

RESEARCH ARTICLE

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Key Points:

- How will C-fluxes, CUE, and C-stocks of the major European forest types may respond to elevated atmospheric CO<sub>2</sub>, warming, and management in the future?
- Results show that managed forests left unthinned will reduce their CUE and their C-stocks capability faster under climate change because of accelerated development
- Results show that thinning may have a large influence on C-sequestration improving forest efficiency in stocking C as also in preventing risks of forest dieback

Supporting Information:

- Supporting Information S1

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# Thinning Can Reduce Losses in Carbon Use Efficiency and Carbon Stocks in Managed Forests Under Warmer Climate

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**Abstract** Forest carbon use efficiency (CUE, the ratio of net to gross primary productivity) represents the fraction of photosynthesis that is not used for plant respiration. Although important, it is often neglected in climate change impact analyses. Here we assess the potential impact of thinning on projected carbon cycle dynamics and implications for forest CUE and its components (i.e., gross and net primary productivity and plant respiration), as well as on forest biomass production. Using a detailed process-based forest ecosystem model forced by climate outputs of five Earth System Models under four representative climate scenarios, we investigate the sensitivity of the projected future changes in the autotrophic carbon budget of three representative European forests. We focus on changes in CUE and carbon stocks as a result of warming, rising atmospheric CO<sub>2</sub> concentration, and forest thinning. Results show that autotrophic carbon sequestration decreases with forest development, and the decrease is faster with warming and in unthinned forests. This suggests that the combined impacts of climate change and changing CO<sub>2</sub> concentrations lead the forests to grow faster, mature earlier, and also die younger. In addition, we show that under future climate conditions, forest thinning could mitigate the decrease in CUE, increase carbon allocation into more recalcitrant woody pools, and reduce physiological-climate-induced mortality risks. Altogether, our results show that thinning can improve the efficacy of forest-based mitigation strategies and should be carefully considered within a portfolio of mitigation options.

## 1. Introduction

Investigating the potential impacts of climate change on terrestrial carbon sequestration and carbon stocks is important and urgently needed, especially within the context of the Paris Agreement and its ambitious goal to remain *well below* the 2 °C target. Complex nonlinear land-atmosphere feedbacks can buffer or amplify anthropogenic climate change (Bonan, 2008) and are currently offsetting a significant fraction of anthropogenic CO<sub>2</sub> emissions (Keenan et al., 2016). Forests play a pivotal role in this feedback response. Recent studies indicate that globally, increasing atmospheric CO<sub>2</sub> concentrations under climate change have led to increased carbon sequestration (Keenan et al., 2016) and leaf area (Zhu et al., 2016) at global scale, and higher primary production at specific sites (Reyer, 2015). Enhanced growth as a result of ecophysiological responses to a changing environment is predicted in the future (Huang et al., 2013; Pretzsch et al., 2014). However, there

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is no evidence that such positive changes will generally continue and species-specific differences as well as local growth decline due to increasing drought stress or other disturbances have also been reported (e.g., Alvarez et al., 2016; Ashraf et al., 2015; Noce et al., 2016, 2017).

Forest plays a pivotal role in this potential feedback response. About 86% of European forests and about 52% of global forests with varying intensity are managed (FAO, 2015; Meyfroidt & Lambin, 2011). Understanding if, how and to what extent different forest management practices may modify the processes that control carbon dynamics during undisturbed stand development and in response to climate change is therefore key to improving our understanding of land-based climate mitigation capacity (Bellassen & Luyssaert, 2014; Naudts et al., 2016; Nolè et al., 2013, 2015).

The ongoing open debate whether forest management practices can increase forest yields and/or carbon sequestration under changing climate conditions is thus crucial (Bellassen & Luyssaert, 2014; Lindner et al., 2014). There is in fact a long-standing interest and a pressing need for including a detailed representation of forest management in coupled land-climate models for scenario analyses (Schelhaas et al., 2015; Yue et al., 2017).

Process-based forest growth models are valuable tools to evaluate forest dynamics, development, management, and changing climate and to assess long-term effects on forest carbon cycling (Kirschbaum et al., 2012; Wang et al., 2013). Model-based assessments of climate scenarios on forest carbon balance are generally based on sound physiological knowledge, but major uncertainties surround the scaling up from the trees to ecosystem and landscapes, long-term dynamics, and the interactions between physiology and stand structural changes (De Kauwe et al., 2013; Fischer et al., 2017; Keenan et al., 2013). In particular, it is still unclear how future climate will affect the balance between photosynthesis and autotrophic respiration (Reich et al., 2016). Accurately quantifying the resulting forest productivity, which is the relatively small difference between these two large fluxes, is fundamental to the net carbon budget of forests and to the global carbon balance (Ibrom et al., 2006).

Vegetation carbon-use-efficiency (CUE), the ratio of net to gross primary productivity, is an effective metric for quantifying the interaction between plant physiology and climate. CUE reflects the fraction of photosynthesis that is not used for autotrophic respiration (Manzoni et al., 2012; Zhang et al., 2013), which is considered one of the key characteristics of both plants and ecosystem functioning (Bradford & Crowther, 2013; Zhang et al., 2013). Despite its importance, CUE is often rarely analyzed (as plant respiration) in climate change scenarios studies. CUE is known to depend on forest age (Chen & Luo, 2015; Luyssaert et al., 2007), forest structure (Goulden et al., 2011), soil fertility (but more specifically as biomass production efficiency [BPE], i.e., biomass production/gross primary production [GPP], Vicca et al., 2012), climate (Frank et al., 2015; Zhang et al., 2017), and disturbances. Therefore, CUE is a metric particularly prone to respond to changes in climate, forest development, aging, and management (Carnioli et al., 2015; Skubel et al., 2015).

Here we present a comprehensive modeling assessment of the carbon budget of managed forests as determined by the interaction among the climatic, structural, and physiological plant features such as stand development and management variables.

The objectives of the analysis are the following:

1. to evaluate model reliability when forced with both historical measured and modeled climate data compared to site measurements of GPP, net primary production (NPP), production of woody compounds ( $NPP_{wood}$ ), and autotrophic respiration ( $R_a$ );
2. to quantify the model's sensitivity to climate change and the role of warming and increasing atmospheric  $[CO_2]$  on plant physiology and functioning, and forest development;
3. to estimate variations in plant CUE and the related changes in carbon sequestration of forest ecosystems due to different climate and management scenarios (see in section 2 the description for the type of management applied).

To address these goals, we first analyze the dynamics of the main key autotrophic components of the carbon budget as the unit mass per unit area per unit time, thus GPP, NPP and  $R_a$ , and relative CUE, as well as carbon allocation. We then analyze how projected changes in CUE affect forest carbon stocks as the unit mass per unit area and the biomass annually stored (namely  $NPP_{wood}$ ) into long-lived tree woody pools (stems and

branches). We focus on the woody pools for their relatively long turnover times and capacity to potentially store assimilated carbon dioxide for many years (Hyvönen et al., 2007). Our management of the forest consists of thinning and harvesting that we analyze by studying carbon allocated into woody pools and harvested wood biomass. Both standing and harvested woody biomass are assumed here to represent a permanent carbon pool, thus reflecting the potential of forests to sequester and stock carbon (i.e., harvested biomass does not back to the atmosphere, for example, through decomposition or its usage). We also include unthinned simulations and a baseline climate and stable  $[\text{CO}_2]$  scenarios as a benchmarking reference. Note that, although important, heterotrophic and soil responses are voluntarily taken out from this analysis to deeply focus on physiological climate-induced responses of plants to climate warming,  $[\text{CO}_2]$  enrichment, and scenarios of forest management.

## 2. Materials and Methods

### 2.1. Model Description

The 3D-CMCC FEM (EuroMediterranean Centre on Climate Change Forest Ecosystem Model, Collalti et al., 2014, 2016, 2017; Marconi et al., 2017) is a stand-scale process-based model simulating photosynthesis, autotrophic respiration, and net primary productivity of representative average trees grouped into cohorts (sensu Fischer et al., 2017), at a daily temporal resolution (for a full description of model principles grounded and formulations, see Collalti et al., 2014, 2016 and Marconi et al., 2017; supporting information Table S1).

Photosynthesis is computed through the light use efficiency approach (Landsberg & Waring, 1997; Monteith, 1972; see below for an in-depth description of model formulations and implementations) where the radiation interception is represented through the Beer's law by a two-stream scheme for a single canopy divided into Sun and shaded leaves (Thornton, 2010) and horizontally crowns are distributed within the grid cell in a similar manner as in the *Perfect Plasticity Approximations* (Strigul et al., 2008).

Autotrophic respiration (as the sum of growth and maintenance respiration) is explicitly simulated and directly controlled by living biomass (see below for an in-depth description of model formulations and implementations). Growth and maintenance respiration of new and living biomass (substrate pools) are computed by each component (i.e., foliage, fine roots, and wood), following the McCree's (1970) paradigm. Changes in live woody pools are controlled annually by fixed species-specific turnover rates. Daily NPP is the result of GPP less autotrophic respiration. Allocation of assimilates to seven different pools (structural pools): that is, stems, branches, leaves, fine and coarse roots, and fruits and one nonstructural carbon compound (nonstructural carbohydrates, NSC), is done with a daily update and strongly coupled to the model's phenology scheme (Arora & Boer, 2005; Collalti et al., 2016; Marconi et al., 2017; Vacchiano et al., 2018). The carbon partitioning ratios are based on species-specific parameters that are dynamically forced by limiting factors (i.e., radiation and water availability) and by phenology (e.g., budburst; Collalti et al., 2014; Friedlingstein et al., 1998; Krinner et al., 2005). The general scheme considers, for example, that nonstructural carbon compounds have priority in carbon allocation for refilling the NSC pool followed by leaf and fine root production and only successively for the other pools (Dietze et al., 2014; Krinner et al., 2005). The ratios on which carbon is allocated for the other structural pools during the year follow the general scheme described in Friedlingstein et al. (1998) for *capturing the most limiting resources* (in our case water and light, see below for in-depth description). The relative nitrogen (N) pools, by fixed C:N ratios for each pool, are updated daily based on the relative amount of carbon in each pool. The use of allometric relationships, for example, to the calculations of monthly diameter at breast height (DBH) from the increased monthly stem biomass pool, is limited into the model avoiding that uncertainties in their usage outside the current climatic conditions, on which they were created, may falsify model results.

Water balance is computed as the balance between inflows (i.e., precipitation) and outflows (canopy evapotranspiration, soil evaporation, runoff, and/or percolation) of the daily water flows. Stomatal conductance is modeled by the Jarvis method (Jarvis, 1976) in which maximum stomatal conductance (a fixed species-specific parameter) is reduced by scaling factors controlled by environmental (e.g., temperature, vapor pressure deficit, and soil water content), as, for example, in the Biome-BGC model (Thornton et al., 2002), and structural (e.g., stand age) variables. Additionally, leaf stomatal conductance is controlled by a specific  $[\text{CO}_2]$  modifier that reduces the maximum stomatal conductance with rising  $[\text{CO}_2]$  as in Franks et al. (2013) and Hidy et al. (2016). Leaf transpiration (as also canopy and soil evaporation) is computed through the

widely used Penman-Monteith approach (Campbell & Norman, 1998; Monteith, 1965) and is computed separately for Sun and shade leaves and subsequently scaled to canopy level. Excess water from the site-specific soil field capacity is lost via runoff or percolation (not distinguished). Long-term model processes include changes in forest structure (e.g., self-pruning), changes in carbon biomass ratio (e.g., variable fraction of living cells within the sapwood biomass) and tree mortality. In 3D-CMCC FEM three different mortalities are simulated. One stochastically accounts yearly for age in which each tree, within cohorts, has a certain probability of death based on species-specific maximum age (a parameter that represents the maximum age likely to be attained by the species). The second considers the annual balance between depletion of NSC through substrate-dependent maintenance respiration and its accrual through net primary productivity; when all over the simulation period the nonstructural carbon pool is fully depleted (i.e., carbon starvation), the model removes such trees (see also Naudts et al., 2015). The third is a crowding competition (e.g., self-thinning) mortality function as described in Sitch et al. (2003) and Collalti et al. (2014).

The meteorological input data include solar radiation ( $\text{MJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ), maximum and minimum air temperature ( $^{\circ}\text{C}$ ), relative humidity (%), and precipitation (mm/day). Model initialization requires the initial stand conditions, that is, species composition, age, tree height, DBH, and stand density. Soil data include physical and chemical characteristics (e.g., soil texture, soil depth, and bulk density) as well as stand topography (e.g., latitude). The species-level parameterization includes ecophysiological traits (e.g., maximum canopy quantum efficiency and maximum stomatal conductance) and allometric characteristics (e.g., maximum and minimum crown diameter to DBH ratio).

To predict the effects of climate change and management on forests, the model version used for this study (i.e., v.5.3.3- Intersectoral Impact Model Intercomparison Project, ISIMIP) implements the current state of the art for several (offline) climate change-dependent processes that differ from previous model versions in order to

1. simulate processes occurring over medium to long time periods (more than 100 years): e.g., self-pruning and -thinning, and age-dependent mortality;
2. account for the physiological effects of rising  $[\text{CO}_2]$  (i.e., fertilization and stomatal acclimation to increasing  $[\text{CO}_2]$ );
3. account for short- to long-term thermal acclimation on maintenance respiration; and
4. account for forest management practices (i.e., thinning and final harvesting, see below for an in-depth description).

## 2.2. Main Model Implementations on the Simulation of Plant Physiology

### 2.2.1. $\text{CO}_2$ Fertilization Effects and Thermal Acclimation on Photosynthesis

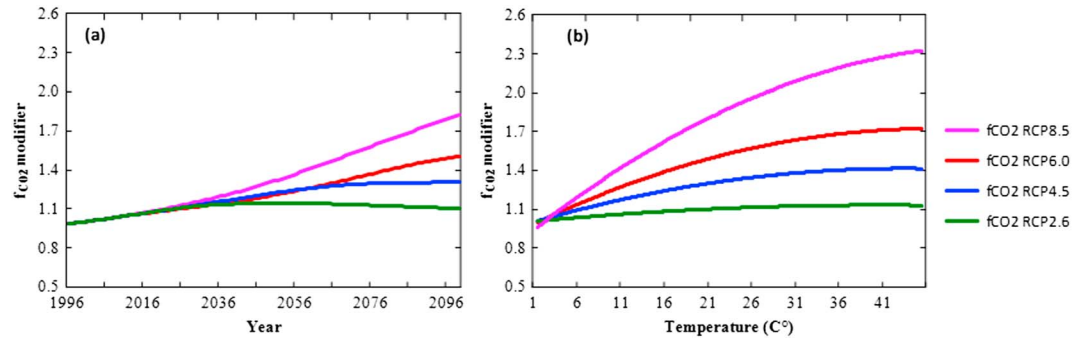
The  $\text{CO}_2$  enrichment is considered to produce a fertilization effect when the atmospheric  $\text{CO}_2$  concentration ( $[\text{CO}_{2\text{curr}}]$ , ppmv) is above the reference level for which the model has been parameterized ( $[\text{CO}_{2\text{ref}}]$ , ppmv; Ainsworth & Long, 2005; Ellsworth et al., 2010; De Kauwe et al., 2013; Medlyn et al., 2015; Nowak et al., 2004; Veroustraete et al., 2002; Zafele et al., 2014) leading to an increase in light use efficiency (Norby et al., 2005). The general equation by which 3D-CMCC FEM versions (see Collalti et al., 2014, 2016) compute daily gross primary productivity ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) is

$$\text{GPP} = \alpha_c \times \text{APAR} \quad (1)$$

where

$$\alpha_c = \alpha_x \times f_n \times (f_T \times f_{\text{CO}_2}) \quad (2)$$

$\alpha_c$  and  $\alpha_x$  are the current and maximum quantum canopy efficiencies ( $\text{mol C}\cdot\text{mol}\cdot\text{PAR}^{-1}$ ), APAR is the Absorbed Photosynthetically Active Radiation (PAR,  $\text{MJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) from the canopy and normalized modifiers ( $f_n$ ). Both modifiers are physiological (i.e., age effect) and environmental scalars (e.g., vapour pressure deficit and soil water) while  $f_T$  is the temperature scalar with values between 0 and 1 (see supporting information Table S1). In 3D-CMCC FEM the  $\text{CO}_2$  fertilization is calculated using a daily  $\text{CO}_2$  modifier ( $f_{\text{CO}_2}$ ) that increases the efficiency at which absorbed light is converted into photosynthates by increasing  $[\text{CO}_2]$  (different from other modifiers,  $f_{\text{CO}_2}$  varies from 1 to 1.x; Figure 1a) and that depends on the daily average temperature (Figure 1b). Following Collatz et al. (1991) and after Veroustraete (1994) and Veroustraete et al. (2002):



**Figure 1.** Trends for the  $f_{\text{CO}_2}$  modifier for assimilation based on the climate change using four Representative Concentration Pathways (RCPs 2.6, 4.5, 6.0, 8.5) used for forcing the model (reference  $[\text{CO}_2] = \sim 370$  ppmv): (a) variations of modifier related to changes of  $[\text{CO}_2]$  along the simulation period at fixed temperature  $20^\circ\text{C}$ ; (b) sensitivity of  $f_{\text{CO}_2}$  modifier at fixed  $[\text{CO}_2]$  (based on the 2099 values for each RCPs) and variable temperature. Parameterization for equations (1)–(4) follows from values given in Veroustraete (1994) and Veroustraete et al. (2002).

$$f_{\text{CO}_2} = \frac{[\text{CO}_2 \text{ curr}] - \frac{[\text{O}_2]}{2\tau}}{[\text{CO}_2 \text{ ref}] - \frac{[\text{O}_2]}{2\tau}} \times \frac{K_m^{\text{CO}_2} \left(1 + \frac{[\text{O}_2]}{K_o}\right) + [\text{CO}_2 \text{ ref}]}{K_m^{\text{CO}_2} \left(1 + \frac{[\text{O}_2]}{K_o}\right) + [\text{CO}_2 \text{ curr}]} \quad (3)$$

where  $[\text{O}_2]$  is the atmospheric oxygen concentration (%),  $K_m^{\text{CO}_2}$  (ppmv  $\text{CO}_2$ ) and  $K_o$  (% $\text{O}_2$ ) are the Michaelis-Menten Rubisco affinity coefficients for  $\text{CO}_2$  and the Michaelis-Menten inhibition coefficient for  $\text{O}_2$ , respectively, and  $\tau$  is the  $\text{CO}_2/\text{O}_2$  specificity ratio (dimensionless). As shown by Badger and Collatz (1977), Veroustraete (1994), and Veroustraete et al. (2002),  $K_m^{\text{CO}_2}$  and  $K_o$  are controlled by daily average temperature according to an Arrhenius relationship:

$$K_m^{\text{CO}_2} = A e^{(-E_a/(R_{\text{gas}} T_K))} \quad (4)$$

Veroustraete (1994) showed that the  $\text{CO}_2$  fertilization has two phases and hence two sets of parameters that are used in the model, based on daily average air temperature. The two phases originate from a conformational change of Rubisco in the membranes and are incorporated as functions of daily average temperature  $T_{\text{avg}}$ :

1. for  $T_{\text{avg}} \geq 15^\circ\text{C}$   $E_a = 59.4$  (KJ/mol) and  $A = 2.419 \times 10^{13}$
2. for  $T_{\text{avg}} < 15^\circ\text{C}$   $E_a = 109.6$  (KJ/mol) and  $A = 1.976 \times 10^{22}$

The inhibition constant  $K_o$  for the oxygen concentration  $\text{O}_2$  is computed as

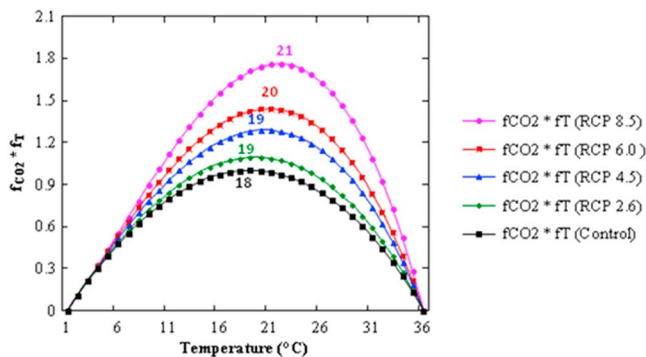
$$K_o = A_0 e^{(-E_{a0}/(R_{\text{gas}} T_K))} \quad (5)$$

with  $A_0 = 8240$  and  $E_{a0} = 13913.5$  (KJ/mol). For both the equations of  $K_m^{\text{CO}_2}$  and  $K_o$ ,  $R_{\text{gas}}$  is the gas constant ( $8.314 \text{ J}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$ ) and  $T_K$  is the daily average air temperature in Kelvin. The temperature dependence of  $\tau$  is computed as

$$\tau = A_\tau e^{(-E_{a\tau}/(R_{\text{gas}} T_K))} \quad (6)$$

wherein  $A_\tau = 7.87 \times 10^{-5}$  and  $E_{a\tau} = -42896.9$  (KJ/mol), and  $R_{\text{gas}}$  again the gas constant.

Physiological studies of leaf photosynthesis, as reported by Sigurdsson et al. (2002) and Medlyn et al. (2011), describe a strong interaction between temperature and  $\text{CO}_2$  responses. When  $f_{\text{CO}_2}$  and  $f_T$  are coupled, their interaction increases optimum temperature at which photosynthesis occurs (Figure 2), for about 1–2  $^\circ\text{C}$ , in line with the values reported by



**Figure 2.** Effects of  $f_{\text{CO}_2}$  and  $f_T$  coupling at fixed  $[\text{CO}_2]$  (based on the 2099  $[\text{CO}_2]$  values for each RCPs) and variable daily average temperature ( $^\circ\text{C}$ ) for the different RCPs. Control  $T_{\text{opt}} = 18^\circ\text{C}$ , resulting  $T_{\text{opt}}$ : RCP 2.6  $T_{\text{opt}} = 19^\circ\text{C}$ , RCP 4.5  $T_{\text{opt}} = 19^\circ\text{C}$ , RCP 6.0  $T_{\text{opt}} = 20^\circ\text{C}$ , RCP 8.5  $T_{\text{opt}} = 21^\circ\text{C}$ , with  $T_{\text{max}} = 35^\circ\text{C}$ ,  $T_{\text{min}} = 0^\circ\text{C}$ . RCP = Representative Concentration Pathway.

Battaglia et al. (1996) and Kirschbaum (2000), and, conversely,  $f_{\text{CO}_2}$  is downregulated, increasing distance from the optimum temperature.

The equation by which all 3D-CMCC FEM versions consider the dependency of photosynthesis to daily temperature, following Waring and McDowell (2002), is given by

$$f_T = \left( \frac{T_{\text{avg}} - T_{\text{min}}}{T_{\text{opt}} - T_{\text{min}}} \right) \left( \frac{T_{\text{max}} - T_{\text{avg}}}{T_{\text{max}} - T_{\text{opt}}} \right)^{\frac{(T_{\text{max}} - T_{\text{opt}})}{(T_{\text{opt}} - T_{\text{min}})}} \quad (7)$$

where  $f_T$  is a daily value (0–1) and  $T_{\text{max}}$ ,  $T_{\text{min}}$ ,  $T_{\text{opt}}$  are maximum, minimum, and optimum temperatures for gross assimilation ( $f_T = 0$  if  $T_{\text{avg}} \leq T_{\text{min}}$  or  $T_{\text{avg}} \geq T_{\text{max}}$ ).

### 2.2.2. Autotrophic Respiration and Its Thermal Acclimation

Maintenance respiration ( $R_m$ ) uses a  $Q_{10}$  relationship with temperature and nitrogen content of live tissues for each tree structural pool. Hence, all species, when respiration is assessed on a proportional basis, exhibit similar degrees of change while, on an absolute basis, the degrees of change is higher for species with the highest N concentration. The model uses different temperature for different organs as, for example, soil temperature for coarse and fine roots, daytime and nighttime temperature for leaves, and daily average temperature for stem and branch respiration. Temperature responses of respiratory  $\text{CO}_2$  efflux rates from plants, soils, and ecosystems are frequently modeled through exponential functions with a constant  $Q_{10}$  value (Reich et al., 2016). This fixed  $Q_{10}$  temperature sensitivity parameter ( $= 2.0$ ; Chen & Zhuang, 2013; Smith & Dukes, 2012; Thornton, 2010) implies that respiration increases exponentially with temperature leading to a gross overestimation or underestimation larger at local scale rather than at global scale (Atkin et al., 2008; Kattge et al., 2009). As discussed by Tjoelker et al. (2001) and Smith and Dukes (2012) there is a compelling body of evidence that plants acclimate, and at the same time there is clear evidence that respiratory  $Q_{10}$  is not likely to be constant but rather depends on both the shape of the temperature-response curve and the range of temperatures used in its empirical determination. It is obvious that extrapolation beyond this range is speculative. Therefore, we included the  $Q_{10}$  modification proposed by Tjoelker et al. (2001), Atkin and Tjoelker (2003), and recently by Smith and Dukes (2012) that more closely matches the instantaneous response of maintenance respiration ( $R_{mTx}$ ,  $\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ; i.e., *Type-I* or *short-term* acclimation, sensu Atkin et al., 2008, 2005; Atkin & Tjoelker, 2003) within the calculation expressed by the two following equations:

$$Q_{10} = 3.22 - 0.046T_x \quad (8)$$

and

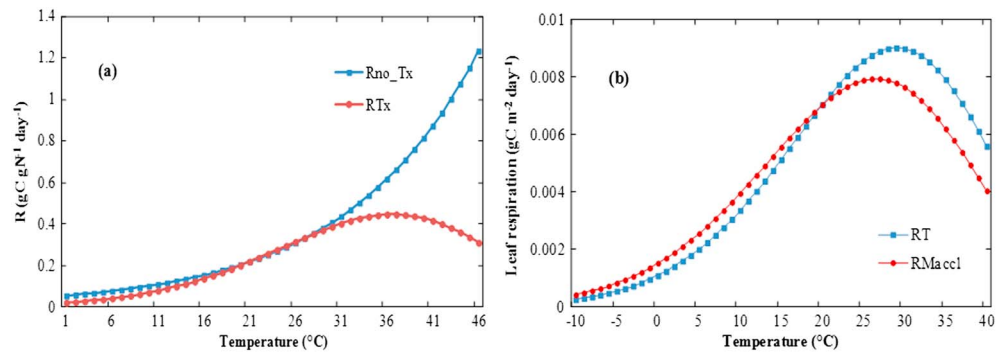
$$R_{Tx} = R_{\text{ref}} Q_{10}^{\left(\frac{T_x - T_{\text{ref}}}{10}\right)} \quad (9)$$

where  $R_{\text{ref}}$  is the basal respiration rates ( $0.218 \text{ g C}\cdot\text{g N}^{-1}\cdot\text{day}^{-1}$ ; Ryan, 1991a; Thornton et al., 2007) at the reference temperature  $T_{\text{ref}}$  ( $= 20^\circ\text{C}$ ; Reich et al., 2016; Thornton et al., 2007). Maintenance respiration for each pool  $x$  is computed as in Cox (2001) based on tissue nitrogen amount ( $N_x$ ,  $\text{g N}\cdot\text{m}^{-2}$ ) within each live biomass pool such that

$$R_{mTx} = R_{Tx} N_x \quad (10)$$

This leads to a decrease in respiration to an increase in temperature at a peak temperature of  $\sim 35^\circ\text{C}$  (as in Smith & Dukes, 2012) via a sixth-degree polynomial function, and it reflects an instantaneous response of respiration to temperature as a biochemical adjustment to this stimulus (Atkin & Tjoelker, 2003; Figure 3a).

The second modification implemented within the model represents the likely result of a biogeochemical plant adjustments and/or biogeochemical feedbacks in the long-term response of respiration rates to temperature ( $R_{\text{Maccl}}$ ,  $\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ; i.e., *Type-II* or *long-term* acclimation, Atkin et al., 2008, 2005; Atkin & Tjoelker, 2003) that leads to a decrease in the temperature-mediated basal rate response curve with increasing temperature as described by Smith and Dukes (2012) through



**Figure 3.** (a) Type-I or short-term acclimation. Comparison of  $Q_{10}$  respiration rate function at varying temperature with no modification (fixed  $Q_{10}$ )  $R_{no\_Tx}$  ( $Q_{10} = 2.0$ ) versus modified (variable  $Q_{10}$ )  $RT_x$  ( $Q_{10} = 3.22 - 0.046T_x$  as in Smith & Dukes, 2012; for both  $R_{refx} = 0.218 \text{ g C g N}^{-1} \cdot \text{day}^{-1}$ ,  $T_{ref} = 20 \text{ }^\circ\text{C}$ , Collalti et al., 2016; Ryan, 1991a; Thornton et al., 2007). (b) Type-II or long-term acclimation. Comparison of daily leaf temperature respiration responses including only Type I ( $RT$ , blue line) and Type-I + Type-II acclimation ( $R_{Maccl}$ , red line). Temperature refers to 10-days average temperature.

$$R_{Maccl} = R_{mT_x} 10^A (T_{10\text{days}} - T_{Ref}) \quad (11)$$

where  $A$  represents a constant temperature correction factor for acclimation ( $-0.00794$ , Atkin et al., 2008, Smith & Dukes, 2012; Figure 3b) and  $T_{10\text{days}}$  the preceding 10 days average daily temperature. Growth respiration (or synthesis respiration;  $R_g$ ,  $\text{g C m}^{-2} \cdot \text{day}^{-1}$ ) is assumed into the model to decrease linearly with aging, from 35% to 25% of the daily assimilates used for structural growth (Larcher, 2003), and is temperature independent (Amthor, 2000). No direct effects of increased  $[\text{CO}_2]$  are modeled since Free-Air Carbon dioxide Enrichment (FACE) experiments, increased respiration rate under elevated  $\text{CO}_2$  was primarily due to increased biomass, and no change in growth respiration rate was observed as reported by Hamilton et al. (2001).

### 2.3. Site Description

The simulation experiments are applied to three European forests sites of the Fluxnet network included within the ISIMIP: a Danish temperate European Beech (*Fagus sylvatica* L.) forest (Sorø, Pilegaard et al., 2011), a Norway Spruce (*Picea abies* (L.) H. Karst) stand in Czech Republic (Bílý Kříž, Godbold et al., 2015), and a Finnish boreal Scots pine (*Pinus sylvestris* L.) forest (Hyytiälä, Makela et al., 2006). These forests are all intensively monitored research sites that represent managed forests of the most common European deciduous and coniferous forest species (Table 1). Moreover, for these sites soil, stand, climate, eddy covariance measurements, and biometric data are available. Species-specific model parameters are reported in Collalti et al. (2014, 2016), whereas details on the observed management during the current simulation period were provided by the site Principal Investigators (henceforth PIs).

### 2.4. Simulation Experiment Design

We performed 100 simulations for each site, combining different components (stable  $[\text{CO}_2]$  or not, thinning interventions or not, and five Earth System Model climate forcing data sets with four different Representative Concentration Pathways, RCPs) including a *no climate change* reference scenario to disentangle the effects of each single component on modeled key variables and model sensitivity by combining

1. five different ESMs climate output data to provide climate boundary conditions and to test the sensitivity of results against different input climate forcing;
2. two  $[\text{CO}_2]$  options: stable  $\text{CO}_2$  after 2000 or varying consistently with RCPs;
3. four different forcing scenarios (RCP2.6, RCP4.5, RCP6.0, and RCP8.5) to test model's sensitivity to warming and  $[\text{CO}_2]$ ;
4. two management options: a control, interrupting management (i.e., leaving the stand to develop with no thinning from 1997, namely *natural* or *unthinned*), and the Business-As-Usual (BAU) management to assess the effects of such management on forests (see below for an in-depth description); and
5. finally, to consider the case of no climate change as a benchmark, the 1997–2005 scenario was randomly repeated up to 2099. This additional climate simulation was named Control (*baseline* climate), and the

**Table 1**  
Sites Description and Stand Initialization Data Used in Simulations (Data Corresponds to the Year 1997)

Site name	Species	Climate	DBH (cm)	Age	Tree height (m)	Density (trees/ha)	LAI (m <sup>2</sup> /m <sup>2</sup> )	Soil type	Reference
Sorø	<i>F. sylvatica</i> L.	Cool temperate, suboceanic	25	80 (even aged)	25	400	5	Mollisoil rich in clay(8–23%)	Dalsgaard et al. (2011), Pilegaard et al. (2011)
Hyytiälä	<i>P. sylvestris</i> L.	Boreal	10.3	28 (even aged)	10	1,800	3	Podzol with sandy and coarse silty glacial till	Mencuccini and Bonosi (2001), Makela et al. (2006)
Bílý Kříž	<i>P. abies</i> L.	Cold continental	7.1	16 (even aged)	5.6	2,408	7.5	Mesozoic Godulas sandstone	Godbold et al. (2015)

Note. DBH = diameter at breast height; LAI = leaf area index.

[CO<sub>2</sub>] in this case was held constant to the value of year 2000 (368.86 ppmv) or let it varies accordingly to the value of the specific year.

The year 1997 was considered as the starting year of the climate series for all sites, consistent with the availability of measured stand data. Simulations were performed up to 2099 with the aim to cover the most economic rotation length for each species (i.e., the rotation age at which the economic revenue of the wood yield literature suggests to be maximized, in our case at Sorø 140 years).

From these simulations, model outputs have been extracted and used for model evaluation (one data set for each ESM) for the period 1997–2005. The model outputs after 2005 were excluded from model evaluation since 2006; the climate data transitions to scenario are forced by different [CO<sub>2</sub>].

We organized the analysis in a factorial design (Mason et al., 2003) across the matrix of the components (100 factorial combinations for each site) to identify the most influential ones that drive model results (supporting information S3).

## 2.5. Forest Management

Forest management represents an anthropogenic perturbation to the natural dynamic of the ecosystem. The Intergovernmental Panel on Climate Change guidelines define managed land as the area *where human interventions and practices have been applied to perform production, ecological, or social functions* (IPCC, 2006).

We implemented a simple BAU management routine that basically simulates an *intensive even-aged approach* forest management following Dunker et al. (2012) through thinning and, at the rotation period, through harvesting, as observed at each of the sites analyzed. Thus, in the present work, forest *management* represents thinning and harvesting practices. These management guidelines differ for each site and species and are characterized by

1. *thinning intensity* (i.e., percentage of stand basal area to remove based on total stand basal area),
2. *Thinning interval* (i.e., years between operations), and
3. *Rotation age* (i.e., stand age at which the final harvest occurs)

Both thinning and harvesting occur at the end of the year and to close both daily, monthly and annual carbon budget, such pools are accounted for before their removal.

For the Sorø site we used the variable values as described for *F. sylvatica* by Cescatti and Piutti (1998) and Hein and Dhote (2006) that closely match with the historical management practices observed also in Sorø (thinning intensity 30% of standing basal area, interval 15 years, stand age for final harvest 140 years).

For the evergreen sites we use the values described in Lasch et al. (2005) and Fürstenau et al. (2007) which, on average report, have a thinning intensity of 30%, an interval of 15 years, and a stand age for final harvest of 120 years for Norway spruce and a thinning intensity of 20%, an interval of 15 years, and a stand age for final harvest of 140 years for Scots pine. To stay compliant with the history of management observed at these sites, harvesting has not been simulated since both Bílý Kříž and Hyytiälä did not reach the age for final felling as Sorø did during simulation. When the stand age for final harvest is reached in Sorø, all trees are completely removed; the below ground fraction into the soil is not taken



into account by the model. At the year after harvesting, the plot is replanted with new trees of the same species (i.e., 6000 trees/ha, dbh = 1 cm, tree height = 1.3 m, and age = 5 years, as described by personal communications with PIs site and as adopted into the ISIMIP protocol) covering mandatory model initial variables needed for model runs.

Our management guidelines are the same as those adopted by the models participating in the ISIMIP. We note that we examine sensitivity to climate and management using synthetic management strategies and do not attempt to replicate a site-specific management scheme. We are aware that forest management may comprise other operations such as soil preparation, ground vegetation control, fire control, drainage, and pest control, which are not, however, considered in this study. Natural regeneration was also not considered since it was not observed in the stands.

### 3. Climate and Evaluation Data

We used climate simulation data from the ISIMIP Fast Track initiative (<https://www.isimip.org/>, Warszawski et al., 2014), based on the Climate Model Intercomparison Project 5 in which Earth System Models (ESMs), were driven by four RCPs associated with different scenarios of greenhouse gas concentrations, namely RCP2.6, RCP4.5, RCP6.0, and RCP8.5 (Moss et al., 2010; van Vuuren et al., 2011; supporting information S1). ISIMIP provides climate simulations under all these RCPs for five ESMs (HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, GFDL-ESM 2M, and NorESM1-M), whose data (1950–2099) were bias corrected and downscaled to a common grid resolution of  $0.5^\circ \times 0.5^\circ$  according to Hempel et al. (2013) (for the ISIMIP ESMs representativeness see McSweeney & Jones, 2016). In terms of meteorological input data for 3D-CMCC-FEM, temperatures, precipitation, and radiation were available as bias-corrected/downscaled variables, while uncorrected values for relative humidity have been used. Climate variables for the selected forest stands were extracted from the grid cell of the downscaled climate forcing data set in which each stand is located.

Model evaluation was performed by comparing simulated GPP against the eddy covariance estimates (night-time method with constant USTAR, Reichstein et al., 2005) as reported in the FLUXNET2015 data set (<http://fluxnet.fluxdata.org/>) for the period 1997–2005. Daily GPP data with low-quality check values (less than 0.5; Papale et al., 2006) were removed from both the measured and modeled data sets. We are aware that eddy covariance GPP is derived from net ecosystem exchange measurements and is not a directly measured flux although it is strongly based on direct measurements (however, for former net ecosystem exchange model validation and discussion, see Marconi et al., 2017). The use of eddy covariance GPP in modeling is, however, largely adopted as testing variable for model robustness (e.g., Bonan et al., 2012).

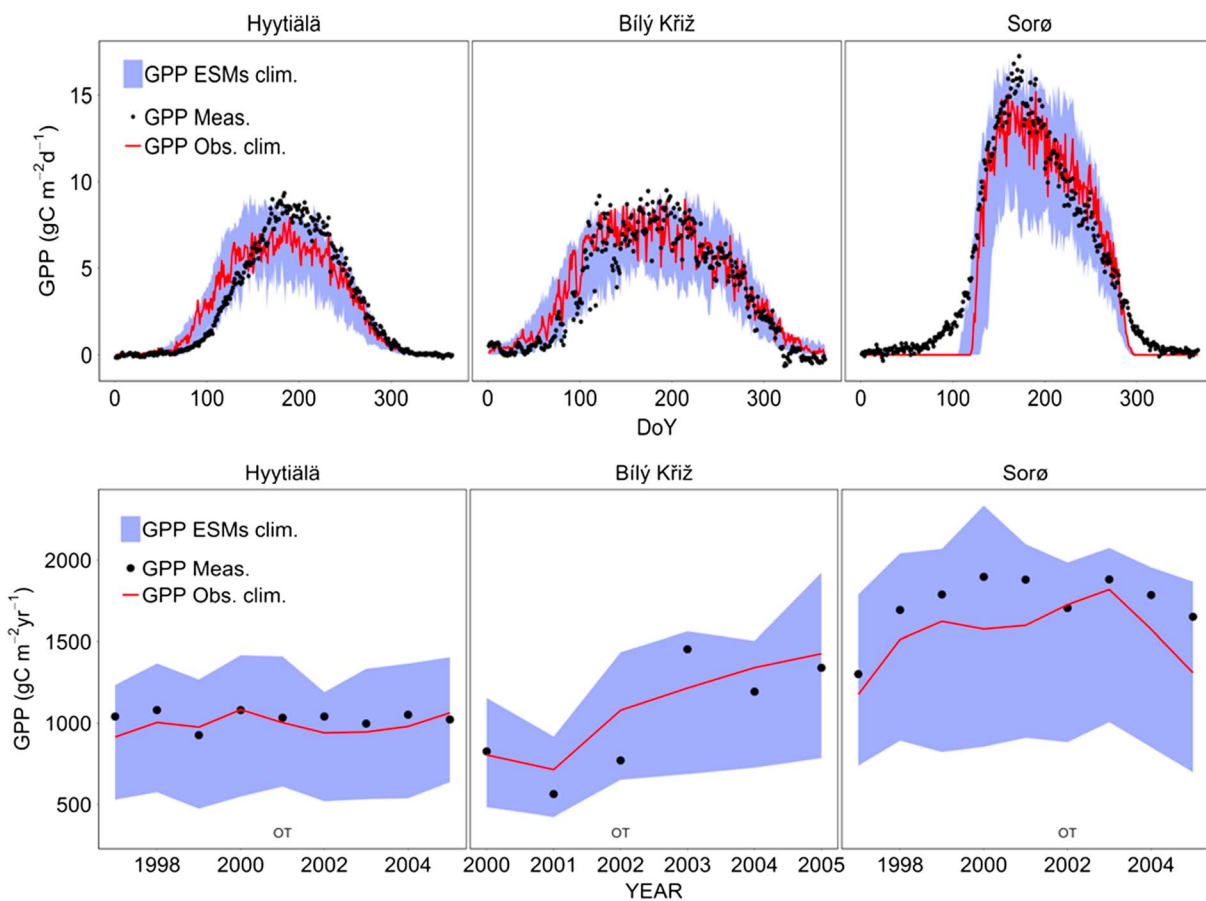
Additionally, we compared each model output produced for each site with the five ESMs available up to 2005; subsequent years were excluded from the comparison since the scenario period in the ESMs starts in 2006, and hence, ESMs are driven by different  $[\text{CO}_2]$  pathways after 2006. Even though the climate pathway in the historical ESM simulations does not reflect the actual observed climate pathway, the bias correction ensures that the simulated climate matches the observed climate on average. Simulated  $\text{NPP}_{\text{wood}}$  was evaluated using data provided by site PIs, while  $\text{NPP}$  and  $R_a$  were evaluated using literature data. In order to check the reliability of meteorological data obtained from downscaling coarse models, we additionally compared the mean daily temperature and precipitation from the ensemble of the ESMs with measurements collected over the three selected sites.

## 4. Results

We focus on the following key variables of the autotrophic ecosystem carbon budget: gross photosynthesis, autotrophic respiration, net primary productivity, carbon use efficiency (CUE) and tree woody stocks (i.e., stems, branches, and coarse roots), and carbon fluxes to tree woody compounds (i.e.,  $\text{NPP}_{\text{wood}}$ ). For each of these variables we first present the intercomparison of model simulation with site observations and then explore the future trends under thinned and unthinned scenarios.

### 4.1. Evaluation

The comparison of GPP simulated by 3D-CMCC-FEM and forced by five ESMs with eddy covariance data over the 1997–2005 historical period shows that the model satisfactorily reproduces the daily GPP cycle at the



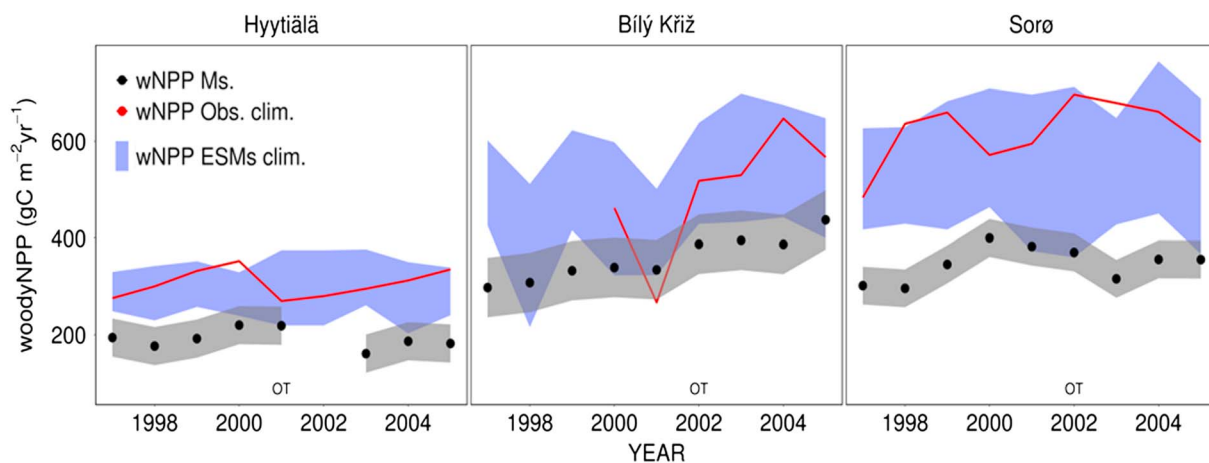
**Figure 4.** Validation for seasonal and annual GPP trends. Top row shows the seasonal course of average daily GPP over the years, bottom row the temporal trend of annual GPP (DoY = day of year). Shaded area represents the maximum and minimum bounds of GPP values among the five ESMs used to force the model (GPP ESM clim.), red line represents the average GPP values when model is forced by observed climate (GPP Obs. clim.), and black dots represent the quality checked and filtered GPP values evaluated at the sites by the eddy covariance technique (GPP Meas.). OT = observed thinning; ESMs = Earth System Models; GPP = gross primary production.

three selected sites (Hyttiälä  $R^2 = 0.78$ , Bílý Kříž  $R^2 = 0.59$ , and Sorø  $R^2 = 0.83$ ); the correlations of 3D-CMCC-FEM forced by climate models are only marginally lower than the same correlations obtained by forcing the model with measured climate data (Hyttiälä  $R^2 = 0.84$ , Bílý Kříž  $R^2 = 0.68$ , and Sorø  $R^2 = 0.89$ ), implying both reliable meteorological forcing and overall model predictability. The model reproduces seasonal GPP changes reasonably well, and it correctly identifies the start and the end of the growing season (Figure 4, top row); the root-mean-square error obtained from daily data is  $1.55 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  for Hyttiälä,  $2.51 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  for Bílý Kříž, and  $2.5 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  for Sorø (supporting information S2).

Observed GPP falls inside the range of variability of the different ESMs, identified by the shaded area in Figure 4 (bottom row and supporting information S2).

Modeled autotrophic respiration rates in the historical period are in line with the autotrophic respiration data reported by Granier et al. (2008) for a beech forest (on average  $751 \pm 52$  versus modeled  $730 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ ) and by Luyssaert et al. (2007) for both boreal evergreen forests ( $558 \pm 24.5$  versus modeled  $489 \pm 83 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ ) and temperate humid evergreen forests ( $726 \pm 110$  versus  $951 \pm 114 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ ).

Modeled NPP (here defined as biomass production plus NSC) during the historical period agreed with data reported by different studies (e.g., Wu et al., 2013). At Sorø and for temperate deciduous forests NPP was  $778 \pm 133 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  modeled versus  $708 \pm 65 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  measured, at Hyttiälä and for boreal evergreen forests  $423 \pm 54 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  modeled versus  $366$  and  $334 \pm 55 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  measured, and for temperate spruce forest at Bílý Kříž  $619 \pm 89 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  modeled versus  $611 \pm 45 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$



**Figure 5.** Comparison of the predicted annual  $\text{NPP}_{\text{woody}}$  values with site observations for the period 1997–2005. Shaded area represents the maximum and minimum bounds of  $\text{NPP}_{\text{woody}}$  values among the five ESMs used to force the model (GPP ESM clim.); red line represents the average  $\text{NPP}_{\text{woody}}$  values when model is forced by observed climate (GPP Obs. clim.). Black dots represent the measured  $\text{NPP}_{\text{woody}}$  values (GPP Meas.), and the gray shaded area represents the relative uncertainty bounds (Campioli et al., 2016; Luyssaert et al., 2007). Observed data for year 2002 at Hyytiälä was missing. OT = observed thinning; ESM = Earth System Model; GPP = gross primary production; NPP = net primary production.

measured. Modeled  $\text{NPP}_{\text{woody}}$  values in the historical period are fairly close to the values measured at sites. Comparison of 1997–2005 measured to modeled data shows that the model tends to overestimate  $\text{NPP}_{\text{woody}}$  at Sorø for  $198 \pm 92 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , at Hyytiälä for  $97 \pm 47 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , and at Bílý Kříž for  $121 \pm 45 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (Figure 5).

Modeled annual CUE in the historical period ranges between 0.46 and 0.53 at Sorø, which is close to the bounds of 0.45 and 0.50 described by Wu et al. (2013) and Knohl et al. (2008) for beech sites. For Hyytiälä modeled CUE is  $\sim 0.44$ , in the range of 0.32 reported by Xiao et al. (2003), and 0.45–0.65 by Vanninen and Mäkelä (2005) for Scots pine. For Bílý Kříž, modeled CUE is  $\sim 0.45$ , similar to reports for other Norway spruce stands (0.45–0.5) published by Luyssaert et al. (2007) and Tang et al. (2014) and those formerly described in Marconi et al. (2017).

## 4.2. Future Projections

### 4.2.1. Gross Primary Productivity

In our simulations GPP is projected to increase in the future relative to the control and exhibits a monotonic increase with  $[\text{CO}_2]$  and warming in all scenarios. One important factor affecting GPP is growing season length. Interestingly, in the near future (NF, 2020–2050) the length of the growing season for Sorø and Bílý Kříž (defined here as the period for conifers in which daily GPP is larger than zero) is similar across all RCPs and longer compared to the baseline control. At these two sites the growing season length is predicted to increase by  $\sim 15$  days until 2050 across all RCPs and in the far future (FF, 2070–2099) by 20–60 days depending on the RCP used. At Hyytiälä the length of the growing season increases on average by 31 days across all RCPs until about 2050, and, on average, by 42 days at the end of the century. It is noteworthy that the variability of the length of growing season is strongly related to the variability among ESMs in distributing temperature seasonality throughout the year.

Thinning effects on GPP are evident for all sites and RCPs and are more apparent at Sorø during harvesting (which in the BAU management occurs at Sorø in 2061–2062, when the beech forest is  $\sim 140$  years old), resulting in a stronger reduction of GPP for the subsequent years (harvesting has not been simulated at the other two sites since they did not reach the age for final felling). Reduction of GPP caused by harvesting is however only partially compensated over the few subsequent years by increased photosynthesis (that is more rapid with increasing warming and raising  $[\text{CO}_2]$ ) from the remaining trees and that accounts for  $\sim 420 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (18%) less GPP when compared in the FF to unthinned scenarios. At canopy closure, GPP increases monotonically, driven by warming and raising  $[\text{CO}_2]$  following the patterns of unthinned simulations. At Hyytiälä in the NF, GPP decreases by about  $205 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  ( $\sim 14\%$ ) in management scenarios, but in the FF it is projected to increase by on average for about  $370 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  ( $\sim 18\%$ ) when compared

**Table 2**

Percentage of Changes for Mean GPP,  $R_a$ , NPP, CUE,  $NPP_{wood}$ , and Carbon Woody Stocks Between Thinned Versus Unthinned Simulations for Near Future (NF, 2020–2050) and Far Future (FF; 2070–2099) Time Windows

RCP	Hyttiälä		Bílý Kříž		Sorø	
	Mean NF	Mean FF	Mean NF	Mean FF	Mean NF	Mean FF
$\Delta GPP\%$						
Control	–14.66	–18.28	–10.68	–13.68	–4.17	–38.55
RCP2.6	–13.70	19.50	–9.78	–13.34	–3.26	–26.71
RCP4.5	–13.65	18.55	–9.84	–12.41	–3.15	–19.12
RCP6.0	–13.75	17.85	–10.00	–11.89	–3.11	–17.38
RCP8.5	–13.45	17.30	–9.43	–11.81	–3.19	–11.21
AVG	–13.64	18.30	–9.76	–12.36	–3.18	–18.61
$\Delta R_a\%$						
Control	–20.27	–25.44	–19.19	–26.39	–18.31	–67.41
RCP2.6	–19.53	–23.47	–17.95	–26.10	–16.99	–60.21
RCP4.5	–19.53	–22.78	–18.03	–24.96	–16.75	–53.53
RCP6.0	–19.56	–22.46	–18.05	–24.28	–16.82	–51.28
RCP8.5	–19.38	–22.52	–17.39	–24.49	–16.78	–45.98
AVG	–19.50	–22.81	–17.85	–24.96	–16.83	–52.75
$\Delta NPP\%$						
Control	–3.84	–2.31	5.19	15.08	20.88	29.06
RCP2.6	–1.69	2.07	6.26	19.49	20.97	63.41
RCP4.5	–1.61	3.22	6.26	20.02	20.52	66.41
RCP6.0	–2.11	2.96	5.35	19.68	20.73	61.86
RCP8.5	–1.30	7.62	5.89	25.16	20.17	77.30
AVG	–1.68	3.97	5.94	21.09	20.60	67.24
$\Delta CUE\%$						
Control	12.56	19.68	18.28	33.99	27.14	113.92
RCP2.6	13.75	22.24	18.43	38.50	26.14	128.13
RCP4.5	13.64	22.40	18.40	37.84	25.09	110.62
RCP6.0	13.19	21.38	17.52	36.57	25.38	101.42
RCP8.5	13.69	26.25	17.53	42.61	24.70	106.84
AVG	13.57	23.07	17.97	38.88	25.32	111.75
$\Delta NPP_{wood}\%$						
Control	7.08	18.59	13.16	31.32	33.26	71.29
RCP2.6	9.21	25.11	11.96	34.37	27.65	110.56
RCP4.5	8.95	24.42	11.98	32.28	26.54	91.47
RCP6.0	8.31	20.92	10.96	29.57	27.51	76.93
RCP8.5	8.86	28.23	10.28	35.27	25.32	90.40
AVG	8.83	24.67	11.30	32.87	26.76	92.34
$\Delta$ Carbon woody stock%						
Control	6.90	41.58	12.32	41.45	9.34	38.09
RCP2.6	7.40	44.62	15.31	45.16	9.28	41.48
RCP4.5	7.49	44.98	15.52	45.15	8.95	40.59
RCP6.0	7.30	43.82	15.07	43.68	9.23	38.94
RCP8.5	7.50	45.71	15.19	44.99	9.01	41.38
AVG	7.42	44.78	15.27	44.74	9.12	40.60

Note. Average values are computed across ESMs considering the four RCPs. Positive values indicate a positive effect of management. ESMs = Earth System Models; RCPs = Representative Concentration Pathways; CUE = carbon use efficiency; NPP = net primary production; NF = near future; FF = far future; GPP = gross primary production.

to unthinned ones (Table 2 and supporting information S4). Bílý Kříž shows a similar behavior to Sorø with lower values of GPP when compared to unthinned simulations both in the NF ( $\sim 186 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ,  $\sim 10\%$ ) and in the FF ( $\sim 260 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ,  $\sim 12\%$ ). In summary, GPP increases at each site with the effects of rising  $[\text{CO}_2]$  and warming, largely in unthinned simulations rather than in managed ones. Absolute values for GPP across different setup combinations and scenarios are in depth shown in the supporting information (S5, S6, S7, S8).

#### 4.2.2. Autotrophic Respiration

Modeled autotrophic respiration at each site tends to clearly increase with temperature. Without thinning, autotrophic respiration increases with biomass accumulation due to warming and then stabilizes with

increasing mortality. When thinning is simulated, modeled  $R_a$  exhibits a saw-tooth behavior at all sites: for a couple of years after thinning a decrease in  $R_a$  occurs, followed by a subsequent increase that strongly depends on the RCP used. These trends are stronger at Sorø rather than at Hyytiälä due to a higher thinning intensity (30% versus 20% of standing basal area, i.e., higher removed biomass) and higher standing biomass. When compared to unthinned simulations, across the full suite of ESMs and RCPs,  $R_a$  decreases on average from 224 (~18%) to 385 g C·m<sup>-2</sup>·year<sup>-1</sup> (~25%) at Bílý Kříž in the NF and FF, respectively, from 178 (~19%) to 301 g C·m<sup>-2</sup>·year<sup>-1</sup> (~23%) at Hyytiälä, and from 208 (~16%) to 875 g C·m<sup>-2</sup>·year<sup>-1</sup> (~52%) at Sorø, respectively (Table 2 and supporting information S4). In summary,  $R_a$  decreases in unthinned simulations with respect to thinned ones as the results of reduced biomass per unit area, while warming tends generally to increase autotrophic respiration per unit of biomass. Absolute values for  $R_a$  across different setup combinations and scenarios are in depth shown in the supporting information (S5, S6, S7, and S8).

#### 4.2.3. Net Primary Productivity

At all sites NPP is projected to increase with rising [CO<sub>2</sub>] both with and without thinning; conversely, when [CO<sub>2</sub>] is maintained at the current level, a general decline is foreseen with the exception of Sorø. Considering the mean across ESMs for each RCP, the positive spikes in NPP following thinning increase with greater warming. Compared to the unthinned case, the decrease of NPP due to forest development is effectively counterbalanced by thinning. At Sorø management practices enhance NPP on average by ~21% in the NF and by ~67% in the FF across ESMs and RCPs (relative to the unthinned scenario). When compared to unthinned cases, NPP shows positive trends across all RCPs also for Bílý Kříž and Hyytiälä. In the NF, NPP at Bílý Kříž is projected to increase on average by 6%, while at Hyytiälä it weakly decreases (~2%). In the FF, NPP is projected to increase at both evergreen sites, from ~19% to ~25% at Bílý Kříž and from ~2% to ~8% with RCP8.5 at Hyytiälä (Table 2 and supporting information S4). Absolute values for NPP across different setup combinations and scenarios are in depth shown in the supporting information (S5, S6, S7, S8).

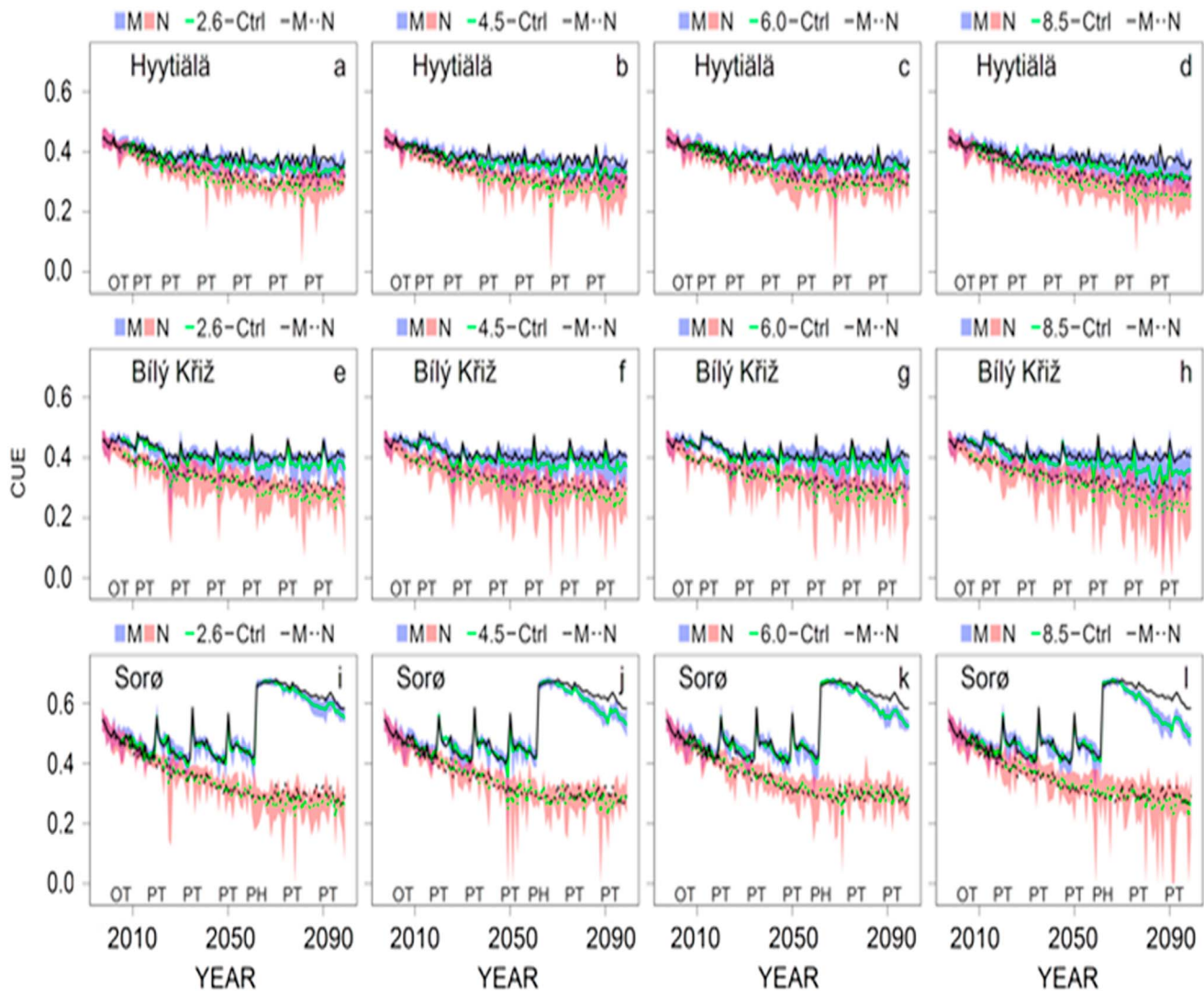
#### 4.2.4. Carbon Use Efficiency

Without thinning CUE is generally projected to slightly decrease with increasing warming. At each site when thinning is not simulated, the lowest values are modeled in the years at the end of the rotation period, down to 0.28 at Sorø and 0.27 at both Hyytiälä and Bílý Kříž sites at the end of simulation period, respectively, which roughly corresponds to ~0.2 units less than at the beginning of simulation. At Sorø, when thinning is considered (supporting information S5 and S7), CUE varies little across the full suite of ESMs, conversely, we found a large variability across RCPs, especially after harvesting, suggesting that CUE is highly responsive to this forest management practice and to stand development and that climatic changes may strengthen these effects. For the period 2070–2099 (i.e., after harvesting), CUE increases up to 0.61 (RCP2.6) and to 0.57 (RCP8.5), an increase twofold compared to unthinned simulations. At Hyytiälä CUE varies only from 0.35 (RCP6.0) to 0.32 (RCP8.5) at the end of century, decreasing from ~0.37 computed during the NF period (Figure 6 and supporting information S6 and S8).

When compared to simulations with the forest left undisturbed, the increase in CUE is ~16% in the NF and ~23% for the FF, respectively, across RCPs. At Bílý Kříž reductions in CUE with thinning are larger for the FF with increasing climate warming, varying from 0.38 with RCP2.6 to 0.35 with RCP8.5, corresponding to a reduction of less than 0.1 units, but still corresponding to ~38% and ~43% when compared to unthinned scenarios (Table 2 and supporting information S4). In summary, in unthinned simulations CUE decreases with stand development, but both thinning and climate change compensate for this trend. Absolute values for CUE across different setup combinations and scenarios are in depth shown in the supporting information (S5, S6, S7, S8).

#### 4.2.5. NPP<sub>wood</sub> and Carbon Woody Stocks

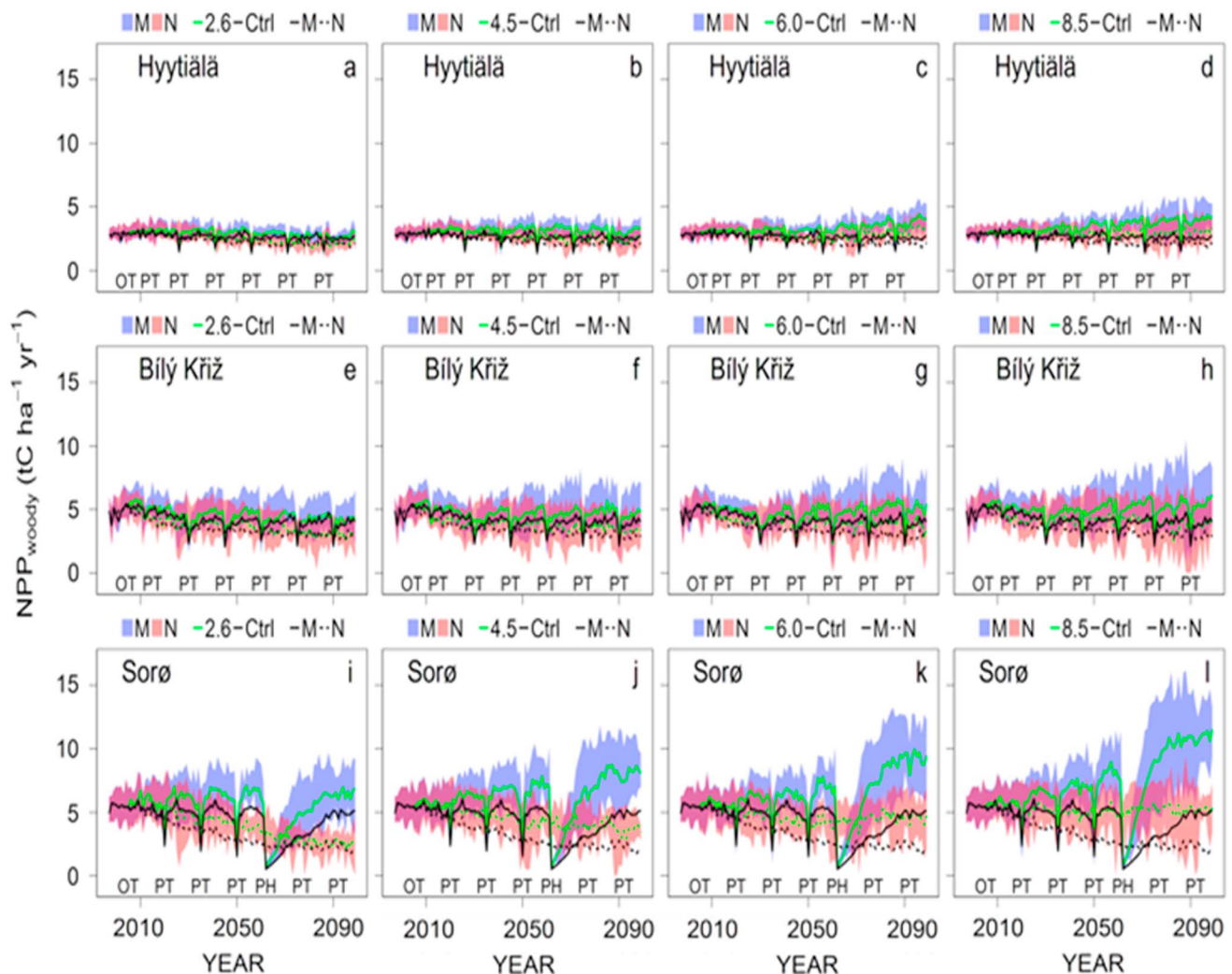
In all simulations, the annual carbon allocated in woody pools and stocks increases with warming and with or without thinning, compensating for age related decline in baseline climate scenarios. Thinning increases the total carbon production at all sites with large variability among ESMs and RCPs. This is more evident at Sorø, where NPP<sub>wood</sub> increases across RCPs, when compared to unthinned conditions, which increases in the NF and FF 1.29 (~27%) and 3.67 t C·ha<sup>-1</sup>·year<sup>-1</sup> (~92%), respectively (Table 2 and supporting information S4). At each temporal time frame (NF and FF) variability in NPP<sub>wood</sub> increases, when compared to natural forest evolution, is fairly weaker to the variability found, across RCPs, for Sorø from on average from 0.39 (~11%)



**Figure 6.** Time series of mean annual CUE over the simulation period. Blue shaded area represents the maximum and minimum values for among ESMs and RCPs when management is considered (M), and red shaded area represents when management is not considered (N). Solid lines represent the average annual values among ESMs for each control (Ctrl) and RCP scenario when management is simulated, and dashed lines represent when management is not simulated (OT = observed thinning, PT = prescribed thinning, PH = prescribed harvesting). (a, e, and i) Simulations under RCP2.6 scenario; (b, f, j) RCP4.5 scenario; (c, g, k) RCP6.0 scenario; and (d, h, l) RCP8.5 scenario. ESMs = Earth System Models; CUE = carbon use efficiency; RCPs = Representative Concentration Pathways.

to  $1.19 \text{ t C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  (~33%) for Bílý Kříž and from on average from  $0.25$  (~9%) to  $0.65 \text{ t C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  (~25%) for Hyttiälä, respectively (Figure 7).

Carbon stocks in woody components (i.e., standing plus harvested woody biomass) increase, across sites and RCPs, in comparison to baseline climate and even more when compared to conditions where management is not simulated, while no appreciable differences among climate scenarios are simulated (Figure 8). Carbon woody stocks increase with thinning, and across RCPs, from ~9% to ~40% (corresponding to 27 and  $175 \text{ t C/ha}$ , respectively) at Sorø, from ~7% to ~45% (corresponding to 12 and  $100 \text{ t C/ha}$ , respectively) at Hyttiälä, whereas at Bílý Kříž they vary from ~15% to ~45% (corresponding to 31 and  $144 \text{ t C/ha}$ , respectively), in the NF and FF (Figure 8). In comparing scenarios to control climate in managed simulations no appreciable differences among sites are found in the NF (Table 2 and supporting information S4). In summary, climate change and thinning and harvesting increase wood production and carbon stocks. Absolute values for  $\text{NPP}_{\text{wood}}$  and carbon woody stocks across different setup combinations and scenarios are in depth shown in the supporting information (S5, S6, S7, and S8).

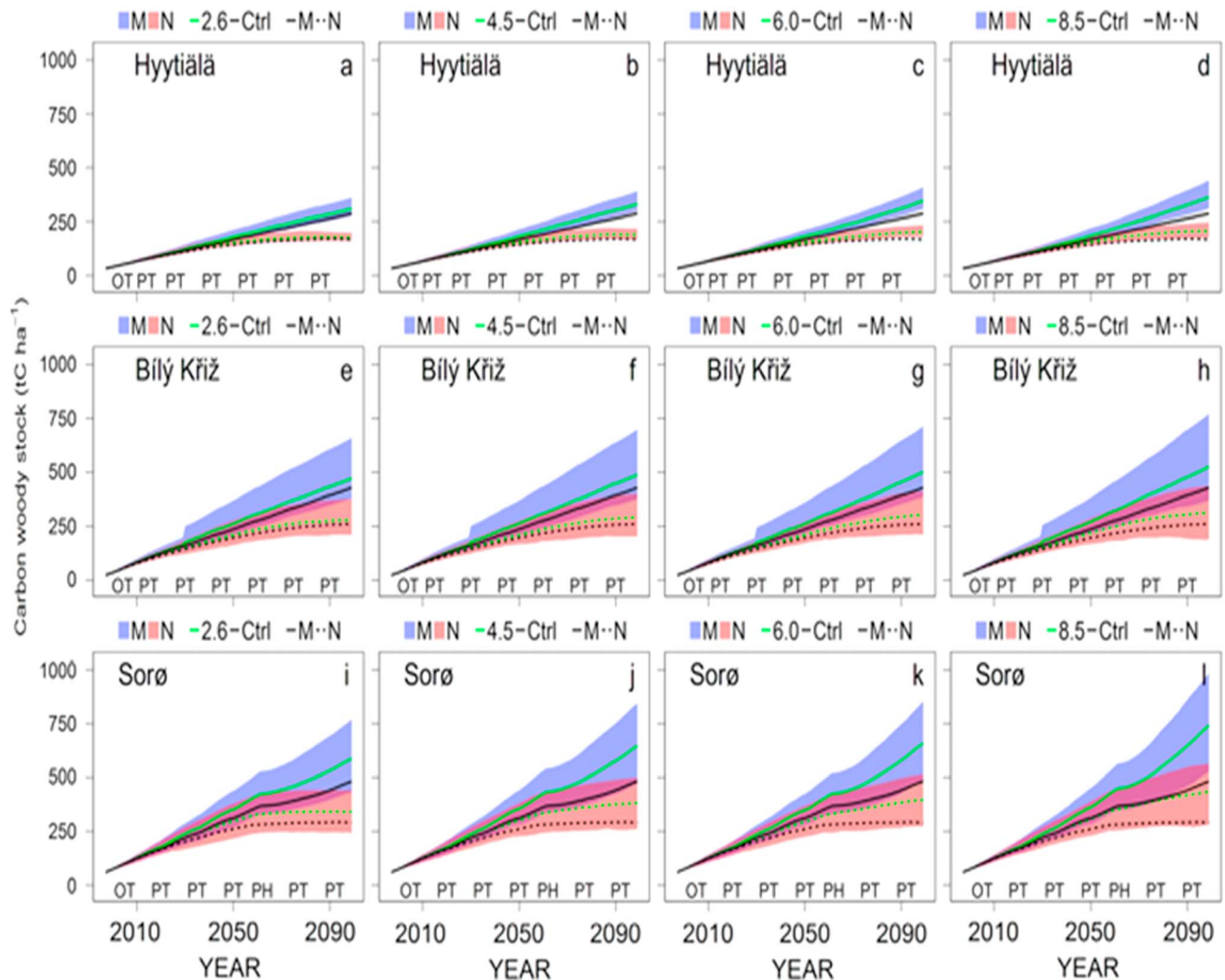


**Figure 7.** Time series of mean annual  $NPP_{wood}$  over the simulation period. Blue shaded area represents the maximum and minimum values for among ESMs and RCPs when management is considered (M), and red shaded area when management is not considered (N). Solid lines represent the average annual values among ESMs for each control (Ctrl) and RCP scenario when management is simulated, and dashed lines when management is not simulated (OT = observed thinning, PT = prescribed thinning, PH = prescribed harvesting). (a, e, and i) Simulations under RCP2.6 scenario; (b, f, j) RCP4.5 scenario; (c, g, k) RCP6.0 scenario; and (d, h, l) RCP8.5 scenario. ESMs = Earth System Models; RCPs = Representative Concentration Pathways; NPP = net primary production.

## 5. Discussion

### 5.1. Forest Carbon Budget Under a Changing Climate

During the historical period the model satisfactorily reproduces the carbon flux observations at the three sites. At both daily and annual temporal resolutions, observed GPP falls into the variability bounds of the modeling results for the five ESMs. Likewise, simulations of annual  $R_g$ , NPP (i.e., biomass production + NSC) and CUE are in agreement with data reported in the literature from different authors (e.g., Campioli et al., 2015; Luyssaert et al., 2007; Tang et al., 2014 and Wu et al., 2013). The comparison between observed and measured annual  $NPP_{wood}$  shows that the model slightly overestimates the carbon allocated to woody pools. This potential overestimation may be due to (i) carbon fluxes usually not considered by models (e.g., carbon exudation to the rhizosphere, transfer to mycorrhizae, and volatile organic compounds) that may represent a significant fraction of annual NPP (Vicca et al., 2012) and (ii) some unaccounted biomass removed through management. It is also possible that observational estimates of  $NPP_{wood}$  might be biased, given the fact that some components (e.g., coarse roots and branches) are often calculated by indirect methods or by allometric relations that are inherently uncertain for specific site conditions (Clark et al., 2001; Wu et al., 2013).



**Figure 8.** Time series of mean annual carbon woody stock (tC/ha) (i.e., the sum of standing and harvested woody biomass) over the simulation period. Blue shaded area represents the maximum and minimum values when management is considered (M), and red shaded area when management is not considered (N). Solid lines represent the average annual values among ESMs for each control (Ctrl) and RCP scenario when management is simulated, and dashed lines when management is not simulated (OT = observed thinning, PT = prescribed thinning, PH = prescribed harvesting). (a, e, and i) Simulations under RCP2.6 scenario; (b, f, j) RCP4.5 scenario, (c, g, k) RCP6.0 scenario, and (d, h, l) RCP8.5 scenario.

In the absence of climate change and thinning, the model behaved in line with the widely accepted theories of Kira and Shidei (1967) and Odum (1969) of a *quasi-equilibrium*, with GPP, NPP, and  $R_a$  increasing over time, leveling off, and then gradually declining as the effect of forest development (Kirschbaum, 2005; Ryan et al., 2004; Zaehle et al., 2006), resulting in narrow bounds of NPP:GPP variability from the short period to medium period (Gifford, 2003; Litton et al., 2007; Waring et al., 1998). Under the control scenario (under both thinned and unthinned simulations), as well as under changing climate, the projected GPP is controlled by the warming rate and by the temperature sensitivity of the different species. Simulated GPP is driven by combined changes in photosynthetic responses and by the lengthening of the growing season (Keenan et al., 2014; Miller-Rushing & Primack, 2008). In particular GPP for the beech stand benefits from warming due to the earlier bud break of leaves, in accordance with other modeling studies (e.g., Chen et al., 2016; Jeong et al., 2013; Loustau et al., 2005). To a lesser extent, also the simulated GPP in Hyttiälä and Bílý Kříž increased because of the positive effects of prolonged growing season as reported by Gauthier et al. (2015).

To our knowledge, this is the first study investigating the role of autotrophic respiration within the framework of *managed-driven* stand development under changing climate. In our simulations plant respiration



increases, in spite the model implementations for short- to long-term acclimation to warming, due to its direct relation to temperature and the increase in the amount of growth and maintenance respiratory substrate (Dore et al., 2012; Lu et al., 2013; Tjoelker et al., 1999). Our factorial analysis confirmed the positive response of simulated autotrophic respiration to warmer RCPs even for the FF (supporting information S3). In the studied forests, however, elevated  $[\text{CO}_2]$ , the lengthening of the growing season, and climate warming all increase forest productivity and biomass accumulation despite the increasing plant respiration. The rate and the speed at which warming will boost respiratory  $\text{CO}_2$  release and the extent to which acclimation will outweigh this increase are however still debated, and estimates have ranged from a likely increase (Piao et al., 2010) to a site-dependent impact of variable magnitude (Lloyd & Farquhar, 2007; Reich et al., 2016; Wu et al., 2016). Other studies have contradicted the idea of a simple temperature-related stimulation of autotrophic respiration particularly when water becomes limiting (Verborg et al., 2005; Zhou et al., 2010). This shows that to date there is no universal consensus on the effects of warming to  $R_a$  (and necessarily also to NPP).

Overall, literature reports that NPP and  $\text{NPP}_{\text{wood}}$  will increase with rising  $[\text{CO}_2]$  and temperature if water or nutrients are not limiting (e.g., Creutzburg et al., 2017; Kirschbaum et al., 2012; Medlyn, 2011), and modeled NPP and  $\text{NPP}_{\text{wood}}$  in Sorø clearly reflect this pattern. However, this tendency is partially dampened under warmer scenarios and over the course of stand development as described by Nabuurs et al. (2002). Likewise, the positive  $\text{CO}_2$  fertilization and temperature effects on NPP and  $\text{NPP}_{\text{wood}}$  increase in Hyytiälä and Bílý Kříž are partially offset by proportionally higher  $R_a$  rates, resulting in greater tree needs for carbon reserve accumulation rather than the increase of structural biomass (see also Tjoelker et al., 1999). In fact, climate warming causes an increase in the autotrophic respiration rate that is proportionally higher than the increase of photosynthesis rate, highlighting the critical role of nonstructural carbon in mediating this imbalance (and plant osmotic regulation, Dietze et al., 2014).

These two main physiological processes are interdependent (but feed-forward) and have different temperature responses (Atkin et al., 2005; Campbell et al., 2007; Way & Sage, 2008), which led to different dynamics at the three different sites. Notably, in the two most productive sites (i.e., Sorø and Bílý Kříž), under warmest climate scenarios with no management (and with/without  $\text{CO}_2$  fertilization effects), the model predicts negative imbalance of carbon with  $R_a:\text{GPP} > 1$  (plant respiration exceeds GPP and stands become a carbon source), causing a climate age-induced die off of the stand during the simulation period. We speculate that these simulation results may occur also in the real world under a frequent and prolonged sequence of extreme climatic events (e.g., heat waves and drought, Allen et al., 2010; Anderegg et al., 2012), which are likely to be increasingly common in highly susceptible regions as Europe (Reichstein et al., 2013). As shown in the recent past for temperate European forests (Brèda et al., 2006; Ciais et al., 2005; Granier et al., 2007), this climate pattern may accentuate the vulnerability and consequent mortality of trees and whole-forest stands as a consequence of downregulated assimilation and a faster depletion of nonstructural carbon compound (e.g., carbon starvation hypothesis, Adams et al., 2017; McDowell, 2011; Rowland et al., 2015), which represents a not often accounted pool in the ecosystem-level carbon budget (Trumbore, 2006) and forest growth and yield models. As shown by Morales et al. (2007) for Fenno-Scandinavia, as well as Anav and Mariotti (2011) and Santini et al. (2014) for Europe, and Bonan (2008) for boreal forests globally, under severe changes in climate, vegetation composition may shift from conifers to broadleaved trees (or by potentially most suited species). This is a significant modeling challenge at all spatial scales (Fischer et al., 2015). In our simulation exercise, however, we assume that the presence of the current species at the sites will continue.

For all sites, the simulated CUE decreases without management and tree carbon stocks level off as forests age. This may seem surprising given the generally positive effects of climate change on forests. However, a decline in productivity and a progressive leveling off in carbon stocks with forest development is a well-known phenomenon, generally attributed, among others, to an increasing fraction of respiring tissues and/or increasing hydraulic limitations (Goulden et al., 2011; Makela & Valentine, 2001; Ryan et al., 1997; Skubel et al., 2015). This is particularly evident at Sorø, which is older than the other two sites. At each modeled site, the overall tendency of decreasing CUE and stabilizing carbon stocks is slightly modified by the scenarios used (ESMs, RCPs, or  $[\text{CO}_2]$ ; Goulden et al., 2011; Noormets et al., 2015) and is thus assumed to be related to forest intrinsic development (aging and biomass accumulation) rather than to specific climatic forcing.

## 5.2. Effects of Thinning on the Forest Carbon Budget

Forest management practices are usually designed to accelerate wood yield and increase wood quality (and the economic revenue of the wood yield) through the thinning of forest canopies that favors penetration of light, soil water, and nutrient availability rather than carbon sequestration (Thornley & Cannell, 2000a). Conversely, undisturbed forests yield no timber but have a high standing biomass and so store large amount of carbon (Harmon et al., 1990). Under management, forest ecosystem carbon storage and natural tree mortality may decrease while GPP and growth in the remaining individual trees increase (Noormets et al., 2015; Wilkinson et al., 2016). These processes are reproduced by the model through thinning and harvesting (at Sorø) and are also confirmed by observations at the investigated sites (Kowalski et al., 2004; Vesala et al., 2005; Wu et al., 2013).

Modeled NPP between thinning events tends to decrease and subsequently rapidly increase afterward due to the removal of standing biomass (see also Thornley & Cannell, 2000b). This is consistent with analysis of Luysaert et al. (2007) that on short time and at local scale, NPP may be largely controlled by management and other nonclimatic factors. Throughout the reference scenarios at both Hyttiälä and Bílý Kříž sites, thinning had variable effect on total net primary productivity as observed also by Kirschbaum (1999). Overall, under climate change scenarios and forest management, NPP is projected to increase at all the analyzed sites. Consequently, thinning effectively counteracts the decrease in CUE due to forest development when compared to unthinned scenarios. These results agree with Campioli et al. (2015), who also found that management can compensate the age effect on BPE (equivalent to  $[NPP-NSC]/GPP$  in our study) for both temperate and boreal forest ecosystems (as documented also in DeLucia et al., 2007).

As the results described above, thinning causes a reduction in  $R_a$  due to partial removal of *respiring* trees at which it corresponds a proportionally lower decrease in GPP (due to a reduction in canopy coverage that is balanced by a slight increase in Leaf Area Index and in higher light and water availability). Hence, this is mirrored in a substantial increase in CUE in the subsequent years after thinning. Therefore, at ecosystem scale thinning increasing the availability of resources and reducing the amount of respiring tissues leads to an increase in CUE. Simulations show that the slope of decreasing rate of CUE between two thinning events is correlated with the temperature trend of the respective scenario. It thus supports a higher acclimation rate to more stressful conditions in the future that can be used to mitigate negative climate change effects.

The dynamic of CUE under warmer scenarios tends to be more pronounced after harvesting, suggesting that climate change may increase the sensitivity of the young forests. This may somehow support the arguments of Ryan (1991b) and Kirschbaum (2005) that climate change may lead young forests to grow faster, mature earlier, and also die younger. Models and experiments (Reich & Oleksyn, 2008) confirm also that there may be little leeway to alleviate this pattern over the NF through current management practices and that alternative management options should be considered for the FF.

Notably, when comparing thinned versus unthinned conditions,  $NPP_{wood}$  increases proportionally more than total NPP. This is confirmed by observations showing that the photosynthates are primarily used to enhance carbohydrate reserve accumulation (used to actively fuel  $R_a$  over the year and budburst in spring) and subsequently growth (Krinner et al., 2005; Scartazza et al., 2013; Trumbore, 2006). This implies that any reduction in autotrophic respiration or proportional increase in photosynthesis (as in our simulations) leads to a more rapid replenishment of the reserve pool and leaves formation and consequently only indirectly increases the allocation of photosynthates into woody tissues. This behavior is well expressed by the model at each site and is also confirmed in other works (Campioli et al., 2015; De Kauwe et al., 2014; DeLucia et al., 2005).

In contrast to other regional and global models that do not consider forest thinning and harvesting and tend to simulate negative effects of physical climate change on productivity for northern sites (Chen & Luo, 2015; Gauthier et al., 2015), we find that negative impacts on forest productivity were almost entirely overruled by the simulated management practices and by positive  $CO_2$  effects on NPP. These findings support the concept of Morales et al. (2007) and Reyer et al. (2014) that NPP is likely to benefit from projected increments in temperature (currently a limiting factor), precipitation, and  $CO_2$  enrichment in boreal climate, and that this benefit may be persistent over the medium term (Nuutinen et al., 2006), in particular if these management practices are applied.

Altogether, these results suggest that climate change coupled with management strategies may enhance biomass production and plants' carbon sequestration in woody compounds in both standing and harvested woody biomass and ultimately boost climate change mitigation. Differences in carbon woody stocks between thinned and unthinned simulations support the initial hypothesis that also under climate change current silvicultural practices may still sustain and even increase the forests mitigation role, and most importantly, this may be independent on the warming scenarios considered. The simulations furthermore show that despite large differences in current carbon sequestration capabilities, all sites' management leads to similar proportional sequestration potentials in the FF.

### 5.3. Model Assumptions and Limitations

Despite the overall good performance of the model in comparison to observed data, there are still major sources of uncertainty related to the processes assumptions and model parameterization under climate change. Different assumptions for acclimation of physiological processes to elevated  $[\text{CO}_2]$  and temperature, changes in carbon allocation patterns, and on nutrient limitation may offset or exacerbate the model results under ESMS and RCPs (Zaehle et al., 2015). For example, the underlying model assumption for photosynthesis and its sensitivity to  $[\text{CO}_2]$  using the Rubisco limitation (rather than RuBP-regeneration limitation) places the model at the *optimistic* end of the spectrum of possible  $\text{CO}_2$  responses (Figures 1a and 1b). The differences in simulated GPP among the three species reflect the model parameterization of the temperature dependence of photosynthesis, and how the model couples rising  $[\text{CO}_2]$  with temperature (Figure 2). Furthermore, more favorable temperatures early in the season may be less relevant for photosynthesis at boreal than at temperate sites, considering the limited incoming radiation during the first months of boreal spring.

For the sake of this analysis a key feature of the model is that the single components of autotrophic respiration are explicitly computed and directly related to temperature. As novelty of this work, we contrast with the common assumption that plant respiration and thus CUE may constitute a priori a fixed fraction of photosynthesis (Friend, 2010; Nemani et al., 2009; Waring et al., 1998) as used in other impact studies on European forests (e.g., Reyer et al., 2014). The constancy of CUE across biomes and stand development has been long debated as well as its correct definition and quantification (e.g., Campioli et al., 2015; Vicca et al., 2012). Inaccurate assumptions related to the effects of climate, stand age, and other environmental conditions on CUE may lead to unrealistic results (Hartley et al., 2006; Smith & Dukes, 2012). Such homeostasis in the plant respiration to assimilation ratio is indeed not expected in responses to an increase in  $[\text{CO}_2]$  and warming (Dewar et al., 1999). This issue is of particular relevance under changing climate that may lead to changing demands of carbon for plant growth and respiration. In fact, some studies show that the NPP:GPP ratio is far from being conservative throughout stand development, as documented by Makela & Valentine (2001) for Scots pine in southern Fennoscandia (and see also Grant et al., 2007). Similarly, Tjoelker et al. (1999) found that CUE decreases in boreal tree species in relation to plant size and warming and Piao et al. (2010), as well as Zhang et al. (2009, 2013), showed that globally CUE exhibits a spatial and temporal pattern strongly associated with climate (i.e., temperature and precipitation) and Atkin et al. (2007) with growth temperature and atmospheric  $[\text{CO}_2]$ . The variability of the ratio can also be derived from the broad range of values that have been derived globally (i.e.,  $\sim 0.2$ – $0.8$ ; DeLucia et al., 2007). We stress that a difference of  $\pm 0.1$  in CUE results in a proportional change of  $\pm 20\%$  in NPP and  $R_a$ , thereby a fixed assumption for NPP:GPP may lead to an unavoidable overestimate/underestimate of forest CUE throughout stand development.

The tested model implementation of a transient  $Q_{10}$  to warming (i.e., short-term acclimation, Figure 3a) seems to have only minor effects at the analyzed sites, since autotrophic respiration strongly saturates in the current model formulation for autotrophic respiration beyond a certain air temperature threshold (Smith & Dukes, 2012). Temperatures at which short-term acclimation of  $Q_{10}$  may occur have only rarely been reached at these sites. Differently, the long-term acclimation (i.e., Type-II acclimation, Figure 3b), increases linearly the model sensitivity under warmer scenarios. However, the effect, the speed, and the magnitude of acclimation on autotrophic respiration remain highly uncertain also at leaf as at the whole plant level in laboratory-controlled experiments (Drake & Tjoelker, 2016; Reich et al., 2016). We highlight that in the present study, changes in processes representation (e.g., allocation patterns) during management are uniquely modeled as quantitative changes in space, light, and water availability and do not depend on specific modifications in model algorithms or parameters.

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Additionally, since the model currently does not consider other carbon fluxes (such as VOCs and root exudates) but does include NSC besides biomass production, the modeled CUE is rather a value in between CUE and BPE (Carnieli et al., 2015). Such missing pools (i.e., VOCs and exudates) may be the causes of the modeled overestimation for NPP.

The 3D-CMCC FEM still does not consider some other potentially relevant processes that are likely to be influenced by climate change, as the nitrogen use efficiency (i.e., variations of plant C/N stoichiometry with increasing [CO<sub>2</sub>] as a consequence of acclimation to temperature) (de Wries et al., 2017; Lombardozzi et al., 2015; Medlyn et al., 2011, 2015). However, recent research supports the view that this effect might not be universal, pointing out that tree species forming s are very responsive to CO<sub>2</sub> fertilization over a large spectrum of nutrient availability (Terrer et al., 2016). In addition, nonmanagement disturbances, such as changes in species composition and ozone (Anav et al., 2011; Seidl et al., 2017), are not currently represented in the model.

## 6. Conclusions

Our findings at the analyzed sites suggest that climate change is likely to impact the autotrophic components of the forests carbon budget, accelerating the main physiological and functional processes and metabolic responses governing autotrophic carbon fluxes. These impacts may alter the carbon allocation patterns (see the role of NSC compound and the carbon starvation hypothesis) that in turn are likely to modify forest growth and other key processes from soil to ecosystem level (e.g., heterotrophic and total ecosystem respiration).

The quantification of the effects of climate change and the applied management practices on plant physiology provides new hypothesis and perspectives about the sensitivity of forests to management as one of the likely key drivers of the carbon cycle for autotroph (but also for heterotroph) organisms. In particular, our results highlight that forests thinning is likely to increase climate and human benefits in the short term and to possibly dampen the described decreases in CUE and carbon woody stock capacity in the long term. However, further analysis under adaptive or alternative management strategies needs to be considered.

Furthermore, our results confirm that appropriate stand/ecosystem scale modeling requires a combined representation of physiological and structural processes along with the consideration of management practices. These needs should also be carefully considered within ESMs, in which the improved representation of land management represents an urgent need.

## References

- Adams, H., Zeppel, M., Anderegg, W., Hartmann, H., Landhäusser, S. M., Tissue, D. T., et al. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology and Evolution*, 1(9), 1285–1291. <https://doi.org/10.1038/s41559-017-0248-x>
- Ainsworth, E., & Long, S. (2005, 165). What we have learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist*, 351–371.
- Allen, C., Macalady, A., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Alvarez, S., Ortiz, C., Diaz-Pinès, E., & Rubio, A. (2016). Influence of tree species composition, thinning intensity and climate change on carbon sequestration in Mediterranean mountain forests: A case study using the CO<sub>2</sub>Fix model. *Mitigation and Adaptation Strategies for Global Change*, 21, 1045–1058.
- Amthor, J. (2000). The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. *Annals of Botany*, 86, 1–20.
- Anav, A., & Mariotti, A. (2011). Sensitivity of natural vegetation to climate change in the Euro-Mediterranean area. *Climate Research*, 46(3), 277–292. <https://doi.org/10.3354/cr00993>
- Anav, A., Menuet, L., Khvorostyanov, D., & Viovy, N. (2011). Impact of tropospheric ozone on the Euro-Mediterranean vegetation. *Global Change Biology*. <https://doi.org/10.1111/j.1365-2486.2010.02387.x>
- Anderegg, W. R. L., Kane, J. M., & Anderegg, L. D. L. (2012). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*. <https://doi.org/10.1038/NCLIMATE1635>
- Arora, V., & Boer, G. (2005). A parameterization for leaf phenology in the terrestrial ecosystem component of climate models. *Global Change Biology*, 11(1), 33–59.
- Ashraf, M., Bourque, C., MacLean, D., Erdle, T., & Meng, F.-R. (2015). Estimation of potential impacts of climate change on growth and yield of temperate tree species. *Mitigation and Adaptation Strategies for Global Change*, 20, 159–178.
- Atkin, O., Atkinson, L., & Fisher, R. (2008). Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model. *Global Change Biology*, 14, 2709–2726.
- Atkin, O., Bruhn, D., Hurry, V., & Tjoelker, M. (2005). The hot and the cold: Unraveling the variable response of plant respiration to temperature. *Functional Plant Biology*, 32, 87–105.

available upon request to the corresponding author or at <https://github.com/CMCC-Foundation/3D-CMCC-LAND>. The authors declare no conflict of interest. Correspondence and requests for materials should be addressed to A. C. ([alessio.collalti@cmcc.it](mailto:alessio.collalti@cmcc.it) or [alessio.collalti@isafom.cnr.it](mailto:alessio.collalti@isafom.cnr.it)).

- Atkin, O., Scheurwater, I., & Pons, T. (2007). Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. *New Phytologist*, *174*, 367–380.
- Atkin, O., & Tjoelker, M. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, *8*, 343–351.
- Badger, M., & Collatz, J. (1977). Studies on the kinetic mechanism of RuDP-carboxylase and oxygenase, with particular reference to the effect of temperature on kinetic parameters. 1976–1677: Carnegie Institution, Annual Report.
- Battaglia, M., Beadle, C., & Loughhead, S. (1996). Photosynthetic response of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiology*, *16*, 81–89.
- Bellassen, V., & Luyssaert, S. (2014). Managing forests in uncertain times. *Nature*, *506*, 153–155.
- Bonan, G. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, *320*, 1444–1449.
- Bonan, G. B., Oleson, K. W., Fisher, R. A., Lasslop, G., & Reichstein, M. (2012). Reconciling leaf physiological traits and canopy flux data: Use of the TRY and FLUXNET databases in the Community Land Model version 4. *Journal of Geophysical Research*, *117*, G02026. <https://doi.org/10.1029/2011JG001913>
- Bradford, M., & Crowther, T. (2013). Carbon use efficiency and storage in terrestrial ecosystems. *New Phytologist*, *199*, 7–9.
- Brèda, H., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*, 625–644.
- Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O., & Hurry, V. (2007). Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist*, *176*(2), 375–389. <https://doi.org/10.1111/j.1469-8137.2007.02183.x>
- Campbell, G., & Norman, J. (1998). *An introduction to environmental biophysics*. New York: Wiley.
- Campioli, M., Malhi, Y., Vicca, S., Luyssaert, S., Papale, D., Peñuelas, J., et al. (2016). Evaluating the covariance between eddy-covariance and biometric methods for assessing carbon budgets of forests. *Nature Communications*, *7*. <https://doi.org/10.1038/ncomms13717>
- Campioli, M., Vicca, S., Luyssaert, S., Bilcke, J., Ceschia, E., Chapin III, F. S., et al. (2015). Biomass production efficiency controlled by management in temperate and boreal ecosystems. *Nature Geoscience*, *8*(11), 843–846. <https://doi.org/10.1038/NNGEO2553>
- Cescatti, A., & Piutti, E. (1998). Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *Forest Ecology and Management*, *102*, 213–223.
- Chen, H., & Luo, Y. (2015). Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. *Global Change Biology*. <https://doi.org/10.1111/gcb.12994>
- Chen, M., Melaas, E., Gray, J., Friedl, M., & Richardson, A. D. (2016). A new seasonal-deciduous spring phenology submodel in the Community Land Model 4.5: Impacts on carbon and water cycling under different future climate scenarios. *Global Change Biology*, *22*(11), 3675–3688. <https://doi.org/10.1111/gcb.13326>
- Chen, M., & Zhuang, Q. (2013). Modelling temperature acclimation effects on the carbon dynamics of forest ecosystems in the conterminous United States. *Tellus*, *65*(1). <https://doi.org/10.3402/tellusb.v65i0.19156>
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., et al. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, *437*(7058), 529–533. <https://doi.org/10.1038/nature03972>
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., & Ni, J. (2001). Measuring net primary production in forests: Concepts and field methods. *Ecological Monographs*, *71*(2), 356–370.
- Collalti, A., Biondo, C., Buttafuoco, G., Maesano, M., Caloiero, T., Lucà, F., et al. (2017). Simulation, calibration and validation protocols for the model 3D-CMCC-CNR-FEM: A case study in the Bonis' watershed (Calabria, Italy). *Forest*, *14*, 247–256. <https://doi.org/10.3832/efor2368-014>
- Collalti, A., Marconi, S., Ibrom, A., Trotta, C., Anav, A., D'Andrea, E., et al. (2016). Validation of 3D-CMCC Forest Ecosystem Model (v.5.1) against eddy covariance data for 10 European forest sites. *Geoscientific Model Development*, *9*(2), 479–504. <https://doi.org/10.5194/gmd-9-479-2016>
- Collalti, A., Perugini, L., Santini, M., Chiti, T., Nòlè, A., Matteucci, G., et al. (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>
- Collatz, G., Ball, J., Griwet, C., & Berry, J. (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer. *Agricultural and Forest Meteorology*, *54*, 107–136.
- Cox, P. (2001). *Description of the "TRIFFID" Dynamic Global Vegetation Model* (pp. 1–16). Berkshire, Hadley Centre, Met Office: Bracknell.
- Creutzburg, M., Scheller, R., Lucash, M., LeDuc, S. D., & Johnson, M. G. (2017). Forest management scenarios in a changing climate: Trade-offs between carbon, timber, and old forest. *Ecological Applications*, *27*, 503–518.
- De Kauwe, M., Medlyn, B., Zaehle, S., Walker, A. P., Dietze, M. C., Hickler, T., et al. (2013). Forest water use efficiency at elevated CO<sub>2</sub>: A model-data intercomparison at two contrasting temperature forest FACE sites. *Global Change Biology*, *19*, 1759–1779.
- De Kauwe, M., Medlyn, B., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y. P., et al. (2014). Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO<sub>2</sub> enrichment sites. *New Phytologist*, *203*(3), 883–899. <https://doi.org/10.1111/nph.12847>
- DeLucia, E., Drake, J., Thomas, R., et al. (2007). Forest carbon use efficiency: Is a respiration a constant fraction of gross primary production? *Global Change Biology*, *13*, 1157–1167.
- DeLucia, E., Moore, D., & Norby, R. (2005). Contrasting responses of forest ecosystems to rising atmospheric CO<sub>2</sub>: Implications for the global C cycle. *Global Biogeochemical Cycles*, *19*, GB3006. <https://doi.org/10.1029/2004GB002346>
- Dewar, R. C., Medlyn, B. E., & McMurtrie, R. E. (1999). Acclimation of the respiration/photosynthesis ratio to temperature: Insights from a model. *Global Change Biology*, *5*, 615–622.
- de Wries, W., Posch, M., Simpson, D., & Reinds, G. J. (2017). Modelling long-term impacts of changes in climate, nitrogen deposition and ozone exposure on carbon sequestration of European forest ecosystems. *Science of the Total Environment*, *605–606*, 1097–1116.
- Dietze, M. C., Sala, A., Carbone, M., Czimeczik, C. I., Mantooth, J. A., Richardson, A. D., et al. (2014). Nonstructural carbon in woody plants. *Annual Review of Plant Biology*, *65*(1), 667–687. <https://doi.org/10.1146/annurev-arplant-050213-040054>
- Dore, S., Montes-Helu, M., Hart, S., Hungate, B. A., Koch, G. W., Moon, J. B., et al. (2012). Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. *Global Change Biology*. <https://doi.org/10.1111/j.1365-2486.2012.02775.x>
- 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>
- Dunker, P., Barreiro, S., Hengevelds, G., Lind, T., Mason, W., Ambroz, S., & Spiecker, H. (2012). Classification of forest management approaches: A new conceptual framework and its applicability to European forestry. *Ecology and Society*, *17*(4), 51.

- Ellsworth, D., Thomas, R., Crous, K., Palmroth, S., Ward, E., Maier, C., et al. (2010). Elevated CO<sub>2</sub> affects photosynthetic responses in canopy pine and subcanopy deciduous trees over 10 years: A synthesis from Duke FACE. *Global Change Biology*, *18*, 223–242.
- FAO (2015). Global Forest Resource Assessment.
- Fischer, R. A., Koven, C. D., Anderegg, W. L. R., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., et al. (2017). Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology*, *24*(1), 35–54. <https://doi.org/10.1111/gcb.13910>
- Fischer, R. A., Muszala, S., Versteinstein, M., Lawrence, P., Xu, C., McDowell, N. G., et al. (2015). Taking off the training wheels: The properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). *Geoscientific Model Development*, *8*(11), 3593–3619. <https://doi.org/10.5194/gmd-8-3593-2015>
- Frank, D., Poulter, B., Saurer, M., Esper, J., Huntingford, C., Helle, G., et al. (2015). Water-use efficiency and transpiration across European forests during the Anthropocene. *Nature Climate Change*. <https://doi.org/10.1038/NCLIMATE2614>
- Franks, P., Adams, M., Amthor, J., Barbour, M. M., Berry, J. A., Ellsworth, D. S., et al. (2013). Sensitivity of plants to changing atmospheric CO<sub>2</sub> concentration: From the geological past to the next century. *New Phytologist*, *197*(4), 1077–1094. <https://doi.org/10.1111/nph.12104>
- Friedlingstein, P., Joel, G., Field, C., & Fung, I. (1998). Toward an allocation scheme for global terrestrial carbon models. *Global Change Biology*, *5*, 755–770.
- Friend, P. (2010). Terrestrial plant production and climate change. *Journal of Experimental Botany*, *31*, 1293–1309.
- Fürstenau, C., Badeck, F., Lasch, P., Lexer, M. J., Lindner, M., Mohr, P., et al. (2007). Multiple-use forest management in consideration of climate change and the interests of stakeholder groups. *European Journal of Forest Research*, *126*(2), 225–239. <https://doi.org/10.1007/s10342-006-0114-x>
- Gauthier, S., Bernier, P., & Kuuluvainen, a. (2015). Boreal forest health and global change. *Science*. <https://doi.org/10.1126/science.aaa9092>
- Gifford, R. (2003). Plant respiration in productivity models: Conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*, *30*(2), 171–186. <https://doi.org/10.1071/FP02083>
- Godbold, D., Vasutova, M., Wilkinson, A., Edwards-Jonášová, M., Bambrick, M., Smith, A. R., et al. (2015). Elevated atmospheric CO<sub>2</sub> affects ectomycorrhizal species abundance and increases sporocarp production under field conditions. *Forests*, *6*(12), 1256–1273. <https://doi.org/10.3390/f6041256>
- Goulden, M., McMillan, A., Winston, G., Rocha, A. V., Manies, K. L., Harden, J. W., et al. (2011). Patterns of NPP, GPP, respiration and NEP during forest boreal succession. *Global Change Biology*, *17*(2), 855–871. <https://doi.org/10.1111/j.1365-2486.2010.02274.x>
- Granier, A., Breda, N., Longdoz, B., Gross, P., & Ngao, J. (2008). Ten years of fluxes and stand growth in a young beech forest at Hesse. *Annals of Forest Science*, *65*(7), 704. <https://doi.org/10.1051/forest:2008052>
- Granier, A., Reichstein, M., Brèda, N., Falge, E., Ciais, P., Grünwald, T., et al. (2007). Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, *143*(1-2), 123–145. <https://doi.org/10.1016/j.agrformet.2006.12.004>
- Grant, R. F., Black, T. A., Humphreys, E. R., & Morgenstern, K. (2007). Changes in net ecosystem productivity with forest age following clear-cutting of a coastal Douglas-fir forest: Testing a mathematical model with eddy covariance measurements along a forest chronosequence. *Tree Physiology*, *27*, 115–131.
- Hamilton, J., Thomas, R., & DeLucia, E. (2001). Direct and indirect effects of elevated CO<sub>2</sub> on leaf respiration in a forest ecosystem. *Plant, Cell and Environment*, *24*(9), 975–982. <https://doi.org/10.1046/j.0016-8025.2001.00730.x>
- Harmon, M. E., Ferrell, W. K., & Franklin, J. F. (1990). Effects on carbon storage of conversion of old growth forests to young forests. *Science*, *247*, 699–702.
- Hartley, I. P., Armstrong, A. F., Murthy, R., Barron-Gafford, G., Ineson, P., & Atkin, O. K. (2006). The dependence of respiration on photosynthetic substrate supply and temperature: Integrating leaf, soil and ecosystem measurements. *Global Change Biology*, *12*(10), 1954–1968. <https://doi.org/10.1111/j.1365-2486.2006.01214.x>
- Hein, S., & Dhote, J. (2006). Effect of species composition, stand density and site index on the basal area increment of oak trees (*Quercus* sp.) in mixed stands with beech (*Fagus sylvatica* L.) in northern France. *Annals of Forest Science*, *63*, 457–467.
- Hempel, S., Frieler, K., Warszawski, J., Schewe, J., & Piontek, F. (2013). A trend-preserving bias correction—The ISI-MIP approach. *Earth System Dynamics*, *4*(2), 219–236. <https://doi.org/10.5194/esd-4-219-2013>
- Hidy, D., Barcza, Z., Marjanović, H., Ostrogović Sever, M. Z., Dobor, L., Gelybó, G., et al. (2016). Terrestrial ecosystem process model Biome-BGCMuSo v4.0: Summary of improvements and new modeling possibilities. *Geoscientific Model Development*, *9*(12), 4405–4437. <https://doi.org/10.5194/gmd-9-4405-2016>
- Huang, J., Bergeron, Y., Berninger, F., Zhai, L., Tardif, J. C., & Denneler, B. (2013). Impact of future climate on radial growth of four major boreal tree species in the eastern Canadian boreal forest. *PLoS One*, *8*(2), e56758. <https://doi.org/10.1371/journal.pone.0056758>
- Hyvönen, R., Ågren, G., Linder, S., Persson, T., Francesca Cotrufo, M., Ekblad, A., et al. (2007). The likely impact of elevated [CO<sub>2</sub>], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: A literature review. *New Phytologist*, *173*(3), 463–480. <https://doi.org/10.1111/j.1469-8137.2007.01967.x>
- Ibrom, A., Jarvis, P., Clement, R., Morgenstern, K., Oltchev, A., Medlyn, B. E., et al. (2006). A comparative analysis of simulated and observed photosynthetic CO<sub>2</sub>. *Tree Physiology*, *26*(7), 845–864. <https://doi.org/10.1093/treephys/26.7.845>
- Intergovernmental Panel on Climate Change (IPCC) (2006). 2006 IPCC Guidelines for National Greenhouse Gas Inventories. Intergovernmental Panel on Climate Change, NGGIP Publications, IGES, Japan.
- Jarvis, P. (1976). The interpretation of the variants in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London*, *273*, 593–610.
- Jeong, S.-J., Medvigy, D., Shevliakova, E., & Malyshev, S. (2013). Predicting changes in temperate forest budburst using continental-scale observations and models. *Geophysical Research Letters*, *40*, 359–364. <https://doi.org/10.1029/2012GL054431>
- Kattge, J., Knorr, W., Raddatz, T., & Wirth, C. (2009). Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, *15*, 976–991.
- Keenan, T., Gray, J., Friedl, M., Toomey, M., Bohrer, G., Hollinger, D. Y., et al. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, *4*(7), 598–604. <https://doi.org/10.1038/NCLIMATE2253>
- Keenan, T., Hollinger, D., Bohrer, G., Dragoni, D., William Munger, J., Schmid, H. P., et al. (2013). Increase in forest water-use efficiency as atmospheric carbon dioxide concentration rise. *Nature*, *499*(7458), 324–327. <https://doi.org/10.1038/nature12291>
- Keenan, T., Prentice, I., Canadell, J., Williams, C. A., Wang, H., Raupach, M., et al. (2016). Recent pause in the growth rate of atmospheric CO<sub>2</sub> due to enhanced terrestrial carbon uptake. *Nature Communications*, *7*. <https://doi.org/10.1038/ncomms13428>
- Kira, T., & Shidei, T. (1967). Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Japanese Journal of Ecology*, *17*, 70–87.

- Kirschbaum, M. (1999). CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecological Modelling*, *118*, 17–59.
- Kirschbaum, M. (2000). Forest growth and species distribution in a changing climate. *Tree Physiology*, *20*, 309–322.
- Kirschbaum, M. (2005). A model analysis of the interaction between forest age and forest responsiveness to increasing CO<sub>2</sub> concentration. *Tree Physiology*, *25*(7), 953–963. <https://doi.org/10.1093/treephys/25.7.953>
- Kirschbaum, M., Watt, M., Tait, A., & Ausseil, A.-G. E. (2012). Future wood productivity of *Pinus radiata* in New Zealand under expected climatic changes. *Global Change Biology*, *18*, 1342–1356.
- Knohl, A., Sørensen, A., Kutsch, W., Göckede, M., & Buchmann, N. (2008). Representative estimates of soil and ecosystem respiration in an old beech forest. *Plant and Soil*, *302*(1–2), 189–202. <https://doi.org/10.1007/s11104-007-9467-2>
- Kowalski, A., Loustau, D., Berbigier, P., Manca, G., Tedeschi, V., Borghetti, M., et al. (2004). Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. *Global Change Biology*, *10*(10), 1707–1723. <https://doi.org/10.1111/j.1365-2486.2004.00846.x>
- Krinner, G., Viovy, N., de Noblet-Ducoudrè, N., Ogée, J., Polcher, J., Friedlingstein, P., et al. (2005). A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles*, *19*, GB1015. <https://doi.org/10.1029/2003GB002199>
- Landsberg, J., & Waring, R. (1997). A generalised model for forest productivity using simplified concepts of radiation-use-efficiency, carbon balance and partitioning. *Forest Ecology and Management*, *172*, 199–214.
- Larcher, W. (2003). *Physiological plant ecology*. Berlin Heidelberg: Springer-Verlag.
- Lasch, P., Badeck, F. W., Suckow, F., Lindner, M., & Mohr, R. P. (2005). Model-based analysis of management alternatives at stand and regional level in Brandenburg. (Germany). *Forest Ecology and Management*, *207*(1–2), 59–74.
- Lindner, M., Fitzgerald, J., Zimmermann, N., Reyser, C., Delzon, S., van der Maaten, E., et al. (2014). Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? *Journal of Environmental Management*, *146*, 69–83. <https://doi.org/10.1016/j.jenvman.2014.07.030>
- Litton, C., Raich, J., & Ryan, M. (2007). Carbon allocation in forest ecosystems. *Global Change Biology*, *13*, 2089–2109.
- Lloyd, J., & Farquhar, G. (2007). Effects of rising temperature and [CO<sub>2</sub>] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B*, *363*(1498), 1811–1817. <https://doi.org/10.1098/rstb.2007.0032>
- Lombardozzi, D., Bonan, G., Smith, N., Dukes, J. S., & Fisher, R. A. (2015). Temperature acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate feedback. *Geophysical Research Letters*, *42*, 8624–8631. <https://doi.org/10.1002/2015GL065934>
- Loustau, D., Bosc, A., Colin, A., Ogee, J., Davi, H., Francois, C., et al. (2005). Modeling climate change effects on the potential production of French plains forests at the sub-regional level. *Tree Physiology*, *25*(7), 813–823. <https://doi.org/10.1093/treephys/25.7.813>
- Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., et al. (2013). Responses of ecosystem carbon cycle to experimental warming: A meta-analysis. *Ecology*, *94*(3), 726–738. <https://doi.org/10.1890/12-0279.1>
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichsteins, M., Papale, D., et al. (2007). CO<sub>2</sub> balance of boreal, temperate and tropical forests derived from global database. *Global Change Biology*, *13*(12), 2509–2537. <https://doi.org/10.1111/j.1365-2486.2007.01439.x>
- Makela, A., Kolari, P., Karimäki, J., Nikinmaa, E., Perämäki, M., & Hari, P. (2006). Modelling five years of weather-driven variation of GPP in a boreal forest. *Agricultural and Forest Meteorology*, *139*(3–4), 382–398. <https://doi.org/10.1016/j.agrformet.2006.08.017>
- Makela, A., & Valentine, H. (2001). The ratio of NPP to GPP: Evidence of change over the course of stand development. *Tree Physiology*, *21*, 1015–1030.
- Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Ågren, G. I. (2012). Environmental and stoichiometry controls on microbial carbon-use efficiency in soils. *New Phytologist*, *196*(1), 79–91. <https://doi.org/10.1111/j.1469-8137.2012.04225.x>
- 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*, *8*, 220–227.
- Mason, R., Gunst, R., & Hess, J. (2003). *Statistical design and analysis of experiments, with applications to engineering and science*. Carthage, MO: Wiley and Sons Publications.
- McCree, K. (1970). An equation for the rate of respiration of white clover plants grown under controlled conditions. In I. Setlik (Ed.), *Prediction and measurement of photosynthetic productivity* (pp. 221–229). The Netherlands: Pudoc, Wageningen.
- McDowell, N. (2011). Mechanism linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology*, *155*, 1051–1059.
- McSweeney, C., & Jones, R. (2016). How representative is the spread of climate projections from the 5 CMIP5 GCMs used in ISI-MIP? *Climate Services*, *1*, 24–29.
- Medlyn, B. (2011). Comment on "drought-induced reduction in global terrestrial net primary production from 2000 through 2009". *Science*, *333*(6046), 1093. <https://doi.org/10.1126/science.1199544>
- Medlyn, B., Duursma, R., & Zeppel, J. (2011). Forest productivity under climate change: A checklist for evaluating model studies. *Climate Change*. <https://doi.org/10.1002/wcc.108>
- Medlyn, B., Zaehle, S. D., de Kauwe, M. G., Walker, A. P., Dietze, M. C., Hanson, P. J., et al. (2015). Using ecosystem experiments to improve vegetation models. *Nature Climate Change*, *5*(6), 528–534. <https://doi.org/10.1038/nclimate2621>
- Mencuccini, M., & Bonosi, L. (2001). Leaf/sapwood area ratios in Scots pine show acclimation across Europe. *Canadian Journal of Forest Research*, *31*(3), 442–456.
- Meyfroidt, P., & Lambin, E. (2011). Global Forest transition: Prospects for end to deforestation. *Annual Review of Environment and Resources*, *36*, 343–371.
- Miller-Rushing, A., & Primack, R. (2008). Global warming and flowering times in Thoreau's concord: A community perspective. *Ecology*, *89*, 332–341.
- Monteith, J. (1965). Evaporation and environment. *19th Symposia of the Society for Experimental Biology*, *19*, 205–234.
- Monteith, J. (1972). Solar radiation and productivity in tropical ecosystem. *Journal of Applied Ecology*, *9*, 747–766.
- Morales, P., Hickler, T., Rowell, D., Smith, B., & Sykes, M. T. (2007). Changes in European ecosystems productivity and carbon balance driven by regional climate model output. *Global Change Biology*, *13*(1), 108–122. <https://doi.org/10.1111/j.1365-2486.2006.01289.x>
- Moss, R., Edmonds, J., & Hibbard, K. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, *463*, 747–756.
- Nabuurs, G.-J., Pussinen, A., Karjalainen, T., Erhard, M., & Kramer, K. (2002). Stemwood volume increment changes in European forest due to climate change: A simulation study with the EFISCEN model. *Global Change Biology*, *8*(4), 304–316. <https://doi.org/10.1046/j.1354-1013.2001.00470.x>
- Naudts, K., Chen, Y., McGrath, J., Ryder, J., Valade, A., Otto, J., et al. (2016). Europe's forest management did not mitigate climate changing warming. *Science*, *351*(6273), 597–600. <https://doi.org/10.1126/science.aac9976>
- Naudts, K., Ryder, J., McGrath, M., Otto, J., Chen, Y., Valade, A., et al. (2015). A vertically discretised canopy description for ORCHIDEE (SVN r2290) and the modifications to the energy, water and carbon fluxes. *Geoscientific Model Development*, *8*(7), 2035–2065. <https://doi.org/10.5194/gmd-8-2035-2015>

- Nemani, R., Hashimoto, H., Votava, P., Melton, F., Wang, W., Michaelis, A., et al. (2009). Monitoring and forecasting ecosystem dynamics using terrestrial observation and prediction system (TOPS). *Remote Sensing of Environment*, *113*(7), 1497–1509. <https://doi.org/10.1016/j.rse.2008.06.017>
- Noce, S., Collalti, A., & Santini, M. (2017). Likelihood of changes in forest species suitability, distribution, and diversity under future climate: The case of Southern Europe. *Ecology and Evolution*. <https://doi.org/10.1002/ece3.3427>
- Noce, S., Collalti, A., Valentini, R., & Santini, M. (2016). Hot Spot maps of forest presence in the Mediterranean Basin. *iForest - Biogeosciences & Forestry*, *9*, 766–774. <https://doi.org/10.3832/for1802-009>
- 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.
- Nolè, A., Collalti, A., Magnani, F., Duce, P., Ferrara, A., Mancino, G., et al. (2013). Assessing temporal variation of primary and ecosystem production in two Mediterranean forests using a modified 3-PG model. *Annals of Forest Science*, *70*(7), 729–741. <https://doi.org/10.1007/s13595-013-0315-7>
- Noormets, A., Epron, D., Domec, J., McNulty, S. G., Fox, T., Sun, G., et al. (2015). Effects of forest management on productivity and carbon sequestration: A review and hypothesis. *Forest Ecology and Management*, *355*, 124–140. <https://doi.org/10.1016/j.foreco.2015.05.019>
- Norby, R., DeLucia, E., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., et al. (2005). Forest response to elevated CO<sub>2</sub> is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(50), 18,052–18,056. <https://doi.org/10.1073/pnas.0509478102>
- Nowak, R., Ellsworth, D., & Smith, S. (2004). Functional responses of plants to elevated CO<sub>2</sub>—Do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist*, *162*, 253–280.
- Nuutinen, T., Matala, J., Hirvela, H., Härkönen, K., Peltola, H., Väisänen, H., & Kellomäki, S. (2006). Regionally optimized forest management under changing climate. *Climatic Change*, *79*(3–4), 315–333. <https://doi.org/10.1007/s10584-006-9098-2>
- Odum, E. (1969). The strategy of ecosystem development. *Science*, 262–270.
- Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., et al. (2006). Towards a standardized processing of net ecosystem exchange measured with eddy covariance technique: Algorithms and uncertainty estimation. *Biogeosciences*, *3*(4), 571–583. <https://doi.org/10.5194/bg-3-571-2006>
- Piao, S., Luysaert, S., Ciais, P., Janssens, I. A., Chen, A., Cao, C., et al. (2010). Forest annual carbon cost: A global-scale analysis of autotrophic respiration. *Ecology*, *91*(3), 652–661. <https://doi.org/10.1890/08-2176.1>
- Pilegaard, K., Ibrom, A., Courtney, M., Hummelshøj, P., & Jensen, N. O. (2011). Increasing net CO<sub>2</sub> uptake by a Danish beech forest during the period from 1996 to 2009. *Agricultural and Forest Meteorology*, *151*(7), 934–946. <https://doi.org/10.1016/j.agrformet.2011.02.013>
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., & Rotzer, T. (2014). Forest stand growth dynamics in central Europe have accelerated since 1870. *Nature Communications*, *5*(1), 4967. <https://doi.org/10.1038/ncomms5967>
- 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>
- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M., Seneviratne, S. I., et al. (2013). Climate extremes and the carbon cycle. *Nature*, *500*(7462), 287–295. <https://doi.org/10.1038/nature12350>
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., et al. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology*, *11*(9), 1424–1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- Reyer, C. P. O. (2015). Projections of changes in forest productivity and carbon pools under environmental change—A review of stand scale modeling studies. *Current Forestry Reports*, *1*, 53–68. <https://doi.org/10.1007/s40725-015-0009-5>
- Reyer, C. P. O., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., & Pilz, T. (2014). Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. *Annals of Forest Science*, *71*(2), 211–225. <https://doi.org/10.1007/s13595-013-0306-8>
- Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., et al. (2015). Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, *528*, 119–122.
- Ryan, M. G. (1991a). Effects of climate change on plant respiration. *Ecological Applications*, *1*(2), 157–167.
- Ryan, M. G. (1991b). A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. *Tree Physiology*, *9*, 255–266.
- Ryan, M., Binkley, D., & Fownes, J. (1997). Age-related decline in forest productivity: Pattern and process. *Advances in Ecological Research*, *27*, 213–262.
- Ryan, M., Binkley, D., Fownes, J., Giardina, C., & Senok, R. (2004). An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs*, *74*(3), 393–414. <https://doi.org/10.1890/03-4037>
- Santini, M., Collalti, A., & Valentini, R. (2014). Climate change impacts on vegetation and water cycles in the Euro-Mediterranean region, studied by a likelihood approach. *Regional Environmental Change*. <https://doi.org/10.1007/s10113-013-0582-8>
- Scartazza, A., Moscatello, S., Matteucci, G., Battistelli, A., & Brugnoli, E. (2013). Seasonal and inter-annual dynamics of growth, non-structural carbohydrates and C stable isotopes in a Mediterranean beech forest. *Tree Physiology*, *33*(7), 730–742. <https://doi.org/10.1093/treephys/tpt045>
- Schelhaas, M.-J., Nabuurs, G.-J., Hengenveld, G., Reyer, C., Hanewinkel, M., Zimmermann, N. E., et al. (2015). Alternative forest management strategies to account for climate change-induced productivity and species suitability changes in Europe. *Regional Environmental Change*, *15*(8), 1581–1594. <https://doi.org/10.1007/s10113-015-0788-z>
- Seidl, R., Vigl, F., Rossler, G., Neumann, M., & Rammer, W. (2017). Assessing resilience of Norway spruce forests through a model-based reanalysis of thinning trials. *Forest Ecology and Management*, *388*, 3–12. <https://doi.org/10.1016/j.foreco.2016.11.030>
- Sigurdsson, B., Robertz, P., Freeman, M., Naess, M., Saxe, H., Thorgeirsson, H., et al. (2002). Impact studies on Nordic forests: Effects of elevated CO<sub>2</sub> and fertilization on gas exchange. *Canadian Journal of Forest Research*, *32*(5), 779–788. <https://doi.org/10.1139/x01-114>
- Sitch, S., Smith, B., Prentice, C., Arneth, A., Bondeau, A., Cramer, W., et al. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*(2), 161–185. <https://doi.org/10.1046/j.1365-2486.2003.00569.x>
- Skubel, R., Altaf Arain, M., Peichl, M., Brodeur, J. J., Khomik, M., Thorne, R., et al. (2015). Age effects on the water-use efficiency and water-use dynamics of temperate pine plantations forests. *Hydrological Processes*. <https://doi.org/10.1002/hyp.10549>
- Smith, N., & Dukes, J. (2012). Plant respiration and photosynthesis in global-scale models: Incorporating acclimation and CO<sub>2</sub>. *Global Change Biology*, *19*, 45–63.



- Strigul, N., Pristinski, D., Purves, D., Dushoff, J., & Pacala, S. W. (2008). Scaling from trees to forests: Tractable macroscopic equations for forest dynamics. *Ecological Monographs*, *78*, 523–545.
- Tang, J., Luysaert, S., Richardson, A., 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>
- Terrer, C., Vicca, S., Hungate, B., Phillips, R. P., & Prentice, I. C. (2016). Mycorrhizal association as a primary control of the CO<sub>2</sub> fertilization effect. *Science*, *353*(6294), 72–74. <https://doi.org/10.1126/science.aaf4610>
- Thornley, J., & Cannell, M. (2000a). Modelling the components of plant respiration: Representation and realism. *Annals of Botany*, *85*, 55–67.
- Thornley, J., & Cannell, M. (2000b). Managing forests for wood yield and carbon storage: A theoretical study. *Tree Physiology*, *20*(7), 477–484. <https://doi.org/10.1093/treephys/20.7.477>
- Thornton, P. E. (2010). Biome BGC version 4.2: Theoretical framework of Biome-BGC. Technical documentation.
- Thornton, P. E., Lamarque, J., Rosenbloom, N., & Mahowald, N. (2007). Influence of carbon-nitrogen cycle coupling on land model response to CO<sub>2</sub> fertilization and climate variability. *Global Biogeochemical Cycles*, *21*, GB4018. <https://doi.org/10.1029/2006GB002868>
- Thornton, P. E., Law, B. E., Gholz, H. L., Clark, K. L., Falge, E., Ellsworth, D. S., et al. (2002). Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agricultural and Forest Meteorology*, *113*(1–4), 185–222. [https://doi.org/10.1016/S0168-1923\(02\)00108-9](https://doi.org/10.1016/S0168-1923(02)00108-9)
- Tjoelker, M., Oleskyn, J., & Reich, P. (2001). Modelling respiration of vegetation: Evidence for a general temperature-dependent Q<sub>10</sub>. *Global Change Biology*, *7*(2), 223–230. <https://doi.org/10.1046/j.1365-2486.2001.00397.x>
- Tjoelker, M. G., Oleskyn, J., & Reich, P. (1999). Acclimation of respiration to temperature and CO<sub>2</sub> in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology*, *49*, 679–691.
- Trumbore, S. (2006). Carbon respired by terrestrial ecosystems — Recent progress and challenges. *Global Change Biology*, *12*, 141–153.
- Vacchiano, G., Ascoli, D., Berzaghi, F., Lucas-Borja, M. E., Caignard, T., Collalti A., et al. (2018). Reproducing reproduction: How to simulate mast seeding in forest models. *Ecological Modelling*, *376*, 40–53. <https://doi.org/10.1016/j.ecolmodel.2018.03.004>
- Vanninen, P., & Mäkelä, A. (2005). Carbon budget for scots pine trees: Effects of size, competition and size fertility on growth allocation and production. *Tree Physiology*, *25*(1), 17–30.
- Verburg, P., Larsen, J., & Johnson, D. (2005). Impacts of an anomalously warm year on soil CO<sub>2</sub> efflux in an experimentally manipulated tallgrass prairie ecosystems. *Global Change Biology*, *11*(10), 1720–1732. <https://doi.org/10.1111/j.1365-2486.2005.001032.x>
- Veroustraete, F. (1994). On the use of ecosystem modelling for the interpretation of climate change effects at the ecosystem level. *Ecological Modelling*, *75-76*, 221–237.
- Veroustraete, F., Sabbe, H., & Eerens, H. (2002). Estimation of carbon mass fluxes over Europe using C-Fix model and Euroflux data. *Remote Sensing of Environment*, *83*(3), 376–399. [https://doi.org/10.1016/S0034-4257\(02\)00043-3](https://doi.org/10.1016/S0034-4257(02)00043-3)
- Vesala, T., Suni, T., Rannik, U., Keronen, P., Markkanen, T., Sevanto, S., et al. (2005). Effect of thinning on surface fluxes in a boreal forest. *Global Biogeochemical Cycles*, *19*, GB2001. <https://doi.org/10.1029/2004GB002316>
- Vicca, S., Luysaert, 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>
- van Vuuren, D., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., et al. (2011). The representative concentration pathways: An overview. *Climatic Change*, *109*(1–2), 5–31. <https://doi.org/10.1007/s10584-011-0148-z>
- Wang, W., Pend, C., Kneeshaw, D., Larocque, G. R., Lei, X., Zhu, Q., et al. (2013). Modelling the effects of varied forest management regimes on carbon dynamics in jack pine stands under climate change. *Canadian Journal of Forest Research*, *43*(5), 469–479. <https://doi.org/10.1139/cjfr-2012-0320>
- Waring, R., Landsberg, J., & Williams, M. (1998). Net primary production of forests: A constant fraction of gross primary production? *Tree Physiology*, *18*, 129–134.
- Waring, R., & McDowell, N. (2002). Use of a physiological process model with forestry yield tables to set limits on annual carbon balances. *Tree Physiology*, *22*, 179–188.
- 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., & Sage, R. (2008). Elevated growth temperatures reduce the carbon gain of black spruce *Picea mariana* (mill.) BSP. *Global Change Biology*, *14*, 624–636.
- Wilkinson, M., Crow, P., Eaton, E., & Morison, J. (2016). Effects of management thinning on CO<sub>2</sub> exchange by a plantation oak woodland in south-eastern England. *Biogeosciences*. <https://doi.org/10.5194/bg-13-2367-2016>
- Wu, C., Liang, N., Sha, L., Xu, X., Zhang, Y., Lu, H., et al. (2016). Heterotrophic respiration does not acclimate to continuous warming in subtropical forest. *Scientific Reports*, *6*(1). <https://doi.org/10.1038/srep21561>
- 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>
- Xiao, C., Yuste, J., Janssens, I., Roskams, P., Nachtergale, L., Carrara, A., et al. (2003). Above and belowground biomass and net primary production in a 73-year old Scots pine forest. *Tree Physiology*, *23*(8), 505–516. <https://doi.org/10.1093/treephys/23.8.505>
- Yue, C., Ciais, P., Luysaert, S., Li, W., McGrath, M. J., Chang, J., et al. (2017). Representing anthropogenic gross land use change, wood harvest and forest age dynamics in a global vegetation model ORCHIDEE-MICT (r4259). *Geoscientific Model Development Discussion*, 1–38. <https://doi.org/10.5194/gmd-2017-118>
- Zaehle, S., Jones, C., Houlton, B., Lamarque, J.-F., & Robertson, E. (2015). Nitrogen availability reduces CMIP5 projections of twenty-first-century land carbon uptake. *Journal of Climate*, *28*(6), 2494–2511. <https://doi.org/10.1175/JCLI-D-13-00776.1>
- Zaehle, S. S., Prentice, I. C., Liski, J., Cramer, W., Erhard, M., Hickler, T., et al. (2006). The importance of age-related decline in forest NPP for modelling regional carbon balances. *Ecological Applications*, *16*(4), 1555–1574. [https://doi.org/10.1890/1051-0761\(2006\)016\[1555:TIOADI\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1555:TIOADI]2.0.CO;2)
- Zahele, S., Medlyn, B., De Kauwe, M., Walker, A., Dietze, M. C., Hickler, T., et al. (2014). Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate free-air CO<sub>2</sub> enrichment studies. *New Phytologist*, *202*(3), 803–822. <https://doi.org/10.1111/nph.12697>
- Zhang, Y., Xu, M., Chen, H., & Adams, J. (2009). Global pattern of NPP to GPP ratio derived from MODIS data: Effects of ecosystem type, geographical location and climate. *Global Ecology and Biogeography*, *18*, 280–290.
- Zhang, Y., Yu, G., Yang, J., Wimberly, M. C., Zhang, X. Z., Tao, J., et al. (2013). Climate-driven global changes in carbon use efficiency. *Global Ecology and Biogeography*, *23*(2), 144–155. <https://doi.org/10.1111/geb.12086>

- Zhang, Z., Zhang, R., Cescatti, A., Wohlfahrt, G., Buchmann, N., Zhu, J., et al. (2017). Effect of climate warming on the annual terrestrial net ecosystems CO<sub>2</sub> exchange globally in the boreal and temperate regions. *Scientific Reports*, *7*(1), 3108. <https://doi.org/10.1038/s41598-017-03386-5>
- Zhou, X., Luo, Y., Gao, C., Verburg, P. S. J., Arnone, J. A. III, Darrouzet-Nardi, A., et al. (2010). Concurred and lagged impacts of an anomalously warm year on autotrophic and heterotrophic components of soil respiration: A deconvolution analysis. *New Phytologist*, *187*(1), 184–198. <https://doi.org/10.1111/j.1469-8137.2010.03256.x>
- Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., et al. (2016). Greening of the Earth and its drivers. *Nature Climate Change*, *6*(8), 791–795. <https://doi.org/10.1038/nclimate3004>