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Modelling managed forest ecosystems in Sweden: An evaluation from the stand to the regional scale

John Bergkvist *, Fredrik Lagergren, Maj-Lena Finnander Linderson, Paul Miller, Mats Lindeskog, Anna Maria Jönsson

Department of Physical Geography and Ecosystem Science, Lund University, Sölvegatan 12, Lund S-223 62, Sweden

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ABSTRACT

Incorporation of a forest management module in the dynamic vegetation model LPJ-GUESS has allowed the study and predictions of management treatment effects on the carbon cycle and on forest ecosystem structure. In this study, LPJ-GUESS is evaluated at the regional scale against observational data from the Swedish National Forest Inventory. Simulated standing volume is compared against observations for the four most common forest types in the country. Furthermore, eddy-covariance flux measurements from the Integrated Carbon Observation System (ICOS) are used to evaluate model predictions of net ecosystem exchange (NEE), gross primary productivity (GPP) and ecosystem respiration (R_{eco}) at the site scale. The model results suggest an adequate representation of standing volume in monocultures of Norway spruce and Scots pine for regional simulations in southern and central Sweden, after an updated parameterization of the species. For northern Sweden, the standing volume in Norway spruce monocultures was overestimated with the updated parameter values. At the stand scale, the model produced mixed results for carbon fluxes when evaluated against eddy-covariance data for two sites, one in central and one in southern Sweden. The interannual variation of GPP was well captured for the central Swedish site, but the modelled average GPP for the period 2015–2019 was overestimated by 9%. For the southern Swedish site, GPP was underestimated by 15% for the corresponding period and the simulated interannual variation was half of the observed. The seasonal estimates of modelled net ecosystem exchange (NEE) deviated from observations and the simulated standing volume was underestimated by 25% for both sites. The results highlight further potential to perform species-specific calibration to capture latitudinal gradients in key ecosystem properties, and to incorporate additional characteristics of site quality which could benefit model accuracy at the scale of individual forest stands, both regarding simulated carbon fluxes and forest stand variables.

1. Introduction

Boreal and temperate forests together cover about 40% of the global forest area and contribute to two thirds of the annual net global forest carbon sink (Harris et al., 2021). The sequestration of carbon by forests is a vital ecosystem service providing mitigation of greenhouse gas emissions and a reduction of the magnitude of harmful effects of changes to the climate of the Earth (IPBES, 2019). The sequestration potential of forest ecosystems depends on multiple environmental factors including climate, soil and topography, previous patterns of disturbance, and on human land use, such as forest management (Harris et al., 2021; Senf and Seidl, 2020; Kljun et al., 2006). In Sweden, forests cover 69% of the total land area and even-aged silvicultural management practices dominate on the vast majority of the productive forest land (SNFI, 2021a; Lindahl et al., 2017). As a consequence, the extraction of biomass is highly efficient: the forests of Sweden provide about 10% of the total global share of produced timber and pulp (Barklund et al., 2009).

Commonly applied at regional to global scales, dynamic vegetation models (DVMs) are useful tools for large scale studies of the carbon cycle and for predicting the response of vegetation to changing climate conditions. DVMs are built from the theoretical understanding of how plants function and explicitly model vital aspects of a terrestrial ecosystem to project vegetation structure and functioning from climate and soil input data. Recent model development in LPJ-GUESS has allowed for projections of the effects of management treatments on the carbon cycle and on ecosystem service provisioning (Lindeskog et al., 2021; Lagergren

* Corresponding author.
E-mail address: john.bergkvist@nateko.lu.se (J. Bergkvist).

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and Jönsson, 2017). Accounting for forest management is especially relevant for studies of forest ecosystems that bear little resemblance to unmanaged natural forests in the same location. Knowledge of disturbance and management history is important for simulating observed vegetation structure and for the accurate recreation of carbon and nitrogen content in the soil in forestry-enabled DVMs (Lindeskog et al., 2021). The simulated fluxes of carbon, nitrogen and water depend on the ecosystem composition, which is influenced by management treatments such as thinning, clear-felling or fertilization. Thinning, for example, controls the extent of competition between individuals and reduces natural mortality, which in turn affects processes such as photosynthesis and heterotrophic respiration which over long timescales can have major implications for the carbon balance (Lindeskog et al., 2021).

A common method of evaluating vegetation models involves the use of measurement data of net ecosystem CO_2 exchange (NEE), the net flux of carbon from the atmosphere to the biosphere, defined as the difference between the total ecosystem respiration (R_{eco}) and gross primary productivity (GPP) (Desai et al., 2007; Pan et al., 2014; Zaehle et al., 2005). Time-series of NEE measured with the eddy-covariance (EC) technique are available for a multitude of sites in Europe through ICOS RI (Integrated Carbon Observations System Research Infrastructure, Heiskanen et al., 2021). While providing high quality observational data, EC sites represent a local measurement heavily influenced by the site conditions of the forest stand in closest proximity to the point of measurement. For this reason, bottom-up methods to scale up measured NEE from the stand to the regional level are challenging and dependent on a modeling approach, and such studies are rare (but see Chi et al., 2019; Desai et al., 2007).

Measurements of forest variables, including biomass, standing stock and productivity, are provided by National Forest Inventories (NFIs), presenting an alternative method of large-scale model evaluation (Pan et al., 2014). In Sweden, long time-series of observational data exist describing the state and change of forest ecosystems at the national scale (Fridman et al., 2014). Using NFI data, Lagergren et al. (2012) evaluated the forestry-enabled DVM LPJ-GUESS at the national scale of Sweden, and found an overestimation of simulated standing volume in southern Sweden. Lindeskog et al. (2021) evaluated the module for forest management at the scale of Europe, showing that simulated biomass and annual increment compares favorably against observational data.

Improved simulation of stand growth and development for forests consisting of monocultures and species mixtures could provide the possibility of more detailed assessments of regulating ecosystem services related to carbon sequestration, or of provisioning ecosystem services related to timber, pulp and bioenergy. Here we update the forestry-enabled dynamic vegetation model LPJ-GUESS with revised parameter settings for the two commercially most important tree species in Swedish forestry, Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst). At the regional scale, the mean standing volume is evaluated for 20-year age classes representing the average forest state during different stages of growth and development for 1996–2015 in Sweden. Birch (*Betula* L.) is evaluated in mixtures with Norway spruce. The approach captures the influence of climate conditions and forest management on volume development for the above-mentioned species both in monocultures and in mixtures, as well as stand growth development in monocultures. Additionally, the model is evaluated at the stand scale against EC data to assess model capacity to simulate carbon fluxes and associated interannual variation. An evaluation of forest stand variables at the stand scale is also included.

Specifically, the aims of the current study were to:

(i) assess the model performance of simulating standing volume at the regional scale by evaluating the results against observational data from the Swedish National Forest Inventory
(ii) improve the species-specific model parameterization for the two dominating tree species based on projections of standing volume at the regional scale
(iii) determine the model's capacity to accurately project stand variables such as mean height, mean stand diameter, stand density and mean stand volume, as well as seasonal and interannual variation at the stand scale for carbon fluxes of NEE, gross primary production (GPP) and ecosystem respiration (R_{eco}) by evaluating the results against eddy-covariance data.

2. Material & methods

2.1. Ecosystem model

LPJ-GUESS is a dynamic vegetation model (DVM) with a process-based representation of ecosystem function and vegetation structure (Smith et al., 2001, 2014). The model incorporates a detailed description of the exchange of carbon and water between the atmosphere and the biosphere (Ahlström et al., 2012) and of nitrogen cycling (Smith et al., 2014). Terrestrial vegetation is simulated in dynamic response to input of external climate data (Fig. 1). The plant physiological processes of photosynthesis, respiration, stomatal regulation and phenological development are simulated at a daily time step within the ecosystem. Soil hydrology and plant water uptake is modelled using a two-layer soil profile. LPJ-GUESS includes dynamic cycling of nitrogen and soil carbon based on the CENTURY model (Parton et al., 1993). Soil nitrogen build-up results from mineralization of litter, from biological nitrogen fixation estimated based on modelled evapotranspiration rates, and from nitrogen deposition. Mineralization and nitrogen fixation are represented as internal model functions described in Smith et al. (2014) and nitrogen deposition is determined from an external dataset.

The model requires a spin-up period of 500 years where the soil carbon, nitrogen and ecosystem vegetation gradually build up from bare land. Vegetation is simulated for cohorts of different plant functional types (PFTs) within patches where competition for resources affect regeneration, growth and mortality (Smith et al., 2014). Species-specific parameters govern tree allometry, longevity and root distribution and influence the competition for light, water and nutrients (N) within each simulated patch (Smith et al., 2001; Wramneby et al., 2008). Bioclimatic limits for establishment and survival determine the natural geographic distribution potential of each PFT (Hickler et al., 2012). The forest management module enables the simulation of even-aged or uneven-aged silvicultural systems through a user-defined regime which initiates a naturally regenerated or planted forest stand at the patch level. It includes a comprehensive set of parameters regulating timing and extent of planting, thinning and clear-cutting for individual tree species (Lindeskog et al., 2021).

2.2. Environmental forcing data

2.2.1. Regional simulations (climate, soil)

Mean monthly values for temperature, precipitation, short-wave radiation and annual values for carbon dioxide concentration were used to drive the model for regional simulations. The climate variables originated from the *CRUNCEP version 7* forcing dataset (Viovy, 2018) and CO_2 concentration data from the Global Carbon Project (Le Quéré et al., 2018). Detrended climate data for 1901–1930 were repeatedly cycled to build up pools of soil carbon and nitrogen over the course of the spin-up period, with the CO_2 value for 1901 representing pre-industrial atmospheric concentrations. A pre-industrial value for nitrogen deposition was used during model spin-up corresponding to 2 kg N ha^{-1} $year^{-1}$. Annual values for CO_2 were prescribed as input during the historical 1901–2015 period for regional simulations, and for 1901–2020 for local simulations. Monthly values of nitrogen deposition at 10-year intervals were used as input based on Lamarque et al. (2011) during 1850–2009. We assumed similar nitrogen deposition rates post 2009 as of 2000–2009. The gridded climate data had a spatial resolution of $0.5 \times 0.5°$. New soil types were created to represent the four most common forest soils throughout the country (Table 1). These were

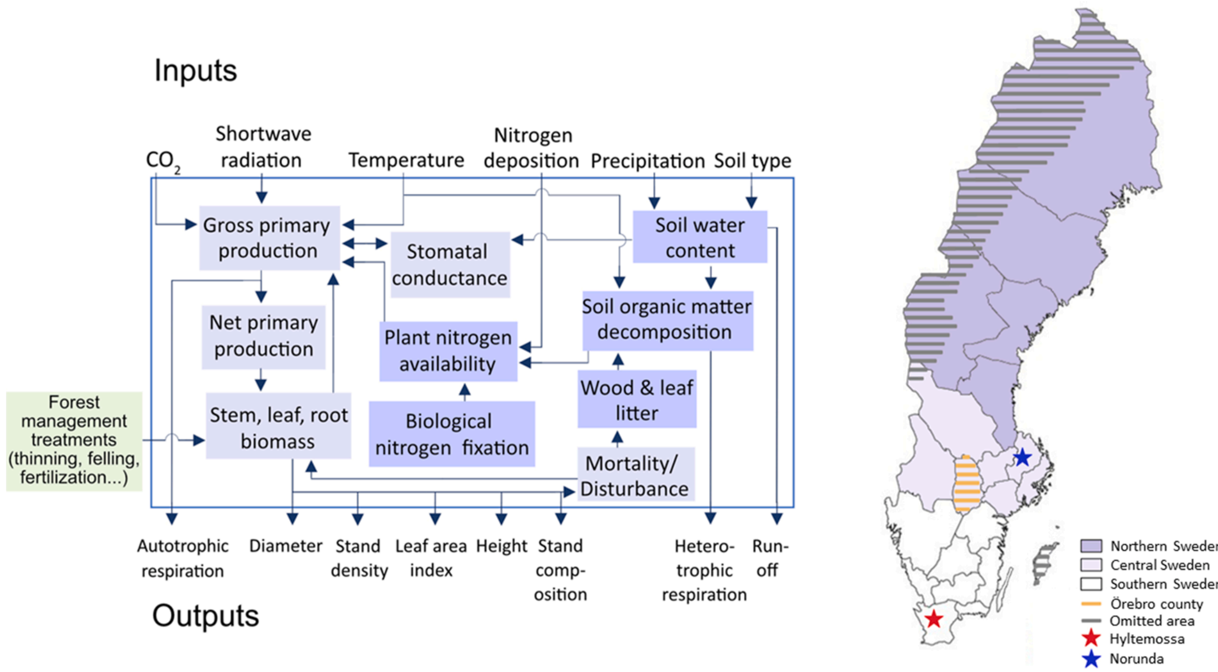

Fig. 1. To the left: simplified conceptual diagram of the LPJ-GUESS model, highlighting the model components of key importance in this study. Gray boxes indicate above-ground processes and structural components, whereas blue boxes signify below-ground processes and associated structural components. To the right: map of Sweden, indicating county borders, and three study regions in southern, central and northern Sweden corresponding to the three country parts Götaland, Svealand and Norrland, respectively. The ICOS sites used in stand scale simulations are indicated with asterisks. Omitted areas were not included in model simulations and are dashed in gray. A sensitivity analysis and optimization of species-specific parameters was performed at the regional scale for Örebro county, here dashed in orange.

Table 1
The relative proportion of grain size within the simulated soil layer for the 4 different soil types considered in this study. K is an empirical parameter governing the percolation rate from the upper to the lower soil layer, as dependent on the water content within the soil layer (in mm/day). H_{max} is the volumetric water holding capacity at field capacity minus the volumetric water holding capacity at wilting point as a fraction of the depth of the soil layer.

Soil Type	Sand (%)	Silt (%)	Clay (%)	K	H_{max}
Till-like coarse sand	95	5	0	5.05	0.10
Till-like fine sand	88	12	0	5.05	0.12
Till-like coarse silt	75	20	5	4.81	0.15
Well-sorted sand	90	10	0	5.05	0.11

determined from a data set received from the Swedish Forest Soil Inventory (SFSI), consisting of 6621 sample sites across productive forest land. The field data had been collected during the period 2003–2012 from permanent sample plots. For the four soil types, the fractions of sand, silt and clay were determined from the classification scheme of Albert Atterberg (Tupek et al., 2016). Because LPJ-GUESS does not include simulation of mineral fractions coarser than sand, fractions representing gravel, stones and boulders were added to the sand fraction. Additional parameters such as soil water holding capacity (H_{max}), percolation rate (K) and soil thermal properties were calculated from these fractions based on Haxeltine and Prentice (1996) to enable model simulations (Table 1).

2.2.2. Stand scale simulations, instrumentation & data processing

To enable model simulations for the sites Norunda in central Sweden (60°05′N, 17°29′E, 45 m asl) and Hyltemossa in southern Sweden (56°06′N, 13°25′E, 115 m asl), site-specific meteorological data were received from the two ICOS (Integrated Carbon Observation System, Heiskanen et al., 2021) stations (Fig. 1). The variables included daily values of measured precipitation, temperature, shortwave radiation, soil temperature and soil water content and originated from the Warm Winter 2020 ecosystem datasets (Heliasz et al., 2022; Mölder et al., 2022).

The site Norunda is situated in the boreonemoral zone and experiences a mean annual temperature of 7.1 °C and precipitation of 565 mm per year (period 1990–2020, SMHI station Uppsala). The site Hyltemossa is located in the nemoral zone in the county of Skåne, with a mean annual temperature of 8.1 °C and precipitation of 786 mm per year (climate period 1991–2020, SMHI stations Klippan and Hörby). The eddy covariance tower in Norunda is located in the center of a mixed coniferous forest stand. The stand consists mainly of Scots pine (*Pinus sylvestris,* 58% of basal area) and Norway spruce (*Picea abies,* 38% of basal area) with dominant trees reaching heights of 30 m (Lindroth et al., 2020). The mean leaf area index (LAI) for 2019 was 2.8 m^2 m^{-2} (Mölder et al., 2021). The forest soil, classified as a dystric regosol, is a stony glacial till with a relatively high proportion of clay and silt (Lundin et al., 1999). The soil contains a large amount of gravel and boulders and the fine material content of the soil (< 2 mm) is about 30%. The forest within the EC tower footprint of Hyltemossa consists of an even-aged Norway spruce monoculture sparsely admixed with downy birch (*Betula pubescens)*. Stand height in 2017 was 14.6 m with a mean leaf area index in 2019 of 4.4 m^2 m^{-2} (Heliasz et al., 2021). The Norway spruce stand was established in 1983 and thinned in 2009 and 2013. The site index is estimated to 36.0 m at 100 years. The soil is classified as a sandy silty glacial till with a shallow organic layer.

For the stand scale simulations, monthly data originating from the *CRU-NCEP* dataset (from the gridcell containing the site) were first bias-corrected based on the averaged differences with the monthly-averaged meteorological data from the sites, over the overlapping period (1995–2013 for Hyltemossa and 1995–2010 for Norunda). The bias-corrected data were then used during the model spin-up phase and the historical period up until 1994. Thereafter, the meteorological data from SMHI weather stations in proximity to the two sites were applied directly, enabling a gradual transition from the spin up and historical periods, covering the years 1995–2013 for Hyltemossa and 1995–2010 for Norunda. Weather data from different stations were combined because of a lack of a complete dataset for the entire transition phase. Weather data for the 1995–2013 transition period of Hyltemossa originated from the nearby Munka-Ljungby and Klippan weather stations for precipitation, and from Backåkra and Munka Ljungby for air temperature. The dataset for the 1995–2010 transition period of Norunda included temperature from Uppsala airport and Dannemora weather station, and precipitation from Harbo, Drälinge and Vattholma. Meteorological data from the stations were used from 2011 for Norunda and 2014 for Hyltemossa covering the evaluation period 2015–2019.

2.3. Forest observational data for comparison with simulations at the regional scale

Data from the Swedish National Forest Inventory (SNFI) were obtained via the interactive tool *TaxWebb* (SNFI, 2021b). The data consisted of quality-controlled measurements of standing volume classified in four forest types for productive forest land in Sweden (Norway spruce monoculture, Scots pine monoculture, Mixed Norway spruce-Scots pine forest, Mixed Norway spruce-Birch forest). Other forest types, such as those containing nemoral broadleaves, were excluded from the study. The standing volume was received in 20-year age classes for each forest type for each of the 20 counties included in this study. The youngest age class (0–20 years) only included measured trees above a height of 1.3 m. The uncertainty of the standing volume estimates provided by the SNFI varies between 2 and 15% at the scale of individual counties (SNFI, 2016). Data were also received for the area cover of each age class within the counties. The county-level estimates of standing volume were weighted by forest area of the age class in each county, enabling the calculation of mean standing volume for each of the three regions of Sweden.

The mean observed standing volume used to evaluate model results represents the average forest state during the period 1996 to 2015 for each age class and region (Fig. 1).

A weighted standard deviation was calculated to indicate the variation in standing volume among the counties of a region for a given age class:

$$sd_w = \sqrt{\frac{\frac{\sum_{i=1}^{N} w_i (x_i - \bar{x}_w)^2}{(N'-1)\sum_{i=1}^{N} w_i}}{N'}} \quad (1)$$

Where w_i is the forest-area based weight for the *i*th county, x_i is the non-weighted mean standing volume of the *i*th county, $\bar{x}_w$ is the weighted mean standing volume, and N' is the number of non-zero weights.

2.4. Eddy covariance (EC) data for comparison with simulations at the stand scale

Model simulations for Hyltemossa and Norunda were validated with monthly and yearly values of net ecosystem exchange (NEE) for the years 2015 to 2019, partitioned into the components of gross primary production (GPP) and total ecosystem respiration (R_{eco}). The datasets originate from the Warm Winter 2020 ecosystem eddy covariance flux product and were processed and quality-controlled following the ICOS protocols (Sabbatini et al., 2018), compliant with the FLUXNET2015 release (https://fluxnet.fluxdata.org/) (Heliasz et al., 2022; Mölder et al., 2022). Evaluation data for stand variables originated from the ICOS L2 ecosystem datasets (Mölder et al., 2021; Heliasz et al., 2021).

Two methods exist for calculating the components of GPP and R_{eco} from NEE. The nighttime method (NT) models R_{eco} from nighttime NEE data based on its relationship to temperature. The R_{eco} model is then extrapolated to daytime and GPP is derived as the difference between measured NEE and modelled R_{eco} (Reichstein et al., 2005). The daytime method (DT) models GPP and R_{eco} from measured NEE, where the GPP component is derived with a light response curve which includes the limiting effect of vapor pressure deficit during daytime. The R_{eco} component is then modelled based on air temperature in a similar manner to the nighttime method (Lasslop et al., 2010). The ecosystem model LPJ-GUESS models GPP based on a mechanistic description of photosynthesis during daytime, which shares more resemblance with the approach of the daytime method compared to the nighttime method. We therefore present the simulation results of annual and monthly carbon fluxes at the stand scale with a comparison against observational DT data. For comparison of methods, annual carbon fluxes are presented also for NT (Appendix A, Fig. A7).

The EC data used in this study were measured and analyzed by ICOS who have developed a standardized approach for post-processing of raw data (Franz et al., 2018). The approach ensures comparability of each dataset to other EC sites and provides a comprehensive quality control (QA/QC) with an assessment of the uncertainty which arises during the measurement and post-processing steps (Heiskanen et al., 2021; Franz et al., 2018).

One of the main contributions to EC data uncertainty is associated with the correct estimation of the threshold for friction velocity (u*). The threshold value varies with site, season and year and indicates a boundary below which measurement data of nighttime ecosystem respiration should be discarded due to low turbulent mixing (Wutzler et al., 2018). Filtering of data based on different values for friction velocity ultimately results in an assessment of the range of uncertainty for a time-series of NEE, GPP and R_{eco}. The method is fully discussed in Pastorello et al. (2020). The uncertainty in the data is indicated by the 16th and the 86th percentiles of the threshold values of u*. We visualized the uncertainty as an overlay for monthly NEE in Fig. 3, for monthly GPP and R_{eco} in Fig. 4, for annual NEE, GPP and R_{eco} in Fig. 5, and for annual GPP and R_{eco} in Fig. A7.

The micrometeorological sign convention for ecosystem fluxes is used in this study, where a positive sign denotes a flow towards the atmosphere and a negative sign a flow towards the ground. The datasets cover years representative of the climate normal period (1991–2020). This includes the drought year 2018, when large parts of Scandinavia and the Baltic was affected by a drought during the summer (Lindroth et al., 2020).

2.5. Model setup of simulations

2.5.1. Regional scale simulations

We applied the forest management module of LPJ-GUESS (version 4.0) within each of the three main regions of Sweden (southern, central and northern) (Fig. 1) with the aim to simulate the standing volume in monocultural and mixed species stands formed by the main tree species; Norway spruce (*Picea abies* L. Karst*)*, Scots pine (*Pinus sylvestris* L.*)* and Birch (*Betula* L.), which together represent 92.2% of standing volume across productive forest land (SNFI, 2021a). Monoculture stands were simulated for Norway spruce and Scots pine. Mixed stands were formed by Norway spruce and Downy birch (*Betula pubescens* Ehrh.), and mixed coniferous stands by Norway spruce and Scots pine. The simulations covered 194 gridcells capturing the 20 counties of mainland Sweden (the island of Gotland was omitted). The number of patches per forest stand was set to 12. Gridcells situated above the treeline, i.e. within alpine environments, were excluded (Fig. 1). Stochastic mortality events were turned off after introduction of management to generate simulations representing the best-case-scenario for each given region.

LPJ-GUESS generates a forest ecosystem in equilibrium with the climate at the end of a 500-year long spin-up period during which carbon and nutrients in the soil gradually are built up. The establishment of managed forest types was initiated at different years during the 19th century by simulating clear-felling and plantation of forest stands, resulting in stands of different ages in the landscape during the period of evaluation. We evaluated the simulated standing volume against the observed for the mean state of the forest during 1996–2015 for each age class.

Five age classes were included for southern and central Sweden for monocultures and mixed coniferous forest (0–20, 21–40, 41–60, 61–80, 81–100 years). An additional age class (101–120 years) was included for northern Sweden as stand rotations are longer within the colder northern climate. Birch is often found with Norway spruce within a mixture during early to mid-rotation, and was therefore represented by three age classes for southern and central Sweden and four in northern Sweden (Hynynen et al., 2009).

The applied forest management treatments represented even-aged management which has characterized forest management during the 20th century in Sweden (Table 2). For the mixed stands, a selective cutting function was set to thin the stands every 12 to 20 years to retain an equal balance of the woody biomass of each of the two species within the mix for all but the two youngest age classes (Lindeskog et al., 2021). As a consequence, the strength of the thinning varied across age classes and gridcells, and the removals are therefore not included in Table 2.

2.5.2. Stand scale simulations

The simulated forest management of both sites aimed to recreate a forest stand representative of current site conditions (2015–2019) based on the available knowledge regarding the history of stand management. A mixed Scots pine and Norway spruce stand was simulated at the Norunda site by initiating planting at the year 1900 following a clearcut of previously unmanaged forest (Table 2). Very little is known regarding the stand management at Norunda during the early 20th century. We assumed the planting density was lower than in contemporary forestry since no formal law for mandatory regeneration had been passed at the time (Ekelund and Hamilton, 2001, p. 37). One pre-commercial thinning and two regular thinnings were assumed at given intervals, as well as a known thinning which occurred in 2008 removing about 15% of the volume (Lindroth et al., 2018). A till-like soil type dominated by sand was used for the Norunda site to represent a very high content of coarse material in the soil (Lundin et al., 1999). As indicated by available stand management information, the Norway spruce monoculture was initiated in Hyltemossa through planting of 3300 stems ha^{-1} in 1983, followed by pre-commercial thinning in 1998 and a thinning in 2010 (Table 2). We assumed one previous rotation had occurred before the current stand was planted. A till-like sandy soil with high silt content was used for Hyltemossa.

2.6. Sensitivity analysis and improvement of parameters

A sensitivity analysis was performed to test the influence of the four key parameters turnover_sap, k_latosa, sla, and cton_sap on the modelled standing volume of Norway spruce and Scots pine. The parameter turnover_sap regulates the proportion of sapwood converted into heartwood, influencing the tree carbon accumulation and respiratory losses (Zaehle et al., 2005). The carbon to nitrogen ratio of the sapwood is determined by the parameter cton_sap, which influences autotrophic respiration by modifying the nitrogen content of the sapwood (Smith et al., 2014). The parameter k_latosa determines the proportion of carbon allocated to leaf and stem biomass (Zaehle et al., 2005). The ratio between leaf area and leaf dry biomass is influenced by the parameter sla (Wramneby et al., 2008). Settings for the two parameters rootdist and leaflong were also changed, but were not included within the sensitivity analysis, as their settings are less uncertain.

The analysis was performed to determine if the species-specific settings could improve model projections of standing volume (Tables A1 & A2, Appendix A). The simulations represented monocultures at the landscape-scale, simulating their different age classes within one gridcell in Örebro county, situated in the boreonemoral zone in central Sweden (Fig. 1). Model climate data input was the same as specified in 2.2.1, representing the grid cell average climate during the period of forest growth. Landscape averages for standing volume derived from the SNFI data for both Scots pine and Norway spruce monocultural forest types were used for evaluating simulated standing volume. During the analysis, 3 of the above-mentioned parameters were kept at their original setting while the 4th was changed to determine the relative influence of the parameter on simulated standing volume. The sensitivity analysis resulted in 21 simulations for each species (Tables A1 & A2, Appendix A). The sensitivity analysis indicated that region-specific parameter settings would generate closer to observed volume estimates. New parameters, called *Opt*, were therefore identified, used and evaluated along with the original parameters for Scots pine and Norway spruce for the three main regions (Table 3). According to Mencuccini and Grace (1995), the leaf to sapwood area ratio (k_latosa) should increase with increasing latitude. For this reason, k_latosa was raised slightly for northern Sweden, and lowered slightly for southern Sweden. Additional specifications and motivations for changed parameter settings are presented in Appendix A.

Results below of simulated standing volume with the new

Table 2
Forest management treatments applied during the simulation of stands within the three regions southern Sweden, central Sweden and northern Sweden, and for stand simulations for Norunda and Hyltemossa. The amount of volume removed during thinnings is indicated in %.

Scale of simulation *Regional*	*Forest type*	Management treatment *Planting density (stems ha^{-1})*	*Pre-commercial thinning*	*1st thinning*	*2nd thinning*	*3rd thinning*	*4th thinning*
Southern Sweden	Scots pine monoculture	2700	15% at 9 years	35% at 21 years	30% at 36 years	25% at 54 years	25% at 72 years
Central Sweden	Scots pine monoculture	2500	15% at 9 years	35% at 24 years	30% at 39 years	25% at 60 years	25% at 81 years
Northern Sweden	Scots pine monoculture	2300	15% at 12 years	30% at 27 years	25% at 60 years	20% at 69 years	
Southern Sweden	Norway spruce monoculture	2700	10% at 6 years	20% at 18 years	15% at 30 years		
Central Sweden	Norway spruce monoculture	2500	10% at 9 years	25% at 24 years	20% at 36 years		
Northern Sweden	Norway spruce monoculture	2300	15% at 12 years	25% at 33 years	20% at 42 years		
Stand	*Forest type*	*Planting density (stems ha^{-1})*	*Pre-commercial thinning*	*1st thinning*	*2nd thinning*	*3rd thinning*	*4th thinning*
Norunda	Scots pine & Norway spruce mixed coniferous forest	1400	10% at 10 years	20% at 32 years	10% at 48 years	15% at 108 years	
Hyltemossa	Norway spruce monoculture	3300	10% at 15 years	25% at 27 years			

Table 3

Original species-specific parameter settings and the optimized parameter values in each region for Scots pine and Norway spruce. Parameters assessed within the sensitivity analysis are given in bold. Additional motivations for the values chosen is given in Appendix A.

Parameter	Description	Scots pine Original setting	Optimized parameter values (Opt)			Norway spruce Original setting	Optimized parameter values (Opt)		
		Global	Southern Sweden	Central Sweden	Northern Sweden	Global	Southern Sweden	Central Sweden	Northern Sweden
k_latosa	Leaf area to sapwood area ratio	3000	3500	4000	4500	4000	3500	4000	4500
sla	Specific leaf area (m2/kg C)	9.3	13	13	13	9.3	12	12	12
cton_sap	Carbon to nitrogen ratio of sapwood	330	270	270	270	330	360	360	360
turnover_sap	Fraction of sapwood converted to heartwood per year as a proportion of sapwood C biomass	0.075	0.045	0.045	0.04	0.05	0.18	0.18	0.16
leaflong	Leaf longevity (years)	2	3	4	4	3	4	5	5
rootdist	Fraction of plant roots within the topmost soil layer	0.6	0.6	0.6	0.6	0.8	0.65	0.65	0.65

parameters are denoted *Opt*, and results with the original estimates are referred to as *Orig*. These simulations were based solely on the till-like fine sand soil type, which here represents the most common soil for all regions of Sweden (Table 1). The optimized model parameters *Opt* were also used within the simulations for Norunda and Hyltemossa in order to generate stand variables, fluxes of gross primary productivity (GPP), net ecosystem exchange (NEE) and ecosystem respiration (R_{eco}). Model runs with differing soil input information were aggregated into mean standing volume within simulations denoted Opt_w. These represent forest established on a wider range of soils differing in soil water holding capacity and percolation rate within each gridcell (Table 1). A comparison of the relative contribution of individual soil types to the weighted standing volume of simulation Opt_w is presented in Fig. A1, Appendix A. This simulation was performed for a monocultural stand of Norway spruce in Örebro county with identical management settings as in the sensitivity analysis above. For the simulations at the regional scale, we assumed that Scots pine was established primarily on sandy soils (Heiskanen and Makitalo, 2002) while Downy birch and Norway spruce were assumed to be primarily established on sandy to silty tills (Heiskanen et al., 2016; Hynynen et al., 2009). We also assumed that the soil types were evenly distributed in the same proportions across all gridcells of Sweden for a given forest type (Table A3, Appendix A).

2.7. Sensitivity analysis and improvement of parameters

Simulated output data were analyzed using the software *Excel (Microsoft, 2019)* and *MATLAB (R2020b, MathWorks Inc.)*. Modelled stem wood biomass (kg C m^{-2}) was transformed to stem wood volume (m^3 ha^{-1}) through application of biomass expansion factors (BEFs) using a constant carbon to dry matter fraction (0.51 kg C per kg dry matter for conifers, and 0.48 kg C per kg dry matter for broadleaves, Aalde et al., 2006). The stem volume was derived from BEFs for different age classes (Lehtonen et al., 2004), an approach suitable for application of tree species in the boreal zone, as constant biomass expansion factors may lead to biased results (Petersson et al., 2012). The resulting volume given for each age class and species was derived for each of the 20 mainland counties of Sweden (Fig. 1). Values for standing volume for each of the three study regions were then calculated as a weighted mean, where counties with larger forested area within a region contributed more to the overall estimate in the same manner as described above for the observational data. A weighted standard deviation was calculated for each age class to indicate the variation in standing volume within a region according to Eq. (1). This method allowed for a direct comparison of simulated standing volume against observed. Alternative methods, such as a comparison of the net simulated periodic increment against the observed for each region, would rely on further calculations, introducing additional uncertainty into the analysis.

Mean annual increment (MAI) was calculated as the total stand production divided by the stand age. The periodic annual increment (PAI) was calculated as the net change in standing volume from a given point during the simulation to the next divided by the number of years between the points. Removed biomass from thinnings and natural mortality during the period was included in the estimate for both MAI and PAI. Model output for carbon fluxes were transformed from daily to monthly and annual values, and were analyzed to determine the deviation from eddy-covariance data by calculating the root mean square deviation (RMSD) (Kobayashi and Salam, 2000). The interannual variation was calculated as the standard deviation of the annual values of the studied period (2015–2019) for each site.

3. Results

3.1. Sensitivity analysis and improvement of parameters

Any change in one of the assessed parameters had an influence on the simulated standing volume for both species. A stepwise increase in the parameter k_latosa reduced simulated volume while an increase in sla, turnover_sap or cton_sap relative to the original setting caused an increase in vegetation carbon and biomass over time (Tables A1 and A2). The original model parameters showed large deviations for both Scots pine and Norway spruce when simulated standing volume was compared to observed for Örebro county.

This motivated a need to increase accumulated biomass for Norway spruce and decrease it for Scots pine. As a consequence, an increase in any of the three parameters turnover_sap, sla, or cton_sap reduced the negative bias in standing volume compared to NFI data for Örebro county for Norway spruce (Table A2). For Scots pine, a reduction in turnover_sap combined with increased values for k_latosa reduced the positive bias (Table A1). The new parameter sets (*Opt*) aimed to improve the species- specific settings (Table 3).

The mean annual increment (MAI) of the Norway spruce monoculture forest simulated in Örebro using the updated parameter set *Opt* showed a consistent increase over the studied period (Fig. 2). Similarly, the Scots pine monoculture simulated using the *Opt* parameters indicated no clear peak of the MAI over the course of the simulation (Fig. 2).

3.2. Evaluation of simulated standing volume for the three regions of Sweden

3.2.1. Scots pine monoculture

The original parameterization (*Orig*) overestimated the standing volume of Scots pine compared to the NFI data for all three regions (Table 4). The new parameterization (*Opt* and Opt_w) improved the overall accuracy, most noticeably for the four oldest age classes in southern and central Sweden (Table 4). The volume estimates with soil type representation Opt_w and average soil type *Opt* differed by less than 5 m^3 ha^{-1} for northern and central Sweden, and less than 10 m^3 ha^{-1} for southern Sweden. The *Orig* setting produced age class specific estimates

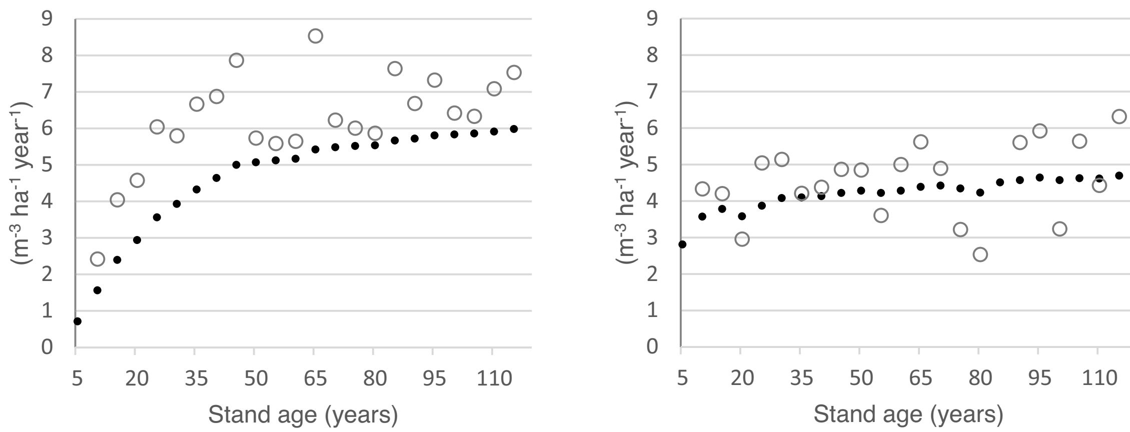

Fig. 2. Mean annual increment (MAI, black dots) and periodic annual increment (PAI, gray circles) for a Norway spruce monoculture stand (left) and a Scots pine monoculture stand (right) simulated in Örebro county using the optimized parameter settings. MAI is given for every fifth year, and PAI was calculated for five-year intervals. Both PAI and MAI include removals from thinning and natural mortality.

Table 4
Modelled and observed mean standing volume (m^3 ha^{-1} ± one standard deviation) per age class for monocultures of Scots pine for the three regions northern Sweden, central Sweden and southern Sweden. The standard deviation indicates the variation in standing volume for a given age class among the counties in a region. Opt (optimized model parameters, one main dominating soil type), Opt_w (optimized model parameters, volume weighted across three soil types), Orig (original model parameters) represent simulated standing volume. NFI represents data from the Swedish National Forest Inventory (SNFI, 2021b).

	Volume per age class (m^3 ha^{-1})					
	0–20	21–40	41–60	61–80	81–100	101–120
Northern Sweden						
Orig	**22** ± 5.5	**78** ± 13.2	**147** ± 13.4	**164** ± 13.9	**256** ± 14.3	**315** ± 17.0
Opt	**28** ± 4.5	**79** ± 5.9	**131** ± 6.7	**136** ± 7.2	**183** ± 9.3	**225** ± 10.9
Opt_w	**28** ± 4.3	**80** ± 5.3	**132** ± 6.1	**137** ± 6.6	**184** ± 8.5	**226** ± 9.9
NFI	**12** ± 3.6	**58** ± 22.8	**105** ± 36.2	**124** ± 34.1	**139** ± 32.7	**164** ± 32.2
Central Sweden						
Orig	**38** ± 7.7	**108** ± 12.4	**175** ± 11.5	**227** ± 9.1	**269** ± 8.9	
Opt	**46** ± 5.5	**106** ± 5.7	**151** ± 7.1	**186** ± 9.3	**218** ± 9.3	
Opt_w	**45** ± 5.3	**104** ± 5.3	**148** ± 6.9	**183** ± 9.2	**214** ± 9.4	
NFI	**22** ± 8.8	**89** ± 15.9	**157** ± 20.2	**201** ± 38.1	**208** ± 46.1	
Southern Sweden						
Orig	**58** ± 2.3	**129** ± 3.3	**191** ± 5.1	**243** ± 6.2	**316** ± 8.4	
Opt	**63** ± 2.0	**121** ± 5.1	**170** ± 8.5	**212** ± 9.6	**269** ± 11.0	
Opt_w	**61** ± 2.0	**118** ± 5.2	**166** ± 8.4	**207** ± 9.5	**262** ± 10.9	
NFI	**33** ± 4.7	**112** ± 7.7	**169** ± 14.3	**203** ± 19.9	**225** ± 11.9	

ranging from 22 to 315 m^3 ha^{-1} for northern Sweden (Table 4), with an overall positive bias of 63%. *Opt_w* and *Opt,* showing similar results, had a bias of 31 and 30%, respectively. In central Sweden, *Orig* had a positive bias of 21%, *Opt* 4% and *Opt_w* 2%. In southern Sweden, standing volume for *Orig* varied from 58 to 316 m^3 ha^{-1} while *Opt_w* and *Opt* ranged from 61 to 269 m^3 ha^{-1}. Both *Opt_w* and *Opt* displayed a major improvement

Table 5
Modelled and observed mean standing volume (m^3 ha^{-1} ± one standard deviation) per age class for monocultures of Norway spruce for the three regions northern Sweden, central Sweden and southern Sweden. The standard deviation indicates the variation in standing volume for a given age class among the counties in a region. *Opt* (optimized model parameters, one main dominating soil type), *Opt_w* (optimized model parameters, volume weighted across three soil types), *Orig* (original model parameters) represent simulated standing volume. *NFI* represents data from the Swedish National Forest Inventory (SNFI, 2021b).

	Volume per age class (m^3 ha^{-1})					
	0–20	21–40	41–60	61–80	81–100	101–120
Northern Sweden						
Orig	**12** ± 2.9	**49** ± 5.8	**79** ± 8.0	**128** ± 11.0	**173** ± 11.3	**203** ± 8.5
Opt	**16** ± 4.5	**85** ± 11.1	**152** ± 13.4	**226** ± 12.1	**288** ± 15.7	**315** ± 19.4
Opt_w	**17** ± 4.8	**87** ± 11.4	**155** ± 13.2	**228** ± 13.3	**293** ± 15.9	**320** ± 20.2
NFI	**13** ± 4.1	**61** ± 28.3	**137** ± 47.8	**183** ± 58.3	**206** ± 53.3	**212** ± 51.1
Central Sweden						
Orig	**23** ± 3.9	**60** ± 3.9	**102** ± 5.1	**146** ± 5.3	**190** ± 10.2	
Opt	**37** ± 6.0	**117** ± 7.6	**192** ± 7.8	**263** ± 12.8	**326** ± 14.7	
Opt_w	**39** ± 6.2	**121** ± 7.5	**198** ± 8.5	**270** ± 13.5	**334** ± 16.4	
NFI	**25** ± 7.8	**123** ± 19.2	**225** ± 20.6	**288** ± 31.0	**294** ± 38.9	
Southern Sweden						
Orig	**33** ± 1.6	**76** ± 2.8	**118** ± 3.2	**150** ± 4.0	**179** ± 4.7	
Opt	**54** ± 3.4	**144** ± 5.2	**221** ± 8.4	**297** ± 11.8	**366** ± 12.7	
Opt_w	**55** ± 3.2	**147** ± 5.1	**226** ± 8.4	**303** ± 11.7	**374** ± 13.2	
NFI	**27** ± 2.9	**163** ± 19.7	**277** ± 32.6	**333** ± 40.9	**343** ± 23.0	

Table 6
Modelled and observed mean standing volume (m^3 ha^{-1}, ± one standard deviation) per age class for mixed coniferous forest for the three regions northern Sweden, central Sweden and southern Sweden. The standard deviation indicates the variation in standing volume for a given age class among the counties in a region. *Opt* (optimized model parameters, one main dominating soil type), Opt_w (optimized model parameters, volume weighted across two dominating soil types), *Orig* (original model parameters) represent simulated standing volume. *NFI* represents data from the Swedish National Forest Inventory (SNFI, 2021b).

	Volume per age class (m^3 ha^{-1})					
	0–20	21–40	41–60	61–80	81–100	101–120
Northern Sweden						
Orig	**20** ± 4.3	**60** ± 7.1	**136** ± 10.8	**183** ± 13.9	**213** ± 17.2	**267** ± 17.9
Opt	**19** ± 4.9	**69** ± 12.2	**153** ± 10.7	**213** ± 15.0	**265** ± 19.6	**317** ± 20.6
Opt_w	**19** ± 4.5	**71** ± 11.1	**155** ± 10.0	**216** ± 13.8	**269** ± 18.1	**322** ± 19.0
NFI	**16** ± 4.5	**61** ± 25.8	**122** ± 44.1	**162** ± 45.0	**180** ± 42.4	**193** ± 42.5
Central Sweden						
Orig	**29** ± 4.7	**78** ± 6.3	**160** ± 10.2	**220** ± 16.7	**256** ± 14.4	
Opt	**45** ± 6.7	**132** ± 6.9	**207** ± 12.0	**296** ± 15.2	**354** ± 19.3	
Opt_w	**45** ± 6.1	**132** ± 6.1	**205** ± 10.6	**292** ± 15.0	**352** ± 18.7	
NFI	**23** ± 4.7	**101** ± 17.6	**181** ± 18.2	**251** ± 28.3	**276** ± 32.3	
Southern Sweden						
Orig	**42** ± 1.9	**107** ± 3.9	**179** ± 8.1	**242** ± 13.0	**295** ± 16.1	
Opt	**62** ± 2.9	**159** ± 3.6	**260** ± 12.3	**327** ± 15.1	**376** ± 17.4	
Opt_w	**61** ± 2.9	**157** ± 3.6	**255** ± 12.1	**321** ± 14.9	**370** ± 17.6	
NFI	**30** ± 7.2	**126** ± 11.7	**203** ± 8.6	**258** ± 4.2	**285** ± 2.6	

for age classes 21–40, 41–60 and 61–80. Overall positive bias was 13% for *Opt*, 9% for Opt_w, and 26% for *Orig*.

3.2.2. Norway spruce monoculture

Simulations with the original setting (*Orig*) underestimated volume for all three regions compared to the NFI data except for the youngest age class in southern Sweden (Table 5). The *Opt* and Opt_w settings improved model results for central and southern Sweden, but the model overestimated standing volume for northern Sweden in comparison to NFI data. Both *Opt* and Opt_w settings produced similar results for standing volume for the three regions, differing by less than 5 m^3 ha^{-1} in northern Sweden, and by less than 10 m^3 ha^{-1} for central and southern Sweden (Table 5). In northern Sweden, the bias was −21% for *Orig*, whereas the bias for *Opt* was 33% and for Opt_w 36%. In central Sweden, the model results deviated only slightly for *Opt* and for Opt_w compared to the observational data for all age classes. Bias for *Opt* was 2% and 0.2% for Opt_w, whereas *Orig* underestimated standing volume for four out of five age classes (Table 5). Results for *Orig* in southern Sweden had a bias of −51%. Bias for *Opt* in southern Sweden was −5% and for Opt_w −4% (Table 5).

3.2.3. Mixed coniferous forest

The *Orig* setting for mixed coniferous forest was relatively well constrained for all three studied regions, whereas *Opt* and Opt_w displayed a stronger positive bias in relation to the NFI data (Table 6). *Opt* and Opt_w generated similar results, differing by 5 m^3 ha^{-1} in northern Sweden, less than 5 m^3 ha^{-1} in central Sweden, and less than 10 m^3 ha^{-1} in southern Sweden. The *Orig* setting in northern Sweden ranged from 20 to 267 m^3 ha^{-1} (Table 6), indicating a positive bias of 20% compared to the NFI data. *Opt* and Opt_w in northern Sweden had a positive bias of 41% and 43%, respectively. In central Sweden, *Orig* had a negative bias of −11% which was reduced to −4% for southern Sweden. In central Sweden, *Opt* ranged from 45 to 354 m^3 ha^{-1} and had a positive bias of 24%, whereas Opt_w ranged from 45 to 352 m^3 ha^{-1} with a positive bias of 23%. *Opt* and Opt_w deviated strongly also from the NFI data in southern Sweden by 31% and 29%, respectively.

3.2.4. Mixed forest

The original model parameters for mixed forest displayed agreement with the observational data for all studied regions. *Opt* and Opt_w differed by 5 m^3 ha^{-1} in northern Sweden and central Sweden and less than 10 m^3 ha^{-1} in southern Sweden (Table 7). In northern Sweden, *Orig* deviated by 6% from the NFI data, whereas *Opt* deviated by 15% and Opt_w by

Table 7
Modelled and observed mean standing volume (m^3 ha^{-1}, ± one standard deviation) per age class for mixed spruce-birch forest for the three regions northern Sweden, central Sweden and southern Sweden. The standard deviation indicates the variation in standing volume for a given age class among the counties in a region. *Opt* (optimized model parameters, one main dominating soil type), Opt_w (optimized model parameters, volume weighted across two dominating soil types), *Orig* (original model parameters) represent simulated standing volume. *NFI* represents data from the Swedish National Forest Inventory, (SNFI, 2021b).

	Volume per age class (m^3 ha^{-1})			
	0–20	21–40	41–60	61–80
Northern Sweden				
Orig	**24** ± 4.0	**87** ± 6.4	**100** ± 8.5	**132** ± 10.8
Opt	**15** ± 4.3	**93** ± 12.8	**114** ± 28.2	**198** ± 11.8
Opt_w	**15** ± 4.3	**95** ± 12.3	**121** ± 30.9	**194** ± 7.7
NFI	**18** ± 7.4	**68** ± 30.2	**122** ± 41.4	**157** ± 54.2
Central Sweden				
Orig	**37** ± 5.0	**113** ± 6.8	**145** ± 19.6	
Opt	**29** ± 6.2	**148** ± 13.9	**177** ± 29.7	
Opt_w	**29** ± 5.9	**148** ± 13.1	**171** ± 27.2	
NFI	**30** ± 3.1	**117** ± 14.1	**192** ± 16.3	
Southern Sweden				
Orig	**48** ± 1.7	**128** ± 5.5	**193** ± 6.6	
Opt	**51** ± 4.9	**181** ± 7.5	**264** ± 18.5	
Opt_w	**50** ± 4.9	**179** ± 8.0	**258** ± 17.9	
NFI	**34** ± 2.7	**130** ± 14.2	**191** ± 15.9	

Table 8
Comparison of simulated (*Opt*) and observed forest variables at the Norunda and Hyltemossa sites. The standard deviation (±) indicates the within-stand variation for observational data when available. Observational data for Norunda for height and diameter were collected in 2017, LAI in 2019, and stand density in 2021 (Mölder et al., 2021). For Hyltemossa, height and diameter were measured in 2017, stand density and LAI in 2019 (Heliasz et al., 2021).

	Species/Forest type	Stand age	Density (stems ha^{-1})	Standing volume (m^3 ha^{-1})	Diameter (cm)	Height (m)	Mean LAI (m^2 m^{-2})
Norunda							
Observed	Scots pine	75–130 years	325	363	35.0 ± 6.8	27.4 ± 4.1	
	Norway spruce	75–130 years	247	62	19.6 ± 11.7	16.7 ± 9.2	
	Mixed stand sum		*572*	*425*			2.8 ± 0.6
Simulated	Scots pine	118	344	283	31.4	18.3	
	Norway spruce	118	192	35	18.8	13.1	
	Mixed stand sum		*536*	*318*			2.7
Hyltemossa							
Observed	Norway spruce	35	1968	308	16.4 ± 5.8	14.6 ± 4.4	4.4 ± 0.5
Simulated	Norway spruce	35	717	232	21.9	14.4	2.4

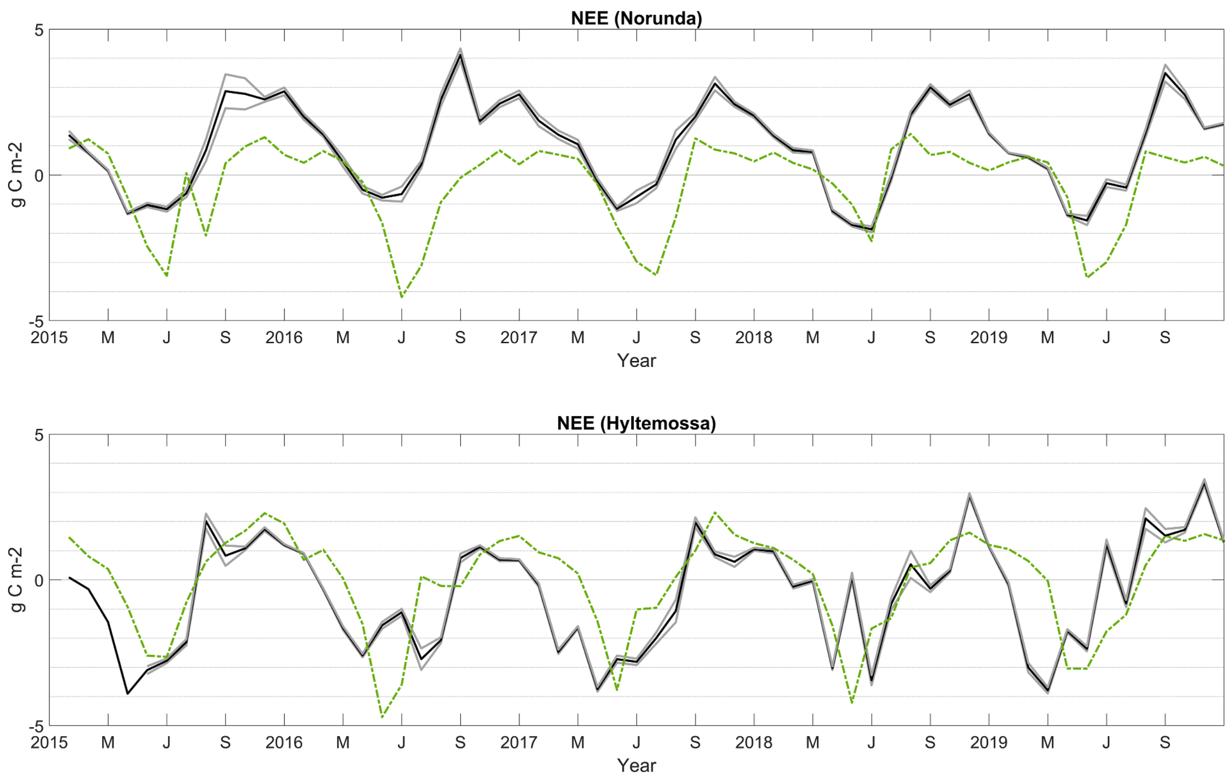

Fig. 3. Modelled and observed monthly averages of daily NEE for both studied sites 2015–2019. The green dashed line indicates simulated values of NEE. The black line indicates the monthly average observed NEE. The range of uncertainty in the observational data is indicated in gray (see 2.4 in 'Material & methods' for additional details).

16%. The model accuracy was reduced for *Orig* in central Sweden with a bias of −13% compared to the NFI data, whereas *Opt* and *Opt*$_w$ improved the results (bias of 5% and 3%, respectively). The *Orig* setting agreed with the observational data regarding standing volume for southern Sweden with a bias of 4% (Table 7) whereas *Opt* and *Opt*$_w$ deviated more strongly with a bias of 40% and 38%, respectively.

3.3. Evaluation of stand scale simulations

3.3.1. Evaluation of simulated forest structure variables

For Norunda, both height and diameter were relatively well captured for Norway spruce within the mixed stand using the *Opt* parameters, but the density was underestimated. The total simulated volume was 25% lower than observed, primarily as a result of a low simulated height and diameter of Scots pine (Table 8). This result indicates a discrepancy between the simulated productive capacity of Scots pine calibrated at the regional scale for central Sweden (*Opt*) and the observed productive capacity for the species at the Norunda site. The simulated mean annual increment (MAI) remained even but showed a tendency towards culmination 110 years after establishment (Fig. A2, Appendix A).

The simulated standing volume in the Norway spruce monoculture in Hyltemossa was 25% lower than the observed. The simulated MAI of the stand did not culminate within the period of study, displaying a growth trend similar to observed for monocultures of Norway spruce in southern Sweden on sites of high quality (Fig. A2, Appendix A). The high planting density caused competition within the simulated stand and elicited self-thinning which offset the increase in standing volume over time. By 2017, 94 m^3 of stemwood volume had been lost to natural mortality, excluding thinnings. In addition, the simulated leaf area index was underestimated by 2 m^2 m^{-2} resulting in a lower light use within the simulated stand, which limited carbon sequestration and growth (Table 8).

3.3.2. Evaluation of simulated carbon fluxes

Net ecosystem exchange: Norunda. Norunda was observed to be a source of carbon for all years, with an average net flux of 343 g C m^{-2} year^{-1} for the 2015–2019 period (hereafter referred to as period average). Carbon emissions ranged from 259 g C m^{-2} in 2019 to 483 g C m^{-2} in 2016 presenting a total range of 224 g C m^{-2} year^{-1} for the studied period, with an interannual variation of 91 g C m^{-2} year^{-1} (Fig. 5). For all years, the site was a carbon sink in spring, and the uptake was offset by high respiration during summer and autumn months (Fig. 3). LPJ-GUESS, forced with station-based climate data, simulated an average modelled net carbon flux of −103 g C m^{-2} year^{-1} for 2015–2019, with a range for the studied period of 280 g C m^{-2} year^{-1} (Fig. 5). The modelled interannual variation was 106 g C m^{-2} year^{-1}. The modelled NEE broadly agreed with the observed during spring months, but the model overestimated carbon uptake during summers (Fig. 3), leading to higher RMSD values (Fig. 6). In 2018, the annual precipitation dropped to 456 mm, which was 19% lower compared to the value for the climate normal period 1990–2020 (565 mm year^{-1}). The mean air temperature for the summer was 17.9 °C, whereas the period average for 2015–2019 was 16.1 °C (Fig. A4, Appendix A). LPJ-GUESS correctly estimated NEE in 2018 as positive but underestimated its magnitude (Fig. 5).

Net ecosystem exchange: Hyltemossa. Hyltemossa had an observed average annual net carbon flux of −175 g C m^{-2} which varied from −363 g C m^{-2} year^{-1} (2017) to −13 g C m^{-2} year^{-1} (2019), a range of 349 g C m^{-2} year^{-1} over the studied period, with an interannual variation of 144 g C m^{-2} year^{-1} (Fig. 5). For three out of the six years, the sink strength of the ecosystem was larger in spring (MAM) than in summer (JJA) (Fig. 3). Both spring and summer seasons displayed a net carbon uptake with the exception of the summer of 2019, when the Norway spruce forest stand was a carbon source for JJA, releasing 77 g C m^{-2} (Fig. 3). The period average NEE was not accurately captured by LPJ-GUESS, simulated as −19 g C m^{-2} year^{-1}. Individual years ranged from −143 g C m^{-2} year^{-1} (2016) to 106 g C m^{-2} year^{-1} (2015), presenting a simulated interannual variation of 93 g C m^{-2} year^{-1} (Fig. 5). Stand observations indicated that photosynthesis started earlier during the years than in the modelled stand. Modelled NEE in February was positive for all years, whereas a net carbon uptake was commonly observed for this month for the studied period (Fig. 3).

Gross primary production & ecosystem respiration: Norunda. The observed average gross primary production for the Norunda site 2015–2019 was 1310 g C m^{-2} year^{-1} and varied from 1138 g C m^{-2} year^{-1} (2017) to 1448 g C m^{-2} year^{-1} (2015) (Fig. 5), a range of 310 g C m^{-2} year^{-1}. The interannual variation was 131 g C m^{-2} year^{-1}. Average R_{eco} for the corresponding period was 1514 g C m^{-2} year^{-1} with a between-year variation of 168 g C m^{-2} year^{-1}, ranging from 1333 g C m^{-2} year^{-1} (2017) to 1753 g C m^{-2} year^{-1}, a total range of 420 g C m^{-2} year^{-1} (2016). Model results for gross primary production were close to observed for Norunda (Fig. 4). The simulated period average GPP was 1423 g C m^{-2} year^{-1}, on average 9% higher than observed, and varied between 1304 g C m^{-2} year^{-1} (2018) and 1583 g C m^{-2} year^{-1} (2015), presenting a range for the period of 279 g C m^{-2} year^{-1}. The interannual variation was 110 g C m^{-2} year^{-1}. The ratio of modelled NPP to GPP was on average 0.25, and varied from 0.17 (2018) to 0.31 (2019).

Modelled R_{eco} period average was 1416 g C m^{-2} year^{-1}, 6% below the observed average, and ranged from 1298 g C m^{-2} year^{-1} (2016) to 1540 g C m^{-2} year^{-1} (2015), a range of 242 g C m^{-2} year^{-1}. The modelled between-year variation was 110 g C m^{-2} year^{-1} (Fig. 5). The modelled soil water content (SWC) in the top 50 cm soil layer broadly agreed with the observed during summers and autumns of most years (Fig. A3, Appendix A). Modelled R_{eco} peaked in late July 2018 as a result of a sudden increase in soil water content following a period of drought, inconsistent with the trends within the observational data (Fig. 4).

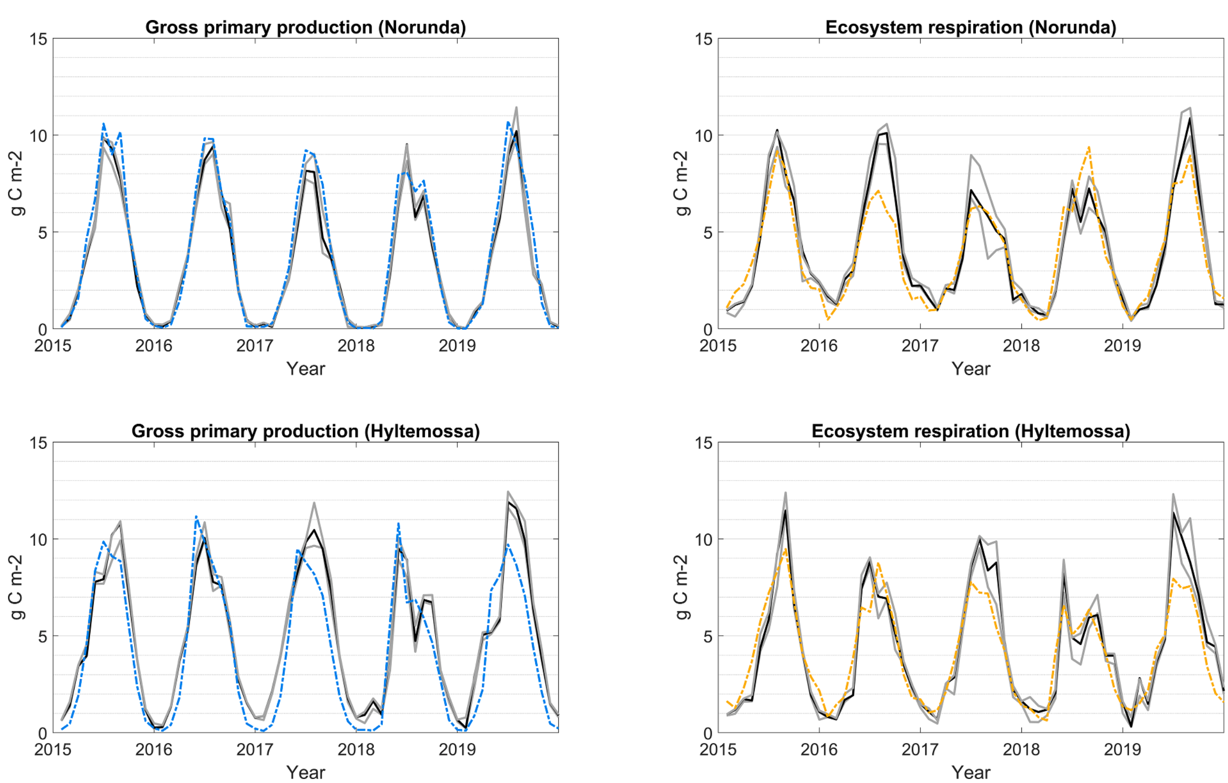

Fig. 4. Monthly averages of daily observed gross primary production and ecosystem respiration (black) for Norunda and for Hyltemossa 2015–2019. Dashed lines are monthly averages of daily simulated values, in blue for gross primary production and in yellow for ecosystem respiration. The range of uncertainty in the observational data is indicated in gray (see 2.4 in 'Material & methods' for additional details).

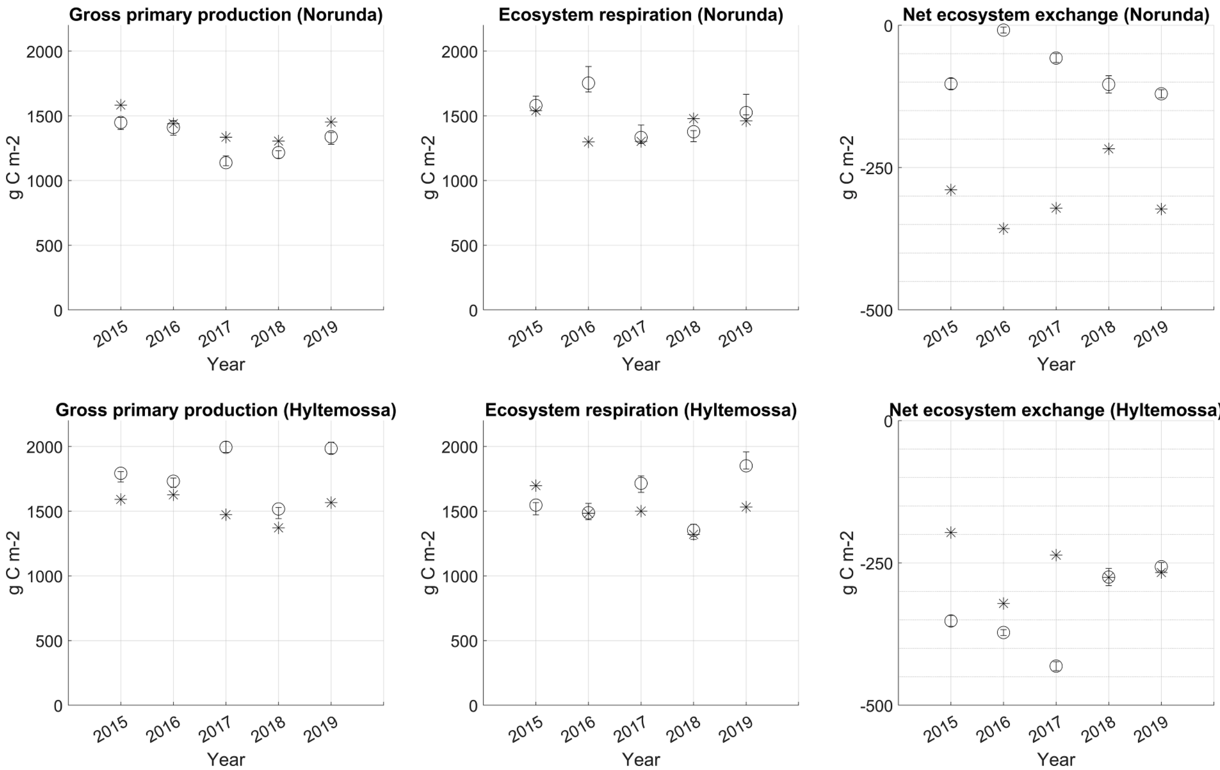

Fig. 5. Yearly sums of simulated (stars) and measured (circles) gross primary production, ecosystem respiration, and net ecosystem exchange for the two sites Norunda and Hyltemossa (2015–2019). A negative sign of NEE denotes a net flow of carbon from the atmosphere to the vegetation. Brackets indicate the range of uncertainty within the observational data for NEE, GPP and R_{eco} (see 2.4 in 'Material & methods' for additional details). Note the difference in vertical axis scale in the rightmost NEE column.

Gross primary production & ecosystem respiration: Hyltemossa. The observed GPP was on average 1804 g C m^{-2} $year^{-1}$ (2015–2019) and varied from 1517 g C m^{-2} $year^{-1}$ (2018) to 1994 g C m^{-2} $year^{-1}$ (2017), a range of 477 g C m^{-2} $year^{-1}$ (Fig. 5). The between-year variation was 198 g C m^{-2} $year^{-1}$. R_{eco} was on average 1591 g C m^{-2} $year^{-1}$ (2015–2019) and varied between 1352 g C m^{-2} $year^{-1}$ (2018) to 1850 g C m^{-2} $year^{-1}$ (2019), a range of 498 g C m^{-2} $year^{-1}$, with an interannual variation of 195 g C m^{-2} $year^{-1}$. The modelled GPP period average was 1525 g C m^{-2} $year^{-1}$, which was 15% below the observed GPP period average, and varied from 1371 g C m^{-2} $year^{-1}$ (2018) to 1625 g C m^{-2} $year^{-1}$ (2016), a range of 219 g C m^{-2} $year^{-1}$ (Fig. 5). The modelled interannual variation was 103 g C m^{-2} $year^{-1}$. The ratio of NPP to GPP was 0.41 for the period 2015–2019, varying from 0.36 (2018) to 0.45 (2019). The range of annual flux values within the observational data for GPP and R_{eco} were larger for Hyltemossa than for Norunda over the observed period (Fig. 5).

The modelled period average R_{eco} was 1506 g C m^{-2} $year^{-1}$ with a range of 377 g C m^{-2} for the studied period. Simulated R_{eco} was 5% lower than observed for the studied period, and varied from 1320 g C m^{-2} in 2018 to 1697 g C m^{-2} in 2015, presenting an interannual variation of 134 g C m^{-2} $year^{-1}$. The model accurately captured the reduction in R_{eco} during 2018, with a negative bias of 2% for this year (Fig. 4).

4. Discussion

4.1. General overview

This study provided an evaluation of the DVM LPJ-GUESS for managed forests in the nemoral and boreal zones of Sweden. An updated parameterization of Norway spruce and Scots pine, based on data from central Sweden, generated regional averages of standing volume in monocultures in southern and central Sweden that were closer to observed values. The new parameters did however not work well for northern Sweden or for mixed stands. The regional scale evaluation was complemented by an assessment of the model's capacity to simulate the structure of two forest stands and associated interannual variation of carbon fluxes. Simulated annual values of NEE were outside of the range of uncertainty presented in the EC data, indicating a mismatch in the representation of site-specific conditions. The model produced acceptable predictions of the magnitude of GPP for Norunda but underestimated GPP for Hyltemossa (Fig. 5). Disagreement between observed and simulated stand variables further suggest potential for additional tuning and site-specific configuration to account for differences in site quality at the stand scale.

4.2. Model application at the regional scale

4.2.1. Northern Sweden

With the new parameters (*Opt*), the model became better suited for application at the regional scale in southern and central Sweden, representing monocultures for age classes relevant to commercial forestry, where stand rotations do not commonly exceed 100 years for Scots pine and Norway spruce. The simulations of conifers in northern Sweden were however not representative of the average regional standing volume in monocultures or mixed coniferous stands. Several aspects may have contributed to the discrepancy. In this study we excluded gridcells within alpine regions in northwestern Sweden. Due to the coarse size of a gridcell (50 × 50 km), some portions of low productive forest land may then also have been omitted, contributing in part to the overestimation of the simulated standing volume per hectare in comparison with NFI data.

The sensitivity analysis of the species-specific parameters was performed for a county in central Sweden, however, the new parameter settings include a decrease in k_latosa with increasing latitude based on evidence from available literature (Mencuccini and Grace, 1995). A

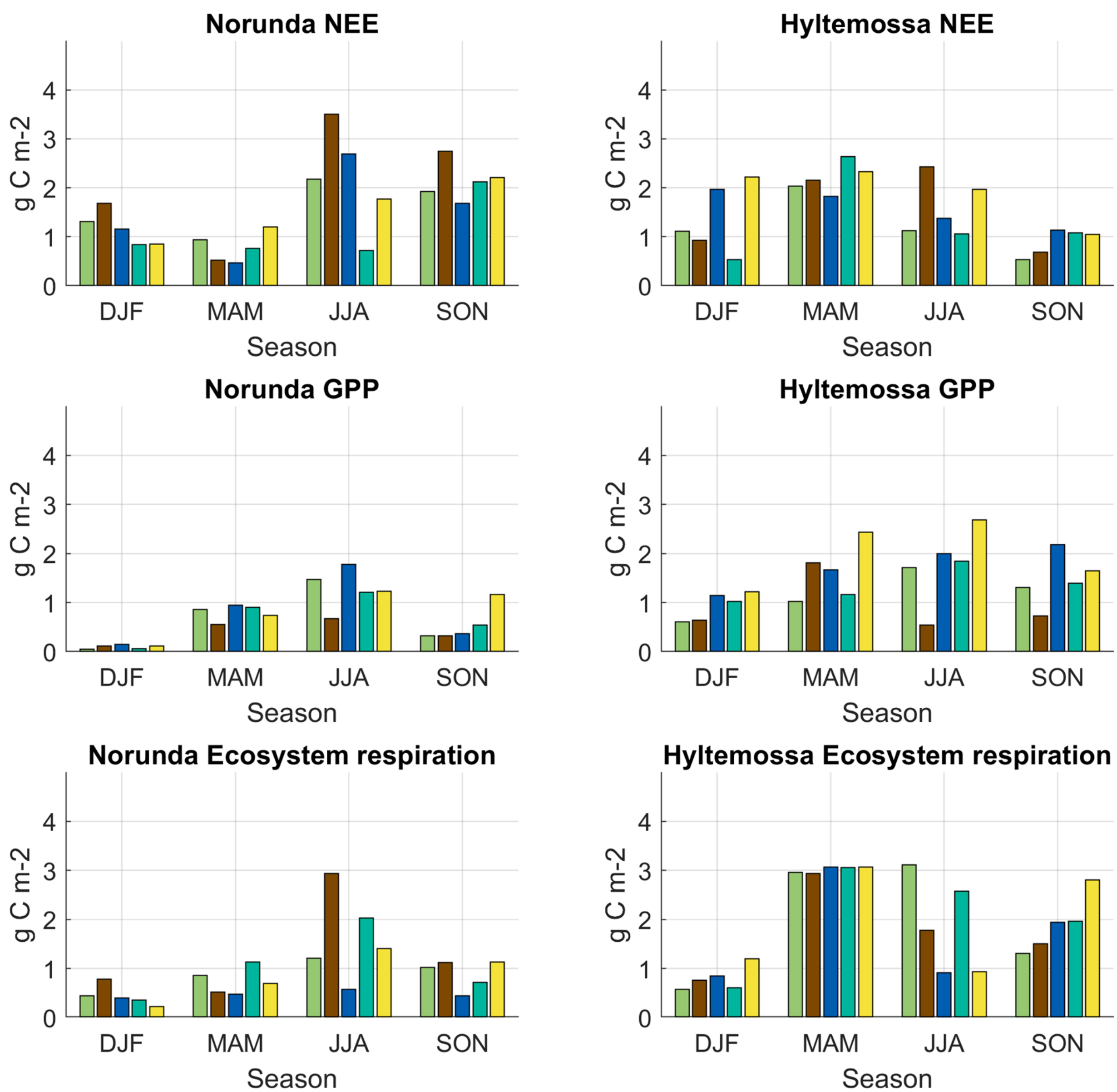

Fig. 6. Root mean square deviation between observed and simulated seasonal average fluxes of NEE, GPP and R_{eco} for both studied sites 2015–2019. To the left: Norunda, to the right: Hyltemossa. MAM = March, April, May, JJA = June, July, August, SON = September, October, November. green = 2015, brown = 2016, blue = 2017, turquoise = 2018, yellow = 2019.

representative setting for leaflong for northern Sweden would likely further improve model results, however, uncertainty regarding the minimum nitrogen content in older needles prevented an increase of leaflong to the observed 8 to 12 years (Reich et al., 2014). Furthermore, to have a firm control of the modeling processes, this study did not include the simulation of random stand-replacing disturbances during the simulation of managed forests, commonly set with a return time of 100 to 400 years (Lindeskog et al., 2021; Gustafson et al., 2021). Enabling this setting may provide results closer to observed, specifically for regions with extensive forest cover such as northern Sweden. The tendency to overestimate biomass production at high latitudes may also result from inadequate descriptions of relevant additional processes that inhibit tree growth. These could include a limiting effect of cold conditions on the synthesis of wood or a simulated loss of carbon representing the exchange of carbohydrates for the uptake of nitrogen through mycorrhizal symbiosis as well as an inhibition of water uptake due to frozen soils in spring and autumn months (Gustafson et al., 2021).

4.2.2. *The influence of changed soil conditions*

Accounting for variation in soil type (Opt_w) had limited influence on the simulated standing volume for a forest type within the landscape as Opt_w outputs resembled those from *Opt* for all studied regions regarding estimated standing volume. The comparison of simulations to highlight the influence of soil type on standing volume indicated that greater proportions of finer grain size material within a soil increases standing volume (Fig. A1, Appendix 1). The small difference between the till-like fine sand and till-like coarse sand soil type may possibly be explained by their similar water holding capacity (Table 1). Determining the influence of individual soil parameters on biomass growth and structure within additional analyses in future studies could provide further valuable information on the influence of soil hydrology on forest growth and productivity. The relative contribution of each soil type to the generated standing volume in Opt_w did also depend on the assumptions made regarding their proportion within a gridcell for these simulations (Table A3). The assumed proportions were largely based on the site requirements of each tree species and the silvicultural recommendations of establishing Scots pine on soils with higher sand content compared to Norway spruce. The small variations in productivity among the two model simulations *Opt* and Opt_w however imply a robustness when accounting for only one dominating soil type across a grid when the objective is to adequately represent a regional average standing volume.

Apart from both climate and soil texture, soil nutrient content, soil depth, and the movement of groundwater also influence growth and productivity within a stand (Skovsgaard and Vanclay, 2013; Bergh et al., 2005). Significant variations in site productivity can exist for the same type of soil: Norway spruce established on a till dominated by fine sand has an estimated site index varying from 30.0 m to 38.0 m at 100 years at the research site Tönnersjöheden in southern Sweden (Johansson, pers. comm). Our modeling approach, relying on variation in soil texture and climate, is therefore not sufficient for capturing the variation in site conditions for individual forest stands. Additional model development adding processes and parameter settings for aspects which further influence productivity would be needed to account for differences in site quality. Such aspects could include variations in soil depth among sites or additional soil layers (Lasota et al., 2016; Bergh et al., 2005). However, the benefit of adding functionality to the model needs to be considered in relation to the uncertainty introduced by additional parameters and equations, which may influence the robustness of the model (Wramneby et al., 2008).

4.2.3. Age-related aspects

The standing volume was overestimated for the two oldest age-classes by *Opt* and Opt_w compared with the NFI data for all three regions for the Norway spruce monoculture forest type. However, the development of the simulated MAI for Norway spruce established in a monoculture in Örebro county displayed a similar trend as described for stands of Norway spruce in the southern boreal zone in Sweden, indicating a representative stand development over time (Bergh et al., 2005). Within commercial forestry, older forest stands are commonly situated on soils with low inherent productive capacity whereas stands situated on fertile soils generally have a shorter rotation period (Bergh et al., 2005; Roberge et al., 2016). High-yielding forest stands are therefore less likely to contribute to the regional volume estimate for higher age classes. We did not account for this in our model simulations. The estimated volume for the youngest age class deviated from the observed both within monocultures and mixed forest types for several regions. The modelled plants have a height of 2 m and are initiated directly after clear-cut, which we consider the main cause for the overestimation of standing volume for this age class. Furthermore, the stand regeneration phase is associated with some challenges which are currently not included in the model such as failed regeneration due to browsing, frost damage to buds, or damage due to pathogens such as the pine weevil (Bergqvist et al., 2014; Wallertz and Petersson 2011; Holmström et al., 2018; Gustafson et al., 2021). Incorporation of these growth reducing factors and alteration to the tree allometry following planting would improve the representation of forest stands and their growth within the establishment and early growth phase (0–20 years).

4.2.4. Mixed coniferous forest

The model results for the *Orig* setting for mixed Birch/Norway spruce forest matched the observed data relatively well for all regions. Furthermore, the original model parameters generated a standing volume of mixed coniferous forest comparable to observational data for southern and central Sweden, likely due to a conservative growth response of Norway spruce in *Orig* (Table 5) in combination with a greater than observed growth of Scots pine in *Orig* (Table 4). The new parameterization *Opt* resulted in higher standing volume of mixed coniferous stands at ages above 60 years in comparison to NFI data. We checked if this result was due to reduced thinning since the mixed forest was simulated with a setting for variable thinning to maintain an even proportion (50/50) of the carbon biomass of each species within the stands, but found no such indications: the average removal of volume was similar but slightly below that of pure Scots pine for higher age classes and similar to Norway spruce for younger age classes. The modelled environment is less complex than an actual ecosystem, with more distinct characteristics of tree species (Hou et al., 2013). The unexpected overestimation could be attributed to reduced competition within simulated mixed stands with the *Opt* parameterization, with modelled species being able to exploit resources more efficiently due to clear differences in functional traits (Kahmen et al., 2006).

4.3. Model application at the stand scale

4.3.1. Forest stand variables

The setting *Opt* generated model results for stand variables which were inconsistent with site data with an underestimation of simulated standing volume for both Norunda and Hyltemossa (Table 8). Our model results indicated an initiation of self-thinning due to a high initial stand density for the Norway spruce stand at the Hyltemossa site, which reduced the stand volume increment. However, the simulated growth was consistent with the observed trend for forest stands of high site productivity in southern Sweden (Fig. A2, Appendix A). The observational data indicated a sustained carbon sequestration and growth in Norway spruce even at high stand densities (Fig. A2, Appendix A). Similarly to this study, Lindeskog et al. (2021) modelled the standing volume for Norway spruce and beech (*Fagus sylvatica*) monoculture stands for 16 sites in Germany using the LPJ-GUESS forest management module. The study found representative model results for stands with low standing volume but a negative bias of 50% or more for stands with high standing volume. The authors pointed to the possibility of including additional plant physiological processes such as hardening and dehardening as a potential way to account for differences in productivity (Lindeskog et al., 2021). Another option, apart from the aspects mentioned above concerning soil characteristics and hydrology, could be to further tune the two species-specific allometric parameters k_allom2 and k_allom3 (Smith et al., 2001, 2014). These parameters influence the mean height and diameter within a stand ($height = k\_allom2 \times diameter^{k\_allom3}$). Bellassen et al. (2010) showed that several forest variables were sensitive to changes in parameter values within similar biomass allometric equations implemented in the ORCHIDEE DVM adapted for forest management. An initial assessment in our study showed improved estimates of stand height and density of Scots pine for the Norunda site when optimized against observational data (Table 8). We decided however not to use site-specific calibration of these parameters due to lack of additional, independent stand data for validation.

4.3.2. Norunda carbon fluxes

The modelled interannual variation of GPP for 2015–2019 of 110 g C m^{-2} was similar to the observed value of 131 g C m^{-2} $year^{-1}$ for the mixed stand at the Norunda site. The modelled ratio of NPP:GPP was on average 0.25 for 2015–2019, and was identical compared to a given estimate for Scots pine in the boreal zone at the observed stand height (Makela and Valentine, 2001). However, the model simulations of NEE indicated Norunda to be an average sink of −103 g C m^{-2} $year^{-1}$ for the period 2015–2019 which disagreed with the observational data showing the site to be a source of 343 g C m^{-2} $year^{-1}$. Previous empirical studies have suggested soil heterotrophic emissions from the site in the range of 240 g C m^{-2} yr^{-1} (Lagergren et al., 2019). Soil measurements at the site have indicated low soil nitrogen (N) content which both restricts stand photosynthesis and increases competition for available N among soil microorganisms. The selective decomposition of old soil organic matter by microbes to make additional nitrogen available is therefore considered a plausible main cause for the net CO_2 emissions from the site (Shahbaz et al., 2022). These aspects, not captured by the model, may therefore partly explain the discrepancy between simulated and observed R_{eco}. Furthermore, the Norunda site has been shown to have very large within-canopy variability of CO_2 fluxes during nighttime, with strong horizontal and vertical advection occurring during clear summer nights with stable conditions. Strong advection can lead to either underestimation or overestimation of CO_2 and therefore influence the estimation of nighttime NEE within the observational data (Feigenwinter et al., 2010). The modelled between-year variation of NEE (106 g C m^{-2} $year^{-1}$) was an accurate estimate of the observed within the stand (91 g C m^{-2} $year^{-1}$). The interannual variation of the site was slightly higher than in a Scots pine stand within a comparable climate in southern Finland of 77 g C m^{-2} (Suni et al., 2003). Empirical studies have found old forest stands to be carbon sinks or close to carbon neutral in the boreal zone indicating that the model represents the average net carbon balance of this age class well given the current management settings (see below) (Luyssaert et al., 2008).

4.3.3. Hyltemossa carbon fluxes

The modelled average NEE estimate for 2015 to 2019 was −19 g C m^{-2}, whereas the observed average for the period was −175 g C m^{-2} for the Hyltemossa site. The annual modelled estimate of GPP was lower than observed, and the modelled LAI was reduced, causing lower light absorption and interception within the stand. An increase of modelled GPP would raise both NPP and modelled autotrophic respiration, and consequently annual R_{eco}, which was underestimated for the site by 5%. The average ratio of NPP to GPP in the Norway spruce stand was 0.40 for 2015–2019 which agreed with the ratio of NPP:GPP for Norway spruce within the boreal zone given in Harkonen et al. (2010), indicating a proportional contribution of the autotrophic respiration component to modelled GPP for the site. An increase in modelled GPP to the observed value would result in an accurate estimate of NEE, assuming this ratio remains constant.

Previous model studies using the forest management module of LPJ-GUESS have shown high estimates for modelled soil carbon stocks compared to observations, which may cause higher-than observed heterotrophic respiration (Lindeskog et al., 2021). In the model simulation for Hyltemossa, forest management was initiated in 1892 by clear-felling to allow for the known occurrence of one completed rotation period of Norway spruce forest before the initiation of the current forest stand in 1982. Records and maps exist which show established forest in 1938, but the land area had however most likely been managed for a longer period of time (O'Dwyer et al., 2021). The accurate recreation of the historical management was important for generating representative soil carbon emissions: initializing management in the early 1920s would have transformed the stand to a weaker carbon source due to increased R_h (*data not shown*). Furthermore, utilizing the original parameter settings for Norway spruce during spin-up is important, as the new parameters *Opt* are not intended for simulating uneven-aged natural forest. Observational data to enable direct comparisons between modelled and observed R_h are currently lacking for Hyltemossa. Such an effort would involve directly measuring the soil emissions within the stand using a closed dynamic system in conjunction with trenching of roots to disentangle the components of autotrophic root respiration and heterotrophic respiration from R_{eco} (Schindlbacher et al., 2009).

4.4. Model uncertainty, development

LPJ-GUESS has been developed with a key aim of modeling natural and managed forest ecosystems at regional to global scales (Smith et al., 2014). The process-based modeling approach supports the view of the forest as a complex dynamic system (Messier et al., 2013), and the model can be considered a working hypothesis of forest structure and functioning (Korzukhin et al., 1996). Previous LPJ-GUESS evaluation studies of forest growth and standing stock in Sweden have focused on simulations at the national scale, without distinguishing the age classes of specific forest types (Lagergren et al., 2012). We implemented a set of new parameters for the two most common coniferous species in Sweden, with an evaluation at the regional scale which improved the predictions for monocultures in central and southern Sweden.

The original parameters were intended for simulation of uneven-aged potential natural vegetation (PNV), but the simulation of managed even-aged forest landscapes presents new and differing conditions for the competition of light, water and nutrients. The new optimized parameters have been developed to represent managed forest and are not intended for the simulation of PNV with LPJ-GUESS. The development of the MAI and PAI over time both for monocultural forests in Örebro (Fig. 2) and for the central and southern Swedish sites (Fig. A2, Appendix A) indicated a growth pattern representative of temperate and boreal forest stands in Sweden. The increase in standing volume of the Norway spruce monoculture at Hyltemossa was reduced due to high natural mortality in the stand, indicating a potential for further tuning to improve the rate of self-thinning for stands experiencing similar conditions.

In this study, 4 model vegetation parameters for Norway spruce and Scots pine were optimized against county-level NFI data using climate data input at the landscape scale. An optimization at the landscape scale is less likely to capture the stand-level characteristics of each tree species. Attempts to achieve greater biological realism in model simulations would benefit from additional tuning at the site scale using local climate model data input and representations of site quality, including variations in soil depth and the movement of groundwater. Given that Scots pine typically is found on poorer soils in Sweden, resulting in less productive stands, we would expect that an attempt to compensate for this at the landscape scale with changing turnover_sap would lead to a negative directional change in turnover_sap, which is what we also observed within the sensitivity analysis (Table A1, Appendix A). We have with the current approach explored the possibility of accounting for differences in site productivity by using different soil types in the simulations, but different soils produced similar estimates (Fig. A1, Appendix A).

In general, the observational data at the stand scale derived with the daytime method suggested improved model performance compared to observational data based on the nighttime method (Fig. A7, Appendix A). We have here chosen to present the model results primarily with a comparison to the daytime method due to a greater similarity between the mechanistic modeling of NPP in LPJ-GUESS based on photosynthesis to the daytime method of Lasslop et al. (2010). The discrepancy in annual and monthly values between the daytime method and the nighttime method in GPP and R_{eco} highlights the fact that the exchange of carbon between the vegetation and the atmosphere is a complex phenomenon (Fig. A7, Appendix A) (Lagergren et al., 2008). The improvements made to the model can present opportunities for more detailed studies of forest ecosystem services such as carbon sequestration at large spatial scales, allowing for better assessments of policy-relevant forest-based mitigation strategies over long timescales.

5. Conclusions

LPJ-GUESS with an operational forest management module is useful for studying the long-term influence of changed climate conditions on managed forest ecosystems and predict the direction of ecosystem responses to large-scale changes in forest management regimes. The new species-specific parameters presented herein are suitable for application to simulate Norway spruce and Scots pine in monocultures, but are not intended for simulation of potential natural vegetation. LPJ-GUESS is in its current form limited in fully accounting for differences in site quality at the scale of individual forest stands. The results highlight the potential to further incorporate additional characteristics of site quality which could benefit model accuracy, including further tuning of species-specific parameters at the site scale. Further analysis of the influence of specific soil parameters on forest growth could provide valuable insight into the role of the soil in stand growth. Additional model development to better capture local conditions could include a more detailed description of soil layers and associated effects on nutrient storage, soil water freezing and thawing, the movement of water and the influence of spatial variations in soil depth.

CRediT authorship contribution statement

John Bergkvist: Conceptualization, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Fredrik Lagergren:** Conceptualization, Writing – review & editing. **Maj-Lena Finnander Linderson:** Formal analysis, Writing – review & editing. **Paul Miller:** Software, Writing – review & editing. **Mats Lindeskog:** Software. **Anna Maria Jönsson:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

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

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.110253.

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