No leeway to enhance carbon sequestration and stock capacity via changes to forest management

Authors: Dalmonech D.[1,†], Marano G.[1,2,*], Amthor J.[3], Cescatti A.[4], Trotta C.[5], Collalti A.[1, †]

1. Forest Modelling Lab., Institute for Agriculture and Forestry Systems in the Mediterranean, National Research Council of Italy (CNR-ISAFOM), Via Madonna Alta 128, 06128 Perugia, Italy
2. Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland
3. Oro Valley, AZ, US
4. European Commission, Joint Research Centre, Directorate for Sustainable Resources, Ispra, Italy
5. Department of Innovation in Biological, Agro-food and Forest Systems (DIBAF), University of Tuscia, via San Camillo de Lellis snc, 01100 Viterbo, Italy

***corresponding author**

[†] ***contributed equally***

Corresponding author: E-mail: gina.marano@usys.ethz.ch

ORCID:

Dalmonech D.: 0000-0002-1932-5011

Marano G.: 0000-0003-2600-984X

Amthor J.: 0000–0002–4980–8487

Cescatti A.: 0000-0002-2769-2591

Trotta C.: 0000-0001-6377-0262

Collalti A.: 0000-0002-4980-8487

Abstract

Forest management interventions can act as value-based agents to remove CO_2 from the atmosphere and slow anthropogenic climate change and thus might play a strategic role in the framework of the EU forestry-based mitigation strategy. To what extent diversified management actions could lead to quantitatively important changes in carbon sequestration potential and stocking capacity at the tree level remains to be thoroughly assessed. To that end, we used a state-of-the-science bio-geochemically based forest growth model to assess effects of multiple alternative forest management scenarios on plant net primary productivity (NPP) and potential carbon woody stocks (pCWS) under differing scenarios of climate change. The experiments indicated that the capacity of trees to assimilate and store atmospheric CO_2 in recalcitrant standing woody tissue is already being attained as its optimum under business-as-usual forest management conditions regardless of the different climate change scenarios investigated. Nevertheless, on the long-term and under increasing atmospheric CO_2 concentration and warming, managed forests show both higher productivity and a larger pool of stored carbon than unmanaged ones as long as forest thinning and tree harvesting are of moderate intensity.

Keywords: alternative forest management, modeling, virtual forests, climate change, carbon sequestration

1. | Introduction

Forest ecosystems have the capability to mitigate anthropogenic climate change by slowing the rate of atmospheric carbon dioxide (CO_2) increase (Pugh et al., 2019; Friedlingstein et al., 2020). A net reduction of CO_2 emissions is the cornerstone and topmost priority in view of climatic neutrality, which is expected to be reached by 2050, and in this context there are important questions about whether forest management may provide a concrete, cost-effective toolset for enhancing land-based mitigation actions at both the ecosystem/landscape (Kauppi et al., 2001; Pussinen et al., 2002; Nolè et al., 2015; Tong et al., 2020) and wood stocks levels (i.e. material substitution purposes; Leskinen et al., 2018; Howard et al., 2021).

European (EU) forests have been shaped through the centuries by human activities, which, affecting carbon (C) fluxes and stocks, have in turn influenced their potential for enhanced C sequestration (Nabuurs et al., 2008). In the EU *circa* 165 Mha of forest lands are managed which contribute to ~–286 Mt CO_2 year^{-1} of the LULUCF net fluxes (Grassi et al., 2017; 2021). Past management strategies were designed to attain the 'normal forest', creating forest conditions where maximum yield and products can be achieved perpetually (Leslie, 1966), specifically aimed at stimulating commercial yield rather than maximizing biomass sequestration and production (Tahvonen, 2016). Present EU country policies envision a move from predominantly wood-based climate neutrality management actions, to more proactive and sustainable forest management portfolios (EU Forest Strategy, 2015) to enhance forest C storage in a changing climate (Churkina et al., 2020; Favero et al., 2020). Substantial uncertainty remains about the effective capacity of managed forests to even hold the current sink under the global changes and thus contribute to climate change mitigation through their sequestration potential in the near-future, as classical silvicultural schemes are shaped on past environmental conditions. In the past decades European forests registered increased productivity and sustained stock increments exceeding the harvesting rates (Ciais et al., 2008; State of Europe's forests 2020). Such increases are the results of combinations of several factors, primarily climate (through the lengthening of the growing season), increased atmospheric CO_2 concentration (stimulating photosynthesis through 'CO_2-fertilization'), nitrogen deposition (stimulating growth through nitrogen fertilization) and forest management (Bellassen et al., 2011; Piao et al., 2020; Walker et al., 2021). There is concern, however, that recent harvesting rates may be approaching, or even exceeding, net tree growth rates (Nabuurs et al., 2013; Ceccherini et al., 2020; Schulze et al., 2020; State of Europe's forests 2020). Past positive trends in gross primary productivity (GPP; photosynthetic assimilation of atmospheric CO_2), and vegetation productivity in the northern hemisphere might not be sustained in the future if the CO_2 fertilization effect is not persistent (Körner, 2005; Walker et al., 2021) or if this is down-regulated or counteracted by direct effects of climate trends including warming and drying (Yuan et al., 2019; Grossiord et al., 2020), disturbances (McDowell et al., 2020; Senf & Seidl, 2021; Gampe et al., 2021), or by age-related effects on net primary productivity (NPP; the balance of photosynthesis and plant respiratory release of CO_2 to the atmosphere)(Ryan et al., 2006; Zaehle et al., 2006; Luyssaert et al., 2007; Tang et al., 2014; Pugh et al., 2019). Hence, a reduction in vegetation sink capacity and a turning point in its capability of loosening anthropogenic CO_2 might be already approaching (Duffy et al., 2015; Peñuelas et al., 2017; Wang et al., 2020), which would likely trigger a double negative effect, by lowering the short- to medium-term potential of vegetation to sequester carbon and levering a non-persistent increase of carbon woody stocks (CWS, i.e. the sum of standing woody biomass and harvested woody products) in the medium- to long-term.

Forest models are extensively used to investigate and to project the effects of climate and management on forest productivity and sustainability with local to regional scale applications, including the support of policymaking (Mäkelä et al., 2000; Morales et al., 2005; Fontes et al., 2010, 2011; Temperli et al., 2012; Vacchiano et al. 2012; Collalti et al., 2018; Maréchaux et al., 2021). In this context, forest models can be used to assess potential effects of climate change on forest carbon storage, how different management strategies can influence that carbon storage, and therefore how management can support climate change mitigation.

This study aimed at questioning the debated role of past-current forest management practices in ensuring forest productivity under future climate conditions. A validated process-based modeling approach was used to better understand controls on CO_2 uptake and C storage in a composite matrix of managed forests taking into account how combinations of climate change and management affect those controls. Specifically, we questioned whether: *i*) relative to the business-as-usual (BAU) management scenarios or, alternative forest management practices can maximize NPP while at the same time maintaining and/or increasing pCWS (potential Carbon Woody Stocks: i.e. when no harvested wood decay is assumed); *ii*) we tried to quantitatively assess and to discuss around the effective role of forests and forest management in respectively responding to and mitigating climate change.

2. | Materials and Methods

2.1 | 3D-CMCC-FEM Model

2.1.2 | Model description

The 3D-CMCC-FEM v.5.5 (Three Dimensional - Coupled Model Carbon Cycle - Forest Ecosystem Model; Collalti et al., 2014; Marconi et al., 2017; Engel et al., 2021) simulates daily gross photosynthesis (GPP) through the Farquhar-von Caemmerer-Berry biochemical model (Farquhar et al., 1980), modified for sun and shaded leaves (de Pury & Farquhar, 1997), and acclimated for temperature (Kattge & Knorr, 2007). Plant respiration (R_a) is simulated explicitly and partitioned into growth (R_g), and maintenance respiration (R_m) as in the growth-and-maintenance-respiration paradigm (Amthor, 2000; McCree, 1970; Thornley, 2000). R_g is considered a fixed fraction (i.e. 30%) of the remaining C once tissue R_m is accounted for and removed from GPP. R_m is computed, for each functional-structural tree C pool (i.e. live wood, leaves and fine roots), using a temperature-acclimated Q_{10} relationship (for details on thermal acclimation see Tjoelker et al., 2001; Atkin et al., 2003; Smith & Dukes, 2012; Collalti et al., 2018) and a mass-based approach using N-content of the specific live respiring tissues (with the base rate of maintenance respiration (m_R) = 0.218 g C g N^{-1} day^{-1}; Ryan et al., 1991; Drake et al., 2011; Oleson et al., 2013; Collalti et al., 2016, 2020a). The sum of daily R_g (if any) and R_m gives R_a. Daily NPP is then GPP less R_a. Allocation of NPP among tree C pools is performed daily, with preference to non-structural carbon (NSC, i.e. starch and sugars), which is used directly to fuel R_m, up to a minimum NSC threshold level. The minimum NSC-threshold level is a fraction (a model parameter) of the live wood C-content (Collalti et al., 2020a). Once (and if) the threshold is reached, C is allocated preferentially for biomass growth (G) for the different tree C-pools depending on the phenological phase as formerly described in Collalti et al. (2016). The only phenological phase during which NSC has no priority in allocation is during bud break, when recent GPP is completely allocated for growth of leaves up to a maximum annual leaf area index (LAI, m^2 m^{-2}), which is computed at the beginning of each year of simulation through the pipe-model (Shinozaki et al., 1964; Mäkelä, 1997), and growth of fine roots. This NSC allocation scheme reflects a quasi-active role of NSC (NSC usually has priority over growth of new structural tissues), as described by Sala (2011), Merganičová et al. (2019) and Collalti et al.

(2020a), and implies that any asynchrony between C-demand (i.e. R_a and G) and C-supply (i.e. GPP) is buffered by tapping the pool of NSC. When NSC pools cannot be refilled (for any reason) and NSC approaches zero, carbon starvation occurs, and tree death is simulated. This overall C-allocation scheme in the 3D-CMCC-FEM model follows the functional balance theory of allocation, similarly to other models (Merganičová et al., 2019). Age related mortality, carbon starvation, and a background mortality (i.e. the as-yet unexplained mortality), represent the different types of mortality simulated by the model; the last one is turned off when forest management is applied. An in-depth description of the model's underlying characteristics, effects of climate change and model parameter sensitivity and uncertainty, as well as model limitations, is in Collalti et al. (2020a) (and references therein).

2.1.2 | Forest management routine

Historically, a large share of the actively managed European forests has been shaped via thinning and clear-cutting which resulted in the establishment of even-aged, often mono-specific stands when the main aim was prioritizing productivity (see Campioli et al., 2015, and references therein; State of Europe's forests 2020). Therefore, in such configurations, forests carbon pools and fluxes strongly depend on rotation lengths (tree age-class distribution), thinning interval, and thinning intensity (Nabuurs et al., 2008).

In this study we varied the three key management variables associated with European managed forests: thinning intensity, thinning interval and rotation age (following Reyer et al., 2020). Thinning intensity is represented in the model by the percentage of stand basal area to remove based on total stand basal area. Thinning interval stands for the number of years between two consecutive operations. Rotation age represents the stand age at which the final harvest occurs, after which the stand is replanted with saplings of the same species as exactly as adopted into the Inter-Sectoral Impact Model Intercomparison Project (ISIMPI, https://www.isimip.org, Warszawski et al., 2014) protocol. The model benchmark was the *Business-as-Usual* (BAU) forest management scheme for the most common European species as described in Reyer et al. (2020) and applied in three contrasting forest stands as in Collalti et al. (2018).

2.2. | Sites, data and experimental design

The model was parameterized for, and simulated C fluxes and tree growth in three even-aged, long-monitored, managed European forest sites which are part of the Fluxnet network (Pastorello et al., 2020), the ISIMIP initiative and the PROFOUND database (Reyer et al., 2020). Specifically, abovementioned sites are: (1) the temperate European beech (*Fagus sylvatica* L.) forest of Sorø, Denmark; (2) the Norway spruce (*Picea abies* (L.) H. Karst) stand of Bílý Křìž in Czech Republic, and (3) the boreal Scots pine (*Pinus sylvestris* L.) forest of Hyytiälä, Finland (Table 1). These sites were selected because they represent the dominant forest types in Europe and their management best corresponds to 'the intensive even-aged forestry' as defined by Duncker et al. (2012).

As input daily forcing data, we used the climate simulation data from the ISIMIP Fast Track initiative based on the Climate Model Intercomparison Project 5 (CMIP5) in which five Earth System Models (ESMs; i.e.: HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, GFDL-ESM2M, and NorESM1-M) were driven by four Representative Concentration Pathways (RCPs) of atmospheric greenhouse gas concentration trajectories, namely RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 (Moss et al., 2010; van Vuuren et al., 2011). The future annual atmospheric CO_2 time series for the period 2016 to 2500 are based on Meinshausen et al. (2011) as described in Reyer et al. 2020. The RCP atmospheric CO_2 concentration values were used to drive the biogeochemical photosynthesis model with values varying at the end of the century from 421.4 µmol mol^{-1} (RCP 2.6) to 926.6 µmol mol^{-1} (RCP8.5). Daily meteorological forcing-data for each site used by 3D-CMCC-FEM were available as bias-corrected/downscaled variables (air temperature, precipitation, solar irradiance) and as non-corrected variables (relative humidity) according to Hempel et al. (2013).

2.2.1. | Virtual stands

Given that the European forested area is composed of a mix of differing-aged stands, and since forest C cycle processes may respond differently to climate factors at different ages (e.g. Vanninen & Makela, 2005; Ryan et al., 2006; Reich et al., 2008; Bouriaud et al., 2015; Collalti & Prentice, 2019; Collalti et al., 2020b; Huber et al., 2018, 2020; Migliavacca et al., 2021), we developed a composite forest matrix (CFM) consisting of a mixture of stands of different age, structure and associated biomass. Starting from the real stands, we generated a prescribed number of virtual stands in order to obtain representative model outputs of a larger set of different age-classes (with their associated forest attributes) to cover an entire rotation period (~140 years, depending on species), similarly as in Bohn & Huth (2017). A Composite Forest Matrix (CFM) was then created by running at each site the model from 1997 to 2199 (to cover the entire rotation length for each species) under a contemporary climate (no climate change) scenario (de-trended and repeated cycles of 1996-2006 weather), with fixed atmospheric CO_2 concentration (368.865 μmol mol^{-1}) and BAU management practices. From each of these simulations data needed to reinitialize the model at every *rotation length*/10 were extracted (Figure 1). Thus, in total, ten virtual additional stands representing different age classes of the composite matrix were selected and included into the CFM. The management scenario analysis was then carried out by means of this new larger number of forest stands (hereafter named '*virtual stands*') as proxy of our representative forest.

2.2.2. | *Alternative management (AM) schemes*

Overall, we considered at each real and virtual stand, and for each of the three sites, 28 management scenarios: the Business-as-Usual and ‘no management’ (NO-MAN: stands left developing in undisturbed conditions) schemes plus 26 alternative management schemes. These alternative forest management scenarios represent all the possible combinations of two different thinning *intensities*, two different thinning *intervals*, and two different *rotation* durations than the ones adopted to simulate BAU. The schemes were grouped (Tables 1 and Table S1) into combinations of: (1) ‘*more intensive*’ (‘AM+’), where at least one out of the three management variables reflect an intensified management case relative to BAU (e.g. higher thinning intensity and/or shortened interval and/or shortened rotation than BAU), and the other one or two (or no) variables are kept as in BAU; (2) ‘*less intensive*’ (‘AM–’), where at least one variable reflects lower thinning intensity and/or prolonged interval and/or prolonged rotation, compared to the BAU case; and (3) ’*mixed schemes*’ (‘MIX’), where at least one management variable was more intensive and at least one management variable was less intensive than the BAU scheme. In the ‘*no management* scheme forest stands are left to develop without any human interventions or change in species composition.

2.2.3 | *Model runs and evaluation*

The starting year for all simulations was 1997, consistent with the availability of measured stand carbon flux data used for the model initialization and evaluation. After creation of the virtual stands, based on de-trended weather time series for period 1996-2006, final climate change simulations were created from 2006 to 2100. Overall, in total – by considering all potential combinations of management and climate change scenarios under different ESMs climate forcing – at each of the three sites we performed 6,160 simulations (i.e.: 5 ESMs * 4

RCPs * 11 stands * 28 management schemes) corresponding overall to 18,480 different model runs for all of the three sites.

Additionally, to gauge model sensitivity to factors controlling our model results we organized the analysis according to factorial design (Mason et al., 2003; Collalti et al., 2018) across a matrix of different factors (i.e. Stand, ESMs and RCPs, generating seven possible combinations from each factor in total) in order to identify the most influential factor among forest structure (as modified also by management) and climate/scenarios used over the main modeled autotrophic carbon variables (GPP, Ra, NPP, CUE, NPP_{woody}, and potential Carbon Woody Stocks). The model was evaluated using 1997-2005 annual GPP and the annual net woody productivity (NPP_{wood}) data for Sorø and Hyytiälä and 2000-2005 for Bílý Křìž by comparing simulated GPP against eddy covariance estimates (http://fluxnet.fluxdata.org/; Pastorello et al., 2020), and compared modeled wood growth against measured NPP_{wood} (Principal Investigator’s site for Hyytiälä and Bílý Křìž under *personal communication*, and Wu et al., 2013 for the site of Sorø) and stem diameter at breast height (DBH; Reyer et al., 2020). Subsequent years were excluded from the model evaluation since the scenario period in the ESMs started in 2006, and hence, ESMs are driven by different atmospheric CO_2 concentration trajectories after 2006.

2.3 | Effects of climate change and management on carbon fluxes and biomass

As carbon fluxes do not scale linearly to stocks (Schulze et al., 2020) data analyses focused on the variables NPP and the pCWS, the sum of standing and previously harvested woody stocks. Net primary productivity can be used as good proxy for evaluating the forest net active carbon sink process (Sha et al., 2022), and the net biomass input to forest ecosystems (Trotsiuk et al., 2020), with decomposition (decay) processes representing the active carbon source process. Net primary production is a dynamic balance between photosynthesis (GPP) and plant respiration (R_a), which respond separately and/or in combination to a range of climatic factors and, in managed forests, to management practices (Collalti et al., 2020a) which are not generally amenable to *in situ* quantification over long periods, especially for climate change issues, hence raising the need for process-based modeling. Harvested wood products are considered here without decay; hence we aim at evaluating only the potential maximum attainable total woody standing stocks under a wide spectrum of possible management schemes without any consideration of the longevity of harvested wood. Data were averaged over the emission scenario simulation period 2006-2099 and aggregated over virtual and real stands and over ESMs but distinguished between RCPs. In spite of site-specific differences in magnitude of response to the different management schemes and climate (see Section S.2 in the Supporting material) the main emerging pattern with increasing intensity of intervention is of similar magnitude. For these reasons, data were also aggregated over sites. Therefore, alternative management results are presented first aggregated according to the groups AM+ and AM– to better highlight the pattern direction when moving from the current management schemes toward a more intensive or a less intensive scenario.

3. | Results

3.1 | Model evaluation

The 3D-CMCC-FEM model was evaluated in the three sites separately and at different temporal scales with robust results regarding both the carbon fluxes, i.e. GPP and NPP_{woody}, and the structural variables, i.e. average stand DBH (Figures S1-S3 and Table S2 and S3 in Supplementary Material). Simulations forced with both observed local climate and with an ensemble of outputs produced by modeled climate under the present day climate compare both well with the eddy-covariance based estimated daily GPP values in the sites of Sorø (period: 1997-2005; mean absolute error, MAE = 1.43 g C m^{-2} day^{-1} with observed climate, and MAE = 1.91 g C m^{-2} day^{-1} with the ensemble across ESMs forcing; Root Mean Square Error, RMSE = 2.15 g C m^{-2} day^{-1} with local climate, and RMSE = 2.98 g C m^{-2} day^{-1} with the ensemble across ESMs forcing; r > 0.86 and n = 3092), as well as for Hyytiälä (period: 1997-2005; MAE = 1.05 g C m^{-2} day^{-1} with observed climate, and MAE = 1.29 g C m^{-2} day^{-1} with the ensemble across ESMs forcing; RMSE = 1.48 g C m^{-2} day^{-1} with local climate, and RMSE = 1.91 g C m^{-2} day^{-1} with the ensemble across ESMs forcing; r > 0.78 and n = 3092) and Bílý Křiž (period: 2000-2005; MAE = 1.52 g C m^{-2} day^{-1} with observed climate, and MAE = 1.99 g C m^{-2} day^{-1} with the ensemble across ESMs forcing; RMSE = 2.07 g C m^{-2} day^{-1} with local climate, and RMSE = 2.69 g C m^{-2} day^{-1} with the ensemble across ESMs forcing; r > 0.67 and n = 1390), respectively (see Supplementary Material Figure S1, S2 and Table S2).

Model performs robustly for GPP even at annual scale at Sorø (1665.7 ± 171.1 g C m^{-2} $year^{-1}$ and 1584.9 ± 189.6 g C m^{-2} $year^{-1}$ under observed and modelled climate vs. 1731.41 ± 184.4 g C m^{-2} $year^{-1}$ measured; here and elsewhere, ± denotes one standard deviation), as well as for Hyytiälä (894.3 ± 57.3 g C m^{-2} $year^{-1}$ and 871.1 ± 52.6 g C m^{-2} $year^{-1}$ under observed and modelled climate vs. 1028.4 ± 50.1 g C m^{-2} $year^{-1}$ measured), and at Bílý Křiž (893.5 g C ± 251.8 g C m^{-2} $year^{-1}$ and 893.3 ± 222.2 g C m^{-2} $year^{-1}$ under observed and modelled climate vs. 1024.48 ± 354.5 g C m^{-2} $year^{-1}$ measured), respectively. Similarly, model shows to reproduce reasonably well the annual values of the net primary productivity fluxes into the tree woody pools (i.e. NPP_{woody}) at Sorø (350.8 ± 61.2 g C m^{-2} $year^{-1}$ and 274.7 ± 63.2 g C m^{-2} $year^{-1}$ under observed and modelled climate vs. 346.9 ± 36 g C m^{-2} $year^{-1}$ measured), a bit less well at Hyytiälä (316.6 ± 20.7 g C m^{-2} $year^{-1}$ and 290.4 ± 24.3 g C m^{-2} $year^{-1}$ under observed and modelled climate vs. 228.4 ± 23.3 g C m^{-2} $year^{-1}$ measured), and satisfactorily well at Bílý Kříž (442.1 ± 78.7 g C m^{-2} $year^{-1}$ and 405 ± 36.1 g C m^{-2} $year^{-1}$ under observed and modelled climate vs. 379.9 ± 38.41 g C m^{-2} $year^{-1}$ measured), respectively. The mean diameter increase, which was only qualitatively compared, is only slightly underestimated at the site of Bílý Kříž (Figure S3). Comparisons with literature data for NPP and R_a as well as for CUE (i.e. NPP/GPP) between modelled with observed climate and with ESMs' climate are shown in Table S3. Notably, results generated with the 3D-CMCC-FEM forced by the EMSs' climates are close to the ones generated by observed weather data in the evaluation period with the observed values falling, in almost the cases, inside the range of variability of the results generated with different ESMs.

3.2 | Lesser intensive management vs. BAU

Simulated average NPP in the less intensive management scenario group (i.e. AM–) is close to the reference BAU values, ranging between 495.4 g C m^{-2} $year^{-1}$ (–1.2%; here and elsewhere, percentages refers to difference when compared to BAU) to 524.7 g C m^{-2} $year^{-1}$ (–3.1%) when compared to 502 g C m^{-2} $year^{-1}$ and 542 g C m^{-2} $year^{-1}$ for RCP 2.6 and 8.5 under BAU, increasing only slightly with increasing warming and atmospheric CO_2 concentration scenarios and more steeply toward the end of the century and without significant differences across RCPs, respectively (Figure 2 and Figure S4, Table 2). Simulated pCWS values increase steadily along the simulation time for all the alternative management scenarios, with time-averaged values between 179.8 t C ha^{-1} (–6.6%) and 198.5 t C ha^{-1} (–7.3%) compared to 192.9 t C ha^{-1} and 198.5 t C ha^{-1} for RCP 2.6 and 8.5 under BAU, respectively (Figure 3 and Figure S4, Table 2). In Figure 4, NPP and pCWS data are reported considering values averaged over the simulation period and with differences to the reference BAU, plotting the NPP versus the pCWS values. Results for each of the RCPs scenarios and all the alternative management options combined are reported separately across the sites in the Supplementary Material (Table S4). Interestingly, a lower reduction in NPP (–0.7%) and higher values of pCWS (2.6%) when compared to BAU are only in the case of a prolonged rotation period under RCP 8.5, while there are higher losses in NPP (–6.1%) with a prolonged rotation and thinning regime, including a reduction in the intensity, under RCP 8.5. Conversely, pCWS shows the greatest reduction (–13.9%) when both thinning intensity and regime only are set to simulate a decreased management intensity under RCP 8.5 (Table S5). In summary, results from AM– simulations show as for both NPP and pCWS, and in most of the cases, there are lower values with reducing intensity of forest management than the reference BAU. These differences vary only slightly across the emissions scenario considered.

3.3 | More intensive management vs. BAU

The AM+ simulations results are characterized by a significant spread within the different modelled schemes, and returning, on average, lower NPP values than the reference BAU scenario, with values ranging between 350.0 g C m^{-2} $year^{-1}$ (–30.2%, RCP 2.6) and 388.1 g C m^{-2} $year^{-1}$ (–28.4%, RCP 8.5), and the other values in between, thus, significantly lower values when compared to the 502 g C m^{-2} $year^{-1}$ and 542 g C m^{-2} $year^{-1}$ for BAU for the same climate scenarios (Figure 2 and Figure S4, Table 2). Conversely, values of pCWS between AM+ and BAU are closer, with values of about 184.3 t C ha^{-1} (–4.4% for RCP 2.6) and 189.7 3 t C ha^{-1} (–4.4% for RCP 8.5) compared to 192.9 t C ha^{-1} and 198.5 t C ha^{-1} for BAU under the same climate scenarios, respectively (Figure 3 and Figure S4, Table 2). Results for each of the RCPs scenarios and under all the alternative management options combined are reported separately across the sites in the Supplementary Material (Table S4). Noteworthy, a lower reduction in NPP (–4.6%) when compared to BAU is in the case of the shortening rotation period only under RCP 8.5 while higher losses in NPP (–55.6%) under a shortened thinning regime including an increase in the intensity, are modelled under RCP 8.5. Conversely, pCWS shows the a net gain (4.14%), compared to the BAU, when only the thinning intensity is set to simulate an increased management intensity under RCP 8.5, while the greatest reduction in pCWS (–14%) is when the full set of management variables are parameterized to simulate an intensified management under RCP 8.5 (Table S5). Ultimately, both NPP and pCWS results from the AM+ schemes are, on average, lower than the ones from the reference BAU. Interestingly, despite management scenarios showing high variability between the several AM+ schemes, there are no significant differences across RCPs scenarios more than the ones across management scenarios.

3.4 | No management vs. BAU

The NPP values in the NO-MAN scenario are, on average, lower than the reference BAU scenario varying from –14.5% (RCP 2.6) to –19.5% (RCP 8.5), with other values in between, and varying across emissions scenarios with values ranging from 429.1 g C m^{-2} $year^{-1}$ (RCP 2.6) to 444.8 g C m^{-2} $year^{-1}$ (RCP 6.0) when compared to values varying from 502 g C m^{-2} $year^{-1}$ 530.5 g C m^{-2} $year^{-1}$ for BAU under the same climate scenarios, respectively (Figure 2, Table 2). However, a site specific variability in the NPP response to the management scenarios applied exists, with differences between NO-MAN and BAU options ranging from 9.0% (for Hyytiälä) to –41.7% (for Bílý Křìž) both under the warmest emission scenario (Table S4). Differences between NO-MAN and BAU become more evident along the simulation and across RCPs scenarios, with the mean NPP value stabilizing or slightly increasing under the BAU (and AM–) option. Conversely, in the NO-MAN scenario the values steadily decreased (Figure 2).

The simulated pCWS, which is represented by the only standing biomass in the NO-MAN scenario, are, on average, lower than in the BAU scenario, with differences in the order of, overall, about –30.0% (from –21.6% to –40% across the different sites) and with values varying between 192.9 t C ha^{-1} and 198.5 t C ha^{-1} for BAU. Along the simulation pCWS values in the NO-MAN option increase slightly at the beginning of the simulation and then decrease significantly toward the end of the century (Figure 3, Table 2). The NO-MAN case returns the lowest average amount of total woody stocks under every emission scenario (Figure 4 and Table 2).

3.5 | Mixed management alternatives and the factorial analysis

A mixed combination of management schemes (namely 'MIX') was also performed (all of the possible combinations are shown in the Table S1). While data were not shown here (but see in Supplementary Material Figure S5 and Table S4, S5), there are no options with simultaneously increases both in NPP and pCWS than the BAU scenarios. Values for NPP range from –1.38%, with both a prolonged thinning regime and rotation, and, at the same time, an increase in thinning intensity under RCP 2.6. On the other side, a reduction in NPP of about –58.4% with prolonged rotation but a shortened thinning regime and increased thinning intensity is shown under RCP 2.6. Similarly, with the same management schemes pCWS shows to decrease of about –16.1% under RCP 6.0, when compared to BAU, while, conversely, pCWS shows to increase of 5.7% under RCP 8.5 by prolonging the regime and increasing the thinning intensity.

The factorial analysis performed over all the main carbon fluxes and stocks variables produced by the model and separated by site, indicates that a significant fraction of the total variability of the key carbon flux variables was mainly driven by the stand factor (i.e. the forest structure as generated by different age classes and management schemes, including different above- and below-ground biomass, Figure S6 and Table S6).

4. | Discussions

4.1 | Limited leeway to increase carbon uptake and woody stocks with alternative management scenarios

The variables NPP and pCWS stand for two sides of the same coin because one (i.e. NPP) represents the short- to medium term active carbon sequestration capacity while pCWS the sequestered (and maintained) carbon over the medium- to long-term. The simulations clearly indicate that even under future climate change scenarios managing forests can support trees in maintaining their carbon sequestration potential, enhancing the plant capability to respond to changing conditions, and increasing, for instance, their productivity compared to the no-management option. Reducing to some degree tree density allows plants to benefit firstly from alleviated competition for potentially limiting resources such as light and soil moisture, responding with an increase of their photosynthesis activity and growth rate (Zeide et al., 2001). This outcome, combined with the fertilization effects of increased atmospheric CO_2 concentration and less ‘respiring’ (live) biomass per unit of photosynthetic (leaf) area (because of shift toward younger stands), potentially drives more productive and efficient forests. This is mirrored in the capability for trees to allocate (partition) more of the photosynthetically assimilated carbon into new woody biomass rather than into nonstructural carbon pools to maintain living woody tissues (Vicca et al. 2012; Campioli et al., 2015; Malhi et al., 2015; Pappas et al., 2020; Martínez-Vilalta et al., 2016; Collalti et al., 2020a; Huang et al., 2021). This is directly mirrored by the increasing HWP over time with more frequent thinning, reduced tree density, replacement and presence of younger forest stands (a component of the pCWS, see for HWP dynamic Figure S7) which potentially can remain in the system (the other component of the pCWS, see for standing woody biomass dynamic

Figure S8). Overall, the model indicates that on average pCWS is expected to be the highest under the BAU management scheme, even in the future.

The potential to extract more wood and more often, i.e. to shorten the harvest interval, and at the same time maintain at least the current forest biomass depends on NPP under the different scenarios. We found, however, that the benefit of BAU forest management under future environmental conditions remains the most favorable scheme and might already be a close-to-optimum management approach for different RCP scenarios (Figure 4) and across the individual sites (Figs. S9-S11). This is an endorsement of past research arriving at today's management practices. With more frequent harvesting and replanting and increasing intensity of intervention compared to the benchmark BAU, the NPP is not shown to increase any further under any RCP scenario, in spite of an average younger and, in theory, more productive forest stand. The net growth rate does not compensate for the increased fellings, while in parallel there is a limited yield in terms of increased carbon woody stocks, as reflecting in a low standing biomass and a likely sign of a critically low tree density. Albeit the BAU reference benchmark is already an intensive management approach with tree fellings as a percentage of net annual increment of 84%, 77% and 101% for Czech, Finland and Denmark, respectively, as reported for 2005 (State of Europe's forests 2020), the first year of our RCP-based climate change response simulations. Similarly, Pussinen et al. (2009) showed that increasing the total harvested products led to a decrease in both NPP and forest standing biomass in some European areas. The difficulties associated with simultaneously increasing both forest standing biomass and wood products were shown in the seminal modeling study of Thornley & Cannell (2000).

An important factor contributing to the apparent lack of significant differences in forest responses across RCPs scenarios, compared to the differences across different management schemes, might come from the combination of counteracting key drivers of plant physiology (e.g. lengthening of the growing season by warming and, in parallel, an increased respiration rate from that same warming) which are considered in the model despite temperature acclimation. Although experimental evidence for the CO_2 fertilization effect on plants sink capacity is strong, and is typically predicted by vegetation models albeit with different degrees of uncertainties, the probability for its persistence into the longer-term future is a hotly debated issue (Nabuurs et al., 2013; Habau et al., 2020; Wang et al., 2020; Gatti et al., 2021; Walker et al., 2021). The biochemical model of photosynthesis used here (Farquhar et al. 1980) itself assumes a theoretical CO_2 acclimation, yet, other environmental drivers, such as temperature and vapor pressure deficit (which scales exponentially with warming), and water availability were shown to interact to down-regulate the positive CO_2 effect on GPP (Grossiord et al., 2020). Data at the biome scale (see Luyssaert et al., 2007) indicated a potentially higher sensitivity of plant respiration to warming that may stabilize NPP over a temperature threshold with no further gains. Warming in low-temperature-limited forest biomes would be expected instead to have a positive effect on annual GPP and NPP (Henttonen et al., 2017; Sedmáková et al., 2019). However a warming-induced increased respiration cost might curb these trends and even offset a positive GPP and/or NPP response to increasing atmospheric CO_2 concentration, as also shown in some other modeling and experimental studies (Way et al., 2008; Gustavson et al., 2017; Collalti et al., 2018, but see Reich et al., 2016). For example, Mathias & Trugman (2021) showed a potential future unsustainable growth for boreal and temperate broadleaved forests, with the net overall effect of decreased NPP. Other studies already indicated that combined impacts of warming and increasing atmospheric CO_2 concentration might cause forests to grow faster and mature earlier but also to die younger (Kirschbaum, 2005; Collalti et al. 2018). With the increasing standing biomass and accumulation of more respiring tissue in older trees, plant respiration might increase more quickly than GPP, as the canopy closure would be reached earlier, capping GPP but with sustained respiratory needs. The use here of many virtual stands of different ages in our simulations might have compensated for (counterbalanced) any different stand-age, biomass and structural related responses to climate change across a landscape. To the extent that that is true, the patterns described the simulations should be related to the effect of climate and forest management (and their multiple combinations) only.

Ultimately, these simulations indicate that increasing the harvest/growth ratio above current values will be difficult. As such, the possibility of simultaneously increasing both carbon sequestration rate and tree carbon (standing biomass) storage capacity while managing forests in a sustainable way may be very limited. A steady intensification or intervention frequency – alone or in combination – compared to the business-as-usual scheme might come at the price of a substantial loss of primary productivity. While the amount of potential harvested woody products still would be significant, we would *de facto* end up reducing the active forest carbon sink and thus the forest's potential to assimilate and sequester CO_2 from the atmosphere.

4.2 | Role of forest management in the context of climate change

In the context of climate uncertainty and because of policy intentions: management practices may no longer prioritize only productivity – which traditionally includes rotation times being adjusted to maximize value of timber – without preserving the forest carbon sink, and ensuring the long-term functionality of forests and the continued provision of their many ecosystem services (Krofcheck et al., 2019). The selection of alternative management practices has been suggested as a mechanism to potentially enhance the climate change mitigation potential of forest ecosystems (Tahvonen, 2016; Yousefpour et al., 2017). Our model results highlight, for Central and Northern European forests, the importance of forest structure to productivity and carbon storage which in turn indicates that management practices may be quantitatively more important than future climate and atmospheric CO_2 concentration trends in regulating the carbon sink strength of forests, and this is in line with some previous modeling studies (Garcia-Gonzalo et al., 2007; Pussinen et al., 2009; Kindermann et al., 2013; Pukkala, 2017; Akujärvi et al., 2019). These simulations indicate that silvicultural practices included in the model will persist as key factors in the regulation of carbon sequestration through the end of this century – for any of the CMIP5 RCP scenarios. In accordance with the modeling study of Kindermann et al. (2013), our results specify the need to sustain the increment of forest growth and hence productivity rather than maximizing the stocks. Our results also point out, however, a narrow operational space surrounding the *business-as-usual* scheme which can be designated as a potentially near-the-optimum condition over a wide and diversified portfolio of alternative management schemes across every expected RCP/ESM-based climate change scenario. Conversely, other studies (Garcia-Gonzalo et al., 2007; Luyssaert et al., 2018) showed that harvest intensity should be loosened in order to maximize the carbon sink. Similarly, Schelhaas et al. (2015), showed how even through changes in species by replanting more suited ones under an adaptive framework, would result, in any case, with a reduction of the net increments without changes in the woody products amount. On the other hand, Pussinen et al. (2009), suggested that it would be possible to increase the fellings and the product and still maintain the same current forest standing biomass under future climate scenarios.

The present simulation study reveals more modest, almost even beneficial, effects of climate change in combination with CO_2 fertilization on NPP with the higher CO_2 concentration pathway scenarios through 2099 for the BAU and AM– management schemes though NPP declined over time for AM+ and the unmanaged schemes. Others have suggested that past and/or future climate change did, or could, negatively affect NPP (Reich & Oleksyn, 2008) in a range of forested and non-forested ecosystems through increased frequency and/or magnitude of large-scale disturbances (e.g. heat waves, windstorms, weather-based pest outbreaks), with significant variation in effects in different ecosystems or forest types and locations (e.g. Thom et al., 2017; Nabuurs et al., 2019; McDowell et al., 2020; Senf & Seidl, 2021; Gampe et al., 2021). Should such increase in disturbance occur and negatively affect a significant fraction of European forests, the robustness of the BAU management scheme specified by our simulations should be called critically questioned, being that the current carbon-sink status of European forests might decline. However, the unmanaged-forest scenario in our simulations resulted the alarmingly and steady decline in NPP through the year 2099 for the average response to the climates projected by all five ESMs driven by all four RCPs.

4.3 | Outlooks and further considerations

In this study pure stands were considered with no species transition/migration under climate change allowed, even in the no-management scenario. The rates of possible species migration or replacement, however, may be incompatible with expected rates of climate change, at least for the high RCP scenarios (Settele et al., 2014) thus perhaps limiting that as a natural mitigation factor. The main evidence of the present study could be further substantiated by dynamic vegetation modeling studies which allow for a much broader geographical extent by means of up-scaling techniques (Fritsch et al., 2020).

In addition, we are aware that our modeled forests only represent a subset of boreal and temperate European forests, although an important subset that currently plays a significant role in European carbon exchange with the atmosphere.

5. | Conclusions

To our knowledge this is the first study of the possibilities and limitations of altering forest management practices to achieve the twofold objective of maximizing forest NPP while at the same time maintaining and/or increasing pCWS in the face of future climate change. The results clearly indicate that there may be little scope to meet this twofold objective because business-as-usual management practices may already be nearly optimal in terms of carbon use and storage, a testament to previous silvicultural research.

Beside the economic value of the extractable wood and the potential for substitution purpose, it is today crucial for the EU countries to ensure forests functionality to maintain and preserve the carbon sink strength of trees in combination with the provision of their derived wood products. Forest management based on scientific principles remains a valuable tool for local, regional and global strategies to maintain forest carbon sinks and provide products under climate change. To date, based on our results, we believe that generating higher expectations on autotrophic forests' capacity to reduce climate change effects and, at the same time, to provide wood products through forest management (more than forests and forest management can already provide), as analyzed here, could be a risky and a potentially failing bet.

Acknowledgements

We are thankful to A. Ibrom, P. Kolari and J. Krejza for providing us data for Sorø, Hyytiälä and Bílý Kříž sites. We would like to thank J. Holder, B. Waring, H. Bugmann, L. Perugini, S. Luyssaert, M. Lindner, M. Michetti, A. Mäkelä and G. Matteucci for comments on a previous version of the manuscripts and/or fruitful discussions. We also thank the ISI-MIP project (https://www.isimip.org/) and the COST Action FP1304 PROFOUND (Towards Robust Projections of European Forests under Climate Change), supported by COST (European Cooperation in Science and Technology) for providing us the climate historical scenarios and site data used in this work. This work used eddy covariance data acquired and shared by the FLUXNET community, including these networks: AmeriFlux, AfriFlux, AsiaFlux, CarboAfrica, CarboEurope-IP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada, GreenGrass, ICOS, KoFlux, LBA, NECC, OzFlux-TERN, TCOS-Siberia, and USCCC. The ERA-Interim reanalysis data are provided by ECMWF and processed by LSCE. The FLUXNET eddy covariance data processing and harmonization was carried out by the European Fluxes Database Cluster, AmeriFlux Management Project, and Fluxdata Project of FLUXNET, with the support of CDIAC and ICOS Ecosystem Thematic Center, and the OzFlux, ChinaFlux, and AsiaFlux offices. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the respective climate modeling groups for producing and making available their model output. The U.S. Department of Energy's Program for Climate Model Diagnosis and Intercomparison at Lawrence Livermore National Laboratory provides coordinating support for CMIP and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals. A.C. was supported by the EFI-Funded FORMASAM (FORest MAnagement Scenarios for Adaptation and Mitigation) project; D.D.

and A.C. were also supported by resources available from the Italian Ministry of University and Research (FOE-2019), under projects 'Climate Changes' (CNR DTA. AD003.474.029); A.C. and G.M. were supported by LANDSUPPORT Horizon 2020 research and innovation programme under grant agreement No. 774234. The 3D-CMCC-FEM model code is publicly available and can be found on the GitHub platform at: https://github.com/Forest-Modelling-Lab/3D-CMCC-FEM). All data supporting this study are publicly available at the Zenodo repository (https://zenodo.org/record/6026117#.YgTfXnXMJhE). Correspondence and requests for additional materials should be addressed to corresponding authors.

Credit authorship contribution statement

D. Dalmonech, G. Marano and A. Collalti performed conceptualization, data curation, formal analysis, investigation, writing the original draft, and editing; C. Trotta ran the model code; J. Amthor and A. Cescatti, supported for writing, reviewing and editing.

References

Akujärvi, A., Shvidenko, A., & Pietsch, S. A. (2019). Modelling the impacts of intensifying forest management on carbon budget across a long latitudinal gradient in Europe. *Environmental Research Letters*, *14*(3). https://doi.org/10.1088/1748-9326/aaf766

Amthor, J.S. (2000). The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later. *Annals of Botany*, 86(1), 1–20. https://doi.org/10.1006/anbo.2000.1175

Atkin OK & Tjoelker M (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, 8: 343-351.

Bellassen, V., Viovy, N., Luyssaert, S., Le Maire, G., Schelhaas, M. J., & Ciais, P. (2011). Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000. *Global Change Biology*, *17*(11), 3274–3292. https://doi.org/10.1111/j.1365-2486.2011.02476.x

Bohn FJ, Huth A. 2017 The importance of forest structure to biodiversity–productivity relationships. *R. Soc. open sci*. 4: 160521. http://dx.doi.org/10.1098/rsos.160521

Bouriaud, L., Bouriaud, O., Elkin, C., Temperli, C., Reyer, C., Duduman, G., Barnoaiea, I., Nichiforel, L., Zimmermann, N., & Bugmann, H. (2015). Age-class disequilibrium as an opportunity for adaptive forest management in the Carpathian Mountains, Romania. *Regional Environmental Change*, *15*(8), 1557–1568. https://doi.org/10.1007/s10113-014-0717-6

Campioli, M., Vicca, S., Luyssaert, S., Bilcke, J., Ceschia, E., Iii, F. S. C., & Ciais, P. (2015). *Biomass production efficiency controlled by management in temperate and boreal ecosystems*. *Nature Geoscience*, https://doi.org/10.1038/NGEO2553

Ceccherini, G., Duveiller, G., Grassi, G., Lemoine, G., & Avitabile, V. (2020). Abrupt Increase in Forest Harvested Area over Europe After 2015. *Nature*, *583*. https://doi.org/10.1038/s41586-020-2438-y

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

Ciais, P., Schelhaas, M. J., Zaehle, S., Piao, S. L., Cescatti, A., Liski, J., Luyssaert, S., Le-Maire, G., Schulze, E. D., Bouriaud, O., Freibauer, A., Valentini, R., & Nabuurs, G. J. (2008). Carbon accumulation in European forests. *Nature Geoscience*, *1*(7), 425–429. https://doi.org/10.1038/ngeo233

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

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

Collalti, A., Trotta, C., Keenan, T. F., Ibrom, A., Bond-Lamberty, B., Grote, R., Vicca, S., Reyer, C. P. O., Migliavacca, M., Veroustraete, F., Anav, A., Campioli, M., Scoccimarro, E., Šigut, L., Grieco, E., Cescatti, A., & Matteucci, G. (2018). Thinning Can Reduce Losses in Carbon Use Efficiency and Carbon Stocks in Managed Forests Under Warmer Climate. *Journal of Advances in Modeling Earth Systems*, *10*(10), 2427–2452. https://doi.org/10.1029/2018MS001275

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

Collalti, A., & Prentice, I. C. (2019). Is NPP proportional to GPP? Waring’s hypothesis 20 years on. *Tree Physiology*, *39*(8), 1473–1483. https://doi.org/10.1093/treephys/tpz034

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

Collalti, A., Ibrom, A., Stockmarr, A., Cescatti, A., Alkama, R., Fernández-Martínez, M., Matteucci, G., Sitch, S., Friedlingstein, P., Ciais, P., Goll, D. S., Nabel, J. E. M. S., Pongratz, J., Arneth, A., Haverd, V., & Prentice, I. C. (2020b). Forest production efficiency increases with growth temperature. *Nature Communications, under review*. https://doi.org/https://doi.org/10.1101/2020.04.15.042275

de Pury DGG & Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell and Environment*, 20, 537–557.

Drake, J. E., & Tjoelker, M. G. (2016). Does physiological acclimation to climate warming stabilize the ratio of canopy respiration to photosynthesis? *New Phytologist*, 211(3), 850–863. https://doi.org/10.1111/nph.13978

Duffy, P. B., Brando, P., Asner, G. P., & Field, C. B. (2015). Projections of future meteorological drought and wet periods in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1421010112

Duncker, P. S., Barreiro, S. M., Hengeveld, G. M., Lind, T., Mason, W. L., Ambrozy, S., & Spiecker, H. (2012). Classification of forest management approaches: A new conceptual framework and its applicability to European forestry. *Ecology and Society*, *17*(4). https://doi.org/10.5751/ES-05262-170451

Engel M., Vospernik S., Toigo M., Morin X., Tomao A., Trotta C., Steckel M., Barbati A., Nothdurft A. Pretzsch H., del Rio M., Skrzyszewski J., Ponette Q., Lof M., Jansons A., Brazaitis G. (2021). Simulating the effects of thinning and species mixing on stands of oak (Quercus petrea (Matt.) Liebl. / Quercus robur L.) and pine (Pinus sylvestris L.) across Europe. *Ecological Modelling*, 442 (109406), https://doi.org/10.1016/j.ecolmodel.2020.109406

European Commission. "Multi-annual implementation plan of the new EU forest strategy." SWD (2015) 164 Final (2015).

Farquhar GD, et al. (1980) A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. *Planta*. 149: 78-90.

Favero, A., Daigneault, A., & Sohngen, B. (2020). Forests: Carbon sequestration, biomass energy, or both? *Science Advances*, *6*(13), 1–14. https://doi.org/10.1126/sciadv.aay6792

Fontes L., Bontemps J.-D., Bugmann H., Van Oijen M., Gracia C., Kramer K., Lindner M., Rötzer T., & Skovsgaard J. P. (2010). Models for supporting forest management in a changing environment. *Forest Systems*, 19, 8-29. https://doi.org/10.5424/fs/201019S-9315

FOREST EUROPE, & FAO, U. and. (2020). *FOREST EUROPE, 2020: State of Europe's Forests 2020*.

Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Hauck, J., Olsen, A., Peters, G. P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S., Aragão, L. E. O. C., Arneth, A., Arora, V., Bates, N. R., … Zaehle, S. (2020). Global Carbon Budget 2020. *Earth System Science Data*, *12*(4), 3269–3340. https://doi.org/10.5194/essd-12-3269-2020

Fritsch, M, Lischke, H, Meyer, KM. Scaling methods in ecological modelling. *Methods Ecol Evol*. 2020; 11: 1368– 1378. https://doi.org/10.1111/2041-210X.13466

Gampe, D., Zscheischler, J., Reichstein, M., O'Sullivan, M., Smith, W. K., Sitch, S., & Buermann, W. (2021). Increasing impact of warm droughts on northern ecosystem productivity over recent decades. *Nature Climate Change*, 11(9), 772-779.

Garcia-Gonzalo, J., Peltola, H., Briceño-Elizondo, E., & Kellomäki, S. (2007). Changed thinning regimes may increase carbon stock under climate change: A case study from a Finnish boreal forest. *Climatic Change*, *81*(3–4), 431–454. https://doi.org/10.1007/s10584-006-9149-8

Gatti, L.V., Basso, L.S., Miller, J.B. et al. Amazonia as a carbon source linked to deforestation and climate change. *Nature* 595, 388–393 (2021). https://doi.org/10.1038/s41586-021-03629-6

Grassi, G., House, J., Dentener, F., Federici, S., Den Elzen, M., & Penman, J. (2017). The key role of forests in meeting climate targets requires science for credible mitigation. *Nature Climate Change*, *7*(3), 220–226. https://doi.org/10.1038/nclimate3227

Grassi, G., Stehfest, E., Rogelj, J., van Vuuren, D., Cescatti, A., House, J., Nabuurs, G. J., Rossi, S., Alkama, R., Viñas, R. A., Calvin, K., Ceccherini, G., Federici, S., Fujimori, S., Gusti, M., Hasegawa, T., Havlik, P., Humpenöder, F., Korosuo, A., … Popp, A. (2021). Critical adjustment of land mitigation pathways for assessing countries' climate progress. *Nature Climate Change*, *11*(5), 425–434. https://doi.org/10.1038/s41558-021-01033-6

Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T. W., Sperry, J. S., & McDowell, N. G. (2020). Plant responses to rising vapor pressure deficit. *New Phytologist*, *226*(6), 1550–1566. https://doi.org/https://doi.org/10.1111/nph.16485

Gustafson, E.J.; Miranda, B.R.; De Bruijn, A.M.G.; Sturtevant, B.R.; Kubiske, M.E. (2017). Do rising temperatures always increase forest productivity? Interacting effects of temperature, precipitation, cloudiness and soil texture on tree species growth and competition. *Environmental Modelling & Software*. 97: 171-183. https://doi.org/10.1016/j.envsoft.2017.08.001.

Hempel, S., Frieler, K., Warszawski, L., Schewe, J., and Piontek, F.: A trend-preserving bias correction – the ISI-MIP approach, *Earth Syst. Dynam.*, 4, 219–236, https://doi.org/10.5194/esd-4-219-2013, 2013.

Henttonen, H. M., Nöjd, P., & Mäkinen, H. (2017). Environment-induced growth changes in the Finnish forests during 1971–2010 – An analysis based on National Forest Inventory. *Forest Ecology and Management*, *386*, 22–36. https://doi.org/10.1016/j.foreco.2016.11.044

Howard, C., Dymond, C. C., Griess, V. C., Tolkien-Spurr, D., & van Kooten, G. C. (2021). Wood product carbon substitution benefits: a critical review of assumptions. *Carbon Balance and Management*, *16*(1), 1–11. https://doi.org/10.1186/s13021-021-00171-w

Huang J., Hammerbacher A., Gershenzon J., van Dam, N.M., Sala, A., McDowell N.G., et al. (2021). Storage of carbon reserves in spruce trees is prioritized over growth in the face of carbon limitation. *PNAS*, 118(33), e2023297118; DOI: 10.1073/pnas.2023297118

Hubau, W., Lewis, S.L., Phillips, O.L. et al. Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature* 579, 80–87 (2020). https://doi.org/10.1038/s41586-020-2035-0

Huber, N., Bugmann, H., & Lafond, V. (2018). Global sensitivity analysis of a dynamic vegetation model: Model sensitivity depends on successional time, climate and competitive interactions. *Ecological Modelling*, *368*, 377–390. https://doi.org/10.1016/j.ecolmodel.2017.12.013

Huber, N., Bugmann, H., & Lafond, V. (2020). Capturing ecological processes in dynamic forest models: why there is no silver bullet to cope with complexity. *Ecosphere*, *11*(5). https://doi.org/10.1002/ecs2.3109

Kauppi, P. E., Sedjio, R., Apps, M., Cerri, C., Fujimori, T., Janzen, H., Krankina, O., Makundi, W., Marland, R., Masera, O., & Nabuurs. (2001). Technological and economic potential of options to enhance, maintain, and manage biological carbon reservoirs and Geo-engineering. In IPCC (Ed.), *Climate Change 2001: Mitigation* (pp. 302–343). Cambridge University Press.

Kattge, J. and Knorr, W. (2007), Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant, Cell & Environment*, 30: 1176-1190. https://doi.org/10.1111/j.1365-3040.2007.01690.x

Kindermann, G.E., Schörghuber, S., Linkosalo, T. et al. Potential stocks and increments of woody biomass in the European Union under different management and climate scenarios. *Carbon Balance Management* 8, 2 (2013). https://doi.org/10.1186/1750-0680-8-2

Kirschbaum, M. (2005). A model analysis of the interaction between forest age and forest responsiveness to increasing CO_2 concentration. *Tree Physiology*, 25(7), 953–963. https://doi.org/10.1093/treephys/25.7.953

Körner, C. (2005). Worldwide positions of alpine treelines and their causes. *The Impacts of Climate Variability on Forests*, 221–229. https://doi.org/10.1007/bfb0009775

Krofcheck, D. J., Remy, C. C., Keyser, A. R., & Hurteau, M. D. (2019). Optimizing Forest Management Stabilizes Carbon Under Projected Climate and Wildfires. *Journal of Geophysical Research: Biogeosciences*, 3075–3087. https://doi.org/10.1029/2019JG005206

Leskinen, P., Cardellini, G., González García, S., Hurmekoski, E., Sathre, R., Seppälä, J., Smyth, C. E., Stern, T., & Verkerk, H. (2018). Substitution effects of wood-based products in climate change mitigation. *From Science to Policy*, *7*(November), 28. https://www.efi.int/publications-bank/substitution-effects-wood-based-products-climate-change-mitigation

Leslie, A. J. (1966). A review of the concept of the normal forest. *Australian Forestry*, *30*(2), 139–147. https://doi.org/10.1080/00049158.1966.10675407

Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J. M., Chambers, J., Ciais, P., … Janssens, I. A. (2007). CO2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, *13*(12), 2509–2537. https://doi.org/10.1111/j.1365-2486.2007.01439.x

Luyssaert, S., Marie, G., Valade, A., Chen, Y. Y., Njakou Djomo, S., Ryder, J., Otto, J., Naudts, K., Lansø, A. S., Ghattas, J., & McGrath, M. J. (2018). Trade-offs in using European forests to meet climate objectives. *Nature*, *562*(7726), 259–262. https://doi.org/10.1038/s41586-018-0577-1

Mäkelä A (1997) A Carbon Balance Model of Growth and Self-Pruning in Trees Based on Structural Relationship. *Forest Science*, 43(1), 7-24.

Mäkelä, A., Landsberg, J. O. E., Ek, A. R., Burk, T. E., Ågren, G. I., Oliver, C. D., & Puttonen, P. (2000). *Process-based models for forest ecosystem management, current state*. 289–298.

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., del Aguila-Pasquel, J., Aragão, L. E. O. C., Araujo-Murakami, A., Brando, P., da Costa, A. C. L., Silva-Espejo, J. E., Farfán Amézquita, F., Galbraith, D. R., Quesada, C. A., Rocha, W., Salinas-Revilla, N., Silvério, D., Meir, P., & Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*. https://doi.org/10.1111/gcb.12859

Marconi, S., Chiti, T., Nolè, A., Valentini, R., & Collalti, A. (2017). The role of respiration in estimation of net carbon cycle: Coupling soil carbon dynamics and canopy turnover in a novel version of 3D-CMCC forest ecosystem model. *Forests*. https://doi.org/10.3390/f8060220

Maréchaux I., Langerwish F., Huth A., Bugmann H., Morin X., Reyer C.P.O., Seidl R., Collalti A., Dantas de Paula M., Fischer R., Gutsch M., Lexer M.J., Lischke H., Rammig A., Rödig E., Sakschewski B., Taubert F., Thonicke K., Vacchiano G., Bohn F.J. (2021), "Modelling forests to address key ecological questions: lessons learned from different modelling communities and possible future paths", Ecology and Evolution, 11(9):3746–3770, https://doi.org/10.1002/ece3.7391

Martínez-Vilalta, J., Sala, A., Asensio, D., Galiano, L., Hoch, G., Palacio, S., ... Lloret, F. (2016). Dynamics of non-structural carbohydrates in terrestrial plants: A global synthesis. *Ecological Monographs*, 86(4), 495–516. https://doi.org/10.1002/ecm.1231

Mathias, J.M. & Trugman, A.T. (2021) Climate change impacts plant carbon balance, increasing mean future carbon use efficiency but decreasing total forest extent at dry range edges. *Ecology Letters*, 00, 1– 11. https://doi.org/10.1111/ele.13945

Mason, R. L., Gunst, R. F., & Hess, J. L. (2003). Factorial Experiments in Completely Randomized Designs. In *Statistical Design and Analysis of Experiments*. https://doi.org/10.1002/0471458503.ch5

Massoud, E. C., Xu, C., Fisher, R. A., Knox, R. G., Walker, A. P., Serbin, S. P., Christoffersen, B. O., Holm, J. A., Kueppers, L. M., Ricciuto, D. M., Wei, L., Johnson, D. J., Chambers, J. Q., Koven, C. D., McDowell, N. G., and Vrugt, J. A.: Identification of key parameters controlling demographically structured vegetation dynamics in a land surface model: CLM4.5 (FATES), *Geosci. Model Dev*., 12, 4133–4164, https://doi.org/10.5194/gmd-12-4133-2019, 2019.

McCree, K. (1970). An equation for the rate of respiration of white clover plants grown under controlled conditions. In I. Šetliik (Ed.), Prediction and measurement of photosynthetic productivity (pp. 221–229). Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation.

McDowell, N. G., Allen, C. D., Anderson-teixeira, K., Aukema, B. H., Bond-lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., … Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science*. https://doi.org/10.1126/science.aaz9463

Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J.-F., Matsumoto, K., Montzka, S. A., Raper, S. C. B., Riahi, K., Thomson, A., Velders, G. J. M., and van Vuuren, D. P. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300, *Clim. Change*, 109, 213, https://doi.org/10.1007/s10584-011-0156-z.

Merganičová, K., Merganič, J., Lehtonen, A., Vacchiano, G., Sever, M. Z. O., Augustynczik, A. L. D., Grote, R., Kyselová, I., Mäkelä, A., Yousefpour, R., Krejza, J., Collalti, A., & Reyer, C. P. O. (2019). Forest carbon allocation modelling under climate change. *Tree Physiology*, *39*(12), 1937–1960. https://doi.org/10.1093/treephys/tpz105

Migliavacca, M., Musavi, T., Mahecha, M.D. et al. The three major axes of terrestrial ecosystem function. *Nature* 598, 468–472 (2021). https://doi.org/10.1038/s41586-021-03939-9

Morales, P., Sykes, M. T., Prentice, I. C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P., Viovy, N., Sabaté, S., Sánchez, A., Pla, E., Gracia, C. A., Sitch, S., Arneth, A., & Ogee, J. (2005). Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. *Global Change Biology*, *11*(12), 2211–2233. https://doi.org/https://doi.org/10.1111/j.1365-2486.2005.01036.x

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., Van Vuuren, D. P., Carter, T. R., Emori, S., Kainuma, M., Kram, T., Meehl, G. A., Mitchell, J. F. B., Nakicenovic, N., Riahi, K., Smith, S. J., Stouffer, R. J., Thomson, A. M., Weyant, J. P., & Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*. https://doi.org/10.1038/nature08823

Nabuurs, G. J., Thürig, E., Heidema, N., Armolaitis, K., Biber, P., Cienciala, E., Kaufmann, E., Mäkipää, R., Nilsen, P., Petritsch, R., Pristova, T., Rock, J., Schelhaas, M. J., Sievanen, R., Somogyi, Z., & Vallet, P. (2008). Hotspots of the European forests carbon cycle. *Forest Ecology and Management*, *256*(3), 194–200. https://doi.org/10.1016/j.foreco.2008.04.009

Nabuurs, Gert Jan, Lindner, M., Verkerk, P. J., Gunia, K., Deda, P., Michalak, R., & Grassi, G. (2013). First signs of carbon sink saturation in European forest biomass. *Nature Climate Change*, *3*(9), 792–796. https://doi.org/10.1038/nclimate1853

Nabuurs, Gert Jan, Verweij, P., Van Eupen, M., Pérez-Soba, M., Pülzl, H., & Hendriks, K. (2019). Next-generation information to support a sustainable course for European forests. *Nature Sustainability*, *2*(9), 815–818. https://doi.org/10.1038/s41893-019-0374-3

Nolè, A., Collalti, A., Borghetti, M., Chiesi, M., Chirici, G., Magnani, F., et al. (2015). The role of managed forest ecosystems: A modelling based approach. In R. Valentini & F. Miglietta (Eds.), The greenhouse gas balance of Italy (pp. 71–85). Berlin-Heidelberg: Springer-Verlag.

Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., ... Yang, Z.L. (2013). Technical description of version 4.5 of the community land model (CLM). Ncar Technical Note NCAR/TN- 503+STR. Boulder, CO: National Center for Atmospheric Research, 422 pp.

Pappas, C., Fatichi, S., Leuzinger, S., Wolf, A., & Burlando, P. (2013). Sensitivity analysis of a process- based ecosystem model: Pinpointing parameterization and structural issues. *Journal of Geophysical Research*, 118, 502–528. https://doi.org/10.1002/jgrg.20035

Pappas, C., Maillet, J., Rakowski, S., Baltzer, J. L., Barr, A. G., Black, T. A., Fatichi, S., Laroque, C. P., Matheny, A. M., Roy, A., Sonnentag, O., & Zha, T. (2020). Aboveground tree growth is a minor and decoupled fraction of boreal forest carbon input. *Agricultural and Forest Meteorology*, *290*(May), 108030. https://doi.org/10.1016/j.agrformet.2020.108030

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

Peñuelas, J., Ciais, P., Canadell, J. G., Janssens, I. A., Fernández-Martínez, M., Carnicer, J., Obersteiner, M., Piao, S., Vautard, R., & Sardans, J. (2017). Shifting from a fertilization-dominated to a warming-dominated period. *Nature Ecology and Evolution*, *1*(10), 1438–1445. https://doi.org/10.1038/s41559-017-0274-8

Piao, S., Wang, X., Park, T., Chen, C., Lian, X., He, Y., Bjerke, J. W., Chen, A., Ciais, P., Tømmervik, H., Nemani, R. R., & Myneni, R. B. (2020). Characteristics, drivers and feedbacks of global greening. *Nature Reviews Earth and Environment*, *1*(1), 14–27. https://doi.org/10.1038/s43017-019-0001-x

Poulter, B., Hattermann, F., Hawkins, E. D., Zaehle, S., Sitch, S., RestrepoCoupe, N. A., ... Cramer, W. (2010). Robust dynamics of Amazon dieback to climate change with perturbed ecosystem model parameters. *Global Change Biology*, 16, 2476–2495. https ://doi.org/10.1111/j.1365-2486. 2009.02157.x

Pugh, T. A. M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., & Calle, L. (2019). Role of forest regrowth in global carbon sink dynamics. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1810512116

Pukkala, T. (2017). Does management improve the carbon balance of forestry? *Forestry*, *90*(1), 125–135. https://doi.org/10.1093/forestry/cpw043

Pussinen, Ari, Karjalainen, T., Mäkipää, R., Valsta, L., & Kellomäki, S. (2002). Forest carbon sequestration and harvests in Scots pine stand under different climate and nitrogen deposition scenarios. *Forest Ecology and Management*. https://doi.org/10.1016/S0378-1127(00)00675-7

Pussinen, A., Nabuurs, G. J., Wieggers, H. J. J., Reinds, G. J., Wamelink, G. W. W., Kros, J., Mol-Dijkstra, J. P., & de Vries, W. (2009). Modelling long-term impacts of environmental change on mid- and high-latitude European forests and options for adaptive forest management. *Forest Ecology and Management*, *258*(8), 1806–1813. https://doi.org/10.1016/j.foreco.2009.04.007

Reich, P. B. et al. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecol. Lett.* 11, 793–801 (2008).

Reich, P. B., & Oleksyn, J. (2008). Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters*, **1**(6), 588–597.

Reich, P., Sendall, K., Stefanski, A., Wei, X., Rich, R. L., & Montgomery, R. A. (2016). Boreal and temperate trees show strong acclimation of respiration to warming. *Nature*, 531(7596), 633–636. https://doi.org/10.1038/nature17142

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

Ryan, M. G. (1991). Effects of climate change on plant respiration. *Ecological Applications*, 1(2), 157–167.

Ryan, M.G., Phillips, N., & Bond, B. J. (2006). The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment*, *29*(3), 367–381. https://doi.org/https://doi.org/10.1111/j.1365-3040.2005.01478.x

Sala, A., Fouts, W., & Hoch, G. (2011). Carbon storage in trees: Does relative carbon supply decrease with tree size? In F. C. Meinzer, B. Lachenbruch, & T. E. Dawson (Eds.), Size- and age-related changes in tree structure and function (pp. 287–306). Dordrecht, the Netherlands: Springer.

Schelhaas, MJ., Nabuurs, GJ., Hengeveld, G. et al. Alternative forest management strategies to account for climate change-induced productivity and species suitability changes in Europe. *Reg. Environ. Change* 15, 1581–1594 (2015). https://doi.org/10.1007/s10113-015-0788-z

Schulze, E. D., Sierra, C. A., Egenolf, V., Woerdehoff, R., Irslinger, R., Baldamus, C., Stupak, I., & Spellmann, H. (2020). The climate change mitigation effect of bioenergy from sustainably managed forests in Central Europe. *GCB Bioenergy*, *12*(3), 186–197. https://doi.org/10.1111/gcbb.12672

Sedmáková, D., Sedmák, R., Bosela, M., Je, M., Bla, M., & Maru, R. (2019). *Dendrochronologia Growth-climate responses indicate shifts in the competitive ability of European beech and Norway spruce under recent climate warming in East- Central Europe*. *54*, 37–48. https://doi.org/10.1016/j.dendro.2019.02.001

Senf, C., & Seidl, R. (2021). *Storm and fire disturbances in Europe : Distribution and trends*. 3605–3619. https://doi.org/10.1111/gcb.15679

Settele J, Scholes R, Betts R, Bunn S, Leadley P, Nepstad D, Overpeck JT, Taboada MA (2014) Terrestrial and inland water systems. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN,MacCracken S, Mastrandrea PR,White LL (eds) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate

Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp 271–359

Sha, Z., Bai, Y., Li, R. et al. The global carbon sink potential of terrestrial vegetation can be increased substantially by optimal land management. Commun Earth Environ 3, 8 (2022). https://doi.org/10.1038/s43247-021-00333-1

Shinozaki K, et al. (1964) A quantitative analysis of plant form – the pipe model theory. I. Basic analyses. *Japanese Journal of Ecology* 14, 97–105

Smith N & Dukes J (2012). Plant respiration and photosynthesis in global-scale models: incorporating acclimation and CO_2. *Global Change Biology*, 19: 45-63.

Tahvonen, O. (2016). Economics of rotation and thinning revisited: The optimality of clearcuts versus continuous cover forestry. *Forest Policy and Economics*. https://doi.org/10.1016/j.forpol.2015.08.013

Tang, J., Luyssaert, S., Richardson, A. D., Kutsch, W., & Janssens, I. A. (2014). Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(24), 8856–8860. https://doi.org/10.1073/pnas.1320761111

Temperli, C., Bugmann, H., & Elkin, C. (2012). Adaptive management for competing forest goods and services under climate change. *Ecological Applications*, *22*(8), 2065–2077. https://doi.org/10.1890/12-0210.1

Thornley, J. H. M., & Cannell, M. G. R. (2000). Modelling the components of plant respiration: Representation and realism. *Annals of Botany*, 85, 55–67. https ://doi.org/10.1006/anbo.1999.0997

Thom, D., Rammer, W., & Seidl, R. (2017). Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Global Change Biology*. https://doi.org/10.1111/gcb.13506

Tong, X., Brandt, M., Yue, Y., Ciais, P., Rudbeck Jepsen, M., Penuelas, J., Wigneron, J. P., Xiao, X., Song, X. P., Horion, S., Rasmussen, K., Saatchi, S., Fan, L., Wang, K., Zhang, B., Chen, Z., Wang, Y., Li, X., & Fensholt, R. (2020). Forest management in southern China generates short term extensive carbon sequestration. *Nature Communications*, *11*(1), 1–10. https://doi.org/10.1038/s41467-019-13798-8

Trotsiuk, V, Hartig, F, Cailleret, M, et al. (2020). Assessing the response of forest productivity to climate extremes in Switzerland using model–data fusion. *Global Change Biology*, 26: 2463– 2476. https://doi.org/10.1111/gcb.15011

Tjoelker M, et al. (2001). Modelling respiration of vegetation: evidence for a general temperature-dependent Q10. Global Change Biology, 7: 223-230.

Valade, A., Bellassen, V., Magand, C., & Luyssaert, S. (2017). Forest Ecology and Management Sustaining the sequestration efficiency of the European forest sector. *Forest Ecology and Management*, *405*, 44–55. https://doi.org/10.1016/j.foreco.2017.09.009

Vanninen P., Mäkelä A., Carbon budget for Scots pine trees: effects of size, competition and site fertility on growth allocation and production (2005), *Tree Physiology*, Volume 25, 17–30, https://doi.org/10.1093/treephys/25.1.17

van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., Kram, T., Krey, V., Lamarque, J. F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S. J., & Rose, S. K. (2011). The representative concentration pathways: An overview. *Climatic Change*. https://doi.org/10.1007/s10584-011-0148-z

Vetter, M., Wirth, C., Böttcher, H., Churkina, G., Schulze, E. D., Wutzler, T., & Weber, G. (2005). Partitioning direct and indirect human-induced effects on carbon sequestration of managed coniferous forests using model simulations and forest inventories. *Global Change Biology*, *11*(5), 810–827. https://doi.org/10.1111/j.1365-2486.2005.00932.x

Walker, A. P., De Kauwe, M. G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R. F., McMahon, S. M., Medlyn, B. E., Moore, D. J. P., Norby, R. J., Zaehle, S., Anderson-Teixeira, K. J., Battipaglia, G., Brienen, R. J. W., Cabugao, K. G., Cailleret, M., Campbell, E., Canadell, J. G., Ciais, P., … Zuidema, P. A. (2021). Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO2. *New Phytologist*, *229*(5), 2413–2445. https://doi.org/https://doi.org/10.1111/nph.16866

Wang, Y., Zhang, C., Meng, F. R., Bourque, C. P. A., & Zhang, C. (2020). Evaluation of the suitability of six drought indices in naturally growing, transitional vegetation zones in Inner Mongolia (China). *PLoS ONE*, *15*(5), 1–15. https://doi.org/10.1371/journal.pone.0233525

Warszawski, L., Frieler, K., Huber, V., Piontek, F., Serdeczny, O., & Schewe, J. (2014). The inter-sectoral impact model intercomparison project (ISI-MIP): Project framework. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(9), 3228–3232. https://doi.org/10.1073/pnas.1312330110

Way, D. A. & Sage, R. F. Elevated growth temperatures reduce the carbon gain of black spruce [Picea mariana (Mill.) B.S.P.] (2008). *Glob. Chang. Biol* 14, 624–636.

Wu, J., Larsen, K., van der Linden, L., Beier, C., Pilegaard, K., & Ibrom, A. (2013). Synthesis on the carbon budget and cycling in a Danish, temperate deciduous forest. *Agricultural and Forest Meteorology*, 181, 94–107. https://doi.org/10.1016/j.agrformet.2013.07.012

Vacchiano G, Magnani F, Collalti A (2012) Modeling Italian forests: state of the art and future challenges. *iForest*, e1–e8

Vicca, S., Luyssaert, S., Peñuelas, J., Campioli, M., Chapin, F. S. III, Ciais, P., et al. (2012). Fertile forests produce biomass more efficiently. *Ecology Letters*, 15(6), 520–526. https://doi.org/10.1111/j.1461-0248.2012.01775.x

Yousefpour, R., Temperli, C., Jacobsen, J. B., Thorsen, B. J., Meilby, H., Lexer, M. J., Lindner, M., Bugmann, H., Borges, J. G., Palma, J. H. N., Ray, D., Zimmermann, N. E., Delzon, S., Kremer, A., Kramer, K., Reyer, C. P. O., Lasch-Born, P., Garcia-Gonzalo, J., & Hanewinkel, M. (2017). A framework for modeling adaptive forest management and decision making under climate change. *Ecology and Society*, *22*(4). https://doi.org/10.5751/ES-09614-220440

Yuan, Z., Ali, A., Jucker, T., Ruiz-Benito, P., Wang, S., Jiang, L., Wang, X., Lin, F., Ye, J., Hao, Z., & Loreau, M. (2019). Multiple abiotic and biotic pathways shape biomass demographic processes in temperate forests. *Ecology*, *100*(5), e02650. https://doi.org/https://doi.org/10.1002/ecy.2650

Zaehle, S., Sitch, S., Smith, B., & Hatterman, F. (2005). Effects of parameter uncertainties on the modelling of terrestrial biosphere dynamics. *Global Biogeochemical Cycles*, 19, 1–16. https://doi.org/10.1029/2004GB 002395

Zaehle, S., Sitch, S., Prentice, I. C., Liski, J., Cramer, W., Erhard, M., Hickler, T., & Smith, B. (2006). The importance of age-related decline in forest NPP for modeling regional carbon balances. *Ecological Applications*, *16*(4), 1555–1574. https://doi.org/10.1890/1051-0761(2006)016[1555:TIOADI]2.0.CO;2

Zeide B. (2001). Thinning and growth: A full turnaround, *Journal of Forestry*, 99(1), 20-25. https://doi.org/10.1093/jof/99.1.20

Figures

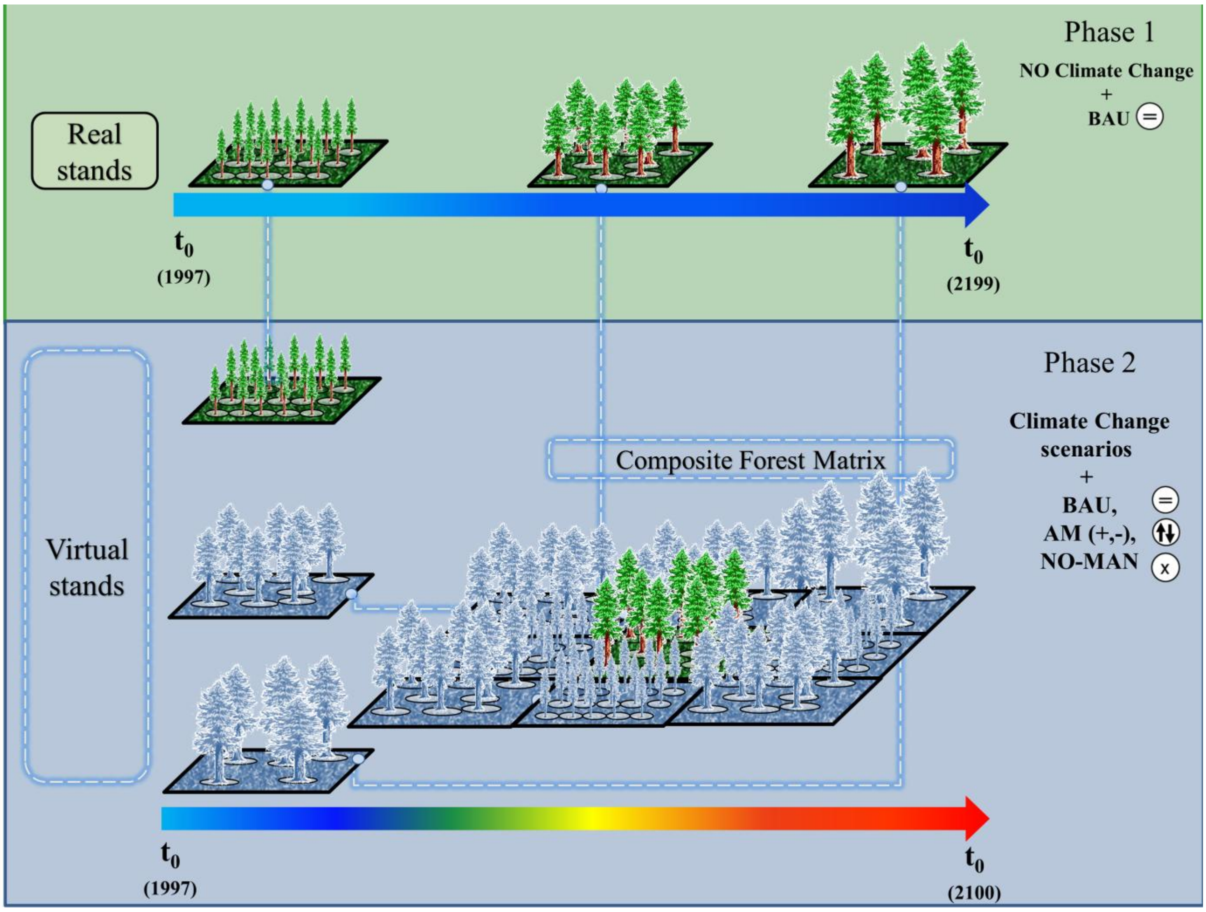


Figure 1 | Conceptual scheme of the virtual stands creation: in Phase 1 the model is initialized with data from the actual forest stands and then simulations are carried out for 202 years of contemporary (1996-2006) weather and atmospheric CO_2 concentration. In Phase 2, multiple stands are drawn from the simulations in Phase 1 and used to build the Composite Forest Matrix (CFM) composed of representative forest stands. The climate change (RCPs) and management scenarios (BAU, Alternative Managements, No-Management) simulations are then applied to the CFM.

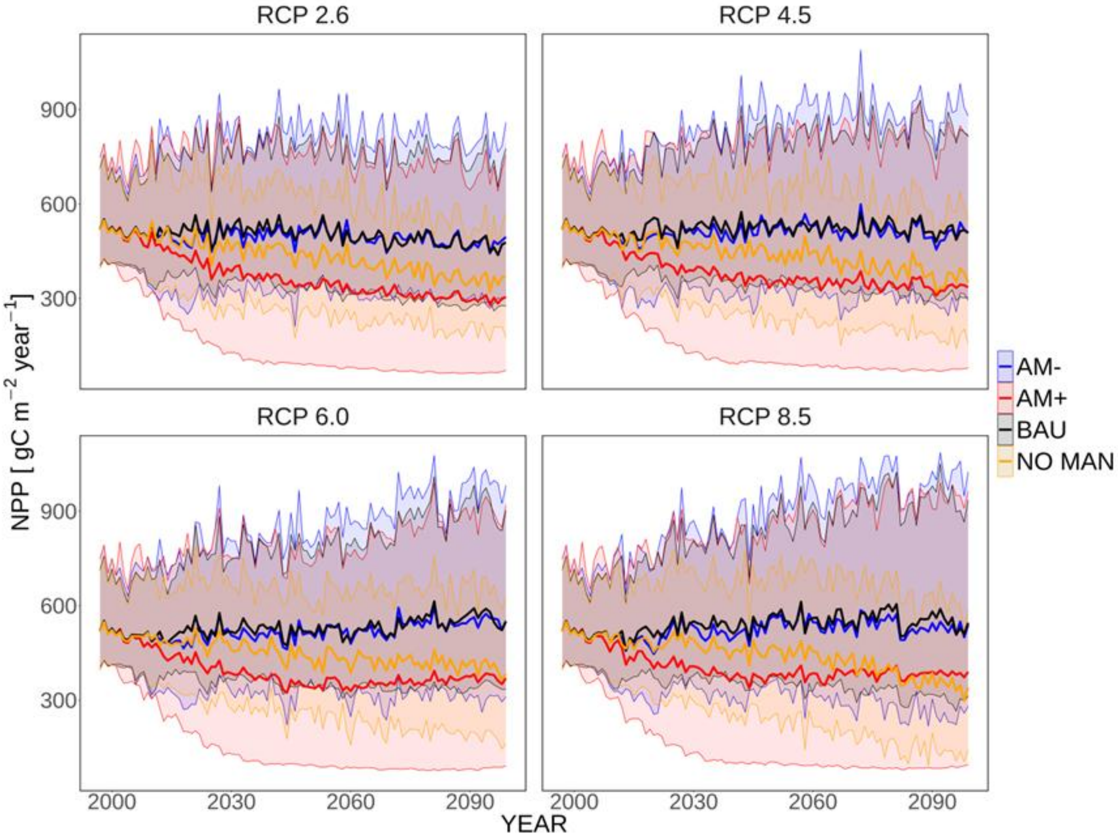


Figure 2 | NPP (Net primary productivity, gC m^{-2} year^{-1}) simulations under different management scenarios (AM+, BAU, AM–) and the NO-MAN scenario for each of the four atmospheric CO_2 concentration pathways (RCPs). NPP, solid line, is averaged across the representative forests, different ESMs and aggregated according to the management regime. Shaded areas represent the maximum and minimum values (5th and 95th percentiles) across the representative forests, different ESMs and aggregated according to the management regime.

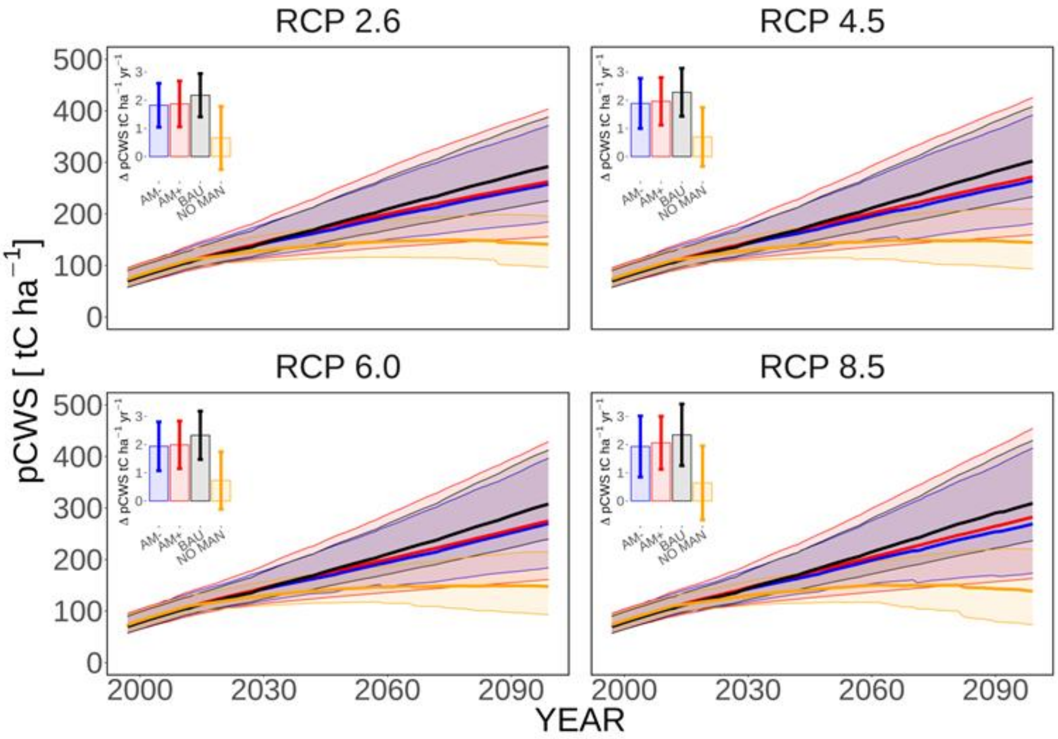


Figure 3 | pCWS (potential Carbon Woody Stock = standing and potential harvested woody biomass; tC ha^{-1}) simulations under different management scenarios (AM+, BAU, AM–) and the NO-MAN scenario divided by different emission scenario RCPs. pCWS, solid line, is averaged across the representative forests, different ESMs and aggregated according to the management regime. Shaded areas represent the maximum and minimum values (5th and 95th percentiles) across the representative forests, different ESMs and aggregated according to the management regime. Carbon sequestration rates (as annual increase of CWS, tC ha^{-1} year^{-1}) in the potential total woody stocks (mean and standard deviation) are reported in the bar plots.

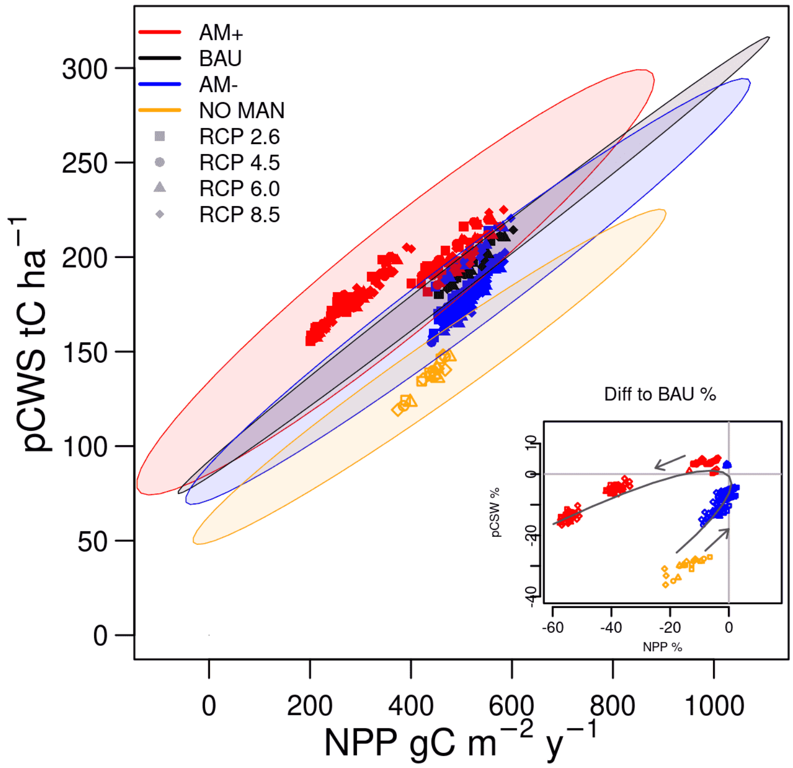
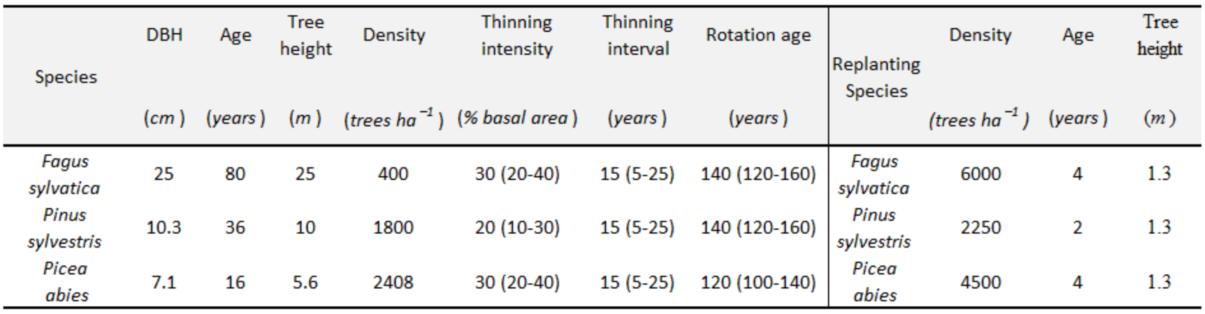


Figure 4 | Average NPP (net primary productivity, gC m^{-2} year^{-1}) vs. pCWS (the sum of standing and potential harvested woody products; tC ha^{-1}) over the period 2006-2099, for the three management scenarios: AM+, AM–, BAU; and the NO-MAN for the 4 RCPs. Reported values refer to data averaged across real and virtual stands and across species. Data ellipses are also reported in shaded colors and refer to all data. NOTE: each single scenario according to Table S1 is reported here (16 in total excluding the mixed ones). In the subplot the differences are expressed as % and are reported along a parametric curve (third order polynomial) with the point (0, 0) representing the reference BAU. Arrows indicate the increasing intensity of management intervention. No significant differences across RCPs were detected.

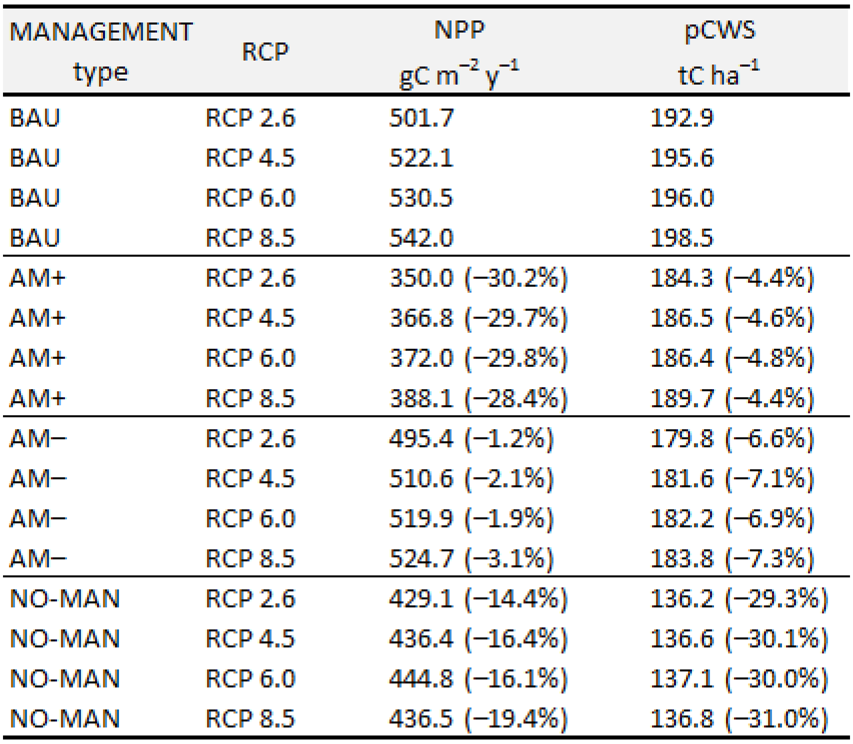
Tables

Table 1 | Site description for model initialization data (corresponding to the year 1997 for Sorø and Hyytiälä and 2000 for Bílý Kříž) to the real stands' characteristics, and management variables used in simulations (see also Collalti et al., 2018; Reyer et al., 2020). Values in brackets represent bounds of variability (the maximum and the minimum absolute values) adopted for alternative management simulations. Re-planting information for the sites in the simulation experiments, according to ISI-MIP protocol as in Reyer et al. (2020). The real stands refer to the monitoring sites in Sorø (*F. sylvatica*, Denmark), Bílý Kříž (*P. abies*, Czech Republic) and Hyytiälä (*P. sylvestris*, Finland).



Species	DBH (*cm*)	Age (*years*)	Tree height (*m*)	Density (*trees ha*$^{-1}$)	Thinning intensity (*% basal area*)	Thinning interval (*years*)	Rotation age (*years*)	Replanting Species	Density (*trees ha*$^{-1}$)	Age (*years*)	Tree height (*m*)
Fagus sylvatica	25	80	25	400	30 (20-40)	15 (5-25)	140 (120-160)	*Fagus sylvatica*	6000	4	1.3
Pinus sylvestris	10.3	36	10	1800	20 (10-30)	15 (5-25)	140 (120-160)	*Pinus sylvestris*	2250	2	1.3
Picea abies	7.1	16	5.6	2408	30 (20-40)	15 (5-25)	120 (100-140)	*Picea abies*	4500	4	1.3

Table 2 | NPP and pCWS computed as average over the simulation period 2006-2099, across all stands and ESMs climate forcing but grouped across RCPs. Mean differences (in percentage) are reported in parenthesis for NPP and pCWS between the alternative management scenarios and the *Business-As-Usual* (BAU) practices used here as the benchmark scenario.



MANAGEMENT type	RCP	NPP $gC\ m^{-2}\ y^{-1}$	pCWS $tC\ ha^{-1}$
BAU	RCP 2.6	501.7	192.9
BAU	RCP 4.5	522.1	195.6
BAU	RCP 6.0	530.5	196.0
BAU	RCP 8.5	542.0	198.5
AM+	RCP 2.6	350.0 (−30.2%)	184.3 (−4.4%)
AM+	RCP 4.5	366.8 (−29.7%)	186.5 (−4.6%)
AM+	RCP 6.0	372.0 (−29.8%)	186.4 (−4.8%)
AM+	RCP 8.5	388.1 (−28.4%)	189.7 (−4.4%)
AM−	RCP 2.6	495.4 (−1.2%)	179.8 (−6.6%)
AM−	RCP 4.5	510.6 (−2.1%)	181.6 (−7.1%)
AM−	RCP 6.0	519.9 (−1.9%)	182.2 (−6.9%)
AM−	RCP 8.5	524.7 (−3.1%)	183.8 (−7.3%)
NO-MAN	RCP 2.6	429.1 (−14.4%)	136.2 (−29.3%)
NO-MAN	RCP 4.5	436.4 (−16.4%)	136.6 (−30.1%)
NO-MAN	RCP 6.0	444.8 (−16.1%)	137.1 (−30.0%)
NO-MAN	RCP 8.5	436.5 (−19.4%)	136.8 (−31.0%)