in GPP (thus excluding that NPP is a fixed fraction of GPP) as some suggest (see Drake et al., 2011), but rather due to increased autotrophic respiration rate (see DeLucia et al., 2007; Goulden et al., 2011; Drake et al., 2011; Collalti & Prentice, 2019; Collati et al., 2020b) caused by the increase of maintenance costs for the living, and thus respiring, biomass as we found here. 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 (mainly nitrogen and phosphorus, see Goulden et al., 2011) and water resources and an increase in stomatal

limitation led to reduced photosynthetic rates, thus, to carbon allocation shifts from leaves and roots to aboveground wood production (Litton et al., 2007; Guillemot et al., 2017; Meng et al., 2023) at the expense of increasing respiratory costs. At the stand-level, such a hypothesis is strengthened by the age-related reductions in population density, despite a single tree-level biomass growth rate increasing continuously with tree size (Stephenson et al., 2014), explaining the simulated stock trends. These findings have remarkable effects in the context of climate-adaptive silviculture, as our experiments were explicitly designed to disentangle the role of management *per se*, even under the assumption of a complete cessation of any 'active' forest management practice.

On the one hand, in our study, NPP is reduced in most conditions, as this response is mainly modulated by a diversified mosaic of age differentiations, which is, in the real world, a product of disturbances such as forest management (but not only). On the other hand, our results suggest that a landscape-level solution such as stand age diversification leads to broad carbon-accumulation patterns, which depend on species-specific responses and age effects. However, our ANOVA analysis shows that age effects are largely dampened by climate effects (and vice versa) when considered together. This holds especially in the beech and spruce sites, which can be primarily attributed, once again, to a diversified initial structure. Indeed, diversified structure results from historical management practices, which are site and species-specific or long-term (~thousands of years) natural stand dynamics.

Climate change affects productivity and C-stocks differently

In our study, the three species show different responses to climate change, which depend, in addition to the auto-ecology of each species and site conditions, but also because of past management legacy that determined the current state of the forest, i.e., the initial conditions of the simulations. As expected, productivity decreases *ceteris paribus* with age, but the temperature effect increases the NPP at the northernmost sites (FI-Hyy and DK-Sor), perhaps reflecting the higher carbon costs of nutrient acquisition in colder climates (Collalti et al., 2020b). Effects of environmental changes on forest ecosystems attract attention in more extreme latitudes and altitudes where species lose or gain area at the edge of their ranges. 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 European beech and sessile/common oak (75 and 46%)(Pretzsch et al., 2023). Many model simulations have been shown not to reproduce this phenomenon. In his review, Reyer (2015) observed that 87% of the simulations (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, with only 13% of the simulations show decreasing forest productivity and declining biomass carbon pools, as the opposite to our study. However, in many of the models investigated in Reyer et al. (2015) and other studies, factors such as acclimation to CO_2 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 thanks to the fertilization effect and the lengthening of the growing season (Peano et al., 2019) *via* increasing GPP. Conversely, the negative feedback on NPP due to increased respiration (both for maintenance and growth respiration at tree and stand level) is not considered. Our study shows that the tCWS increases in all scenarios (including CCS) and stabilizes around 2075, showing an onset of decline for all age classes at the end of the century. The peak in tCWS was reached by the oldest classes, as already found in other studies (Keith et al., 2009; Goulden et al., 2011; Uri et al., 2022). This phenomenon is accentuated by the severity of the scenario (i.e., the strongest decline is observed in the RCP 8.5 scenario, the least in the RCP 2.6). This result is consistent with the theory that growth increases with temperature up to a maximum level and then rapidly declines beyond some optimum thermal conditions (Shenk, 1996; Marchand et al., 2023). Approaching the physiological optima for the species may benefit the biomass synthesis through an augmented photosynthesis supply but may eventually increase the respiratory costs of tissue growth and maintenance despite a strong acclimation capacity (Collalti et al., 2020b). High respiratory costs combined with the decline of NPP in the older age classes (112, 126, and 140 years old, data not shown) leads already, after a few decades of simulation, to repeated mortality phenomena (for carbon starvation), indicating that the environment has likely reached its carrying capacity and the competition for limited resources, such as light and water, is excessively high to sustain with the assimilation alone more biomass in the oldest age classes. The beech forest at DK-Sor's appears to be the one that more positively responds and in a clearer way to the different climate change scenarios, with productivity increasing up to RCP 8.5 in all the age classes. This suggests that the direct so-called fertilization effect of CO_2 outweighs other limiting factors, such as precipitation and soil moisture shortage and increasing temperature, with increasing vapor pressure deficit, directly affecting negatively stomatal conductance and the photosynthetic process. However, temporal NPP patterns show how productivity reaches a plateau or starts declining in the most stringent climate scenario, with environmental conditions that expose beech to drought-induced decline (Diers et al., 2023; Puchi et al., 2023 in prep). In synthesis, the central and northern European beech forests are

346 expected to remain productively stable under most climate change scenarios due to the temperature
347 increase, except for the RCP 8.5. When considering carbon accumulation, the climate effects seem a
348 less important driver compared to age, with older stands accounting for the most carbon accumulation,
349 in contrast to the findings of Förster et al. (2021), who found that the species and the silvicultural
350 practices had a greater effect in beech stands characterized by low tCWS (~150 MgC ha–1). On the
351 contrary, Norway spruce proved to be the most susceptible species, showing a strong decrease in NPP
352 even in the CCS scenario, suggesting that the species is already at its optimum and that even slight
353 climatic variations will affect the resistance and resilience of this species. Indeed, several studies
354 already highlight the lower resistance and resilience of the species to water shortage and subsequent
355 drought conditions (Vital et al., 2017; Bosela et al., 2021; Mensah et al., 2021; Marchand et al., 2023i).
356 This condition is even more evident in the youngest age class, where the lengthening of the growing
357 season likely contributes to biomass growth, leading to an increase in plants' respiration not
358 compensated by a likewise increase in GPP, ultimately causing C-starvation and death. On the other
359 end side of the age spectrum, the older cohorts undergo expected senescence towards the end of the
360 century; however, with the occurrence of stand mortality with increasing emissions scenarios as
361 demonstrated by the abrupt declines in carbon accumulation.
362 Scots pine at FI-Hyy had an intermediate pattern concerning the other two species. The species showed
363 a steady decline in productivity for the older age classes compared to the younger ones. Uri et al.
364 (2022), studying the dynamics of C storage and fluxes in a Scots pine forest, found that the maximum
365 levels of NPP are observed during the pole and middle-aged developmental stages, corresponding to
366 the period of highest C accumulation in trees. Scots pine showed a certain level of adaptability to
367 temperature changes, adjusting its physiological processes in response to temperature variations.
368 However, rising temperatures beyond the species' optimal range will reduce growth and increase
369 vulnerability to environmental stressors.

370 **The dampening effect of age on climate change and implications for management**

371 That NPP and tCWS run fast in the juvenile age, inflect at maturity, and then (more or less) abruptly
372 decline for older ages is something already observed, although guiltily underestimated in vegetation
373 models. At the same time, the direct effects of climate change on the carbon budget are largely debated
374 with models that simulate an overall increase in NPP and tCWS, possibly due to the fixed relation
375 between NPP and GPP (e.g., Reyer 2015) and GPP mainly positively driven by temperature and CO2
376 in the model assumption, and those models that return an increase in tree and stand respiratory costs

over e.g. the positive effects on GPP because of both CO2 fertilization, prolonging vegetative seasons or structural changes, (Collalti et al., 2018).

However, while these two effects, i.e., age and climate change (if singularly taken), at different levels, are primarily discussed and reported in the literature, their interaction effects are largely overlooked, although they may provide reasons for observed patterns in the real world. Indeed, our analyses show that, independently of species, when considered individually, stand age and climate show equally significant effects on both productivity and carbon stock decrease. However, their interaction surprisingly cancels them out when considering the combination of these two factors. This first evidence proves that there is indeed a dampening effect of forest heterogeneity at the landscape level on the climate sensitivity of forests, which can be related to the fact that multi-aged forests benefit from an increasing structural complexity (Jandl et al., 2019; deWergifosse et al., 2022; Asbeck et al., 2023). Structurally, a forest with different age groups will combine young, middle-aged, and mature trees, creating vertical stratification that enhances ecosystem complexity and stability. This stratification provides gradients in biomass (deadwood and living aboveground biomass), different ways to allocate Carbon (Merganičová et al., 2019), as well as ecological niches for flora and fauna (although not simulated here), promoting biodiversity and the capacity to respond more proactively to environmental disturbances (Lafond et al., 2014; Pardos et al., 2021).

From a functional perspective, a forest with diverse ages will exhibit various physiological and life cycle characteristics among its trees. This translates into a greater capacity to absorb and store carbon, thereby mitigating the effects of climate change even in a mosaic of even-aged patches as we simulated here. Young trees in the present day will proliferate and absorb significant amounts of CO2 from the atmosphere compared to young trees of the same age class growing in the historical, leading to contribute more to capturing carbon and are more efficient in converting photosynthates into biomass (DeLucia et al., 2007; Campioli et al., 2015; Collalti et al., 2020b). Yet at the cost of a likely shorter lifespan. In contrast, older trees will accumulate more biomass and serve as long-term carbon sinks and regeneration shelters. Maintaining forests with diverse ages in the landscape, facilitated through active management, thus becomes crucial to fully harness the ecological and climatic benefits offered by structural and functional diversity and to compensate for the positive and negative effects of each age class.

To this respect most of Dynamic Global Vegetation Models (DGVMs) are too coarse to resolve the age distribution of local forest and, hence, limited in their representation of forests on biomass accumulation across forest age. Such models tends thus to return systematically large carbon sink for

old-growth forests as shown in Yang et al. (2023), while our results are more in line with the modelling results shown in Pugh et al. (2018) and with satellite based estimate data as in Yang et al. (2023). The presence of diversified ages within a forest population is crucial for ensuring functional diversity under changing climatic conditions, as this diversity offers benefits in terms of resilience and adaptation (Ehbrecht et al., 2021; Zampieri et al., 2021; Kauppi et al., 2022). On the other hand, several studies argue that if we let forests age without any management, they become a less effective weapon against climate change (Drake et al., 2011; Jandl et al., 2019; Dalmonech et al., 2022). Indeed, aged forests tend to lose their growth and carbon absorption capacity due to factors such as competition among trees, reduced nutrient availability, and increased risk of diseases and pests, which in turn translate to a higher probability of mortality. Consequently, the ability of aging forests to act as carbon sinks and mitigate the effects of climate change may be compromised (Collalti et al., 2019; Zhu et al., 2019). Another recent study (Peng et al., 2023) suggested that reducing the forest harvesting rate could become an effective mitigation option based on the claims that forest harvesting has annualized carbon costs comparable to the annual emissions from land-use change due to agricultural expansion. Such conclusions were drawn based on strong assumptions that are not necessarily verifiable or will occur, such as the "higher value" of short-term mitigation actions or the eventuality that we do not shift toward other emission sources. From a long-term mitigation perspective, stating that near-term emissions and mitigations have a "higher value" than future ones seems ill-founded based on the short simulations period (2010 – 2050) analyzed, an extremely short time when dealing with forests and long-lasting wood products. Finally, the assumption that there is no shift in other emission activities in the absence of harvesting is decidedly too simplistic and unrealistic. Wood has always been an essential raw material throughout human history. Stop harvesting would force us to replace wood with other materials, whose environmental impact could be even more significant. For this reason, we claim that diversifying forest age through management practices makes sense not only due to the faster growth of juvenile trees but, more generally, because the advantage of other classes can compensate for the disadvantage of each age class. Promoting a mosaic of different aged patches will benefit other vital factors, such as biodiversity, resistance, and resilience to biotic and abiotic stressors.

Furthermore, management prevents forest abandonment and aging, increasing susceptibility to wildfires as they accumulate more combustible material, particularly in Mediterranean areas (Llovet et al., 2009; Ursino & Romano, 2014). Therefore, it is essential to adopt (pro-)active forest management practices, including selective cutting, natural regeneration, and promoting structural and functional diversity, to maintain a combination of forests of different ages, which should reflect the different

441 responses to climate. This way, forests can continue to play a fundamental role in climate change
442 mitigation, carbon sequestration, and biodiversity conservation, ensuring a sustainable future for forest
443 ecosystems, especially under uncertain future climatic trajectories.
444
445 **Limitations**
446 The study presented here has certainly some limitations. Indeed, the study does not consider the
447 indirect effects of climate change such as altered disturbance regimes and extreme events (if not
448 already included in the climate scenarios used here) such as fire, insects, or storms to reduce
449 confounding effects related to productivity and carbon accumulation. The assessment of different
450 environmental drivers focuses on direct climate change effects and increasing atmospheric CO_2
451 concentrations without considering other drivers such as Nitrogen (N), Phosphorus (P) or Ozone (O_3),
452 although these have been identified as important drivers of forest productivity (De Marco et al., 2022a,
453 2022b) and across age classes (Ye et al., 2023). In particular, N deposition rates are expected to at least
454 double before reaching a plateau (LeBauer and Treseder, 2008), increasing its fertilization effect in
455 temperate forests and that P rather than N limits tree growth, especially for small trees (Ye et al., 2023).
456 Also, the greater N availability could partially compensate for the decline in NPP observed in the
457 simulations, as found by LeBauer and Treseder (2008). Last, although important, heterotrophic and soil
458 responses are taken out from this study to avoid confounding effects and focus on tree–level
459 physiological responses of different age classes to the joint effects of altered CO_2, temperature, and
460 precipitation, because of its direct implication for the forestry sector and mitigation potential over both
461 short and long temporal scales. We did not account for potential new species migrating into the study
462 areas. However, the effectiveness of tree species change as a mitigation factor in unmanaged forests
463 may be limited due to the potential mismatch between the rates of species migration or replacement and
464 the expected rates of climate change, particularly in the more severe RCP scenarios (Settele et al.,
465 2014; Noce et al., 2016).

466 # Conclusions
467 In the context of future climate uncertainty and changing environmental conditions, the long-term
468 functioning of forests and the apparently seamless supply of multiple ecosystem services will be
469 selectively affected depending on the species, the location of the site regarding species distribution
470 range, stand-level structural characteristics, and stand development stage. Under future climate change,

young stands are expected to grow faster and mature earlier, but they might also die younger. The combination of increased stressors associated with climate change, such as increased temperatures, altered precipitation patterns, and increased frequency of extreme weather events, will pose additional challenges and reduce the overall longevity of European forests. Understanding the dynamics and interactions between different age classes is crucial for predicting how to better preserve and manage European forests in the future under climate change. Adaptive forest management practices, such as promoting species diversity, maintaining forest age diversity, and facilitating natural regeneration, can help support the resilience of European forests across various age classes in the face of climate change. These findings highlight the importance of considering age classes and species-specific responses when assessing the impacts of climate change on forest productivity and carbon storage. The varying responses of different tree species underscore the need for tailored management strategies and conservation efforts to enhance the resilience and adaptability of forests in the face of changing climatic conditions.

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; **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. 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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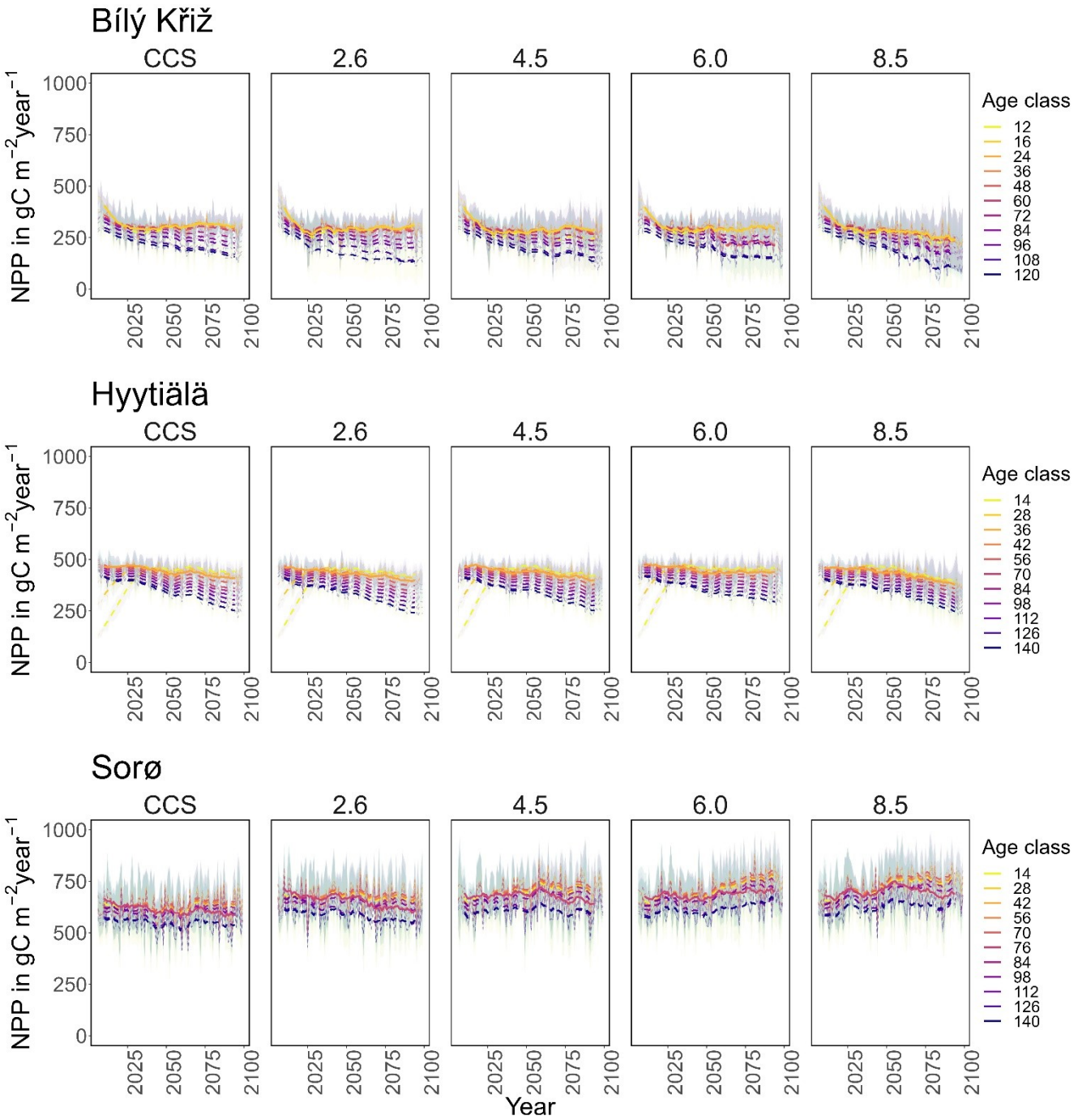

Figure 1 | NPP (gC m^{-2} year^{-1}) for age classes at the three sites in all scenarios along the simulation period (2006-2099). Lines represent the moving average of 10 years. The solid line corresponds to the real stand, while the dotted line to the virtual one. The shaded area represents two standard deviations from the mean predictions of the five ESMs models. In the legend of Figure 1A – for CZ-BK1, FI-Hyy and DK-Sor respectively – the age classes represented by 1) are 12, 14, 14 years-old classes and so on until 11) are 120, 140, 140 years-old classes.

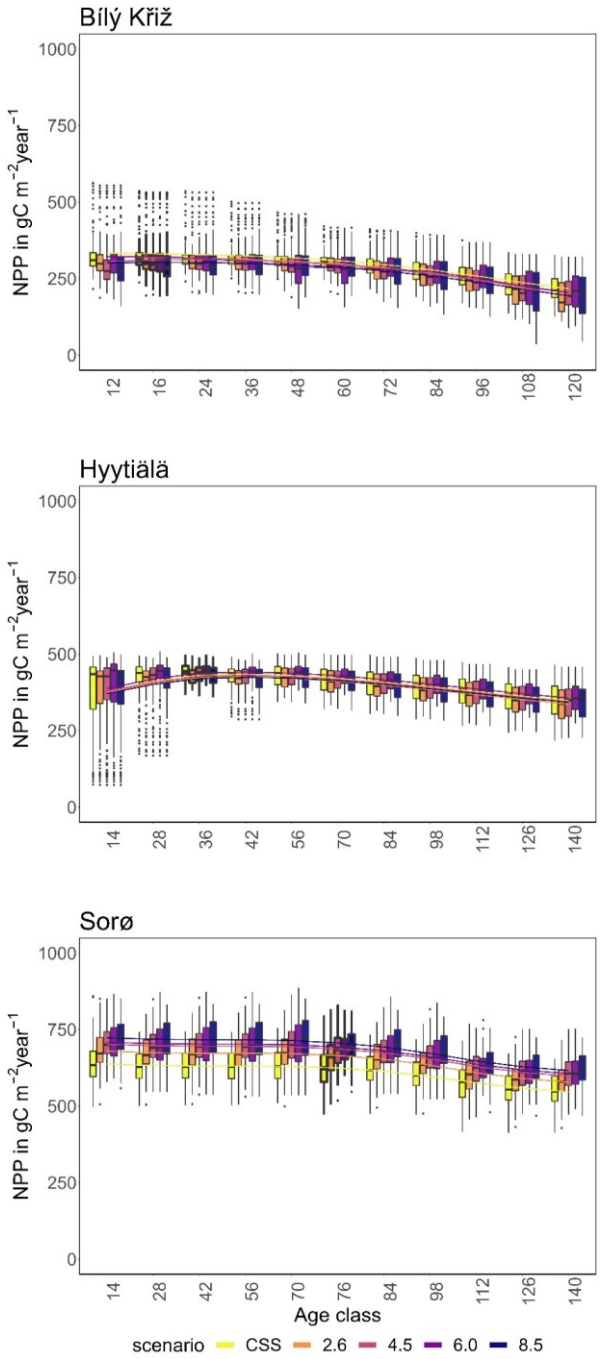

Figure 2 | Boxplot NPP (gC m^{-2} year^{-1}) by age classes at the three sites in the four RCPs scenario compared to the CCS one for the different age classes. The thick line corresponds to the real stand. Lines are fitted throughout the median of the NPP values using a generalized additive model. In the legend of Figure 2A – for CZ-BK1, FI-Hyy and DK-Sor respectively – the age classes represented by 1) are 12, 14, 14 years old classes and so on until 11) are 120, 140, 140 years-old classes.

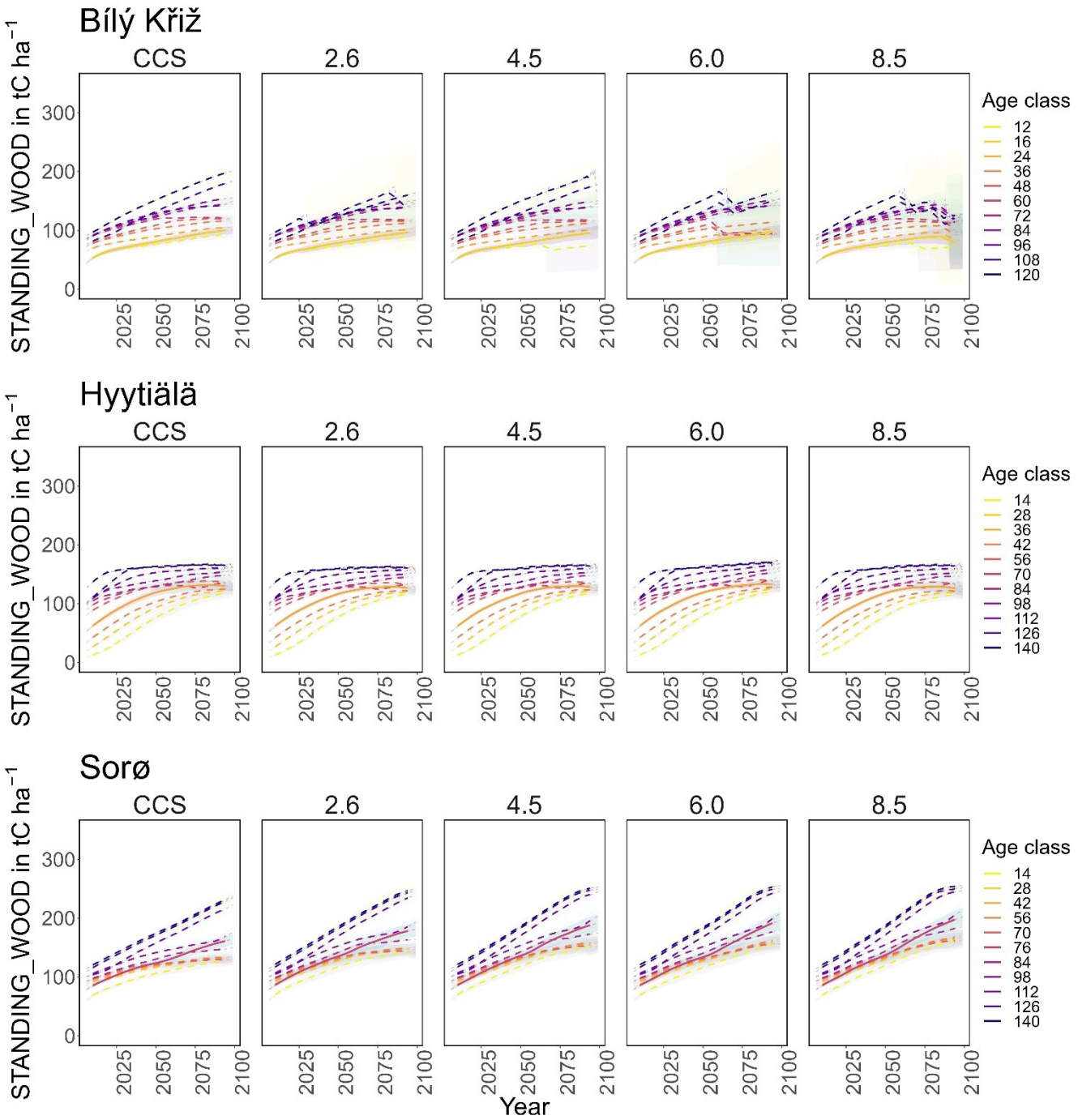

Figure 3 | Modeled tCWS (tC ha^{-1}) for age classes at the three sites in all scenarios along the simulation period (2006-2099). Lines represent the moving average of 10 years. The solid line corresponds to the real stand, while the dotted lines to the virtual ones. The shaded area represents two standard deviations from the mean predictions of the five ESMs models. In the legend of Figure 3A – for CZ-BK1, FI-Hyy and DK-Sor, respectively – the age classes represented by 1) are 12, 14, 14 years-old classes and so on until 11) are 120, 140, 140 years-old classes.

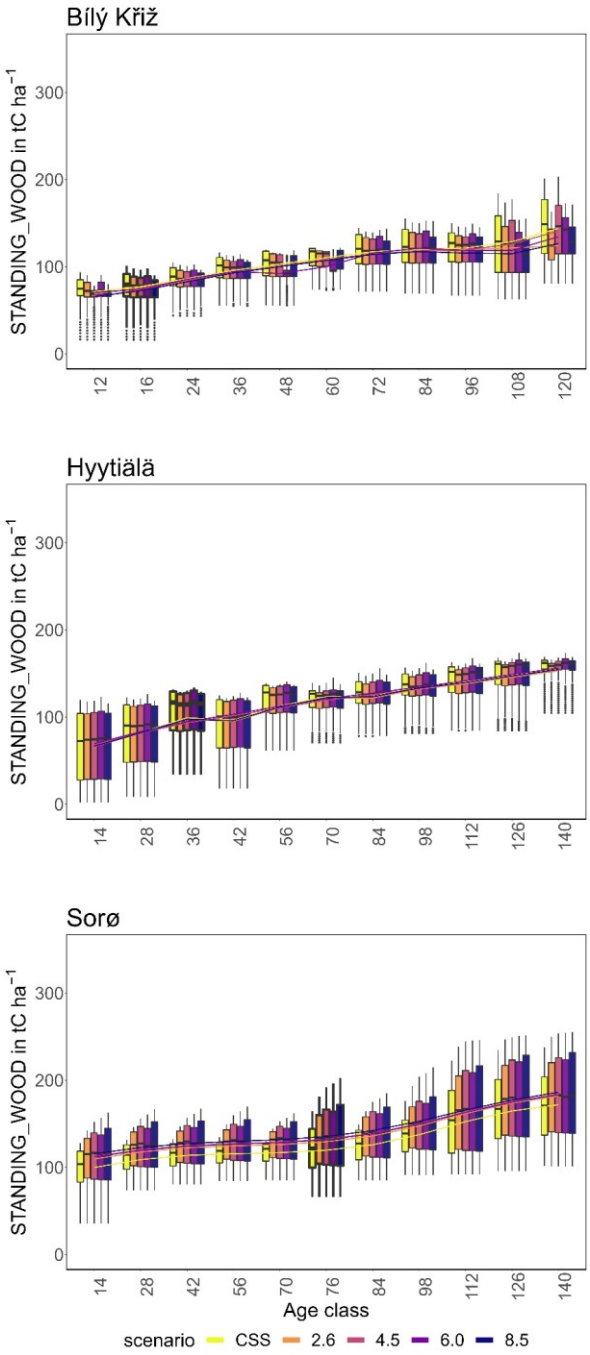

Figure 4 | Boxplot of modeled tCWS (tC ha^{-1}) for age classes at the three sites in the four RCPs scenarios compared to the CCS (current climate scenario) one for the different age classes. The thick line corresponds to the real stand. Lines are fitted throughout the median of the NPP values using a generalized additive model. In the legend of Figure 4A – for CZ-BK1, FI-Hyy and DK-Sor respectively – the age 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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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

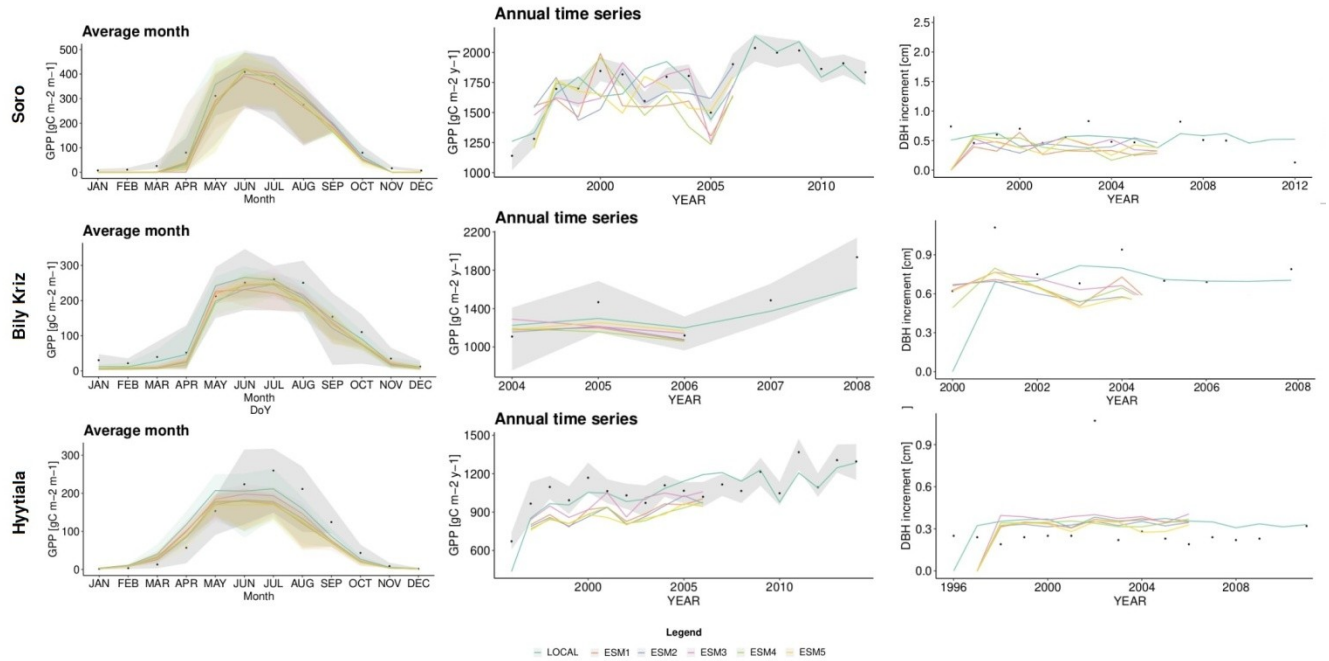

Figure S1| Evaluation of monthly seasonal GPP (gC m–2 day–1) fluxes (left column) and annual values (central column) for the sites of Sorø, Bily Kriz and Hyytiala (rows). Quality-checked and -filtered GPP values evaluated at the sites by the eddy covariance technique are reported as black dots. The shaded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

		Age class										
Site	**Scenario**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
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.

		RCP scenario				
Site	**Age class**	**CCS**	**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.

		Age class										
Site	**Scenario**	**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.

			RCP scenario			
Site	**Age class**	**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

Statistical analysis

ANOVA – HSD di Tukey (α=0.050)

Tables S6 | Factorial ANOVA for NPP and tCWS analyzing the age class and climate scenario factors and the interaction between the two (when at least one interaction was significant), for the CZ–BK1 site. Significance between means was determined using the Tukey *post hoc* multiple comparisons of means test at the 95% family-wise confidence level (p = 0.05).

NPP

Age class					
24	A				
16	A				
36	A	B			
12	A	B			
48	A	B			
60		B	C		
72		B	C		
84			C	D	
96				D	
108					E
120					E

Scenario			
rcp0p0	A		
rcp6p0	A	B	
rcp2p6		B	C
rcp4p5		B	C
rcp8p5			C

938
939 **tCWS**
940
941

Age_class								
120	A							
108		B						
84		B	C					
96		B	C					
72			C					
60				D				
48					E			
36					E			
24						F		
16							G	
12								H

942
943

Scenario				
rcp0p0	A			
rcp4p5		B		
rcp2p6		B		C
rcp6p0		B		C
rcp8p5				C

944
945

Scenario*Age_class							
120,rcp0p0	A						
120,rcp4p5	A						
120,rcp6p0	A	B					
120,rcp8p5		B	C				
108,rcp0p0		B	C	D			
120,rcp2p6		B	C	D	E		
108,rcp4p5		B	C	D	E		
84,rcp0p0			C	D	E	F	
108,rcp2p6			C	D	E	F	
84,rcp6p0			C	D	E	F	
96,rcp0p0			C	D	E	F	
96,rcp6p0			C	D	E	F	
84,rcp2p6			C	D	E	F	G
84,rcp4p5			C	D	E	F	G H

72,rcp0p0	C	D	E	F	G	H	I															
96,rcp2p6	C	D	E	F	G	H	I															
96,rcp4p5	C	D	E	F	G	H	I															
108,rcp6p0	C	D	E	F	G	H	I															
84,rcp8p5	C	D	E	F	G	H	I															
72,rcp6p0	C	D	E	F	G	H	I															
96,rcp8p5	C	D	E	F	G	H	I															
72,rcp2p6		D	E	F	G	H	I															
72,rcp4p5		D	E	F	G	H	I															
72,rcp8p5			E	F	G	H	I															
108,rcp8p5				F	G	H	I	J														
60,rcp0p0				F	G	H	I	J	K													
60,rcp2p6					G	H	I	J	K	L												
60,rcp4p5						H	I	J	K	L												
60,rcp8p5							I	J	K	L	M											
48,rcp0p0								J	K	L	M	N										
48,rcp2p6									K	L	M	N										
48,rcp8p5									K	L	M	N										
60,rcp6p0									K	L	M	N										
48,rcp4p5									K	L	M	N										
36,rcp0p0										L	M	N	O									
36,rcp6p0											M	N	O	P								
36,rcp2p6												N	O	P	Q							
36,rcp4p5												N	O	P	Q							
36,rcp8p5												N	O	P	Q	R						
48,rcp6p0												N	O	P	Q	R						
24,rcp0p0													O	P	Q	R	S					
24,rcp6p0														P	Q	R	S	T				
24,rcp2p6															Q	R	S	T	U			
24,rcp4p5															Q	R	S	T	U			
24,rcp8p5																R	S	T	U	V		
16,rcp0p0																	S	T	U	V	W	
16,rcp6p0																		T	U	V	W	
16,rcp2p6																		T	U	V	W	
16,rcp4p5																			U	V	W	
12,rcp0p0																				V	W	
16,rcp8p5																				V	W	
12,rcp6p0																					W	
12,rcp2p6																					W	
12,rcp8p5																					W	
12,rcp4p5																					W	

Tables S7 | Factorial ANOVA for NPP and tCWS analyzing the age class and climate scenario factors and the interaction between the two (when at least one interaction was significant), for the FI–Hyy site. Significance between means was determined using the Tukey *post hoc* multiple comparisons of means test at the 95% family–wise confidence level (p = 0.05).

NPP

Age_class						
56	A					
42	A	B				
36	A	B				
28	A	B	C			
70		B	C	D		
84		B	C	D		
98			C	D	E	
14			C	D	E	F
112				D	E	F
126					E	F
140						F

tCWS

Age_class										
140	A									
126		B								
112			C							
98				D						
84					E					
70						F				
56						F				
36							G			
42								H		
28									I	
14										J

Tables S8 | Factorial ANOVA for NPP and tCWS analyzing the age class and climate scenario factors and the interaction between the two (when at least one interaction was significant), for the DK–Sor site. Significance between means was determined using the Tukey's *post hoc* multiple comparisons of means test at the 95% family–wise confidence level (p = 0.05).

NPP

Age_class			
42	A		
14	A		
28	A		
70	A	B	
76	A	B	
56	A	B	
98	A	B	
84	A	B	
112		B	C
140			C
126			C

Scenario		
rcp8p5	A	
rcp6p0	A	
rcp4p5	A	
rcp2p6	A	
rcp0p0		B

tCWS

Age_class							
140	A						
126	A						
112			B				
98				C			
84					D		
76					D	E	
70						E	F
56						E	F
42							F

28					F	
14						G

Scenario			
rcp8p5	A		
rcp4p5	A	B	
rcp6p0	A	B	
rcp2p6		B	
rcp0p0			C