Stand age diversity weakens forests sensitivity to climate change

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Abstract

Forest age is the result of population dynamics, disturbance regimes, silviculture and plays an important role in the global Carbon (C) cycle. To examine the shaping effects of forest age on Carbon budget 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 under four representative climate scenarios over a matrix of 11 age classes for each stand. We find that the Net Primary Production (NPP) peak was reached in the middle-aged class (42- to-70-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 as 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. ANOVA analysis applied as factorial analysis to model outputs shows that age and climate scenarios have all effects on forest carbon budget only if taken singularly while their combination reduces - if not totally weakens - any effect.
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 gear 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) as long as they are alive. Once they die, they release the CO_2 back into the atmosphere. Their contribution to climate change carbon-based mitigation is therefore labile and very uncertain (Yousefpour & Hanewinkel, 2016). While some studies report a boost in growth, probably driven by rising atmospheric CO_2, others question this fertilization effect (Duffy et al., 2021) and report in addition an increase in both the severity and return period of climate change-induced disturbances (Senf & Seidl, 2021) which alter the trajectories of forest dynamics with even more uncertain consequences for these ecosystems functionality (Anderson-Teixeira et al., 2013; Thom et al., 2016; Potočić et al., 2021; Senf et al., 2021; Patacca et al., 2023; Dunkl et al., 2023). Indeed, the effects of climate change, with changes in temperature and precipitation regimes, water availability and atmospheric CO_2 concentration, alter wood production by modifying the rates of photosynthesis and respiration rates of trees (Reyer et al., 2014; He et al., 2023). Wood production is influenced by several factors, such as CO_2 fertilization, climate extremes, nitrogen deposition, light availability, precipitation and temperature (Barford et al., 2001; D'Andrea et al., 2020, 2021). In the temperate biome, positive effects on wood production as well as negative ones have been found (Jump et al., 2006). However, it remains unclear why forests react differently to temperature change. In addition to the influence of climate drivers (temperature, radiation, precipitation), wood production is also affected by stand dynamics and structural features which can be grouped into: properties which describe forest structure and properties that describe species composition (deWergifosse et al., 2022). Changes in productivity can be caused, for example, by changes in the leaf area index (Vilà et al., 2013), in the site conditions or by the heterogeneity of stands in the forest (Asner et al., 2003; Bohn and Huth, 2017). Some authors have also found a positive effect of rising temperature on wood production fades with forest aging in temperate deciduous forest. The traditional view of forest dynamics, as described in textbooks, reports that after an initial stepwise increase the forest productivity stabilizes and then slightly declines (Kira and Shidei, 1967; Odum, 1969). But despite the validity of this ecological cornerstone, which has solid foundation under past/present-day climate, this has been scarcely questioned under climate change conditions. Indeed,

high levels of CO_2 are considered to produce a fertilization effect and are boosting temperatures, which expected impacts especially in colder regions. Warmer temperatures accelerate tree growth at the northern latitudes and in mountain areas, even through prolonging vegetation periods. Under climate change, therefore, forests are expected to grow faster, to mature earlier but also to potentially die younger (Collalti et al., 2019) implying that forests of different ages will respond differently (Anderson-Teixeira et al., 2013). 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). Despite the large uncertainty in modeled forests' productivity response (see Reyer, 2014), existing modeling studies consistently show that SRM (solar radiation modification) would increase the global terrestrial carbon sink relative to a high-CO_2 world without SRM (high confidence). Based on available evidence, SRM with high CO_2 would increase global mean forests' net primary production (NPP) and carbon storage in woody tissues (tCWS) on land compared to an unperturbed climate, mainly because of CO_2 fertilization on photosynthesis (Glienke et al., 2015; Yang et al., 2020). 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 (Dunkl et al., 2023). Particularly, 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). Human intervention, through silvicultural practices, shapes the distribution, the structure and age of forests (Noce et al., 2016; Latterini et al., 2023). It is important to quantify carbon storage and flux sensitivity to climate change in different vegetation types and developmental stages and to analyze the mechanisms involved in the carbon cycle to better monitor the processes that control CO_2 uptake and wood production. The dynamic balance between growth (in terms of both GPP and NPP) and respiration is climate-dependent, but responds differently with stand age (Goulden et al., 2011; Collalti 2020a, 2020b). Process-based models (PBMs) make it possible to investigate the effects of climate change and atmospheric CO_2 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. In this context, assessing stock and fluxes via NPP and tCWS offer the possibility to analyse stand dynamics through two aspects of the same phenomenon, as NPP (i.e. the annual carbon sequestration capacity), depends on the gross primary production (mainly dependent on the incoming solar radiation) and the respiration, while tCWS (i.e. the standing woody

biomass at the site), depends mainly on age and long-term climate trends. Existing models struggle in predicting forest growth and carbon dynamics in uneven-aged forests given their high structural complexity as they are composed by multiple age cohorts (Vacchiano et al., 2012; Marèchaux et al., 2021). Although climate change will potentially affect forests of all ages, we lack prospective understanding of how climate change will interact with forest age particularly given that few models studied the interplay of cohorts age and C-cycle (Anderson-Teixeira et al., 2013). 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 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. We investigated: (i) how climate change 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 does forest age can modulate stand dynamics in response to climate change.

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, we extract 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. For more detailed information on the study site characteristics and climate data, see also Collalti et al. (2018), 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) they are under anthropogenic influence as management actively takes place, 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, 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 validated under observed climate, and based on data availability, for GPP and NPP_{woody} (gC m^{-2} $year^{-1}$, see 'Model validation' in Supplementary Material; Dalmonech et al., 2022) and then forced with the climate scenario corresponding to the RCP atmospheric CO_2 concentration values for the period 2016 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 atmospheric CO_2 concentration from 1996-2006 meteorology, 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 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 meteorology from 1996 to 2006 and the observed BAU management practices. Data required to re-initialize the model at every tenth of the rotation length were retrieved from each of these simulations. Hence, ten additional 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 due to the past silvicultural practice and climate. These new stands were used to assess impact of climate forcing to the full range of age classes, as the model has already shown to be sensitive to forest stand development and the relative standing biomass (Collalti et al., 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. Climate change simulations started in 2006 (the final year of the current detrended meteorological data used to create the CFM) 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 following the methodology reported in Dalmonech et al. (2022; see Table S1 in Supplementary Materials). We compare GPP and NPP_{woody} against eddy covariance estimated 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 compare the modeled NPP_{woody} and 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 and scenarios during the simulation period. 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 test and Levene's test, 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).

Results

Statistical analysis

The results of the factorial ANOVA show significant differences in all sites for the age and scenario factors for the NPP variable (Table 1, *p* value <0.001). The interaction between the two factors is still significant in all sites, however, both age and different scenarios have a bearing if singularly taken, but much less when taken together in a non-additive effect. In FI-Hyy site the effect of the scenario is greater because at the *post hoc* test the scenarios show significant differences between them, except for scenarios RCP 2.6 and 4.5, while CZ-BK1 the only scenario that has an effect is the CCS one and the others do not differ (*post hoc* Table S7 in Supplementary Material). The RCP 8.5 caused a drastic reduction in NPP in all age classes compared to the other climate forcing. In fact, in every age class it ranks last or second-to-last, and even in the latter case the differences with the last scenario are not statistically significant (see Bílý Krìz and Hyytiälä *post hoc* Table S7 and S8 in Supplementary Material).

In DK-Sor's site, the strongest effect of age, among the other sites, was observed. In particular, these are separated into well-defined categories: young, mature and old. The NPP is thus closely related to age class, i.e. the younger ones showed higher values that gradually decreased as age increases (at class 76 there is a reversal of the trend). In the CZ-BK1 site, the *Post hoc* test (see Table S7 in 'Statistical analysis' in Supplementary Material) revealed that two age classes (12- and 48-year-old, respectively) did not exhibit any significant differences, whereas the 24-year-old age class differed significantly from all other age classes. The age class trend does not show a definite course: this indicates a greater weight of scenario factor shown for high significance reported in Table 1. Significant effects are shown in relation to RCP 6.0 for age classes 12, 24 and 120 (younger classes are likely more affected by the CO_2 fertilization effect which increases productivity, while older classes show a decrease). 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 S6-9 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 * climate scenarios) taken together tends to reduce 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**
Overall	0.0001***	0.0001***	1	0.0001***	0.0001***	0.901
CZ-BK1	0.0001***	0.0001***	0.4442	0.0001***	0.0001***	0.0001***
FI-Hyy	0.0001***	0.0001***	0.9982	0.0001***	0.0001***	0.9993
DK-Sor	0.0001***	0.0001***	1	0.0001***	0.0001***	0.9969

Effect of age classes and climate change on productivity

Simulated NPP averaged across sites shows, independently on the climate scenarios, a negative trend over the century, yet with different rates, declining for the CCS between 600 for the youngest class and 400 gC m^{-2} $year^{-1}$ for the oldest one, while under RCP 8.5 between about 550 for the youngest class and about 300 gC m^{-2} $year^{-1}$ for the oldest one at the end of the century, with the older stands showing, overall, a steeper decline in productivity (Figure 1A). Overall, NPP shows a peak, independently of the climate scenario, for the middle-aged classes around 550 gC m^{-2} $year^{-1}$, with percentages varying between +7% and +9% depending on age class and the lowest values for the oldest class, at around 420 gC m^{-2} $year^{-1}$, with percentages varying between –10% and –13.5% when compared to the youngest age class (Figure 2A and Table S2 in Supplementary Material). When comparing the same class but within the four climate scenarios (considering the CCS as the benchmark) NPP under RCP 2.6 shows all over the age classes the highest reduction in terms of annual NPP (see Table S3 in Supplementary Material).

At the CZ-BK1, NPP values vary under CCs from ~600 to ~350 gC m^{-2} $year^{-1}$, while from ~400 to ~200 gC m^{-2} $year^{-1}$ in a similar way across all RCPs (Figure 1B). Interestingly, the youngest age class under all four RCPs show diffuse mortality within the stand at the end of the century. Also, at CZ-BK1, NPP shows a peak, independently of the climate scenarios considered in the middle age classes (i.e. 48- to 72-year-old class), but with higher values under CCS of ~400 gC m^{-2} $year^{-1}$ and ~250 gC m^{-2} $year^{-1}$ for all other RCPs, with percentages varying from +57% (48-year-old age class under RCP 2.6) when compared to the youngest age class and lowest values at ~200 gC m^{-2} $year^{-1}$ for the youngest age class (12-year-old class) independently of the climate scenario considered (Figure 3B and Table S2 in Supplementary Material). Differently from the overall case, at CZ-BK1, no clear pattern emerges when comparing the same age classes across different climate scenarios although 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 (~200 gC m^{-2} $year^{-1}$), step wisely increasing and then stabilizing at the middle of the century at ~450 gC m^{-2} $year^{-1}$ and then declining, more in the oldest age classes, from ~400 gC m^{-2} $year^{-1}$ under RCP 2.6 to ~250 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 ~500 gC m^{-2} $year^{-1}$ under CCS and ~450 gC m^{-2} $year^{-1}$ for all other RCPs, with percentages +17% (42-year-old class under CCs) and lowest values at ~300 gC m^{-2} $year^{-1}$ for the oldest age class and under RCP 8.5 with a percentage of -16 of NPP when compared to the youngest age class (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 (see Table S3 in Supplementary Material). Last, at DK-Sor, results show similar patterns as in the overall case and as in the CZ-BK1 with NPP at the end of the century varying from ~850 gC m^{-2} $year^{-1}$ (under CCS) to ~750 gC m^{-2} $year^{-1}$ (under RCP 8.5) and then with NPP that smoothly decreasing in the less severe climate scenarios and for the oldest age classes under RCP 6.0 and 8.5 while stabilizing in the youngest ones around (~750 gC m^{-2} $year^{-1}$)(Figure 1D). Mean annual NPP has the maximum values for the middle-age classes, with a peak for the 70-year-old one and +6% in annual NPP under CCS when compared to the youngest age class and lowest values for the oldest age classes (112- to 140-year-old) corresponding to ~650 gC m^{-2} $year^{-1}$ and a reduction of –14.9% (120-year-old-class) when compared to the youngest age class (Figure 2D and Table S2 in Supplementary Material). 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

Overall, tCWS (tC ha^{-1}) averaged across sites shows a positive trend in all five scenarios but with different magnitudes among scenarios and age classes (Figure 3A). Under CCS, the tCWS of the youngest class increased from 48 to 130 tC ha^{-1} over the century while the oldest class increased from 135 to 250 tC ha^{-1}. Under RCP 8.5 the same classes went from 41 to 96 C ha^{-1} and from 128 to 178 tC ha^{-1} (for the youngest and oldest classes, respectively). Overall, tCWS peaked, independently of the climate scenario, for the oldest classes around 210 tC ha^{-1} under CCS and 176 tC ha^{-1} under all other scenarios (Figure 4A). The tCWS differences between each age class and the youngest one ranged from ~11% (for the 2nd youngest class under CCS) to 100% (for the oldest class under RCP 2.6) (Table S4 in Supplementary Material). Comparing the differences in tCWS of each age class under different scenarios (using CCS as the benchmark) shows a reduction of ~20%, independently from the age and scenario considered (Table S5 in Supplementary Material). Norway spruce at CZ-BK1 shows mean tCWS values among age classes ranging between ~95 to ~175 tC ha^{-1} under CCS over the century, while from ~84 to ~115 tC ha^{-1} until mid-century, then decreasing to ~80 tC ha^{-1} at the end of the century, consistently across all RCPs (Figure 3B). The same mortality observed in the NPP was found in tCWS for the youngest age class. Interestingly, stands older than 72 years also begin to show signs of decay. 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 (~230 tC ha^{-1}) and the lowest under RCP 8.5 (~155 tC ha^{-1}) (Figure 4B), with percentages differences compared to the youngest age class varying between +3.5% (16-year-old age class under CCS) and 330% (120-year-old class under RCP 2.6) (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 ~24 (for the 120-year-old class) and ~50 (for the 12-year-old class) 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 2075 (at ~150 tC ha^{-1} under CCS and ~130 tC ha^{-1} under all RCPs scenarios) and eventually declining by the end of the century around 120 tC ha^{-1}, independently of the scenario, while the older classes showed a more stable trend all over the century (Figure 3C). The Scot pine reached the peak in tCWS at 126 years old (~155 tC ha^{-1} under CCS versus ~140 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 27% (for the 16-year-old class under RCP 6.0) and 150% (for the 140-year-old class under CCS)(Figure 4C and table S4 in Supplementary Material). Interestingly, the difference in mean tCWS between CCS and other RCPs scenarios increased with age and varied from –6.4% (14-year-old class under RCP 6.0) to –11.5% (70-year-old class under RCP 8.5) with the smallest differences in RCP 6.0 (Table S5 in Supplementary Material). Similar to NPP, at DK-Sor, results for tCWS show similar patterns as in the overall case with values ranging between ~220 tC ha^{-1} (under CCS) to ~230 tC ha^{-1} (under RCP 8.5) at the end of the century with the least tCWS under RCP 2.6. 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) keep growing (Figure 3D). Mean annual tCWS reached the maximum for the oldest classes (140-year-old), showing a sharp increase for age classes older than 70 years (Figure 4D). Comparing the mean tCWS of each age class against the youngest one led to an increase between 10% and 66% (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 a decrease in tCWS when compared to the CCS scenario, higher for stands older 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

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 carbon budget is controlled by age confirms the effects of climate change on cohorts suggesting that the age effect is more significant than climate change itself, mostly in terms of the amount of standing biomass in the stands rather than because of age. In our case age is not a *per se* effects but rather the resulting behavior of, among the others, biomass accumulation, changes in forest structure (closing canopies), reduction in stomatal conductance (and its effect on photosynthesis), change in Non-structural carbon usage (Collalti et al., 2016). All these processes have a control on, mainly, the photosynthesis and autotrophic respiration which are the main inflow and outflow fluxes for trees.

Overall, a general reduction in NPP becomes more pronounced as the severity of the climate scenario and forest aging increases. For tCWS, simulations show very different trends compared to NPP as it accumulates over time, saturates for the oldest age class, but not necessarily at the end of the simulation period. The peak of productivity was reached in the intermediate classes (i.e. 48-70-year-old-stand)(Figure 3A), as also found by Goulden et al. (2011), while in older stands, NPP was drastically reduced. This mechanism is yet to be understood, but it appears that the reduction in NPP is not due (or potentially not only) to the decrease in GPP (thus excluding that NPP is a fixed fraction of GPP) as some suggests (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., 2020) 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 (especially, nitrogen and phosphorus)(Goulden et al., 2011) and water resources, and an increase in stomatal limitation lead 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 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). These findings have remarkable effects in the context of climate-adaptive silviculture, as our experiments were specifically designed to disentangle the role of management per se even under the assumption of a complete cease of management practices. On the one hand, our results provide further evidence for larger scale studies such as Roebroek et al. (2023) according to which global forest carbon would increase by ~15% in the unlikely no-management scenario, as in our case under all conditions NPP is reduced no matter the climatic severity (e.g. temperature increase and precipitation deficit), as this response is mostly and uniquely modulated by a diversified mosaic of age differentiations which is, in the real world, a product of disturbances such as forest management. On the other hand, our results suggest that a landscape-level solution such as stand age-diversification leads to unpredictable carbon-accumulation patterns which are much depending on species-specific responses and age effects. However, as our ANOVA analysis show, it seems as climate effects are largely dampened by age effects no matter the species or site conditions, which can be largely attributed once again to a diversified structure which is the result of management practices or long-term (~thousands of years) natural stand dynamics which can likely

be observed in the remaining old-growth primeval forests (Lingua et al. 2011; Motta et al., 2015; Colangelo et al., 2021).

Climate change effects on productivity and C-stocks differently

In our study, the three species show different responses to climate change effects which depend, in addition to the auto-ecology of each species, on the site conditions where they vegetate concerning the specie's distribution, such as soil conditions, nutrient availability, but also past management legacy effects. As expected, productivity decreases *ceteris paribus* with age, but the temperature effect is to increase 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). Current ecosystem models have shown to not reproduce this phenomenon. In his review of forest productivity, Reyer (2015) describes as many models predict an increase in NPP for European forests under most climate change scenarios, in opposite to our study. We argue that so far, and in the models investigated in the abovementioned review and many studies (see review of Reyer 2014), the NPP is a fixed fraction of the GPP (see Collalti & Prentice, 2019), and as main consequence under climate change scenarios the NPP increases thanks to the fertilization effect and the lengthening of the growing season (Peano et al., 2019), but the negative feedback on NPP due to increased respiration from increased GPP is not considered. Our study shows that the tCWS increase in all scenarios (including CCS) and stabilizes around 2075, showing an onset of decline at the end of the century for all age classes. 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 is assumed to increase with temperature up to a maximum level, and then rapidly decline beyond some optimum thermal condition (Shenk 1996; Marchand et al., 2023). Approaching the physiological optima for the species may benefit the biomass synthesis through an augmented photosynthates supply but may eventually increase the respiratory costs of tissue growth and maintenance, despite a strong acclimation capacity (Collalti et al., 2020). High respiratory costs combined with the decline of NPP in the older age classes (112, 126 and 140-years-old, data to shown) leads already after a few decades of simulation to repeated mortality phenomena, indicating the environment has reached its carrying capacity and the competition for limited resources, such as light and water, is excessively high to sustain more biomass in the oldest age classes. The beech forest at

DK-Sor's appears to be the one that responds best 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 changes in precipitation regimes and temperature increases. Hence, an increase in temperatures and the lengthening of the growing season is tolerable up to a certain threshold. Indeed, NPP starts to decline as the concentration of CO_2 in the atmosphere increases, the temperature becomes too high and available water becomes limiting, all conditions which expose beech to drought-induced decline (Diers et al., 2023). In synthesis, the central and northern European beech forests are expected to remain productively stable under most climate change scenarios due to the temperature increase except for the RCP 8.5 with a drastic drop in productivity. As for carbon accumulation, the age effect seems a more important driver, with older stands accounting for the most carbon accumulation, in contrast to the findings of Förster et al. (2021), who found that the species and the silvicultural practices had a greater effect in beech stands characterized by low tCWS (~150 MgC ha^{-1}). On the contrary, Norway spruce proved to be the most susceptible species, showing a strong decrease in NPP even in the CCS scenario, suggesting that the species is already at its optimum and that even slight climatic variations will affect the resistance and resilience of this species. Indeed, several studies highlight the lower resistance and resilience of the species to water shortage and subsequent drought conditions (Marchand et al., 2023, Mensah et al., 2021, Bosela et al. 2021, Vitali et al. 2017). This condition is even more evident in the youngest age class, where the lengthening of the growing season causes biomass growth leading to an increase in respiration not compensated by a stable increase in GPP, ultimately, leading to C-starvation and death. The older cohorts, undergo as expected senescence towards the end of the century demonstrated by abrupt declines in carbon accumulation Scots pine at FI-Hyy had an intermediate pattern with respect to the other two species. For the older age classes, the species showed a steady decline in productivity compared to the younger ones. Uri et al. (2022), studying the dynamics of C 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, corresponding to the period of highest C accumulation in trees. Scots pine showed a certain level of adaptability to temperature changes, adjusting its physiological processes in response to temperature variations. However, rising temperatures beyond the species' optimal range will lead to reduced growth and increased vulnerability to water stress.

The dampening effect of age on climate change

That Net Primary Production and Carbon Woody Stock run fast in the juvenile age, inflect at maturity and then (more or less) abruptly decline for older ages is something already observed from centuries, although guiltily underestimated in vegetation models. At the same time, effects of climate change on forest Carbon budget is largely debated with models which simulates an overall increase in NPP and tCWS because of fixed relation between net and gross primary productivity (Reyer 2014) and those models which assume an increase in respiratory costs over the positive effects on photosynthesis because of both CO_2 fertilization and prolonging vegetative seasons (Collalti et al., 2018). But while these two effects (if singularly taken), at different levels, are largely discussed and reported in literature, the effects of their interaction, i.e. age and climate change, are largely overlooked in literature, although they may provide reasons for observed patterns in the real world. Indeed, the ANOVA analysis applied to models outputs shows that, independently on species, when considered individually, stand age and climate show equally significant effects in terms both productivity and carbon stocks losses, yet when considering the combination of these two factors, their interaction surprisingly cancels them out. This first evidence proves that there is indeed a dampening effect of forest heterogeneity at landscape level on climate sensitivity of forests which can be related to the fact that multi-aged forest 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 have a combination of 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, promoting biodiversity and the capacity to respond more proactively to environmental disturbances (Pardos et al. 2021, Lafond et al. 2014).

From a functional perspective, a forest with diverse ages will exhibit a variety of 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, will grow rapidly and absorb significant amounts of CO_2 from the atmosphere, contributing to carbon capture and are more efficient in converting pothosynthates in biomass (DeLucia et al., 2007; Campioli et al., 2015; Collalti et al., 2020b). 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 eventually through active management, thus becomes crucial to fully harness the ecological and climatic benefits offered by structural and functional diversity and to

compensate positive and negative effects of each age class. As consequence, 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 to climate change (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. 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). Furthermore, abandoned and aged forests can become more susceptible to wildfires as they accumulate more combustible material and may exhibit greater vulnerability to higher temperatures and drought conditions, particularly in Mediterranean areas (Llovet et al., 2009; Ursino &Romano, 2014). Forest fires will in turn release significant amounts of carbon into the atmosphere, further contributing to greenhouse gas concentrations and extinguish the carbon pools stored in the necromass. Therefore, it is essential to adopt (pro-)active forest management practices, including selective cutting, natural regeneration, and the promotion of structural and functional diversity, to maintain a combination of forests with different ages. This way, forests can continue to play a critical role in climate change mitigation, carbon sequestration, and biodiversity conservation, ensuring a sustainable future for forest ecosystems especially under uncertain future climatic trajectories.

Limitations

The study presented here does not consider the indirect effects of climate change such as altered disturbance regimes and extreme events (if not already included in the climate scenarios used here) such as fire, insects, or storms to reduce confounding effects related to productivity and carbon accumulation. The assessment of different environmental drivers focuses on climate change and increasing atmospheric CO_2 concentrations without considering other drivers such as Nitrogen (N), Phosphorus (P) or Ozone (O_3), although these have been identified as important drivers of forest productivity (De Marco et al., 2022a, 2022b) and across age classes (Ye et al., 2023). In particular, N deposition rates are expected to at least double before reaching a plateau (LeBauer and Treseder, 2008), increasing its fertilization effect in temperate forests and that Phosphorus rather than N limits tree growth, especially for small trees (Ye et al., 2023). Also, the greater N availability could partially

compensate for the decline in NPP observed in the simulations, as found by LeBauer and Treseder (2008). Last, although important, heterotrophic and soil responses are taken out from this study to avoid confounding effects and focus on physiological responses of different age classes to the joint effects of altered CO_2, temperature, and precipitation. We did not account for potential new species migrating into the study areas. The effectiveness of tree species change as a mitigation factor in unmanaged forests may be limited due to the potential mismatch between the rates of species migration or replacement and the expected rates of climate change, particularly in the more severe RCP scenarios (Settele et al., 2014; Noce et al. 2016).

Conclusions

In the context of climate uncertainty and changing environmental conditions, the long-term functioning of forests and the apparently seamless supply of multiple ecosystem services will be selectively affected depending on the species, the location of the site in respect to species distribution range, stand-level structural characteristics and stand development stage. Under future climate change young stands are expected to grow faster, to mature earlier but nevertheless 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 species-specific responses and age classes 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; **E. Cioccolo**: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing; **G. Marano**: Writing – original draft, Writing – review & editing; **D. Dalmonech**: Investigation, 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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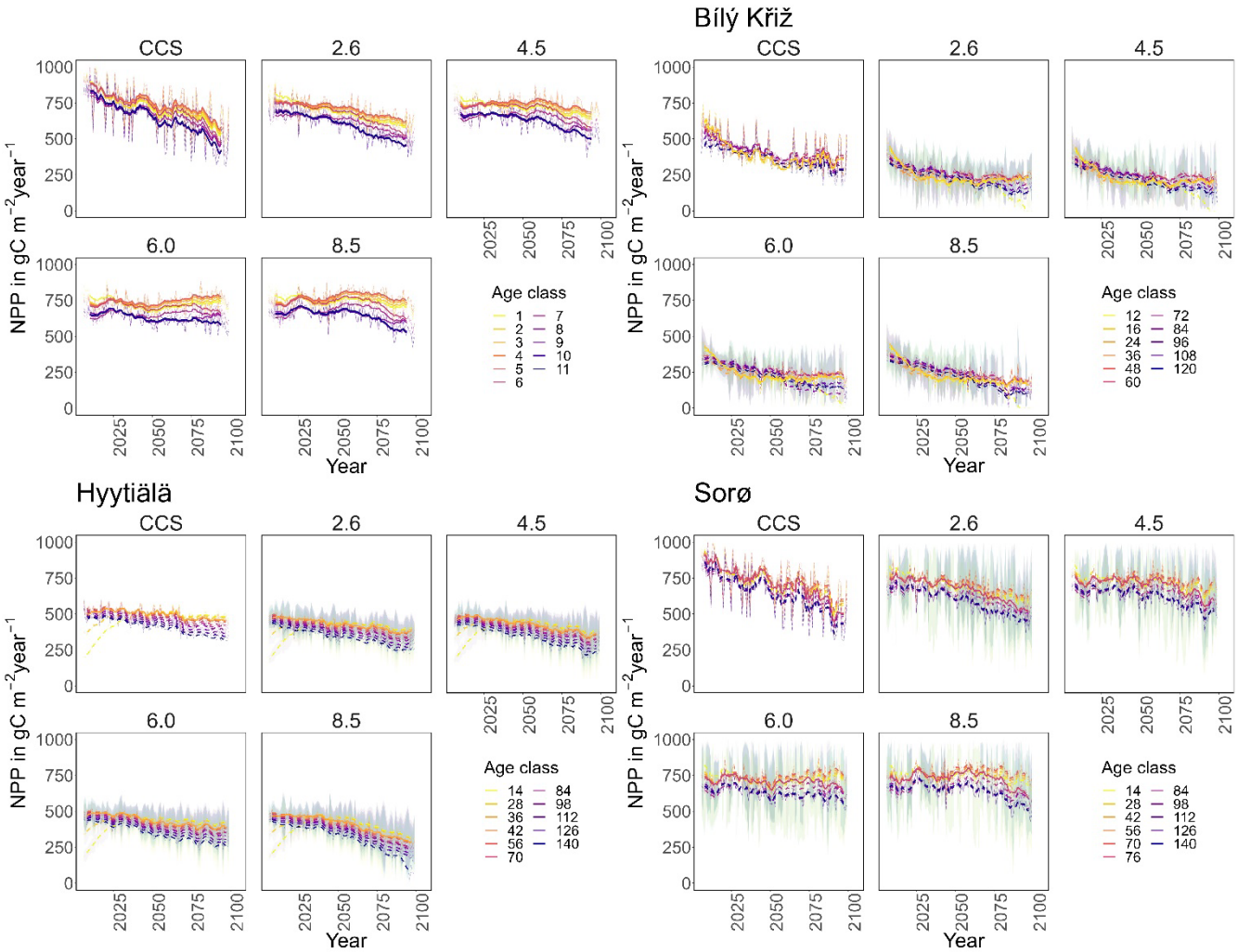

Figure 1 | NPP (gC m^{-2} year^{-1}) for age classes at the three sites in all scenarios along the simulation period (2006-2099). Lines represent the moving average of 10 years. The solid line corresponds to the real stand, while the dotted line to the virtual one. The shaded area represents two standard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

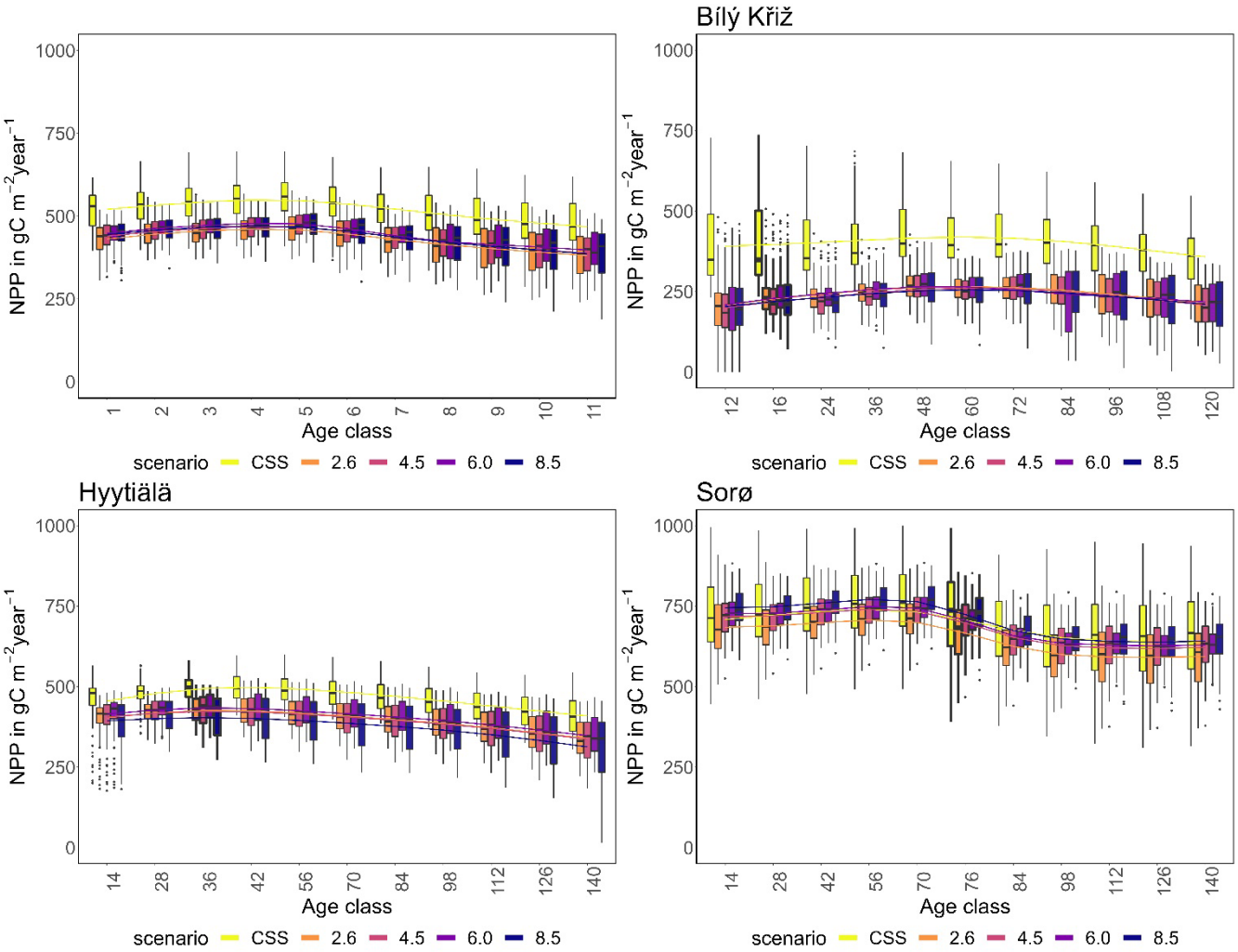

Figure 2 | Boxplot NPP (gC m^{-2} year^{-1}) by age classes at the three sites in the four RCPs scenario compared to the CCS one for the different age classes. The thick line corresponds to the real stand. Lines are fitted throughout the median of the NPP values using a generalized additive model. In 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.

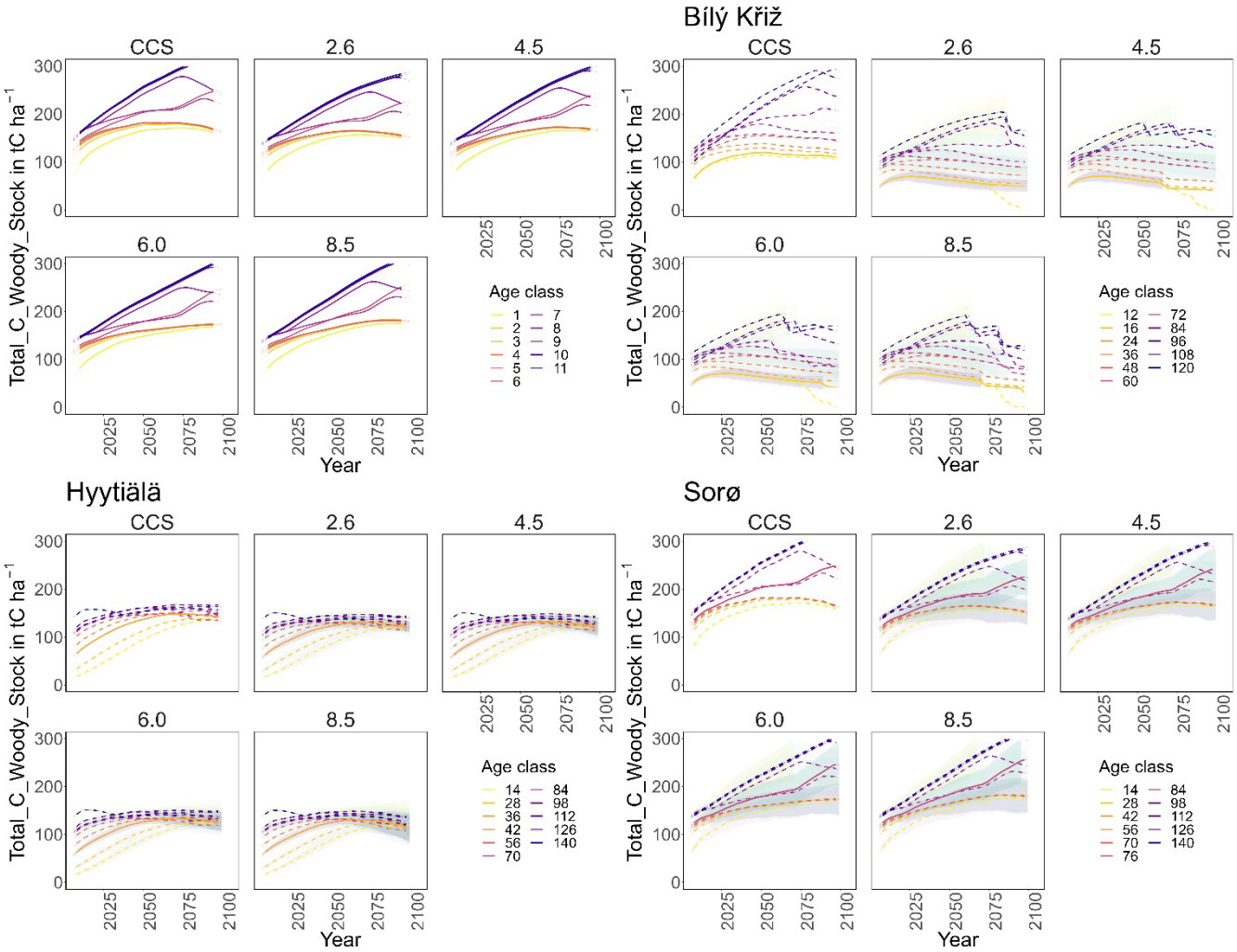

Figure 3 | Modeled tCWS (tC ha^{-1}) for age classes at the three sites in all scenarios along the simulation period (2006-2099). Lines represent the moving average of 10 years. The solid line corresponds to the real stand, while the dotted lines to the virtual ones. The shaded area represents two standard 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.

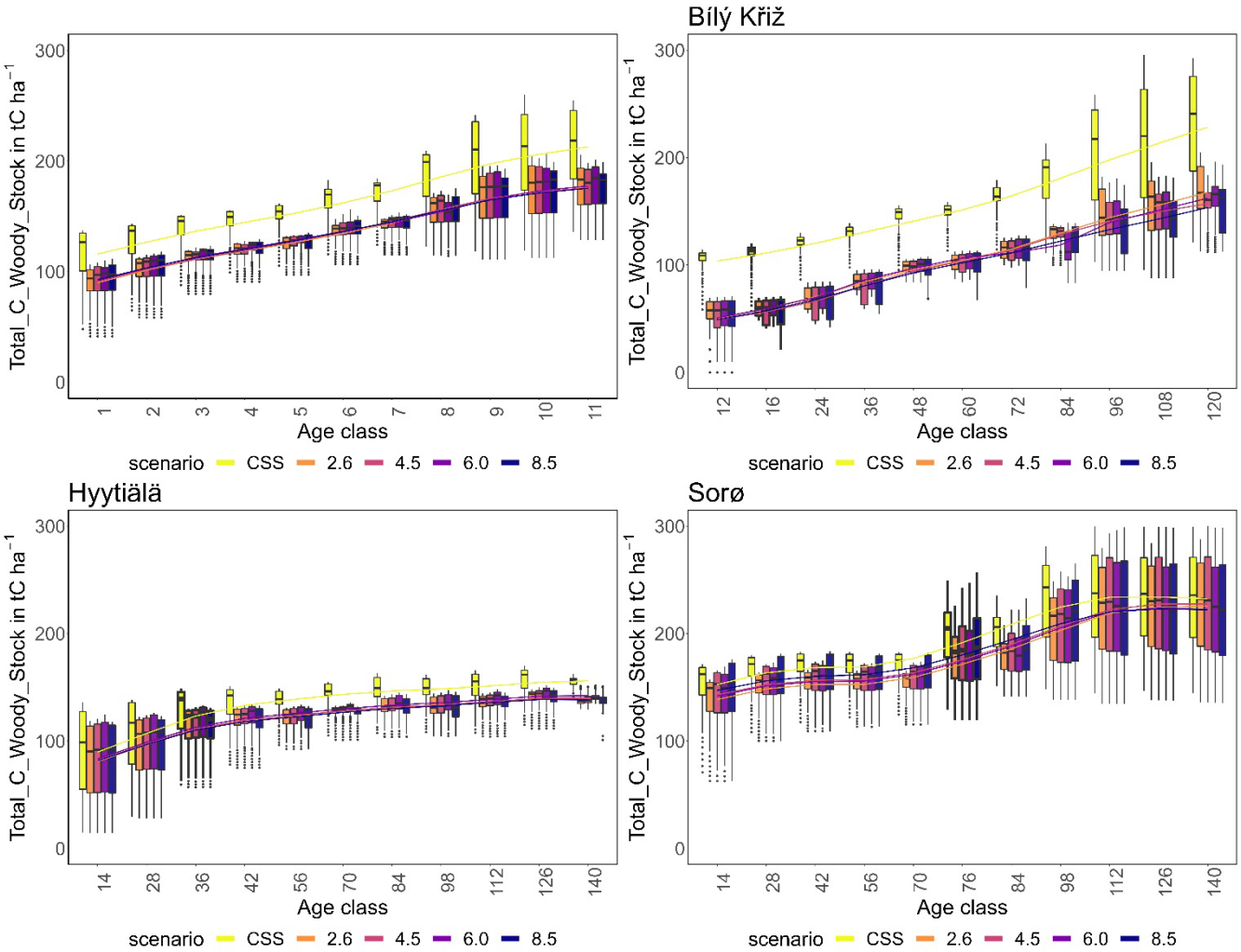

Figure 4 | Boxplot of modeled tCWS (tC ha^{-1}) for age classes at the three sites in the four RCPs scenarios compared to the CCS (current climate scenario) one for the different age classes. The thick line corresponds to the real stand. Lines are fitted throughout the median of the NPP values using 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.