

# Amount of carbon fixed, transit time and fate of harvested wood products define the climate change mitigation potential of boreal forest management—A model analysis

Holger Metzler<sup>a,\*</sup>, Samuli Launiainen<sup>b</sup>, Giulia Vico<sup>a,1</sup>

<sup>a</sup> Department of Crop Production Ecology, Swedish University of Agricultural Sciences (SLU), PO Box 7043, Uppsala, 750 07, Sweden

<sup>b</sup> Natural Resources Institute, Latokartanonkaari 9, Helsinki, 00790, Finland

## ARTICLE INFO

Dataset link: <https://doi.org/10.5281/zenodo.10848284>

### Keywords:

Boreal forest  
Wood production  
Carbon sequestration  
Transit time  
Climate change mitigation  
Process-based modeling

## ABSTRACT

Boreal forests are often managed to maximize wood production, but other goals, among which climate change mitigation, are increasingly important. Hence, it is necessary to examine synergies and trade-offs between forest production and its potential for carbon sequestration and climate change mitigation in forest stands. To this aim, we develop a novel mass-balanced process-based compartmental model that allows following the carbon path from its photosynthetic fixation until its return to the atmosphere by autotrophic or heterotrophic respiration, or by being burnt as wood product. Following carbon in the system allows to account for how long forest ecosystems and wood products retain carbon away from the atmosphere (i.e., the carbon transit time). As example, we apply the model to four management scenarios, i.e., mixed-aged pine, even-aged pine, even-aged spruce, and even-aged mixed forest, and contrast metrics of performance relative to wood production, carbon sequestration, and climate change mitigation potential. While at the end of an 80 yr rotation the even-aged forests held up to 31% more carbon than the mixed-aged forest, the mixed-aged forest was superior during almost the entire rotation when factoring in the carbon retention time away from the atmosphere, i.e., in terms of climate change mitigation potential. Importantly, scenarios that maximize production or amount of carbon stored in the ecosystems are not necessarily the most beneficial for carbon retention away from the atmosphere. These results underline the importance of considering carbon transit time when evaluating forest management options for potential climate change mitigation.

## 1. Introduction

Boreal forests are one of the largest biomes on Earth and strongly regulate global climate through land-surface energy, water and carbon cycles (Bonan, 2008; Chapin et al., 2000; Baldocchi et al., 2000). These forests are in large part managed (Högberg et al., 2021), often to maximize timber production and economic income (Millennium Ecosystem Assessment, 2005). They comprise approximately 45% of the global stock of growing timber (Vanhanen et al., 2012), contributing to the economic well-being and cultural heritage of the Nordic societies (Millennium Ecosystem Assessment, 2005; Vanhanen et al., 2012) and providing numerous ecosystem services (Maes et al., 2016; Vihervaara et al., 2010). Nevertheless, the focus on production has led to degradation of other important ecosystem services, among which climate regulation, collectable goods, recreation, water regulation and purification,

maintenance of soil productivity and air-quality regulation (Pohjanmies et al., 2017).

There is an increasing commitment to more sustainable forest management and preservation of ecosystem services (Larsen et al., 2022; Kellomäki, 2022). There is also an increasing interest in carbon sequestration by boreal forests to support the rapid net emission reductions required to avoid exceeding global tipping points of the climate system (Lenton et al., 2008). Indeed, boreal forests have potential for climate change mitigation by holding CO<sub>2</sub> away from the atmosphere (Pan et al., 2011). To which extent carbon retention potential and wood production clash is a key question when planning management strategies for the future.

A commonly employed metric of carbon sequestration and climate change mitigation potential is the net ecosystem carbon gain over a certain amount of time (Pukkala, 2020). This metric, however, ignores

\* Correspondence to: Department of Forest Ecology and Management, Swedish University of Agricultural Sciences (SLU), Skogsmarksgränd 17, Umeå, 901 83, Sweden.

E-mail address: [holger.metzler@slu.se](mailto:holger.metzler@slu.se) (H. Metzler).

<sup>1</sup> Present address: Department of Ecology, Swedish University of Agricultural Sciences (SLU), PO Box 7044, Uppsala, 750 07, Sweden.

<https://doi.org/10.1016/j.ecolmodel.2024.110694>

Received 4 September 2023; Received in revised form 22 February 2024; Accepted 12 March 2024

Available online 26 March 2024

0304-3800/© 2024 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

the time span between carbon fixation via photosynthesis and its release back to the atmosphere, later referred to as *transit time* (Bolin and Rodhe, 1973; Sierra et al., 2017). Together with the amount of carbon stored, the time the photosynthesized CO<sub>2</sub> remains stored in living plants, residues, soil or wood products determines the *avoided radiative effect* (Sierra et al., 2021) of greenhouse gases in the atmosphere (i.e., the Global Warming Potential; Shine et al. 1990). Also the fate of legacy carbon, i.e., carbon already in the ecosystem and wood products at the beginning of the forest management cycle, and of harvested carbon needs to be considered when evaluating climate change mitigation potential of alternative management regimes. The fate of legacy carbon is of particular relevance to climate change mitigation potential when management is applied to old-growth forests (Luyssaert et al., 2008; Schulze et al., 2020). Despite its importance for climate change mitigation, the role of transit time of carbon outside the atmosphere when assessing alternative forest management scenarios in their climate performance has not been systematically analyzed.

Forest management strategies differ in their synergies and trade-offs among economic, biodiversity, and climate change mitigation targets (Pohjanmies et al., 2017). Even-aged forestry with one to three thinnings to promote tree growth, followed by a clear cut at the end of the rotation and subsequent regeneration has been the prevailing management regime in the boreal zone (Pohjanmies et al., 2017). In the recent decades, there has been increasing interest and pressure to move towards selection harvests. The maintenance of a continuous forest cover of mixed-age, mixed-size, and multi-species stands has been suggested to better address environmental and societal concerns stemming from even-aged management (Kuuluvainen et al., 2012; Larsen et al., 2022; Kellomäki, 2022). The climate change mitigation potentials in even-aged, mixed-aged, and mixed-species management strategies and their trade-offs with wood production remain unclear, particularly if considering not only the amount of carbon sequestered during a fixed rotation period but also the carbon transit time and the timescale of interest. Importantly, we do not know whether and to what extent ensuring both short- and long-term carbon sequestration and climate change mitigation reduces biomass and/or wood production (Pohjanmies et al., 2017).

The long 60 to 100-yr rotation periods make process-based modeling a powerful tool to evaluate the ecosystem services provided by boreal forests differing in age, species distribution, and management. Most ecological growth and yield models developed for boreal forests, however, focus mainly on wood production (SORTIE, Pacala et al. 1996; CROBAS, Mäkelä 1997; 3-PG, Landsberg and Waring 1997) and less frequently on carbon sequestration (Pukkala 2014, 2020). Importantly, none of these models allows to track carbon flows through trees, soil, and harvested wood products. These carbon flows are essential to compute the carbon transit times and to evaluate the importance of legacy carbon and wood-product use when comparing climate performances of alternative management strategies. The available analyses of the effects of legacy carbon, wood products, and fossil fuel substitution on carbon sinks (Wutzler, 2008; Böttcher et al., 2008a,b) have not included the transit time aspect.

Here, we develop a process-based mass-balanced forest and forest-product model to compute carbon transit times for even-aged, mixed-aged, or mixed-species stands. The model enables following the carbon path from its fixation via photosynthesis, through its fate in the forest stand affected by competition and management, until the moment of its return to the atmosphere by respiration or wood-product burning. We use the model to quantify four metrics of performance: wood production, carbon sequestration, and two alternative estimates of climate change mitigation potential. We demonstrate how these different metrics of performance lead to contrasting conclusions. We consider four idealized management scenarios during an 80-yr rotation: a continuous-cover, mixed-aged pine forest and even-aged mono- (pine or spruce), or mixed-species (pine and spruce) stands established after clear cutting, and ask:

- How do metrics of carbon sequestration and climate change mitigation potential compare in different management scenarios?
- How important is the fate of harvested wood products when assessing carbon sequestration and climate change mitigation potential?
- Are there trade-offs between the capacity of forests to produce biomass and sequester carbon and keep it away from the atmosphere?

We focus on pure and mixed Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) stands under current climatic conditions for southern Finland. In its current version, our model serves the purpose of qualitatively comparing metrics of carbon sequestration and transit-time based climate change mitigation potential. A more quantitative investigation of concrete management decision requires further model development and testing under different site conditions.

## 2. Materials and methods

Our primary aim is to compare and contrast different metrics of carbon sequestration and climate change mitigation potential, and to analyze whether these goals are in conflict with wood production. Based on the general mathematical framework for compartmental models (Section 2.1), we introduce different metrics of stand performance representing wood production, carbon sequestration, and climate change mitigation potential (Section 2.2). To determine these metrics, we develop and parameterize a mass-balanced, process-based compartmental model (Section 2.3) that allows us to track the carbon path through the trees, soil, and wood products, as needed by one of the climate change mitigation potential metrics. We compare the performance metrics relative to four scenarios of forest management, differing in age- and species composition (Section 2.4).

### 2.1. Mathematical framework for compartmental models

Compartmental models are mass-balanced, nonnegative dynamical systems that describe the flow of a material (here carbon) into, through, and out of a set of interconnected and well-mixed compartments or, equivalently, pools (here tree organs, soil, and wood products) (Anderson, 1983; Jacquez and Simon, 1993; Luo and Weng, 2011; Sierra and Müller, 2015; Sierra et al., 2018). They can be described mathematically by a  $d$ -dimensional system of nonlinear and nonautonomous ordinary differential equations,

$$\begin{aligned} \frac{d}{dt} \mathbf{x}(t) &= \mathbf{B}(\mathbf{x}(t), t) \mathbf{x}(t) + \mathbf{u}(\mathbf{x}(t), t), \quad t > 0, \\ \mathbf{x}(0) &= \mathbf{x}^0. \end{aligned} \quad (1)$$

Here  $\mathbf{x}(t) \in \mathbb{R}^d$  (gC m<sup>-2</sup>) is the vector of the carbon pools considered at time  $t \geq 0$  (yr),  $\mathbf{x}^0$  gives their initial sizes (at time  $t = 0$ ) and the vector-valued function  $\mathbf{u}$  (gC m<sup>-2</sup> yr<sup>-1</sup>) represents the input to the system (in our case via photosynthesis, i.e., the gross primary productivity of all trees in the system). The matrix-valued function  $\mathbf{B}$  (compartmental matrix) governs the internal carbon cycling and the release of carbon from the system (in our case to the atmosphere). The matrix entry  $B_{mj}$  (yr<sup>-1</sup>) denotes the rate of carbon transferred from pool  $j$  to pool  $m$ . The dimension  $d$  of the equation system is the number of considered pools that describe the carbon in the trees, soil, and wood products.

The fluxes (gC m<sup>-2</sup> yr<sup>-1</sup>) from pool  $j$  to pool  $m$  at time  $t$  are given by

$$F_{mj}(t) = B_{mj}(\mathbf{x}(t), t) x_j(t), \quad t \geq 0. \quad (2)$$

The solution of Eq. (1) is given by Brockett (2015, Theorem 1.6.1)

$$\mathbf{x}(t) = \Phi(t, 0) \mathbf{x}^0 + \int_0^t \Phi(t, \tau) \mathbf{u}(\tau) d\tau, \quad (3)$$

where the first term on the right hand side is the part of legacy carbon that has not yet left the system until time  $t$ , and the second term is the

amount of carbon that has entered the system and remained since the beginning of the simulation. Legacy carbon, given by  $\mathbf{x}^0$ , is the initial amount of carbon in the tree biomass, the soil, and the wood products at time  $t = 0$ . The matrix-valued function  $\Phi$  denotes the state-transition operator given as the numerical solution of the matrix equation

$$\begin{aligned} \frac{d}{dt}\Phi(t, s) &= \mathbf{B}(t)\Phi(t, s), \quad 0 < s \leq t, \\ \Phi(s, s) &= \mathbf{I}, \end{aligned} \quad (4)$$

where  $\mathbf{I}$  is the identity matrix. For a vector  $\mathbf{x}(s)$  of carbon stocks in different pools at time  $s$ , the vector  $\Phi(t, s)\mathbf{x}(s)$  describes the remaining mass (not yet returned to the atmosphere) and its distribution over the pools at time  $t \geq s$ .

This mathematical framework enables us to compute the *transit times* of carbon through the system (Rasmussen et al., 2016; Metzler et al., 2018), which are at the basis of the climate change mitigation potential of the system (Sierra et al., 2021) (see Section 2.2.2).

## 2.2. Stand performance metrics

We assess the performance of forest stands relative to four metrics: wood production, carbon sequestration as net carbon gain, and two climate change mitigation potential estimates. The climate change mitigation potential estimates are based on the carbon transit time, i.e., the time during which the fixed carbon remains in the system and hence away from the atmosphere.

### 2.2.1. Wood production

The wood-product yields till time  $T$  are quantified as the integrated carbon fluxes entering the wood-product pools ( $WP_S$  and  $WP_L$ , since we consider short- and long-lasting wood products  $Y_S$  and  $Y_L$ , respectively; see Section 2.3.4). Let  $S$  and  $L$  be the indices of  $WP_S$  and  $WP_L$  in the carbon content vector  $\mathbf{x}$ , i.e.,  $x_S = WP_S$  and  $x_L = WP_L$ . Then

$$\begin{aligned} Y_S(T) &= \int_0^T \sum_{j \neq S} B_{Sj}(t) x_j(t) dt \quad \text{and} \\ Y_L(T) &= \int_0^T \sum_{j \neq L} B_{Lj}(t) x_j(t) dt. \end{aligned} \quad (5)$$

### 2.2.2. Carbon sequestration and climate change mitigation potential

We quantify carbon sequestration and the potential for climate change mitigation via three metrics. We contrast the results relative to the entire system (including wood products) with those for the forest stand only, because the wood products can be a crucial factor for whether a forest stand subject to a specific management scenario is a carbon sink or source (Liski et al., 2001).

As metric of carbon sequestration we use the Integrated Net Carbon Balance,  $INCB(T)$ , i.e., the net carbon gain or loss over the time interval  $[0, T]$ , defined as the integrated carbon inputs to the system minus the integrated outputs from the system. Note that  $INCB(T)$  does not consider *when* the carbon uptake or release have taken place. Mathematically,

$$INCB(T) = \int_0^T \|\mathbf{u}(t) - \mathbf{r}(t)\| dt = \|\mathbf{x}(T)\| - \|\mathbf{x}^0\|, \quad (6)$$

where the carbon inputs at a generic time  $t$  are given by  $\|\mathbf{u}(t)\|$ , with  $\|\mathbf{u}(t)\| = \sum_m u_m(t)$ , and the carbon outputs from pool  $j$  are given by

$$r_j(t) = - \sum_m B_{mj}(t) x_j(t). \quad (7)$$

$INCB$  is closely related to integrated net ecosystem production (NEP, Randerson et al. 2002), with the difference that  $INCB$  includes wood-product carbon.  $INCB$  has dimensions of mass, because it is the result of integrating fluxes (which have dimension mass/time) over time.  $INCB$  can also be described as the total carbon stocks at time  $t = T$  minus the total stocks at time  $t = 0$ . Hence, to compute  $INCB$  over the rotation,

only the total carbon stocks at the beginning and end of the rotation are needed.

As first metric of climate change mitigation potential we use the Integrated Inputs Transit Time (IITT), originally named Carbon Sequestration (CS) by Sierra et al. (2021). IITT accounts for both the amount of carbon entering the system during the period of interest (via photosynthesis in our case) and the time that it spends in the system. IITT for the time period  $[0, T]$  is given by

$$IITT(T) = \int_0^T \int_\tau^T \|\Phi(t, \tau)\mathbf{u}(\tau)\| dt d\tau = \int_0^T \int_0^t \|\Phi(t, \tau)\mathbf{u}(\tau)\| d\tau dt. \quad (8)$$

Computing IITT requires the time each atom of carbon has spent inside the system, i.e., in practice a compartmental model (Section 2.1), whose state transition operator  $\Phi$  allows us to track all carbon fluxes in the system during the rotation. IITT is a measure of climate change mitigation potential rather than simply carbon sequestration. Nevertheless, IITT neglects the legacy carbon, i.e., the carbon that was in the system at the beginning of the considered time interval.

To overcome the limitation of IITT not considering legacy carbon, we use an additional metric of climate change mitigation potential, the Integrated Carbon Stocks (ICS). This metric is based on the same transit-time concept as IITT but additionally includes the fate of the legacy carbon already in the system at  $t = 0$ . The ICS for the period  $[0, T]$  is computed as

$$ICS(T) = \int_0^T \|\Phi(t, 0)\mathbf{x}^0\| dt + IITT(T) = \int_0^T \|\mathbf{x}(t)\| dt. \quad (9)$$

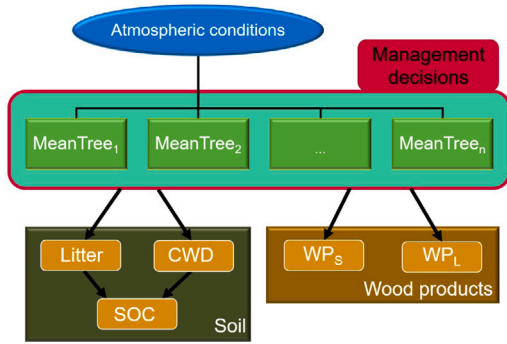
As follows from the second part of Eq. (9), the computation of ICS merely requires the time series of total carbon stocks included in all pools during the rotation. Hence, taking legacy carbon into account, somewhat surprisingly, simplifies the computation compared with IITT, because ICS emerges to be the integral of the total carbon stocks in the system over the rotation. The dimension of both IITT and ICS is mass  $\times$  time, because they are integrals of mass over time.

## 2.3. Model description

To compute the introduced performance metrics, particularly IITT, we developed a tree and stand level model describing the carbon dynamics in a horizontally homogeneous forest stand comprising  $n$  different tree cohorts competing for light. The stand structure is affected by growth, mortality, and management decisions. Furthermore, we describe dynamics of carbon in the soil and in the wood products (Fig. 1).

The stand comprises several cohorts of trees of density  $N_i$  ( $\text{ha}^{-1}$ ), identical in species, age, and size, each represented by a *MeanTree*  $i$ . This allows to describe not only even-aged mono-specific forest stands, but also mixed-aged and/or mixed-species stands. The carbon dynamics and growth of each *MeanTree* are modeled combining physiologically-based carbon fixation and statistical descriptions of tree allometry. For the latter, we developed an extension of the Allometrically Constrained Growth and Carbon Allocation model (ACGCA, Ogle and Pacala, 2009) to explicitly consider the carbon allocation to tree organs based on statistical allometries derived from large experimental data (Lehtonen, 2005; Repola, 2009; Repola and Ahnlund Ulvcrone, 2014). The model describes carbon stocks and fluxes entering the system via photosynthetic  $\text{CO}_2$  fixation and then exchanged among the carbon pools within each *MeanTree*, three soil carbon pools and two wood-product carbon pools, and eventually released back to the atmosphere. The key state variables of the model are the carbon contents of each pool (Table 1).

The model consists of four inter-linked modules: (1) a photosynthesis module, computing the annual gross primary productivity of each *MeanTree* ( $\text{GPP}_i$ ), based on the Atmosphere-Plant Exchange Simulator (APES, Launiainen et al. 2015); (2) a tree module, allocating  $\text{GPP}_i$  to the organs of *MeanTree*  $i$  as structural and nonstructural biomass, describing tree-internal and -external fluxes such as growth and maintenance respiration and tissue turnover based on the ACGCA model (Ogle



**Fig. 1.** Scheme of the model. Several *MeanTrees* interact with the soil and the wood-product components. The atmospheric conditions are the forcing of the carbon dynamics. The photosynthesis module quantifies for each *MeanTree*  $i$  the annual GPP <sub>$i$</sub>  to be distributed to ten tree carbon compartments (carbon pools shown in Fig. 2). Management decisions (i.e., planting, thinning, and cutting) are applied to each *MeanTree* and affect the stand composition and tree carbon distribution to soil and wood-product pools.

**Table 1**  
State variables of the different model components (gCm<sup>-2</sup>).

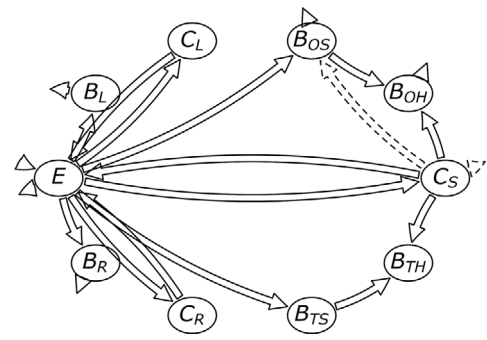
Tree carbon pools	
$E$	transient, available for growth and maintenance
$B_L$	leaf biomass
$C_L$	labile, stored as leaf glucose
$B_R$	fine root biomass
$C_R$	labile, stored as fine root glucose
$B_{OS}$	“other” sapwood
$B_{OH}$	“other” heartwood
$B_{TS}$	trunk sapwood
$B_{TH}$	trunk heartwood
$C_S$	labile, stored as sapwood glucose
Soil carbon pools	
Litter	fast decomposing litter
CWD	coarse woody debris
SOC	soil organic carbon
Wood-product carbon pools	
WP <sub>S</sub>	short-lasting wood products
WP <sub>L</sub>	long-lasting wood products

and Pacala, 2009) but with an improved carbon allocation driven by statistical allometries derived from forest inventory data; (3) a soil carbon module; and (4) a forest management module, describing the rules for planting and harvesting of *MeanTrees* (Fig. 1) in specific sample scenarios and allocation of harvested wood as wood products. The photosynthesis module is solved at half-hourly time step, while the other modules have annual time step. The complete model description and its parameterization are provided in the Supplementary Information (SI, Section A). The environmental conditions (model forcing) are provided in SI, Section B.

In order to calculate the stand performance metrics  $Y_S$ ,  $Y_L$ , INCB, IITT, and ICS (Eqs. (5)–(9)) with this model, the involved integrals are computed as sums over yearly time steps through the rotation. For the computation of  $Y_S$ ,  $Y_L$ , and IITT we are required to reconstruct the compartmental matrix  $B(t_k)$  in each yearly time step  $t_k$ . This is done using a discretized version of the analogous continuous-time approach presented in Metzler et al. (2020). Transit-time related computations involving the state-transition matrix  $\Phi$  are supported by the Python package “CompartmentalSystems” (freely available at <https://github.com/goujou/CompartmentalSystems>).

### 2.3.1. Photosynthesis module

The photosynthesis module (SI, Section A.1) computes carbon and water fluxes in the forest stand, considering competition for light



**Fig. 2.** Carbon budget and flows in a *MeanTree*. Symbols inside the pools are the state variables of the tree module (Table 1). In the “static” and “shrinking” states, there is an additional flux from the labile carbon storage ( $C_S$ ) to  $B_{OS}$  to support the regrowth of “other” wood; the associated growth respiration flux leaves from  $C_S$  (dashed arrows).

among the *MeanTrees*. The module provides the *MeanTree* annual GPP <sub>$i$</sub>  — the carbon input to the tree module. The stand structure, i.e., the maximum leaf-area index (LAI) and leaf-area density profiles and heights of each *MeanTree*, are provided by the tree module (Section 2.3.2) at the beginning of each year. The light environment and leaf photosynthesis and transpiration rates are solved separately for the sunlit and shaded parts of each canopy layer (1 m height each), using well-established biogeochemical model and stomatal optimality principles (Farquhar et al., 1980; Medlyn et al., 2012; Launiainen et al., 2015). The photosynthesis module includes sub-models to account for the seasonal leaf-area dynamics and photosynthetic acclimation (Launiainen et al., 2015, 2019), and the feedback of restricted soil water availability in the root zone to leaf gas-exchange (Launiainen et al., 2022). The root zone is described as a single water storage equally accessible to each *MeanTree*.

### 2.3.2. Tree module

The tree module (SI, Section A.2) describes the partitioning of the annual GPP =  $\sum_{i=1}^n$  GPP <sub>$i$</sub>  to maintenance and growth of a *MeanTree*'s organs (Fig. 2). All tree module variables are shown in SI, Table A.2.

Each *MeanTree* has ten carbon pools, representing structural ( $B$ ) and nonstructural ( $C$ ) carbon in leaves ( $B_L, C_L$ ), fine roots ( $B_R, C_R$ ), coarse roots and branches sapwood ( $B_{OS}$ , subscript “O” stands for “other”) and heartwood ( $B_{OH}$ ), as well as the trunk sapwood ( $B_{TS}$ ) and heartwood ( $B_{TH}$ ). Coarse roots and branches and the trunk share a single nonstructural labile storage pool  $C_S$ , and carbon input from photosynthesis is temporarily stored in a transient pool  $E$  (Fig. 2).

At the beginning of each year, in each *MeanTree* the GPP from the previous year is placed in the transient pool  $E$ . Losses from this pool occur via maintenance respiration ( $R_M$ ) of leaves, fine roots, sapwood, and growth respiration. Respired tree carbon returns directly to the atmosphere. Tissues are also lost at tissue-specific senescence rates. When senescing biomass leaves the *MeanTree*, the associated carbon in the labile storage pool ( $C_L, C_R$ , or  $C_S$ ) returns to the transient pool  $E$ , where it becomes available again for allocation during the subsequent year. The structural carbon of senescing biomass becomes input for the soil module.

Thinning and cutting events reduce the number of trees ( $N_i$ ) represented by a *MeanTree*  $i$ . Part of the carbon stored in the harvested biomass is turned into short- (WP<sub>S</sub>) or long-lasting (WP<sub>L</sub>) wood products (SI, Section A.5) with the partitioning depending on dimensions of the harvested trunk wood. The cutting residues are either left on site and provide litter or coarse woody debris input for the soil module or can become short-lasting bioenergy (part of WP<sub>S</sub>).

The carbon available for allocation after the annual maintenance respiration is  $C_{alloc} \Delta t := E - R_M \Delta t$ , where  $\Delta t = 1$  yr. When the tree is healthy, its allocation to labile storage, tissue growth, and growth respiration is based on species-specific statistical allometric relationships



linking the *MeanTree* organs' biomasses to its diameter at breast height (dbh) (SI, Section A.3.1). These dynamic relationships are based on forest inventory data (Repola, 2009; Repola and Ahnlund Ulvcrona, 2014; Lehtonen, 2005) and overcome a limitation of the original ACGCA model, where the tree allometries were defined by time-invariant parameters (SI, Section A.3.2). For simplicity, the species-specific fine root-to-leaf biomass ratio ( $\rho_{RL}$ ) is assumed constant.

With the allometrically-based information on tree organ biomasses based on dbh, we apply an iterative root-search algorithm to identify the annual radial growth  $\Delta dbh$  such that all available carbon ( $C_{alloc} \Delta t$ ) is used to regrow tissue lost by senescence and to grow new tissue. The density  $\rho_W$  of newly produced sapwood and the sapwood to heartwood ratio are determined dynamically for each year, so that the trunk biomass follows the external allometric relationships.

The carbon allocated to leaves is split into three components, tissue growth ( $B_L$ ), transfer into the labile storage pool ( $C_L$ ), and growth respiration ( $G_L$ ), so that the ratio of labile storage to leaf structural biomass remains constant ( $\delta_L$ ). The same approach is applied to fine roots ( $B_R$ ,  $C_R$ ,  $\delta_R$ ). Conversely, for "other" and trunk, who share a common labile storage pool ( $C_S$ ), the ratio of labile storage to structural biomass is variable and depends on the density of newly produced sapwood ( $\rho_W$ ) and species-dependent sapwood parameters (SI, Tables. A.3 and A.4).

Should the available photosynthetic carbon input be low, the tree reverts to a "static" physiological state (see SI, Section A.4), in which the regrowth of senescent tissue is prioritized ( $\Delta dbh = 0$ ). The regrowth of lost sapwood and heartwood of coarse roots and branches exploits carbon resources from the labile storage pool  $C_S$ . If  $C_{alloc} \Delta t$  is insufficient to cover the costs of replacement of senescing leaves and fine roots, the tree switches to a "shrinking" state, where it loses leaf and fine root biomass proportionally, while "other" organs are regrown from the labile storage. If in subsequent years  $C_{alloc} \Delta t$  returns to being sufficient to cover all the carbon needs (e.g., due to stand management or favorable environmental conditions), the tree reverts directly to the "healthy" state. If instead the GPP remains low and the labile carbon storage  $C_S$  depletes, the *MeanTree* dies.

### 2.3.3. Soil module

The soil module (Fig. 1; SI, Section A.7) describes soil carbon dynamics based on three pools: fast decomposing litter (Litter), slowly decomposing coarse woody debris (CWD), and soil organic carbon (SOC). We included only one soil organic carbon pool because our interest in yearly to decadal timescales limits the need for a separation into fast and slowly decomposing SOC (Manzoni and Porporato, 2009). The carbon from the *MeanTrees*' senescing leaves and fine roots provides input to the Litter pool, while sapwood and heartwood carbon enters the coarse woody debris pool (CWD). Further soil carbon input occurs from cutting residues that are not removed from the ecosystem and are partitioned similarly to litter fall from living trees (see SI, Section A.5).

For simplicity, the decay rates and transfer coefficients between pools are set constant, i.e., we neglect the role of inter-annual climatic variability. Annually decomposing carbon from Litter and CWD is partly respired to the atmosphere and partly moved to SOC, from where it is eventually respired.

### 2.3.4. Management and wood-product module

The forest management module defines the management actions applied to *MeanTrees* in the stand. Management includes (i) initial planting of new *MeanTrees* of given species and initial size (dbh<sub>i</sub>) at a density  $N_i$ ; (ii) thinning (i.e., partial reduction of a *MeanTree*'s  $N_i$ ); (iii) cutting (complete removal of the *MeanTree*), and (iv) potential replanting of a new *MeanTree* after cutting. The cutting can be planned or caused by the death of the *MeanTree*.

When a tree in a stand is removed by thinning or cutting, the tree carbon is transferred to the soil and to short- and long-term wood-product pools depending on the tree's species, size, and its taper curve

(see SI, Section A.5). The carbon transferred to wood-product pools is removed from the stand. The modularity of our model allows an easy change of the applied partitioning of harvested wood into different wood-product compartments.

## 2.4. Simulations and explored management scenarios

To generate the results below, starting with empty tree carbon pools, we run a common 160-yr spinup consisting of a mono-specific mixed-aged pine forest stand made of four *MeanTrees* to initialize the stand structure and tree, soil, and wood-product carbon pools (SI, Section C). From this single initial state, we consider four sample alternative management scenarios leading to different stand compositions and, likely, different wood production, carbon sequestration, and climate change mitigation potential:

### • Mixed-aged pine stand

We maintain a mixed-aged pine stand with a continuous canopy cover. At the beginning of the rotation, the oldest *MeanTree* from the spinup is cut and a new *MeanTree* seedling is planted. Thereafter, every 20 yr the oldest *MeanTree* is cut and a seedling replanted, thus maintaining four *MeanTrees* of ages ranging from 0 to 80 yr and differing among them by 20 yr.

### • Even-aged single-species stands

After a clear cut of the spinup stand, four *MeanTree* pines (or spruces) are planted. We plant four slightly differently sized *MeanTree* seedlings (dbh = 1.0, 1.2, 1.4, 1.6 cm) to approximate the initial size distribution. The effects of small initial size differences can compound in time due to unequal access to light.

### • Even-aged mixed-species stand

After a clear cut of the spinup stand, we plant two pine *MeanTrees* and two spruce *MeanTrees*. For both species the initial dbh values are 1.2 and 1.4 cm.

In all even-aged scenarios, the *MeanTree*  $i$  initially comprises  $N_i = 500 \text{ ha}^{-1}$  identical trees, while in the mixed-aged scenario  $N_i = 375 \text{ ha}^{-1}$ . All scenarios start with the same initial condition, last for 80 yr, and end with a final felling of all trees, where all tree carbon is transferred to soil- or wood-product pools. The same environmental forcing is used in all simulations, consisting of re-cycled 20-yr meteorological data from Hyttiälä SMEAR II-research station (61.51°N, 24.00°E) in Southern Finland (Launiainen et al., 2022).

In even-aged scenarios, a pre-commercial thinning is executed as soon as the mean tree height reaches 3.0 m. All *MeanTrees* are then equally thinned such that the total stand density is reduced from 2000 to 1500 trees per hectare, which equals the stand density of the mixed-aged scenario. When the stand basal area (SBA) reaches  $25 \text{ m}^2 \text{ ha}^{-1}$  during any simulation, all *MeanTrees* are uniformly thinned to reduce SBA to  $18 \text{ m}^2 \text{ ha}^{-1}$ , resembling current recommendations in Finland (Kellomäki, 2022; Kellomäki et al., 2008; Yrjölä, 2002). Such thinning is, however, skipped if a scheduled partial harvest (in the mixed-aged pine scenario) or the final felling (in all simulations) is planned for within the following 10 yr.

In the mixed-aged pine scenario, when a *MeanTree*  $i$  is cut, it is replanted at density  $N_i = 375$  trees per hectare with a delay of 4 yr. This delay in replanting is implemented because the allometric relationships used here are not valid below dbh = 1.0 cm.

When the forest stand becomes increasingly dense, a *MeanTree* might not gather enough carbon from photosynthesis to sustain maintenance and regrowth of senescent biomass. In this case the growth of the *MeanTree* is reduced and it uses its labile storage ( $C_S$ ) to regrow senescent coarse roots and branches (see SI, Section A.4). Upon depletion of  $C_S$ , the *MeanTree* dies and is removed from the stand by cutting it down and transferring its carbon to the soil and to wood products. This process resembles self-thinning, and is called *emergency removal of the MeanTree*. At the time of an emergency removal of a dying *MeanTree*, the remaining stand is also equally thinned down to  $\text{SBA} = 18 \text{ m}^2 \text{ ha}^{-1}$  in order to minimize the number of thinnings that have to be executed.

### 3. Results

#### 3.1. Dynamics of stand attributes and biomass

Despite the common starting point at the end of the spinup, the dynamics of stand attributes and carbon pools differ significantly among the sample management scenarios (Fig. 3).

All the even-aged scenarios involve an initial clear cut of the spinup trees and replanting. As a result, mean stand dbh, stand basal area (SBA) and tree carbon stocks are low compared with the mixed-aged pine forest (Fig. 3). Planted trees then grow until SBA reaches the  $25 \text{ m}^2 \text{ ha}^{-1}$  thinning threshold or a *MeanTree* dies due to persistent light limitations and is subsequently cut. Which event occurs first, and its timing, depends on the scenario. In the even-aged pine scenario (orange lines) SBA reaches the thinning threshold after 50 and 60 yr; the uniform thinning of all four *MeanTrees* reduces stand density to 1056 and further to 740 trees per hectare, respectively.

In the even-aged spruce scenario (green lines), emergency removals due to persistent light limitations occur after 40 and 49 yr in the suppressed (small) spruces. The remaining *MeanTrees* are equally thinned to  $\text{SBA} = 18 \text{ m}^2 \text{ ha}^{-1}$ . After 61 yr the SBA-dependent thinning threshold is reached and the two remaining *MeanTrees* are equally thinned. After 65 yr another emergency removal occurs, leaving only one *MeanTree* till the end of the rotation, without any additional thinning. The final stand density in the even-aged spruce scenario is 202 trees per hectare.

In the mixed-species scenario (red lines) SBA reaches the  $25 \text{ m}^2 \text{ ha}^{-1}$  thinning threshold after 42, 52, and 61 yr; the uniform thinning of all *MeanTrees* subsequently reduces stand density to 1069, 765 and finally to 547 trees per hectare. In all scenarios, when thinning occurs, tree density declines and SBA (Fig. 3B) temporarily decreases. In case of an emergency removal, mean dbh increases (Fig. 3A) because the smallest (light-limited) *MeanTree* is removed.

The mixed-aged pine forest scenario has radically different stand dynamics (blue lines in Fig. 3), because only the tallest *MeanTree* is cut down at the beginning of the simulation and one new small *MeanTree* seedling is planted. The mean dbh (Fig. 3A) decreases at removal of the largest tree and more so when the seedlings are planted four years later, although changes are small compared with even-aged forests. Also SBA (Fig. 3B) and the total tree carbon stock (Fig. 3D) drop upon removal of the dominant *MeanTree*. Every 20 yr the oldest *MeanTree* has a dbh around 20 cm and is cut and substituted by a seedling, leading to periodicity in SBA.

#### 3.2. Wood production

The mixed-aged pine scenario is the most productive over the 80-yr rotation, having the largest total wood product yield ( $Y_S + Y_L = 13.6 \text{ kgC m}^{-2}$ ). Between 1.7 and  $2.0 \text{ kgC m}^{-2}$  are transferred to the soil pools, and between 2.3 and  $2.7 \text{ kgC m}^{-2}$  to the wood-product pools at each cutting. At the end of the rotation, all trees are cut down and 2.7 and  $3.0 \text{ kgC m}^{-2}$  move to the soil and wood products, respectively. This scenario is used as reference in further comparisons (see values in Fig. 4A and Table 2). In terms of wood products, the even-aged pine scenario is about 88% as productive in total and 94% and 83% in terms of short- and long-lasting wood products, respectively. The even-aged spruce scenario emerges as the least productive, with total wood products of 69% and short- and long-lasting products of 45% and 83% of that of the mixed-aged pine.

In both mixed-aged and the even-aged pine stands ca. 60% of the harvested wood met the dbh and length criteria for long-lasting wood products (SI, Section A.5). Additional mixed-aged pine simulations showed that this percentage strongly increases when light competition is reduced by decreasing stand density from  $N = 2000 \text{ ha}^{-1}$  to  $N = 1000 \text{ ha}^{-1}$ . This, however, reduces the total carbon stock in the system, climate change mitigation potential, and the yield of short-lasting wood products (SI, Fig. E.2).

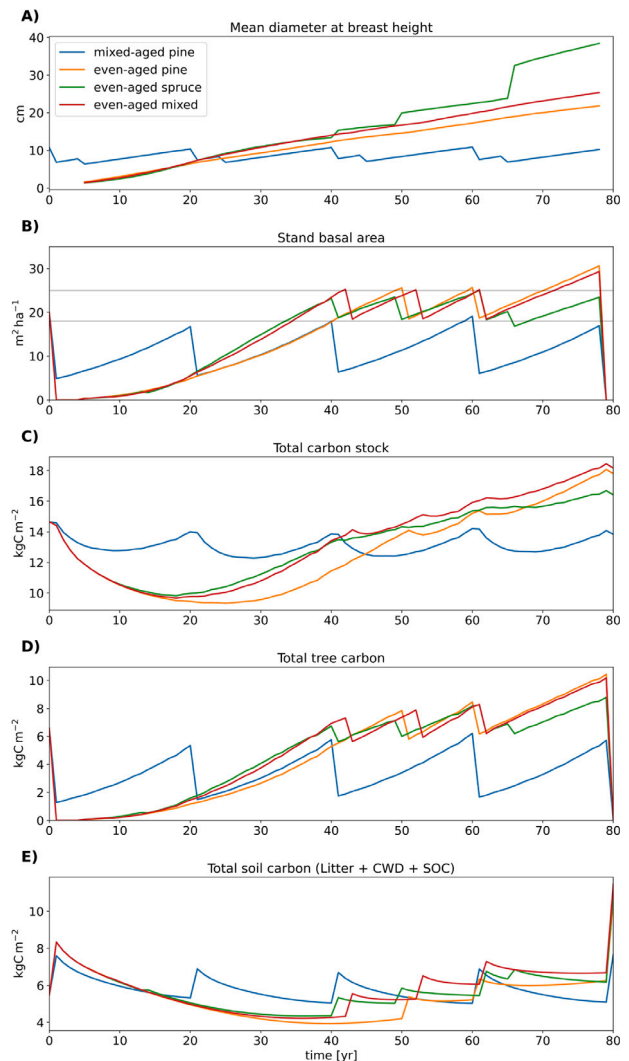


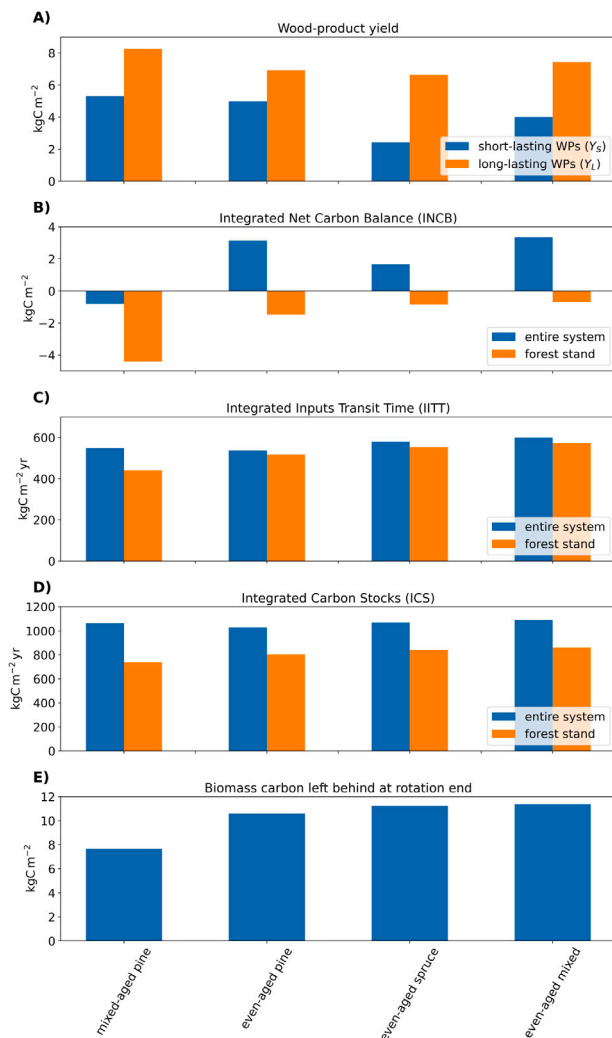
Fig. 3. Temporal evolution of key model outputs (panels) for the four management scenarios (colors): (A) Tree mean diameter at breast height, averaged over all trees in the stand. (B) Stand basal area; grey lines correspond to  $\text{SBA} = 25$  and  $\text{SBA} = 18 \text{ m}^2 \text{ ha}^{-1}$ , i.e., the upper and lower ends of SBA-dependent thinning. (C) Total carbon stock including trees, soil, and wood products ( $\text{kgC m}^{-2}$ ). (D) Total tree carbon stock. (E) Total soil carbon (Litter + CWD + SOC) stock. A detailed attribution of tree carbon to single *MeanTrees* is shown in SI, Fig. E.1.

#### 3.3. Carbon sequestration and climate change mitigation potential

The modeled dynamics of dbh, SBA, carbon stocks, and wood production (Fig. 3) offer insights into the carbon sequestration and the potential for climate change mitigation.

In the even-aged scenarios, the initial clear cut drastically reduces tree carbon stocks and stand carbon uptake, while wood-product and soil carbon is continuously lost as  $\text{CO}_2$  (Fig. 3D, E). During the first 18 (spruce and mixed) to 25 yr (pine) the total carbon stock (trees + soil + wood products) in the system decreases by  $\approx 5 \text{ kgC m}^{-2}$ , and at the minimum it is less than two thirds of the pre-harvest level. The soil carbon stock is lowest ca. 40 yr after the clear cut, approximately half of the initial value. Later in the rotation, all even-aged scenarios lead to higher total carbon stock than the continuous-cover scenario (Fig. 3C). About 50 yr into the rotation, the initial losses are regained (Fig. 3C); this period is referred to as “payback time” in, e.g., Rolls and Forster (2020).

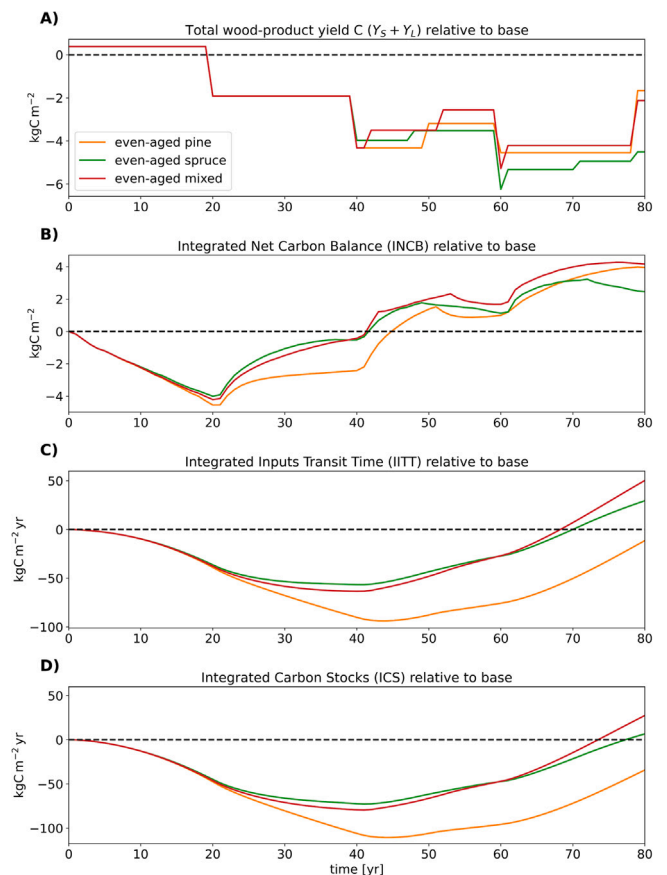
The differences in tree carbon stocks at the end of the rotation are small among the even-aged scenarios (Fig. 3D), but the total carbon



**Fig. 4.** Performance of management scenarios over the rotation when wood-product carbon is included (blue bars), and when excluded (i.e., tree and soil carbon only; orange bars). Panels refer to the following metrics: (A) Yield of short-lasting ( $Y_S$ ) and long-lasting ( $Y_L$ ) wood-products (Eq. (5)). (B) Integrated Net Carbon Balance (INCB, Eq. (6)). (C) Integrated Inputs Transit Time (IITT, Eq. (8)). (D) Integrated Carbon Stocks (ICS, Eq. (9)). (E) The carbon left at the site after final felling; includes carbon in litter, coarse woody debris, and soil organic carbon.

stock is highest in the even-aged pine scenario, followed by even-aged mixed and even-aged spruce (Fig. 3C). Conversely, the total carbon stock recovery early in the rotation is most rapid in the fast-growing young spruce stand. In the even-aged scenarios, it takes 42–46 yr before the total carbon stocks (Integrated Net Carbon Balance, INCB, Fig. 5B) have recovered from the initial clear-cut loss and are at the level of the mixed-aged (continuous-cover) scenario. However, if considering the time during which carbon is retained from the atmosphere (Integrated Inputs Transit Time, IITT, Fig. 5C), it takes 68 yr in the mixed-species and 70 yr for the spruce stand to compensate the lost climate change mitigation potential. The even-aged pine forest does not reach this compensation point within the simulated 80-yr rotation.

Differences among management scenarios are even more pronounced when considering also the fate of legacy carbon, i.e., carbon in the system at the beginning of rotation (Integrated Carbon Stocks, ICS, Fig. 5D). The even-aged mixed and spruce scenarios are level with the mixed-aged simulation only after 72 and 78 yr, respectively. Similar to IITT, the even-aged pine scenario ICS fails to recover over the entire rotation. The net effect of legacy carbon on climate change mitigation can be computed as the difference between ICS and

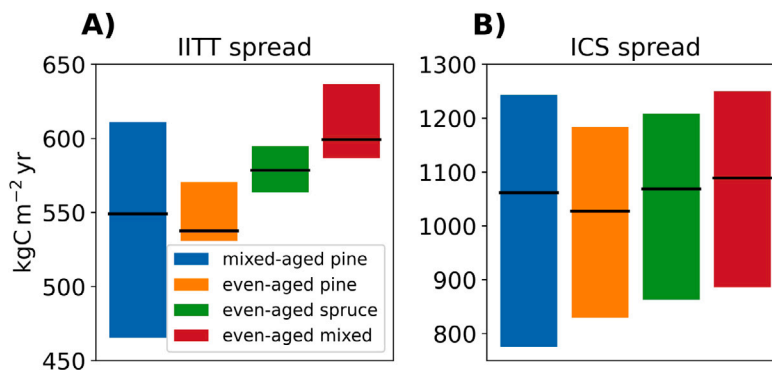


**Fig. 5.** Time series of wood production, carbon sequestration, and climate change mitigation potential metrics. Values are differences from the baseline, here the mixed-aged scenario. (A) Total wood-product yield ( $Y_S + Y_L$ , Eq. (5)). (B) Integrated Net Carbon Balance (INCB, Eq. (6)). (C) Integrated Inputs Transit Time (IITT, Eq. (8)). (D) Integrated Carbon Stocks (ICS, Eq. (9)).

IITT. As shown in SI, Fig. E.3, the negative effect of an initial clear cut of legacy carbon in an established forest stand on climate change mitigation increases over time, when compared to the effect of legacy carbon in the mixed-aged pine forest.

The absolute values of both IITT and ICS, i.e., the climate change mitigation potential, increase when carbon retention times of wood products are included in the analysis (Table 2, Entire system). Relative increases by including wood products are clearly highest in the mixed-aged pine scenario (IITT: +25%, ICS: +44%). Also some rankings of the management scenarios change when wood products are included (Table 2).

In order to assess the effect of different categorization schemes of wood products (FAO, 2022), we additionally assumed wood-product distribution with two extreme wood-product set-ups: short-lasting only and long-lasting wood products only. This analysis provides the ranges of climate change mitigation potential metrics (IITT and ICS) that encompass all potential ways to categorize the harvested wood (Fig. 6). Both IITT (panel A) and ICS (panel B) become more beneficial the more wood is allocated to long-lasting products. Our wood end-use with a short- and a long-lasting pool as described in SI, Section A.5, is located between the two extreme cases (black horizontal lines). In the mixed-aged pine scenario wood end-use has the biggest effect on both IITT and ICS. While wood end-use as only short-lasting wood products makes the mixed-aged pine scenario rank last in terms of climate change mitigation potential, a strong priority on long-lasting wood products lifts the mixed-aged pine scenario to the second rank.



**Fig. 6.** Effect of wood end-use on the climate change mitigation potential metrics in the four different scenarios. The lower end of each bar represents wood end-use as short-lasting wood products only, the upper end long-lasting wood products only. The black horizontal line represents the wood end-use with short- and long-lasting wood products as described in SI, Section A.5. (A) Integrated Inputs Transit Time (IITT, Eq. (8)). (B) Integrated Carbon Stocks (ICS, Eq. (9)).

**Table 2**

Ranking of management scenarios according to carbon sequestration (INCB) and climate change mitigation potential metrics (IITT, ICS) after one complete rotation ( $T = 80$  yr), with respect to the entire system (trees, soil, and wood products) and the stand only (trees and soil), and short-lasting ( $Y_S$ ), long-lasting ( $Y_L$ ) and combined ( $Y_S + Y_L$ ) wood-product yield. The values correspond to those in Fig. 4.

Metric	Scenario	Entire system		Stand only	
		Rank	Value	Rank	Value
INCB (kgC m <sup>-2</sup> )	mixed-aged pine	4	-0.8	4	-4.4
	even-aged pine	2	3.2	3	-1.5
	even-aged spruce	3	1.8	2	-0.9
	even-aged mixed	1	3.5	1	-0.6
IITT (kgC m <sup>-2</sup> yr)	mixed-aged pine	3	549.0	4	440.0
	even-aged pine	4	537.5	3	516.4
	even-aged spruce	2	577.4	2	550.1
	even-aged mixed	1	600.0	1	573.4
ICS (kgC m <sup>-2</sup> yr)	mixed-aged pine	3	1061.7	4	737.2
	even-aged pine	4	1027.5	3	803.8
	even-aged spruce	2	1067.3	2	837.5
	even-aged mixed	1	1090.0	1	860.8
$Y_S$ (kgC m <sup>-2</sup> )	mixed-aged pine	1	5.3		
	even-aged pine	2	5.0		
	even-aged spruce	4	2.4		
	even-aged mixed	3	4.0		
$Y_L$ (kgC m <sup>-2</sup> )	mixed-aged pine	1	8.3		
	even-aged pine	3	6.9		
	even-aged spruce	4	6.9		
	even-aged mixed	2	7.5		
$Y_S + Y_L$ (kgC m <sup>-2</sup> )	mixed-aged pine	1	13.6		
	even-aged pine	2	11.9		
	even-aged spruce	4	9.4		
	even-aged mixed	3	11.6		

#### 4. Discussion

The performance of boreal forestry has been commonly assessed through the economic perspectives and wood production over fixed planning horizons (e.g., 60–100-yr rotation cycles). The increasing interest in climate change mitigation and biodiversity conservation (Astrup et al., 2018; Triviño et al., 2023) makes these metrics insufficient. Forest performance needs to be assessed via a combination of metrics describing forest productivity, management and climate change mitigation synergies and trade-offs. In particular, to assess the climate change mitigation potential of forest management, it is necessary to quantify the amount and timing of carbon fixation and to track the carbon path through the forest — wood product system until its release via decomposition or burning of wood products.

#### 4.1. Climate change mitigation potential depends on management decisions and target timescale

We explored how stand management decisions affect wood-product yield and alternative climate change mitigation potential metrics under a fixed 80-yr rotation period, considering four management scenarios that represent idealized cases of typical management chains in the Nordic countries. Despite identical initial carbon stocks in trees, soil, and wood products, different management alternatives lead to drastically different pathways of carbon stocks and climate change mitigation potential metrics (Figs. 3 and 5). Importantly, the ranking of the management scenarios according to their net carbon sequestration (ICNB) or transit-time based metrics (IITT and ICS) depends on the timescale considered (Fig. 5).

Over the 80-yr rotation, all even-aged scenarios lead to higher carbon stock increases compared with the mixed-aged simulation (ICNB; Fig. 4 and Table 2). However, the initial clear cut and planting at  $t = 0$  cause decreasing carbon stocks during the first ca. 20 yr. It takes 40–43 yr before ICNB reaches again the level of the mixed-aged scenario. In terms of wood products, mixed-aged and mixed-species stand management scenarios were the most productive (Table 2).

Comparing the dynamics and scenario-ranking of INCB to those of the transit-time based metrics IITT and ICS (Table 2 and Fig. 5) shows that wood production and carbon sequestration are relevant for forest owners and forest industry but insufficient to evaluate the climate impacts of boreal forest management. In even-aged scenarios, the decrease in carbon stock and reduced carbon uptake early in the rotation (Fig. 3C) have a strong negative effect on climate change mitigation potential (Fig. 5C, D). The transit-time based metrics suggest that all the even-aged scenarios are inferior to the mixed-aged stand for most part of the rotation period, as it takes almost the entire 80-yr rotation to compensate for the lost climate change mitigation potential caused by the initial clear cut. Thus, the climate change mitigation potential of a management scenario strongly depends on the time scale considered. Long-term effects and short-term impacts can be in conflict: clear-cut management has negative effects on short-term ( $\leq 50$  yrs) climate goals (Fig. 5), and can thus compromise reaching short-term climate targets such as Finland’s goal of reaching carbon neutrality by 2035 (Huttunen et al., 2022).

Our idealized scenarios also suggest the higher climate change mitigation potential (at least in the short-term) of mixed-aged management does not compromise wood production, in line with, e.g., Pukkala et al. (2009), Pukkala (2014), Kuuluvainen et al. (2012). Similarly, despite lacking an explicit facilitation effect in the model, the simulated species mixture yielded ca. 9% more total wood products than a theoretical 50–50 mix of mono-specific forests (Table 2). Such overyielding is in line with Ruiz-Peinado et al. (2021). We also conclude that pine contributes slightly more than spruce to IITT in the mixed-species simulation (55%



compared with 45%). In particular, during the first 50 yr the contribution of pine is much higher than the one of spruce, and later the relative contribution of spruce increases. However, we cannot disentangle the contributions of different species to INCB and ICS because we cannot attribute the effects of legacy carbon to a specific species. While the even-aged single/mixed-species scenarios mimic rotational forestry and the mixed-aged scenario resembles continuous-cover management, we emphasize that these results are, however, far from conclusive for making management decisions because the consequences of age and species diversity for stand productivity are shown to be highly site- and species-specific in general (Mikola, 1984; Lähde et al., 2010; Huuskonen et al., 2021; Holmström et al., 2018).

#### 4.1.1. Wood end-use is central for climate change mitigation potential

The Food and Agriculture Organization of the United Nations (FAO) suggests 14 different categories of wood products (FAO, 2022). We considered here only short-lasting ( $WP_S$ ) and long-lasting ( $WP_L$ ) wood products, as this simplification allows us to study the magnitude of the effects of carbon stored in wood products on climate change mitigation potential without delving into economical considerations or wood markets, which would be out of the scope of this manuscript. We attributed harvested trunk wood to  $WP_S$  and  $WP_L$  according to its diameter and length (SI, Section A.5) to reveal how wood end-use affects the alternative metrics of climate change mitigation potential. Both IITT and ICS increase when carbon retention in wood products is included in the analysis (Table 2, Entire system vs. Stand only), affecting also the ranking of the management scenarios.

We further studied two extreme cases of wood allocation to only short-lasting or only long-lasting wood products. This allows us to cover the effects of a whole range of potential alternative wood-product categorizations on climate change mitigation potential. Fig. 6 shows that long-lasting wood products have a strong positive effect on climate change mitigation potential. Over the 80-yr horizon considered here, wood end-use has a stronger effect than the differences among stand management scenarios, making it crucial to consider wood end-use and wood-product lifetimes when evaluating climate impacts of forestry (Hurmekoski et al., 2023). A potential increase in using large diameter wood for short-lasting bioenergy products would have negative effects on the climate change mitigation potential in all the considered management scenarios.

#### 4.2. Implications for planning climate-smart forest management

Managed forests need to provide biomass while increasingly supporting climate change mitigation efforts. These goals are often in contrast (Jandl et al., 2007b; Noormets et al., 2015; Jandl et al., 2007a), calling for robust approaches and metrics to evaluate benefits and drawbacks of different management strategies in support of the scientific and public debate (Sierra et al., 2021). While a practically realizable approach to climate-smart forestry needs to take economic aspects into account (Nabuurs et al., 2014; Yousefpour et al., 2018), the theoretical foundation for climate change mitigation requires focus on carbon transit times because the time carbon fixed via photosynthesis remains stored in living plants, residues, soil, or wood products is central to determine the avoided global warming effect of carbon sequestration.

Our model makes it possible, for the first time, to contrast boreal forest stand management with respect to different wood-product ( $Y_S$ ,  $Y_L$ ), carbon sequestration (INCB), and climate change mitigation potential (IITT, ICS) metrics simultaneously. The INCB (Eq. (6)), IITT (Eq. (8)) and ICS (Eq. (9)) increase whenever more carbon enters the system compared with the carbon released. However, only the latter two metrics increase if this carbon spends more time in the system (and hence outside of the atmosphere). These metrics account for the timing of carbon uptake and release, which matters for climate change mitigation potential. For example, a large amount of carbon entering

the system towards the end of the rotation has a large impact on INCB, but contributes little to IITT and ICS. Thus, only the transit-time based metrics IITT and ICS measure climate change mitigation potential. Conversely, INCB is suitable to quantify carbon sequestration, and not climate change mitigation potential, although it is often used for the latter purpose (Pukkala, 2020). A reason for the frequent use of INCB is likely that computing the explicit transit times, i.e., using IITT, requires a detailed compartmental model as the one developed in this study.

ICS is an alternative to IITT as climate change mitigation potential metric, as, somewhat surprisingly, it is implicitly a transit-time based metric (Eq. (9)). Its main advantage is that its computation does not explicitly require transit times and a compartmental model, rather just the time series of total carbon stocks during the rotation. This makes ICS and equivalent metrics such as rotation-average carbon stocks (Lundmark et al., 2018) a powerful and widely applicable means to assess climate change mitigation potential, as long as soil- and wood-product carbon is taken into account. However, in order to disentangle the effects of legacy carbon and carbon fixed during the rotation, we need to compute both ICS and IITT, and the latter requires a detailed compartmental model. The net effect of legacy carbon on climate change mitigation potential, as shown in SI, Fig. E.3, can provide a first starting point for exploring compensation mechanisms for maintaining a continuous-cover forest instead of switching to a clear-cut based strategy.

Both the explored boreal forest management scenarios and the newly developed model focus on the level of a single forest stand. The stand is the fundamental unit at which management operations are planned and executed. It is also the scale on which virtually all forest growth models, carbon balance models, and forest decision support simulators such as MOTTI (Hynynen et al., 2005) and Heureka (Lämås et al., 2023) operate. Therefore, the stand level was also the natural scale to analyze and interpret the differences in carbon sequestration and climate change mitigation potential metrics in this study. We acknowledge that climate change mitigation potential of forest management and its trade-offs, e.g., with wood production within a given region and timescale, depend on the initial stand attributes, site type distribution, and management history (Hiltunen et al., 2021). Therefore, scenario simulations to broadly address climate change mitigation potential of forest management require, at minimum, simulating representative sub-samples from the true distribution of forest stands in the region of interest (e.g., Lehtonen et al. 2023, Matala et al. 2009). Our results show that ICS is a powerful metric for such an analysis because of its simple computation and its implicit transit-time dependence. The proposed process-based model framework can also support scenario analyses under changing forest product demands, management methods, and climate conditions not well covered by the commonly used statistical-empirical forest simulators. Leveraging the full capability of the proposed model for specific management decisions requires extensive evaluation and parameter optimization against, e.g., National Forest Inventory data and growth experiments, to obtain parameter values and allometric equations for specific species mixtures (Riofrío et al., 2019; Ruiz-Peinado et al., 2021) and for sites located on a large geographical grid to investigate carefully the averaged performance metrics on a larger scale (Lemprière et al., 2013).

#### 4.3. Model properties

To quantify metrics of production, carbon sequestration, and climate change mitigation potential at different time scales, we developed a process-based, mass-balanced model that combines an improved version of the Allometrically Constrained Growth and Carbon Allocation model (ACGCA, Ogle and Pacala, 2009) with process-based photosynthesis and soil carbon modules, and incorporates harvested wood-product pools. Compared with existing tree- and stand-level growth models (see reviews by Hawkes 2000, Le Roux et al. 2001, Busing

and Maily 2004) and allocation schemes (see reviews by Ågren and Wikström 1993, Cannell and Dewar 1994, Lacoite 2000), our model has the advantage of resting on a mass-balanced approach described by discretely implemented ordinary differential equations.

The model allows computing the carbon age distributions and transit times directly (Sections 2.1 and 2.2), quantifying not only the forest stand carbon storage in different pools but also the *avoided* atmospheric radiative warming provided by the storage of carbon (Sierra et al., 2021) in both forest stand and wood products. The quantification of storage time is necessary to evaluate the reduction of the Global Warming Potential (Shine et al., 1990) of different management scenarios. The model developed was necessary to overcome the limitations of the majority of current forest models such as FORMIND (Köhler and Huth, 1998), CABLE (Wang et al., 2010) and 3-PG (Landsberg and Waring, 1997), which either include only tree biomass carbon pools or would require a substantial mathematical reformulation to recast the model as an ordinary differential equation in compartmental form to compute transit times (Section 2.1, Rasmussen et al. 2016, Metzler et al. 2018).

The process-based photosynthesis model quantifies carbon fixation for each *MeanTree* (part of APES, Launiainen et al., 2015), and allows to describe directly the effects of species traits, soil, and climatic conditions. The explicit description of the light environment in the canopy enables the consideration of among-tree competition for light, necessary to simulate mixed-species and mixed-aged forests. As such, we can evaluate also the prospects of novel management strategies with no or little historical data to rely on. The inclusion of the nonstructural carbohydrate reserve ( $C_S$ ) allows us to consider the effect of light competition and reduced carbon fixation on tree health and mortality (see SI, Section A.4). The depletion of tree labile carbon storage under prolonged light limitation mimics self-thinning. Indeed, the modeled stand densities in the even-aged spruce and pine scenarios largely follow Reineke's rule (Reineke, 1933), which links tree density and mean dbh (SI, Fig. E.4).

A mass-conserving approach is used to compute maintenance and growth respiration and carbon flows based on annually available GPP within each *MeanTree*. This provides a true carbon age distribution for autotrophic respiration, which is comparable with radiocarbon measurements (Carbone et al., 2007, 2013; Muhr et al., 2013). These increasingly available data could support identifying model parameters related to, e.g., nonstructural carbohydrate pools ( $\delta_L$ ,  $\delta_R$ ,  $\delta_S$ ) that are otherwise hard to estimate.

Carbon allocation to tree organs is described via empirical allometric equations linking tree organ biomass to dbh, derived from species-specific forest inventory data (SI, Section A.3.1). This is a compromise between a minimalist description and detailed physiology-based functions (Bugmann, 2001) and ensures that organ growth follows observed allocation patterns in the studied species, while the total biomass growth rate is determined by stand structure and environmental conditions. The allometric equations are based on even-aged and mostly mono-specific stands from Finland (Repola and Ahnlund Ulvcróna, 2014; Repola, 2009; Lehtonen, 2005). Nevertheless, in reality allometries in mixed-species stands can deviate from those of single-species stands (Riofrío et al., 2019). In the current version of the model, allocation does not change with climatic conditions or site fertility - a simplification that could be relaxed by a source-sink based approach as implemented, e.g., in the Quincy model (Thum et al., 2019), which probably amounts to a research project of a size comparable to the one presented here. The species-specific but fixed parameterization of biomass maintenance and growth costs and the fine root-to-leaf biomass ratio neglect tree adaptation to given environmental conditions. For instance, a reduction in the fine root-to-leaf biomass ratio ( $\rho_{RL}$ ) would lead to reduced carbon allocation to roots and hence more carbon available for trunk growth. We addressed this issue in a sensitivity analysis (see Section 4.3.1).

The species- and age-mixtures are considered in a simplified way. Among-tree competition for water and nutrients and the facilitating

effects due to canopy niche complementarity are not considered. However, the modular structure of the model enables easy development of existing modules and inclusion of additional processes. For example, inclusion of broadleaf species such as birch or other mixtures of three or more species in the simulations is possible. Also understory vegetation, currently omitted, could contribute substantially to the stand carbon dynamics and fill spatial or functional niches. Also the allometric relationships could be altered to accommodate forests growing in different and changing conditions, via dynamic rules or competition on water and nutrients among the *MeanTrees*, in case data is available. Similarly, the soil carbon module could include dynamic decay rates and transfer coefficients between pools to capture the role of inter-annual climatic variability (e.g., as in Roth-C, Jenkinson and Rayner 1977 or Century, Parton et al. 1987).

#### 4.3.1. Benchmarking and sensitivity analysis

We used sub-modules based on well-established approaches extensively tested earlier. For example, the photosynthesis module has been applied successfully for boreal forests in Fennoscandia (Launiainen et al., 2015; Leppä et al., 2020; Launiainen et al., 2019, 2022). The carbon dynamics of the tree module is, to a large extent, based on ACGCA, which has previously been successfully used in simulations of tree growth (Fell et al., 2018), gap dynamics (Ogle and Pacala, 2009; Fell and Ogle, 2018), and labile carbon dynamics (Ogle and Pacala, 2009). We further benchmarked the modules against representative observations and data from the literature and provide more in-depth tests of the model behavior in SI, Section D.

The key model outputs, such as annual mean diameter growth (SI, Fig. D.1, Repola 2009, Table 3) and total biomass growth rate (Fig. 3, Berggren Kleja et al. 2007, Fig. 3a) were reasonably well aligned with observations from even-aged single-species forests, lending support to our model and results. The reliable estimates of mean diameter (dbh) growth over 5 yr ensure that also trunk volume growth and resulting yield of short- and long-term wood products are reasonably well simulated over time. Because dbh drives the tree allometry via the external statistical allometries (Lehtonen, 2005; Repola, 2009; Repola and Ahnlund Ulvcróna, 2014), accordance of modeled mean radial growth with observations lends support to the modeled biomass of the tree organs. Moreover, the mean trunk wood densities ( $481 \text{ kg}_{\text{dw}} \text{ m}^{-3}$  for even-aged pine and  $385 \text{ kg}_{\text{dw}} \text{ m}^{-3}$  for even-aged spruce) were just outside the ranges observed for pine and spruce forests (Repola 2006, Fig. 4).

At stand level and averaged over the rotation, the carbon use efficiency (CUE), i.e., the complement to autotrophic respiration to gross primary productivity ratio,  $(\text{GPP} - R_a)/\text{GPP}$ , was comparable (0.49 and 0.32 for even-aged pine and spruce, respectively) with values observed for jack pine (0.34 to 0.43) and black spruce (0.29 to 0.39), respectively (Ryan et al., 1997, Table 7).

During the process of development and calibration, the model proved most sensitive to four parameters: maintenance respiration rate of leaves ( $R_{mL}$ ), senescence rate of fine roots ( $S_R$ ), maximum carboxylation rate at  $25^\circ\text{C}$  ( $V_{\text{cmax},25}$ ), and fine root-to-leaf biomass ratio ( $\rho_{RL}$ ). To analyze whether the parameter uncertainty has major impact on answering the research questions, we ran the four management scenarios by varying the four above mentioned parameters, one at a time, from 90 to 110% of the values reported in Tables A.1, A.3, and A.4. We computed the relative spread (the difference between the maximum and minimum values divided by the values from simulation with default parameters) of the analyzed metrics, i.e., total carbon stock, total wood-product yield ( $Y_S + Y_L$ ), Integrated Net Carbon Balance (INCB), Integrated Inputs Transit Time (IITT), and Integrated Carbon Stocks (ICS) at the end of the rotation period.

The total carbon stock in the even-aged spruce scenario was the most sensitive metric, with particularly high sensitivity to the root-associated parameters  $S_R$  and  $\rho_{RL}$  (Table E.1). This sensitivity can be explained by the high level of light competition by shading in dense

spruce stands. Any carbon additionally allocated to roots instead of above-ground biomass growth comes with the risk of carbon starvation due to low light availability, and mortality of suppressed trees negatively affects the total amount of carbon in the stand. In general, the wood-product yield, IITT, and ICS vary less than 15% when parameter values of  $R_{mL}$ ,  $S_R$ , and  $\rho_{RL}$  vary up to  $\pm 10\%$  away from their default values. All three metrics showed the strongest sensitivity with respect to variations in leaf-level carbon assimilation capacity (i.e.,  $V_{cmax,25}$ ). The sensitivity analysis showed that, although the values of the different metrics naturally vary with parameter values, the specific choice and uncertainty of parameter values do not alter the interpretation of our results and conclusions.

## 5. Conclusions

Boreal forests are increasingly expected to cater to different, often contrasting goals, from biomass production to climate change mitigation. We illustrated how conclusions regarding the performance of forest stands depend on the metric used, even when considering the same goal, like climate change mitigation potential. To that end, we developed a novel forest growth and carbon-balance model capable of tracking the carbon path through the system. The model combines process-based modules for gross-primary productivity as well as autotrophic and heterotrophic respiration with mass-conserving statistical carbon allocation in a tree. It allows to compute the age distribution of carbon in the tree stand-soil-wood product system, enabling the quantification of wood production, carbon sequestration, and climate change mitigation potential across an entire rotation of single- or mixed-species stands.

Using the model, we quantified four metrics of performance: wood production, mass-only based carbon sequestration as expressed by the Integrated Net Carbon Balance (INCB), and transit-time based climate change mitigation potential as expressed by the Integrated Inputs Transit Time (IITT) and the Integrated Carbon Stocks (ICS).

We show that wood production, mass-only based carbon sequestration, and transit-time based climate change mitigation potential provide different information and hence ranks of management scenario performances. For example, when comparing four sample management scenarios over an 80-yr rotation, the wood production was highest in the mixed-aged pine scenario, while carbon sequestration was higher in the even-aged scenarios. However, the even-aged scenarios had lower climate change mitigation potential for most of the rotation compared to the mixed-aged scenario. The initial clear-cut effects on carbon stocks were compensated after 42–45 yr, and ultimately even-aged scenarios sequestered more carbon over the rotation cycle (i.e., had higher INCB). However, the transit-time based metrics, accounting for the retention time of carbon away from the atmosphere (ICS, IITT), show that it takes a typical 80 yr rotation or more to compensate for the lost climate regulation caused by an initial clear cut. It is thus necessary to select the evaluation metrics based on the desired goal and time scale, and to consider the fate of the legacy and wood-product carbon. In short, this means clearly defining the system boundaries and goal of the analysis.

When evaluating climate change mitigation options of forest management, it is necessary to resort to transit-based metrics to determine the avoided radiative effects of greenhouse gasses in the atmosphere. Nevertheless, an effective metric of climate change mitigation does not necessarily need to rest on tracking the path of carbon in the system. We show that ICS is implicitly a transit-time based metric as it accounts for both the amount and the storage time of carbon uptake in the system (Eq. (9)). The computation of ICS requires only time series of total carbon stocks during the rotation. Therefore, ICS and equivalent metrics such as rotation-average carbon stocks (Lundmark et al., 2018) emerge as widely applicable and powerful metrics to assess climate change mitigation potential, as long as soil- and wood-product carbon is taken into account. The in-depth understanding of the different metrics provides support to future multi-criteria decision making on forest resource use.

## CRediT authorship contribution statement

**Holger Metzler:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Samuli Launiainen:** Writing – review & editing, Validation, Software, Funding acquisition. **Giulia Vico:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

All code and data are available at: <https://doi.org/10.5281/zenodo.10848284>.

## Acknowledgments

Funding was provided by the Swedish Research Council for Sustainable Development FORMAS (grant number 2018-01820), the Research Council of Finland (grant number 348102), the Knut and Alice Wallenberg Foundation, Sweden (grant number 2018.0259), and the GreenFeedBack project from the EU Horizon Europe – Framework Programme for Research and Innovation (grant number 101056921). We thank Carlos A. Sierra, Henrik Hartmann, and David Herrera from Max Planck Institute for Biogeochemistry Jena, Germany, and Johannes Larson from SLU in Umeå for fruitful discussions and input. We are particularly grateful to Carlos A. Sierra for providing access to computing facilities. We also thank two anonymous reviewers for their constructive suggestions which allowed us to significantly improve the manuscript.

## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.ecolmodel.2024.110694>.

## References

- Anderson, David H., 1983. *Compartmental Modeling and Tracer Kinetics*, vol. 50, Springer Science & Business Media.
- Astrup, Rasmus, Bernier, Pierre Y., Genet, H el ene, Lutz, David A., Bright, Ryan M., 2018. A sensible climate solution for the boreal forest. *Nature Clim. Change* 8 (1), 11–12.
- Baldocchi, Dennis, Kelliher, Francis M., Black, T. Aet, Jarvis, Paul, 2000. Climate and vegetation controls on boreal zone energy exchange. *Global Change Biol.* 6 (S1), 69–83.
- Berggren Kleja, Dan, Svensson, Magnus, Majdi, Hooshang, Jansson, Per-Erik, Langvall, Ola, Bergkvist, Bo, Johansson, Maj-Britt, Weslien, Per, Truusb, Laimi, Lindroth, Anders,  Agren, G oran I., 2007. Pools and fluxes of carbon in three Norway spruce stands along a climatic gradient in Sweden. *Biogeochemistry*.
- Bolin, Bert, Rodhe, Henning, 1973. A note on the concepts of age distribution and transit time in natural reservoirs. *Tellus* 25 (1), 58–62.
- Bonan, Gordon B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320 (5882), 1444–1449.
- B ottcher, Hannes, Freibauer, Annette, Obersteiner, Michael, Schulze, Ernst-Detlef, 2008a. Uncertainty analysis of climate change mitigation options in the forestry sector using a generic carbon budget model. *Ecol. Model.* 213 (1), 45–62.
- B ottcher, Hannes, Kurz, Werner A., Freibauer, Annette, 2008b. Accounting of forest carbon sinks and sources under a future climate protocol—factoring out past disturbance and management effects on age-class structure. *Environ. Sci. Policy* 11 (8), 669–686.
- Brockett, Roger W., 2015. *Finite Dimensional Linear Systems*, vol. 74, SIAM.
- Bugmann, Harald, 2001. A review of forest gap models. *Clim. Change* 51 (3), 259–305.
- Busing, Richard T., Mailly, Daniel, 2004. Advances in spatial, individual-based modelling of forest dynamics. *J. Veg. Sci.* 15 (6), 831–842.



- Cannell, M.G.R., Dewar, R.C., 1994. Carbon allocation in trees: a review of concepts for modelling. *Adv. Ecol. Res.* 25, 59–104.
- Carbone, Mariah S., Czimczik, Claudia I., Keenan, Trevor F., Murakami, Paula F., Pederson, Neil, Schaberg, Paul G., Xu, Xiaomei, Richardson, Andrew D., 2013. Age, allocation and availability of nonstructural carbon in mature red maple trees. *New Phytol.* 200 (4), 1145–1155.
- Carbone, Mariah S., Czimczik, Claudia I., McDuffee, Kelsey E., Trumbore, Susan E., 2007. Allocation and residence time of photosynthetic products in a boreal forest using a low-level  $^{14}\text{C}$  pulse-chase labeling technique. *Global Change Biol.* 13 (2), 466–477.
- Chapin, III, F.S., McGuire, A.D., Randerson, J., Pielke, R., Baldocchi, Dennis, Hobbie, S.E., Roulet, Nigel, Eugster, W., Kasiskche, E., Rastetter, E.B., et al., 2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biol.* 6 (S1), 211–223.
- FAO, 2022. Classification of forest products. *Sci. Rep.* <http://dx.doi.org/10.4060/cb8216en>.
- Farquhar, G.D., Caemmerer, S.V., Berry, J.A., 1980. A biochemical model for photosynthetic  $\text{CO}_2$  assimilation in leaves of  $\text{C}_3$  species. *Planta* 149 (1), 78–90.
- Fell, Michael, Barber, Jarrett, Lichstein, Jeremy W., Ogle, Kiona, 2018. Multidimensional trait space informed by a mechanistic model of tree growth and carbon allocation. *Ecosphere* 9 (1), e02060.
- Fell, Michael, Ogle, Kiona, 2018. Refinement of a theoretical trait space for North American trees via environmental filtering. *Ecol. Monograph* 88 (3), 372–384.
- Hawkes, Corinna, 2000. Woody plant mortality algorithms: description, problems and progress. *Ecol. Model.* 126 (2–3), 225–248.
- Hiltunen, M., Strandman, H., Kilpeläinen, A., 2021. Optimizing forest management for climate impact and economic profitability under alternative initial stand age structures. *Biomass Bioenergy* 147, 106027.
- Högberg, P., Ceder, L.A., Astrup, R., Binkley, D., Dalsgaard, L., Egnell, G., Filipchuk, A., Genet, H., Ilintsev, A., Kurz, W.A., et al., 2021. Sustainable Boreal Forest Management Challenges and Opportunities for Climate Change Mitigation. Swedish Forest Agency.
- Holmström, Emma, Goude, Martin, Nilsson, Oscar, Nordin, Annika, Lundmark, Tomas, Nilsson, Urban, 2018. Productivity of Scots pine and Norway spruce in central Sweden and competitive release in mixtures of the two species. *Forest Ecol. Manag.* 429, 287–293.
- Hurmekoski, Elias, Kunttu, Janni, Heinonen, Tero, Pukkala, Timo, Peltola, Heli, 2023. Does expanding wood use in construction and textile markets contribute to climate change mitigation? *Renew. Sustain. Energy Rev.* 174, 113152.
- Huttunen, Riku, Kuuva, Petteri, Kinnunen, Markku, Lemström, Bettina, Hirvonen, Petri, 2022. Carbon Neutral Finland 2035 - National Climate and Energy Strategy. Ministry of Economic Affairs and Employment of Finland.
- Huuskonen, Saija, Domisch, Timo, Finér, Leena, Hantula, Jarkko, Hynynen, Jari, Matala, Juhon, Miina, Jari, Neuvonen, Seppo, Nevalainen, Seppo, Niemistö, Pentti, et al., 2021. What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia? *For. Ecol. Manag.* 479, 118558.
- Hynynen, Jari, Ahtikoski, Anssi, Siitonen, Juha, Sievänen, Risto, Liski, Jari, 2005. Applying the MOTTI simulator to analyse the effects of alternative management schedules on timber and non-timber production. *Forest Ecol. Manag.* 207 (1–2), 5–18.
- Jacquez, John A., Simon, Carl P., 1993. Qualitative theory of compartmental systems. *Siam Rev.* 35 (1), 43–79.
- Jandl, Robert, Lindner, Marcus, Vesterdal, Lars, Bauwens, Bram, Baritz, Rainer, Hagedorn, Frank, Johnson, Dale W., Minkkinen, Kari, Byrne, Kenneth A., 2007a. How strongly can forest management influence soil carbon sequestration? *Geoderma* 137 (3–4), 253–268.
- Jandl, Robert, Vesterdal, Lars, Olsson, Mats, Bens, Oliver, Badeck, Franz, Roc, J., 2007b. Carbon sequestration and forest management. *CABI Rev.* (2007), 16–pp.
- Jenkinson, D.S., Rayner, J.H., 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Sci.* 123 (5), 298–305.
- Kellomäki, Seppo, 2022. Management of Boreal Forests: Theories and Applications for Ecosystem Services. Springer Nature.
- Kellomäki, Seppo, Peltola, Heli, Nuutinen, Tuula, Korhonen, Kari T., Strandman, Harri, 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. *Philos. Trans. R. Soc. B* 363 (1501), 2339–2349.
- Köhler, Peter, Huth, Andreas, 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model FORMIND. *Ecol. Model.* 109 (3), 301–321.
- Kuuluvainen, Timo, Tahvonen, Olli, Aakala, Tuomas, 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. *Ambio* 41 (7), 720–737.
- Lacointe, André, 2000. Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. *Ann. For. Sci.* 57 (5), 521–533.
- Lähde, Erkki, Laiho, Olavi, Lin, C. Julian, 2010. Silvicultural alternatives in an uneven-sized forest dominated by *Picea abies*. *J. For. Res.* 15 (1), 14–20.
- Lämäs, Tomas, Sängstuvall, Lars, Öhman, Karin, Lundström, Johanna, Årevall, Jonatan, Holmström, Hampus, Nilsson, Linus, Nordström, Eva-Maria, Wikberg, Per-Erik, Wikström, Peder, et al., 2023. The multi-faceted Swedish Heureka forest decision support system: context, functionality, design, and 10 years experiences of its use. *Front. For. Glob. Chang.* 6, 1163105.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manag.* 95 (3), 209–228.
- Larsen, Jørgen Bo, Angelstam, Per, Bauhus, Jürgen, Carvalho, João Fidalgo, Diaci, Jurij, Dobrowolska, Dorota, Gazda, Anna, Gustafsson, Lena, Krumm, Frank, Knoke, Thomas, et al., 2022. Closer-to-Nature Forest Management. From Science to Policy 12, vol. 12, EFI European Forest Institute.
- Launiainen, Samuli, Guan, Mingfu, Salmivaara, Aura, Kieloaho, Antti-Jussi, 2019. Modelling boreal forest evapotranspiration and water balance at stand and catchment scales: a spatial approach. *Hydrol. Earth Syst. Sci.* 23 (8), 3457–3480.
- Launiainen, Samuli, Katul, Gabriel G., Lauren, Ari, Kolari, Pasi, 2015. Coupling boreal forest  $\text{CO}_2$ ,  $\text{H}_2\text{O}$  and energy flows by a vertically structured forest canopy – Soil model with separate bryophyte layer. *Ecol. Model.* 312, 385–405.
- Launiainen, Samuli, Katul, Gabriel G., Leppä, Kersti, Kolari, Pasi, Aslan, Toprak, Grönholm, Tiia, Korhonen, Lauri, Mammarella, Ivan, Timo, Vesala, 2022. Does increasing atmospheric  $\text{CO}_2$  explain increasing carbon sink of a boreal coniferous forest? *Global Change Biol.*
- Le Roux, Xavier, Lacointe, André, Escobar-Gutiérrez, Abraham, Le Dizès, Séverine, 2001. Carbon-based models of individual tree growth: a critical appraisal. *Ann. For. Sci.* 58 (5), 469–506.
- Lehtonen, Alekski, 2005. Estimating foliage biomass in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) plots. *Tree Physiol.* 25 (7), 803–811.
- Lehtonen, Alekski, Eyvindson, Kyle, Härkönen, Kari, Leppä, Kersti, Salmivaara, Aura, Peltoniemi, Mikko, Salminen, Olli, Sarkkola, Sakari, Launiainen, Samuli, Ojanen, Paavo, et al., 2023. Potential of continuous cover forestry on drained peatlands to increase the carbon sink in Finland. *Sci. Rep.* 13 (1), 15510.
- Lemprière, T.C., Kurz, W.A., Hogg, E.H., Schmolli, C., Rampley, G.J., Yemshanov, D., McKenney, D.W., Gilson, R., Beach, A., Blain, D., et al., 2013. Canadian boreal forests and climate change mitigation. *Environ. Rev.* 21 (4), 293–321.
- Lenton, Timothy M., Held, Hermann, Krieger, Elmar, Hall, Jim W., Lucht, Wolfgang, Rahmstorf, Stefan, Schellnhuber, Hans Joachim, 2008. Tipping elements in the Earth's climate system. *Proc. Natl. Acad. Sci.* 105 (6), 1786–1793.
- Leppä, Kersti, Korhonen, Mika, Nieminen, Mika, Laiho, Raija, Hotanen, Juha-Pekka, Kieloaho, Antti-Jussi, Korpela, Leila, Laurila, Tuomas, Lohila, Annalea, Minkkinen, Kari, Mäkipää, Raisa, Ojanen, Paavo, Pearson, Meeri, Penttilä, Timo, Tuovinen, Juha-Pekka, Launiainen, Samuli, 2020. Vegetation controls of water and energy balance of a drained peatland forest: Responses to alternative harvesting practices. *Agric. Forest Meteorol.* 295, 108198.
- Liski, Jari, Pussinen, Ari, Pingoud, Kim, Mäkipää, Raisa, Karjalainen, Timo, 2001. Which rotation length is favourable to carbon sequestration? *Can. J. Forest Res.* 31 (11), 2004–2013.
- Lundmark, Tomas, Poudel, Bishnu Chandra, Stål, Gustav, Nordin, Annika, Sonesson, Johan, 2018. Carbon balance in production forestry in relation to rotation length. *Can. J. Forest Res.* 48 (6), 672–678.
- Luo, Yiqi, Weng, Ensheng, 2011. Dynamic disequilibrium of the terrestrial carbon cycle under global change. *Trends Ecol. Evol.* 26 (2), 96–104.
- Luyssaert, Sebastiaan, Schulze, Ernst-Detlef, Börner, Annett, Knobl, Alexander, Hoesenmüller, Dominik, Law, Beverly E., Ciais, Philippe, Grace, John, et al., 2008. Old-growth forests as global carbon sinks. *Nature* 455 (7210), 213–215.
- Maes, Joachim, Liqueste, Camino, Teller, Anne, Erhard, Markus, Paracchini, Maria Luisa, Barredo, José I., Grizzetti, Bruna, Cardoso, Ana, Somma, Francesca, Petersen, Jan-Erik, et al., 2016. An indicator framework for assessing ecosystem services in support of the EU Biodiversity Strategy to 2020. *Ecosyst. Serv.* 17, 14–23.
- Mäkelä, Annikki, 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. *For. Sci.* 43 (1), 7–24.
- Manzoni, Stefano, Porporato, Amilcare, 2009. Soil carbon and nitrogen mineralization: Theory and models across scales. *Soil Biol. Biochem.* 41 (7), 1355–1379.
- Matala, Juhon, Kärkkäinen, Leena, Härkönen, Kari, Kellomäki, Seppo, Nuutinen, Tuula, 2009. Carbon sequestration in the growing stock of trees in Finland under different cutting and climate scenarios. *Eur. J. For. Res.* 128, 493–504.
- Medlyn, Belinda E., Duursma, Remko A., Eamus, Derek, Ellsworth, David S., Prentice, I. Colin, Barton, Craig V.M., Crous, Kristine Y., Angelis, Paolo De, Freeman, Michael, Wingate, Lisa, 2012. Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biol.* 18 (11), 3476.
- Metzler, Holger, Müller, Markus, Sierra, Carlos A., 2018. Transit-time and age distributions for nonlinear time-dependent compartmental systems. *Proc. Natl. Acad. Sci.* 115, 201705296. <http://dx.doi.org/10.1073/pnas.1705296115>.
- Metzler, Holger, Zhu, Qing, Riley, William, Hoyt, Alison, Müller, Markus, Sierra, Carlos A., 2020. Mathematical reconstruction of land carbon models from their numerical output: Computing soil radiocarbon from  $^{14}\text{C}$  dynamics. *J. Adv. Modelling Earth Syst.* 12 (1).
- Mikola, P., 1984. Selection forestry. *Silva Fennica* 18, 293–301.
- Millennium Ecosystem Assessment, MEA, 2005. Ecosystems and human well-being, vol. 5, Island press Washington, DC.



- Muhr, Jan, Angert, Alon, Negrón-Juárez, Robinson I., Muñoz, Waldemar Alegria, Kraemer, Guido, Chambers, Jeffrey Q., Trumbore, Susan E., 2013. Carbon dioxide emitted from live stems of tropical trees is several years old. *Tree Physiol.* 33 (7), 743–752.
- Nabuurs, Gert-Jan, Schelhaas, Mart-Jan, Orazio, Christophe, Hengeveld, Geerten, Tome, Margarida, Farrell, Edward P., 2014. European perspective on the development of planted forests, including projections to 2065. *New Zealand J. For. Sci.* 44, 1–7.
- Noormets, Asko, Epron, Daniel, Domec, Jean-Christophe, McNulty, S.G., Fox, T., Sun, G., King, J.S., 2015. Effects of forest management on productivity and carbon sequestration: A review and hypothesis. *Forest Ecol. Manag.* 355, 124–140.
- Ogle, Kiona, Pacala, Stephen W., 2009. A modeling framework for inferring tree growth and allocation from physiological, morphological and allometric traits. *Tree Physiol.* 29 (4), 587–605.
- Pacala, Stephen W., Canham, Charles D., Saponara, John, Silander, Jr., John A., Kobe, Richard K., Ribbens, Eric, 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66 (1), 1–43.
- Pan, Yude, Birdsey, Richard A., Fang, Jingyun, Houghton, Richard, Kauppi, Pekka E., Kurz, Werner A., Phillips, Oliver L., Shvidenko, Anatoly, Lewis, Simon L., Canadell, Josep G., et al., 2011. A large and persistent carbon sink in the world's forests. *Science* 333 (6045), 988–993.
- Parton, William J., Schimel, David S., Cole, C. Vernon, Ojima, Dennis S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Am. J.* 51 (5), 1173–1179.
- Pohjanmies, Tähti, Triviño, María, Le Tortorec, Eric, Mazziotto, Adriano, Snäll, Tord, Mönkkönen, Mikko, 2017. Impacts of forestry on boreal forests: An ecosystem services perspective. *Ambio* 46 (7), 743–755.
- Pukkala, Timo, 2014. Does biofuel harvesting and continuous cover management increase carbon sequestration? *For. Policy Econ.* 43, 41–50.
- Pukkala, Timo, 2020. Calculating the additional carbon sequestration of Finnish forestry. *J. Sustain. For.* 1–18.
- Pukkala, Timo, Lähde, Erkki, Laiho, Olavi, 2009. Growth and yield models for uneven-sized forest stands in Finland. *Forest Ecol. Manag.* 258 (3), 207–216.
- Ågren, Göran I., Wikström, J. Fredrik, 1993. Modelling carbon allocation — a review. *NZ J. For. Sci.* 23, 343–353.
- Randerson, J.T., Chapin, III, F.S., Harden, J.W., Neff, J.C., Harmon, M.E., 2002. Net ecosystem production: a comprehensive measure of net carbon accumulation by ecosystems. *Ecol. Appl.* 12 (4), 937–947.
- Rasmussen, Martin, Hastings, Alan, Smith, Matthew J., Agosto, Folashade B., Chen-Charpentier, Benito M., Hoffman, Forrest M., Jiang, Jiang, Todd-Brown, Katherine E.O., Wang, Ying, Wang, Ying-Ping, Luo, Yiqi, 2016. Transit times and mean ages for nonautonomous and autonomous compartmental systems. *J. Math. Biol.* 73 (6–7), 1379–1398. <http://dx.doi.org/10.1007/s00285-016-0990-8>.
- Reineke, Lester Henry, 1933. Perfecting a stand-density index for even-aged forest. *J. Agric. Res.* 46, 627–638.
- Repola, Jaakko, 2006. Models for Vertical Wood Density of Scots Pine, Norway Spruce and Birch Stems, and Their Application to Determine Average Wood Density. Finnish Society of Forest Science.
- Repola, Jaakko, 2009. Biomass Equations for Scots Pine and Norway Spruce in Finland. Finnish Society of Forest Science.
- Repola, Jaakko, Ahnlund Ulvcróna, Kristina, 2014. Modelling Biomass of Young and Dense Scots Pine (*Pinus sylvestris* L.) Dominated Mixed Forests in Northern Sweden. Finnish Society of Forest Science.
- Riofrío, José, del Río, Miren, Maguire, Douglas A., Bravo, Felipe, 2019. Species mixing effects on height–diameter and basal area increment models for Scots pine and maritime pine. *Forests* 10 (3), 249.
- Rolls, Will, Forster, Piers M., 2020. Quantifying forest growth uncertainty on carbon payback times in a simple biomass carbon model. *Environ. Res. Commun.* 2 (4), 045001.
- Ruiz-Peinado, Ricardo, Pretzsch, Hans, Löf, Magnus, Heym, Michael, Bielak, Kamil, Aldea, Jorge, Barbeito, Ignacio, Brazaitis, Gediminas, Drössler, Lars, Godvold, Kšištof, Granhus, Aksel, Holm, Stig-Olof, Jansons, Aris, Makrickienė, Ekaterina, Metslaid, Marek, Metslaid, Sandra, Nothdurft, Arne, Otto Juel Reventlow, Ditlev, Sitko, Roman, Stankevičienė, Gintarė, del Río, Miren, 2021. Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) productivity along a climatic gradient across Europe. *Forest Ecol. Manag.* 482, 118834. <http://dx.doi.org/10.1016/j.foreco.2020.118834>, URL <https://www.sciencedirect.com/science/article/pii/S0378112720316030>.
- Ryan, Michael G., Lavigne, Michael B., Gower, Stith T., 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *J. Geophys. Res.: Atmos.* 102 (D24), 28871–28883.
- Schulze, Ernst Detlef, Sierra, Carlos A., Egenolf, Vincent, Woerdehoff, Rene, Irslinger, Roland, Baldamus, Conrad, Stupak, Inge, Spellmann, Hermann, 2020. The climate change mitigation effect of bioenergy from sustainably managed forests in Central Europe. *GCB Bioenergy* 12 (3), 186–197.
- Shine, K.P., Derwent, R.G., Wuebbles, D.J., Morcrette, J.J., 1990. Radiative Forcing of Climate in Climate Change: The IPCC Scientific Assessment, Report Prepared for the Intergovernmental Panel on Climate Change by Working Group 1. Cambridge University Press, Cambridge, NY and Melbourne, Sydney.
- Sierra, Carlos A., Ceballos-Núñez, Verónica, Metzler, Holger, Müller, Markus, 2018. Representing and understanding the carbon cycle using the theory of compartmental dynamical systems. *J. Adv. Modelling Earth Syst.* <http://dx.doi.org/10.1029/2018MS001360>.
- Sierra, Carlos A., Crow, Susan E., Heimann, Martin, Metzler, Holger, Schulze, Ernst-Detlef, et al., 2021. The climate benefit of carbon sequestration. *Biogeosciences*.
- Sierra, Carlos A., Müller, Markus, 2015. A general mathematical framework for representing soil organic matter dynamics. *Ecol. Monograph* 85 (4), 505–524. <http://dx.doi.org/10.1890/15-0361.1>.
- Sierra, Carlos A., Müller, Markus, Metzler, Holger, Manzoni, Stefano, Trumbore, Susan E., 2017. The muddle of ages, turnover, transit, and residence times in the carbon cycle. *Global Change Biol.* 23 (5), 1763–1773.
- Thum, Tea, Caldaranu, Silvia, Engel, Jan, Kern, Melanie, Pallandt, Marleen, Schnur, Reiner, Yu, Lin, Zaehle, Sönke, 2019. A new model of the coupled carbon, nitrogen, and phosphorus cycles in the terrestrial biosphere (QUINCY v1.0; revision 1996). *Geosci. Model Dev.* 12 (11), 4781–4802.
- Triviño, María, Morán-Ordoñez, Alejandra, Eyvindson, Kyle, Blattert, Clemens, Burgas, Daniel, Repo, Anna, Pohjanmies, Tähti, Brotons, Lluís, Snäll, Tord, Mönkkönen, Mikko, 2023. Future supply of boreal forest ecosystem services is driven by management rather than by climate change. *Global Change Biol.* 29 (6), 1484–1500.
- Vanhanen, Heidi, Jonsson, Ragnar, Gerasimov, Yuri, Krankina, Olga, Messieur, Christian, et al., 2012. Making Boreal Forests Work for People and Nature. IUFRO Special Project on World Forest, Society and Environment (IUFRO-WFSE).
- Vihervaara, Petteri, Kumpula, Timo, Tanskanen, Ari, Burkhard, Benjamin, 2010. Ecosystem services—a tool for sustainable management of human–environment systems. Case study Finnish Forest Lapland. *Ecol. Compl.* 7 (3), 410–420.
- Wang, Y.P., Law, R.M., Pak, Bernard, 2010. A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences* 7 (7), 2261–2282.
- Wutzler, Thomas, 2008. Effect of the aggregation of multi-cohort mixed stands on modeling forest ecosystem carbon stocks. *Silva Fennica* 42 (4), 535–553.
- Yousefpour, Rasoul, Augustynczyk, Andrey Lessa Derci, Reyer, Christopher P.O., Lasch-Born, Petra, Suckow, Felicitas, Hanewinkel, Marc, 2018. Realizing mitigation efficiency of European commercial forests by climate smart forestry. *Sci. Rep.* 8 (1), 1–11.
- Yrjölä, Tiia, 2002. Forest Management Guidelines and Practices in Finland, Sweden and Norway. European Forest Institute, pp. 1–46.