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Evaluating vegetation carbon storage by primary forests in Sweden using LPJ-GUESS

Sacha van der Vleuten

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

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Supervisor: Anders Ahlström,
Department of Physical Geography and Ecosystem Analysis, Lund University

Exam committee:
Thomas Pugh,
Department of Physical Geography and Ecosystem Analysis, Lund University
Harry Lankreijer,
Department of Physical Geography and Ecosystem Analysis, Lund University

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Abstract

Over the past 200 years, the structure of forests in Sweden has changed drastically, with forestry becoming the dominant land use. This has led to the loss of primary forests, which has major impacts on different ecosystem services, including carbon storage. Primary forests are unique ecosystems that are untouched by humans and have been sequestering carbon for centuries.The effects of this shift from no land use to land use on the vegetation carbon storage is poorly understood. The difference in carbon storage between primary and managed forests could give an indication of the effects of land use. LPJ-GUESS is a dynamic vegetation model that can estimate both potential natural vegetation and managed ecosystems. However, the ability of LPJ-GUESS to simulate potential natural vegetation has not been evaluated. Here, a unique dataset on 11 primary forests in Sweden was used to evaluate the potential natural vegetation. The vegetation carbon storage and different aspects of primary forest structure were investigated using a regression analyis and compared with bootstrapped field data.

The results showed that LPJ-GUESS overestimated carbon storage, but the adjustement of the bole height ratio to 0.25, the disturbance interval to 143 years and the leaf longevity to 7 years improved the model performance. With these improvements, the model could accurately explain 40% of the variation in the field data. The improvements however negatively affected the maximum tree height and further overestimated carbon storage in spruce trees. Furthermore, the same postive results to the adjustments of the parameters were not found for primary forest data form the Swedish national forest inventory.

The initial overestimation of the modelled vegetation carbon storage could be explained by the simulation of very thin trees and the inclusion of grass in the vegetation carbon storage.

The improvements had a good effect on most investigated structural parameters, but the changes within parameters, especially the leaf longevity for pine, were found to impact the tree type composition.

In conclusion, the results showed that LPJ-GUESS could simulate potential natural vegetation moderately well and that this method could thus be used to more efficiently estimate vegetation carbon storage in primary forests. This method could further be used to contrast carbon storage in primary forests with managed forests and the results have a general relevance when simulating natural vegetation in LPJ-GUESS.

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1 Introduction

Since the late 1800s, the structure of Swedish forests, including stand volume, tree age and species composition has changed drastically. Primary forests have largely been converted into managed forests by a combination of logging, the introduction of silviculture and fire-elimination (Linder & Ostlund, 1998). This loss of primary forests has led to the loss of different ecosystem services such as the habitat for wildlife, including many red listed species, as well as sequestration of carbon and prevention of flood and erosion (Linder & Ostlund, 1998; Wirth et al., 2009).

Nowadays, primary forests are relatively rare in Europe, only covering 0.7% of Europe's forested area (Sabatini et al., 2018). Of which, the majority in the Northern hemisphere occurs in the boreal region (Luyssaert et al., 2008; Sabatini et al., 2018). In Sweden, 358 sites with a combined size of 16 565 km^2 of primary ecosystems are known, of which 9 926 km^2 is covered by forest. This is only 2% of the total forest cover in Sweden (Ahlström et al., 2020).

Primary forests can be defined as "Naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed" (FAO, 2018). These natural boreal forests are characterized by many large diameter living and standing dead trees and are dominated by trees with ages over 200 years (Linder & Ostlund, 1998). In Sweden, primary forests generally consist of *Pinus sylvestris* (Scots pine) and *Picea abies* (Norway spruce) (Linder & Ostlund, 1998).

1.1 Carbon uptake in primary forests

Until recently, primary forests were thought to be carbon neutral and were thus excluded from carbon budget estimations (Odum, 1969). However, Luyssaert et al. (2008) found a carbon sequestration of about 2.4 ± 0.8 Mg C ha^{-1} yr^{-1}. Their finding thus suggests that the 15% of the global forest area which consists of primary forests provides at least 10% of the net ecosystem productivity (NEP). In contrast, Gundersen et al. (2021) estimate a 30% lower carbon uptake than Luysseart et al. (2008). Despite differences in the exact value, both sources thus suggest that primary forests act as a carbon sink globally.

Primary forest can accumulate carbon for centuries and therefore form an important carbon sink (Jacob et al., 2013; Luyssaert et al., 2008). Temperate and boreal forests in the Northern hemisphere are estimated to have a total annual sink of 1.3 +/- 0.5 gigatonnes of carbon (Luyssaert et al., 2008). This is a significant portion of the global terrestrial carbon storage and thus highlights the importance of primary forests not just for biodiversity (Jacob et al., 2013; Luyssaert et al., 2008).

Forest ecosystems absorb atmospheric CO_2 through photosynthesis. A large part of the fixed carbon is emitted back to the atmosphere through auto- and heterotrophic respiration, but part of the fixed carbon is sequestered in above- and belowground biomass (Canadell et al., 2007; Zhou et al., 2006). It is expected that if these primary forest are disturbed, much of the carbon stored in these forests will be emitted back to the atmosphere (Luyssaert et al., 2008). Furthermore, logging turns forests into a carbon sources for at least 14 years, and the regrowth forests remain weaker sinks than primary forests for many years (Schulze et al., 1999).

1.2 Primary forests as a baseline to understand land use impacts

About 75% of land globally is used for agriculture, grazing or forestry (Erb et al., 2007). In Sweden, forestry is a dominant land use but its impacts on carbon storage are not well understood (Erb et al., 2016; Erb et al., 2018). Land use affects the carbon stock and turnover significantly (Erb et al., 2016; Erb et al., 2007). Currently biomass stores about 450 petagrams of carbon globally, but with no land use this could be doubled to 916 petagrams according to Erb et al. (2018). One way to estimate long term impacts of land use on vegetation carbon storage is to contrast unmanaged ecosystems with managed ecosystems.

The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) is a dynamic vegetation model that incorporates both nitrogen (N) and carbon (C) cycling in ecosystems. LPJ-GUESS is a state-of-the-art model that can simulate both potential natural vegetation and managed ecosystems (Smith et al., 2014). By using such a model, it is thus possible to estimate the impact of historical and future land use on the carbon cycle and carbon storage. However, since little data exists on carbon storage in primary forests, it remains largely unknown if LPJ-GUESS accurately simulates potential natural vegetation. In this study, the model is tested using a unique dataset of vegetation carbon from 11 primary forest in Sweden. Moreover, parameters within the model are modified to more accurately simulate these forests. This study therefore contributes to future studies investigating the impacts of land use using LPJ-GUESS.

1.3 Aim of the study

This research aims to evaluate how well LPJ-GUESS can estimate vegetation carbon storage by primary forests in Sweden. This will be achieved by answering the following research questions:

1) How well does LPJ-GUESS estimate vegetation carbon storage in primary forests using the default set-up?
2) How well does LPJ-GUESS estimate the forest structure of primary forests?
3) How well could LPJ-GUESS estimate vegetation carbon storage when parameters are adjusted to more accurately represent primary forests in Sweden?

2 Methodology

2.1 General overview

A general overview of the methods used in this study are depicted in *Figure 1*. The steps shown in this figure will be further explained in the following sections. Two types of field data were used for the methods in this study. Most of the results are based on primary forest data, but data from the Swedish national forest (NFI) inventory are also used.

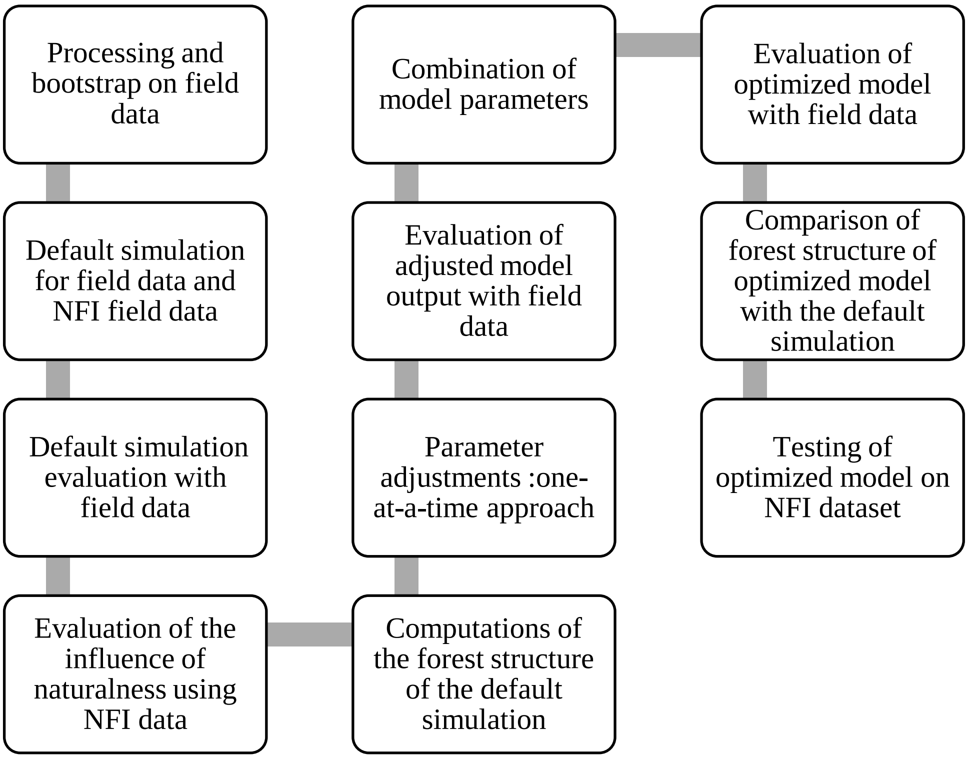


Figure 1. Simplified flow chart depicting the methodology used in this study. When field data is mentioned, field data on primary forests is used and when NFI field data is mentioned, data from the Swedish national forest inventory is used.

2.2 The LPJ-GUESS dynamic vegetation model

In this section the dynamic vegetation model that was used in this study will be explained as well as the model set-up.

2.2.1 Model description

LPJ-GUESS (Smith et al., 2001) is a dynamic vegetation model that is suitable for studies on regional to global scale. The model uses plant functional types (PFTs) to represent different vegetation types. Each PFT is defined by several variables, as can be seen in *Figure 2*. Each parameter is expressed in carbon biomass per area (kg C m^{-2}). For woody PFTs (trees), each average individual falls within an age class in which individuals have the same size and growth rate. The density of the individuals is a resulting parameter. For herbaceous PFTs (grasses), one average individual represents the whole population. Density is thus not taken into account here.

The model simulates a number of patches. Patches are defined as 0.1ha, which is assumed to be the maximum area within which a single tree can have influence on its neighbours. Within a patch, the composition of PFTs is dependent on bioclimatic limits. The establishment of individuals is further influenced by stand structure and crowding over the years. An overview of the different PFTs that were used within this study and their properties can be seen in *Table 1*. The leaf duration and shade tolerance of the used PFTs influence amongst others the canopy conductance and the maximum establishment rate. The PFTs are simulated using a 500 years spin-up time to establish carbon, nutrient and water storage in the various pools that are in equilibrium with the climate at the start of the transient period, 1901. The model further simulates patch destroying disturbances at specific intervals and wild fires (Smith et al., 2014).

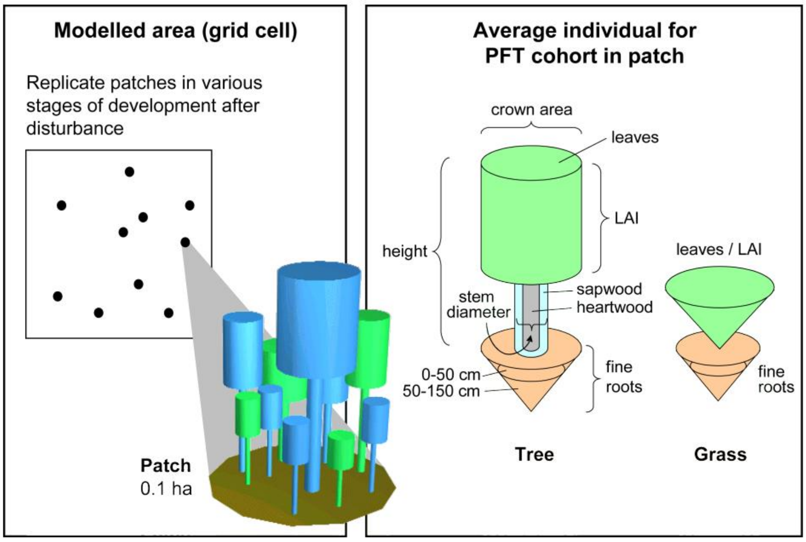


Figure 2. Figure showing how vegetation is modelled in LPJ-GUESS (Smith et al., 2014).

Table 1. The different PFTs used in this study and their properties

PFT	**Climate zone**	**Growth form**	**Leaf type**	**Leaf duration**	**Shade tolerance**
BNE	Boreal	W	Needle	Evergreen	Shade tolerant
BINE	Boreal	W	Needle	Evergreen	Shade intolerant
TeBS	Temperate	W	Broad	Summer green	Shade tolerant
IBS	Temperate	W	Broad	Summer green	Shade intolerant
C3G	Boreal/temperate	H	Grass	-	-

W= Woody, H=Herbaceous. BNE= Spruce and BINE=Pine

2.2.2 Model set-up

The model input consisted of climate forcing data with monthly time steps from CRU-NCEP (Climate Research Unit and National Centers for Environmental Prediction) between 1901 to 2015 (Wei et al., 2014). This data was interpolated to daily timesteps using the Global Weather generator (Sommer & Kaplan, 2017). The atmospheric nitrogen deposition data consisted of monthly averages from the ACCMIP (Atmospheric Chemistry and Climate Model Intercomparison Project) (Lamarque et al., 2010). The soil data originates from WISE 3.0 (Wide-field Infrared Survey Explorer, version 3) (Batjes, 2005) with calculations on hydrological properties of the soil following Olin et al. (2015). Further input consisted of the coordinates for each primary forest.

The model was run in cohort mode. In this setting, which is the most common setting used, the model simulates trees grouped in age classes (cohorts) with varying number of individuals. The individuals in the cohorts therefore have identical size and form. The model was set to use the average of 50 replicate patches to estimate each individual forest, as this resulted in a steady model output with less variability arising from disturbances and successions, see *Figure A* in *Appendix A*, and was thus deemed sufficient. Model estimations for the most recent year, 2015, were used in the model evaluations.

2.3 The field data

Two kinds of field data were used in this study. The main model evaluations were based on primary forest field data, described in *2.3.1 Primary forest field data*. Further field data was used to evaluate the influence of the degree of naturalness and the model optimization, this field data is described in *2.3.2 Swedish inventory field data*.

2.3.1 Primary forest field data

The primary forests field data that was used in this study consists of preliminary data that was stratified randomly sampled based on soil moisture data to represent the average Swedish forest. The data was based on a subset of 11 forests from the primary forest map from Ahlström et al. (2020), see *Figure 3*. This subset was chosen because these forest included the most natural forests and had a wide spread over Sweden. The data was sampled in circles with a 7 m radius, within this area all trees with a diameter at breast height (DBH) over 5 cm were included. The field data consisted of 15 to 26 sample plots per forest. Each sampled forest had a relatively high naturalness on the Buchwald scale (Buchwald, 2005), with values of 7 and 8.

The Buchwald scale is a way of defining the level of naturalness of a forest. This scale ranks natural forests from 0-10 based on how natural they are. Factors that separate the different levels include the dominance of native flora, the presence of key species, the presence of human modifications (e.g. logging), the continuity of forests, and the presence of management (e.g. hunting). The different degrees of naturalness are further explained in Buchwald (2005).

The field data included the tree species, diameter and height of the measured trees. The dry weight of biomass was calculated using the NFI standard biomass functions based on Marklund (1988).

The field data was processed before it could be used as input and comparison with the model. Firstly, the coordinates were converted into GCS WGS 1984 and transformed into WGS 1984 World Mercator. The mean of the different coordinates for each forest was then computed to use as input for the model in order to find the closest 0.5 × 0.5 degree grid cell. Secondly, the total carbon stored in live biomass was calculated by taking 50% of the dry weight of live biomass (Sandström et al., 2007). Then, a bootstrap was performed on the field data. This was done to first of all give a better representation of the forest, as field samples were few, and secondly to give an indication of the accuracy of the used vegetation carbon storage means. The field data was resampled into 100 values per forest using the mean. The mean of all the bootstrapped means was then used to compare with the model output. The95% confidence interval of this mean was calculated using the 100 bootstrapped means and shown as error bars in the figure.

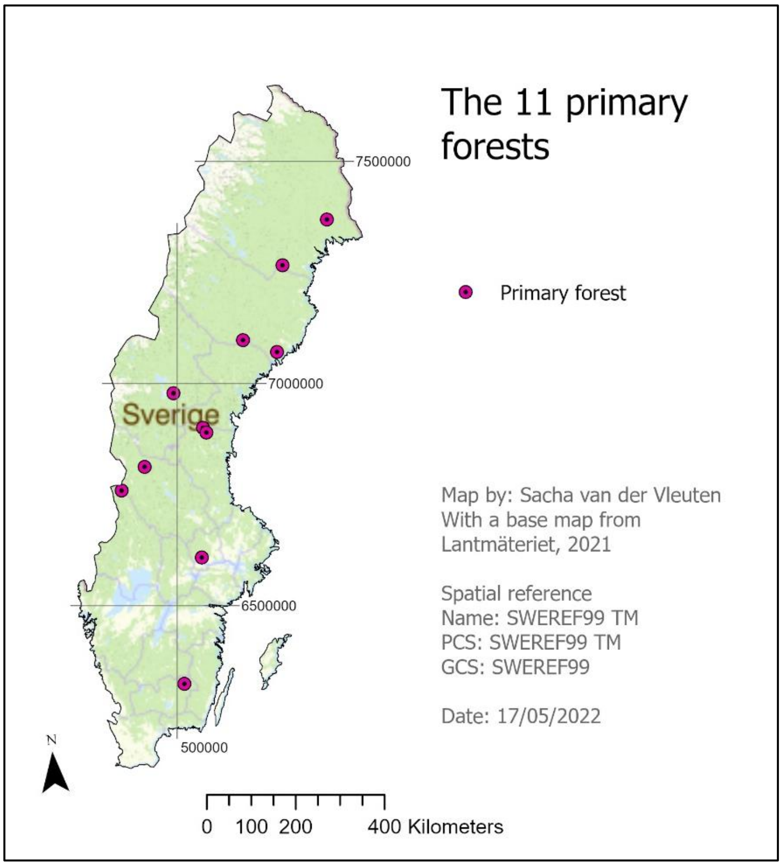


Figure 3. Map showing the locations of the centres of the 11 primary forests used in this study.

2.3.2 Swedish national forest inventory field data

The Swedish national forest inventory (NFI) field data was sampled based on grids and included all types of land use. The data included amongst others, age, height and the dry weight per area (Fridman et al., 2014; Ståhl et al., 2011). The naturalness for each forest according to the Buchwald scale (Buchwald, 2005) was also determined, by overlaying the data with the primary forest map by Ahlström et al. (2020).

The data contained forest data from many different years, all data sampled before the year 2000 was removed, since this was considered too far from the model estimations for 2015. Furthermore, data that had a Buchwald naturalness value below 5 was removed, as 5 and above represents primary forests according to the Buchwald scale (Buchwald, 2005). This resulted in the data points seen in *Figure 4*. Lastly, the carbon content was calculated by taking 50% of the dry weight and was then averaged over each forest (Sandström et al., 2007).

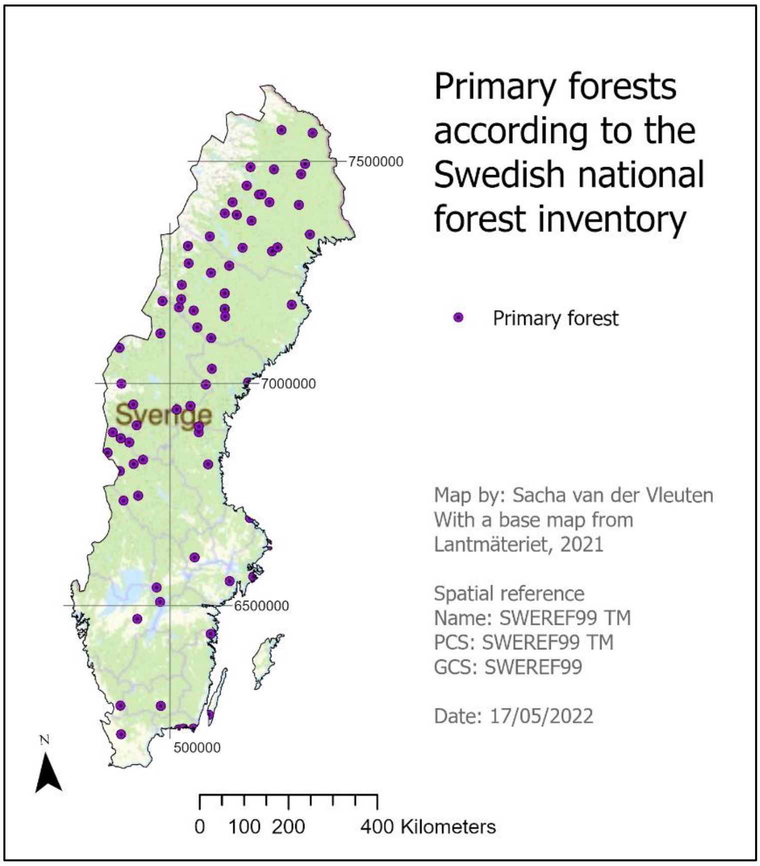


Figure 4. Map showing the locations of the data on primary forests from the Swedish national forest inventory.

2.4 Parameter adjustment

Four different model parameters were adjusted to evaluate their impact on the model fit. The specific parameters were chosen based on expectations by an expert (Stefan Olin), and on what properties are unique for primary forests, as well as what could be specific for the boreal region. In addition, a new parameter to the model was used, the bole height ratio. The values for the adjusted parameters were chosen from literature and the maximum and minimum value with two intermediate values were used. The different values were adjusted within the model input using a one-at-a-time approach, which means only one parameter differed from the default set-up per model run. More information on each parameter can be found in the following sections.

2.4.1 Disturbance interval

Firstly, the parameter for the disturbance interval was adjusted. The disturbance interval refers to the time between stand replacing disturbances. These events can be for example windstorms and landslides. Disturbance events can remove trees from patches or completely destroy the patch, changing the disturbance interval could thus impact the amount of carbon stored in vegetation.

Primary forests in Sweden potentially have a higher disturbance interval than the model default. The initial value for the disturbance interval in the model was set to be 100 years. However, in a study on primary forests in Eastern Europe, a higher average and maximum past disturbance interval were found. A maximum of 300 years was used in this study, as this was the maximum interval that was found by Rodrigo et al. (2022). An intermediate value of 200 years, which was more common, and an intermediate value of 143 years, which was the average, were also used, with the minimum value being the model default (Rodrigo et al., 2022).

2.4.2 Leaf longevity and leaf turnover

Secondly, the parameter for the leaf longevity was changed. The leaf longevity refers to the amount of time before a leaf is shed. When the leaf longevity is changed, the leaf turnover should also be adjusted. The leaf turnover value refers to the fraction of leaves that are shed each year. The turnover can be calculated using the following equation.

$$\text{Leaf turnover} = \frac{1}{\text{Leaf longevity}}$$

Where leaf longevity is the duration of one leaf on the tree in years. For a leaf longevity of 7 years, the turn-over would thus be roughly 0.14. Which means that each year 14% of the leaves are regenerated.

Changing the leaf longevity and turnover would impact the specific leaf area (SLA), which in turn affects the photosynthetically active radiation (FPAR) taken up by the plant. Furthermore, the tree height is impacted by an increase in leaf longevity. When SLA (cm^2 g^{-1}) decreases, tree height will increase as they have an inverse relationship in LPJ-GUESS (Smith et al., 2014). Prolonging the leaf longevity will thus possibly reduce the carbon storage and increase the tree height.

This parameter was only changed for the pine trees (PFT=BINE), because it was found that the model overestimates carbon storage in this tree type the most. Scots pine (*Pinus sylvestris*) is the most common type of pine in Swedish primary forests, leaf longevity values for this species were thus used (Linder & Ostlund, 1998). The default leaf longevity for pine was 3 years in the model and was used as the minimum value for the parameter. Jankoski et al. (2017) found a leaf longevity of 3-7 years for Scots pine from the South to the North of Sweden. 7 years was therefore chosen as the maximum value and 5 as the intermediate one. 6 years was further used as an intermediate value, because so many forests were located in the north.

2.4.3 Respiration coefficient

Thirdly, the value for the respiration coefficient for boreal vegetation was changed. The respiration is deducted from the gross primary productivity (GPP) to compute the net primary productivity (NPP) (Smith et al., 2014). Increasing the respiration might thus decrease the amount of carbon stored within vegetation by reducing growth.

The respiration coefficient was originally set at 1 g-C $g\text{-}N^{-1}$ day^{-1} $°C^{-1}$ for boreal and temperate vegetation. According to Van Dijk & Dolman (2004) a maximum value of 2.5 g-C $g\text{-}N^{-1}$ day^{-1} $°C^{-1}$ could be used for the respiration rate, with values more commonly ranging between 1 g-C $g\text{-}N^{-1}$ day^{-1} $°C^{-1}$ and 2 g-C $g\text{-}N^{-1}$ day^{-1} $°C^{-1}$. A minimum of 1 g-C $g\text{-}N^{-1}$ day^{-1} $°C^{-1}$, intermediate values of 1.5 and 2 g-C $g\text{-}N^{-1}$ day^{-1} $°C^{-1}$ and a maximum value of 2.5 g-C $g\text{-}N^{-1}$ day^{-1} $°C^{-1}$ were thus used.

2.4.4 Bole height ratio

Lastly, the bole height ratio was adjusted. The bole height ratio refers to the fraction of the stem that is branchless. Originally, the bole height ratio was decided based on the PFT specific minimum photosynthetically active radiation. However, this value could now manually be adjusted. Increasing the bole height ratio would decrease the number of branches and therefore decrease vegetation carbon storage.

A value of 0 was used for the minimum, because this would use the original way to calculate the bole height ratio. Some manually put in values were also used. An absolute maximum of 0.5 was used and intermediate values 0.1 and 0.25 were also used.

2.5 Evaluation of naturalness influence on model fit

The definition of primary forests can be quite broad, including many degrees of naturalness. According to the Buchwald scale, values above 5 are considered primary forest. But the scale goes all the way up to 10 (Buchwald, 2005). Therefore there is a broad range of what forests are considered primary forests. It was thus evaluated how the degree of naturalness impacts the model accuracy.

For this, the NFI data was used, because this data contained many data points with a high variance in naturalness. The naturalness could be incorporated into the model by changing the input coordinates to only include forests with certain values on the Buchwald scale. The model was run using data on each Buchwald value over 5 that was available. The percentage that the model differs from the field data was then computed by calculating the difference between the observed and simulated vegetation carbon storage and then dividing it by the observed value. This was multiplied with 100% to give the percentage difference.

2.6 Evaluation of forest structure

Different aspects of the structure of primary forests were evaluated to see where the model performed well and where the model had difficulties in accurately simulating primary forests. Furthermore, the model optimization could be better evaluated with these factors.

2.6.1 The tallest tree

The size of the modelled trees was evaluated as an indicator of stand structure. To evaluate how well the model estimates the tall trees present in primary forests, the maximum tree height was calculated in two different ways. Firstly, the absolute maximum value over all patches and samples for each forest were used. This was compared with the maximum tree height over all samples that was found for each forest in the field.

Secondly, the meanvalue of the maximum tree height for all patches in the model and samples in the field were used. Because the model had more patches the chances of getting a tall tree were higher, this way the odds were more equal. The average maximum tree height for the field data was then plotted against the average maximum simulated tree height.

2.6.2 Tree density (>5 cm)

The tree density of the simulated forests was compared with the field data. For this, trees with a diameter over 5 cm were used, as was done in the field data. The density was then calculated by dividing the number of trees by the patch or sample area and then averaging this per forest. The field density was then plotted against the simulated density.

2.6.3 Individual tree species carbon storage

The amount of carbon stored per tree species in the model simulations was also evaluated. The different PFTs present in the study areas are shown in *Table 1*. For these tree types, the average carbon stored per m^2 was calculated. Since there was a low amount of broadleaf trees present (PFTs= IBS and TeBS) the carbon storage in these tree types were combined. For the field data, the sampling sites were averaged for each forest. These values were then compared with the model output.

2.7 Statistical analysis

The model output and the field data were compared using a regression analysis. The modelled values for the most recent year (2015) were plotted against the field data for the corresponding forest. A trendline was computed and the RMSE and R^2 were calculated. The RMSE showed the difference between the observed data and the modelled date and the R^2 indicated how well the model represents the variability between primary forests in terms of vegetation carbon storage. A 1:1 line was also computed as this showed the ideal model fit. Average values for all forests were also plotted.

2.8 Model optimization

The results of the one-at-a-time approach were evaluated based on their influence on the R^2 and RMSE values for the regression of the modelled vegetation carbon and the observed vegetation carbon. Based on these values, the 2 best parameters were selected and used in the model optimization, where all combinations were used for a model run. During this selection, the parameter values that gave the highest R^2 values amongst the lowest RMSE values were chosen. This resulted in the following combinations for model runs as seen in *Table 2*. For each run, the R^2 and RMSE were also computed, to evaluate which combination of parameters gives the highest model accuracy.

Table 2. The different combinations of parameters for the model optimization attempts

	Bole 0.1	**Bole 0.25**	**DI 100**	**DI 143**	**LL 5**	**LL 7**	**R 1**	**R 1.5**
Run 1	x		x		x		x	
Run 2	x			x	x		x	
Run 3	x		x			x	x	
Run 4	x			x		x	x	
Run 5		x	x		x		x	
Run 6		x		x	x		x	
Run 7		x	x			x	x	
Run 8		x		x		x	x	
Run 9	x		x		x			x
Run 10	x			x	x			x
Run 11	x		x			x		x
Run 12	x			x		x		x
Run 13		x	x		x			x
Run 14		x		x	x			x
Run 15		x	x			x		x
Run 16		x		x		x		x

Where Bole is the bole height ratio, DI is the disturbance interval in years, LL is the leaf longevity in years and R is the respiration rate in g-C^{-1} g-N^{-1} day^{-1} °C^{-1}.

Note: The default run used a bole height ratio of 0, disturbance interval of 100 years, leaf longevity of 3 years and a respiration coefficient of 1 g-C^{-1} g-N^{-1} day^{-1} °C^{-1}.

2.9 Optimized model evaluation

The optimized model was chosen based on the highest R^2 amongst the lowest RMSE values. The results from this optimization were further evaluated using the same methods as described under *2.6 Evaluation of forest structure*. The outcomes were then compared with the forest structure of the default model run.

2.10 Optimized model with NFI data

The optimized model was further used to evaluate how well the combination of parameters worked on a different dataset. For this, the default and optimized model were run with the NFI data. The R^2 and RMSE were also computed to evaluate the impact of the optimization.

3 Results

In this section, the results from the above described in section *2 Methodology* will be presented and described.

3.1 Default simulation evaluation

The results from the default simulation, see ***Error! Reference source not found.***, showed that overall the model overestimates vegetation carbon storage. The average modelled vegetation carbon was 9.64 kg m^{-2}, whereas the average observed carbon was 8.52 kg m^{-2}. The values of the different forests were grouped together with only one clear outlier at observed: 15.7 kg m^{-2} and simulated carbon: 9.2 kg m^{-2}. This was one of the two more southern forests and had the highest observed vegetation carbon. This high carbon storage was clearly underestimated by the model. Overall, the data had a horizontal trendline and thus a low R^2. The value for the RMSE was moderate.

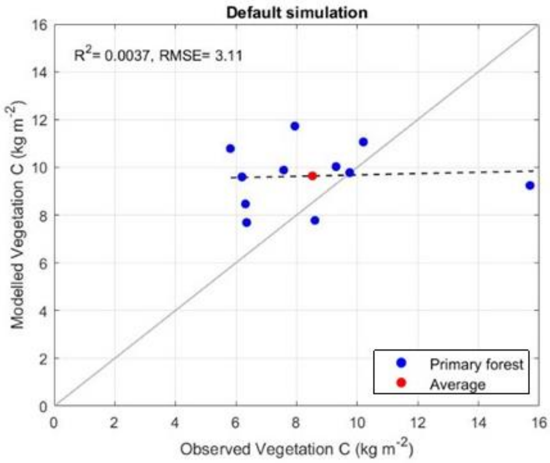


Figure 5. Results from the default simulation. Showing both the 11 primary forests and the average over all forests, as well as the trend.

3.1.1 Bootstrapped field data

The effect of the bootstrap on the average vegetation carbon for each forest was small, see *Table 3*.The bootstrap eliminated the difference in sample number for the field data, with each forest now having 100 samples. The bootstrap further gave insight into the confidence of the used means. The 95% confidence interval for all used bootstrapped means can also be found in Table 3, the average deviation from the mean was around 2 kg m^{-2}. This deviation was small enough that an overall estimation of the field data was 95% certain as seen in *Figure 6*. A high underestimation of the southernmost forest was also certain.

Table 3. Results from the bootstrap on the mean vegetation carbon storage in primary forests field data

Forest number	Mean (kg m^{-2})	Number of resamples	Bootstrapped mean (kg m^{-2})	95% Confidence interval of bootstrapped mean (kg m^{-2})
1	8.55	100	8.61	(6.11, 11.03)
2	6.26	100	6.31	(4.70, 7.90)
3	6.07	100	6.2	(4.87, 7.65)
4	5.81	100	5.82	(4.57, 7.39)
5	9.31	100	9.3	(7.65, 11.86)
6	9.79	100	9.75	(8.55, 11.24)
7	7.53	100	7.57	(6.49, 8.55)
8	6.26	100	6.35	(5.31, 7.71)
9	10.23	100	10.2	(7.64, 13.76)
10	15.68	100	15.7	(11.96, 19.56)
11	7.81	100	7.94	(5.87, 10.13)

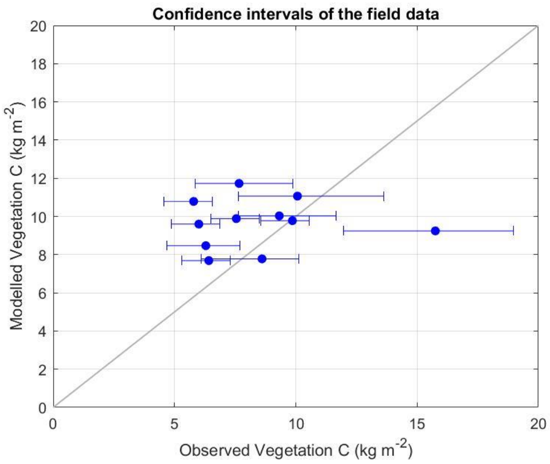


Figure 6: Figure showing the confidence interval of the used means for the primary forests plotted against the modelled vegetation carbon.

3.1.2 Primary forest structure evaluation

LPJ-GUESS systematically underestimated the average maximum tree height, see *Figure 7A*. Although, there was one outlier where vegetation carbon was overestimated, at observed: 21.8mand simulated: 26.6m, which was the most Southern forest. When the overall maximum tree height was considered on the other hand, the model actually overestimated the maximum tree height, see *Figure 7B*. Both figures showed a relatively small spread in the data with a trendline that was almost parallel to the 1:1 line. This relatively good relationship was also reflected in the high R^2 values.

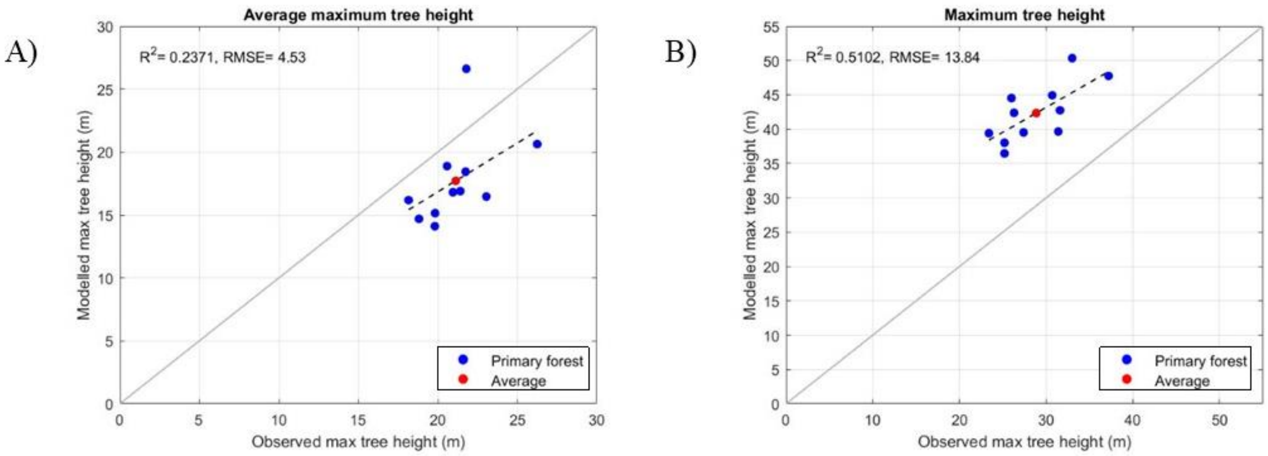


Figure 7. Figures showing the observed and simulated maximum tree height for primary forests. Figure A shows the average maximum tree height and figure B the overall maximum tree height. The modelled values were based on the default settings.

The density of trees over 5 cm in diameter was underestimated by the model, see *Figure 8*. Of which, the most dense forests were the most underestimated. The statistics here showed a moderate to good trend with an R^2 of 0.29. The RMSE showed a moderate spread in the data, with an average difference between the observed and modelled data of 306 trees ha^{-2}.

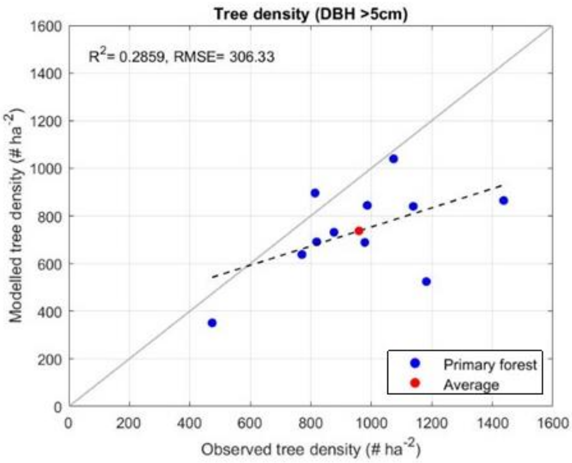


Figure 8. The tree density of the 11 primary forests. The modelled values were based on the default settings.

Vegetation carbon storage in spruce trees, the most common tree species according to the field data, was both under- and overestimated by the model, see *Figure 9A*. In forests with higher amounts of carbon in spruce trees (>4 kg m^{-2}) the carbon storage in spruce was underestimated, whereas in forests with lower carbon storage in spruce trees, the storage was overestimated. This resulted in a near horizontal trend in the data. The R^2 value was close to 0, but the spread of the data was low, which was reflected in the RMSE.

For pine trees, there was a general overestimation in vegetation carbon storage, see *Figure 9B*. This was further reflected in the average over all forests. Also for this tree type there was a near horizontal trend in the data. There was a large spread between the data on carbon storage for pine trees, which is reflected in the high RMSE value. The R^2 was again close to 0.

Generally, broadleaf trees stored little carbon in the field data, see *Figure 9C*. LPJ-GUESS also simulated low values for vegetation carbon storage, but underestimated values above 0.5 kg m^{-2}. One value was hugely overestimated by the model, the observed value was 0 kg m^{-2} whilst the simulated value was 8.1 kg m^{-2}. This was the average vegetation carbon storage of the most southern primary forest. This one outlier had a massive impact on the average and trendline, leading to a R^2 close to 0 and a high RMSE of 2.59 kg m^{-2}.

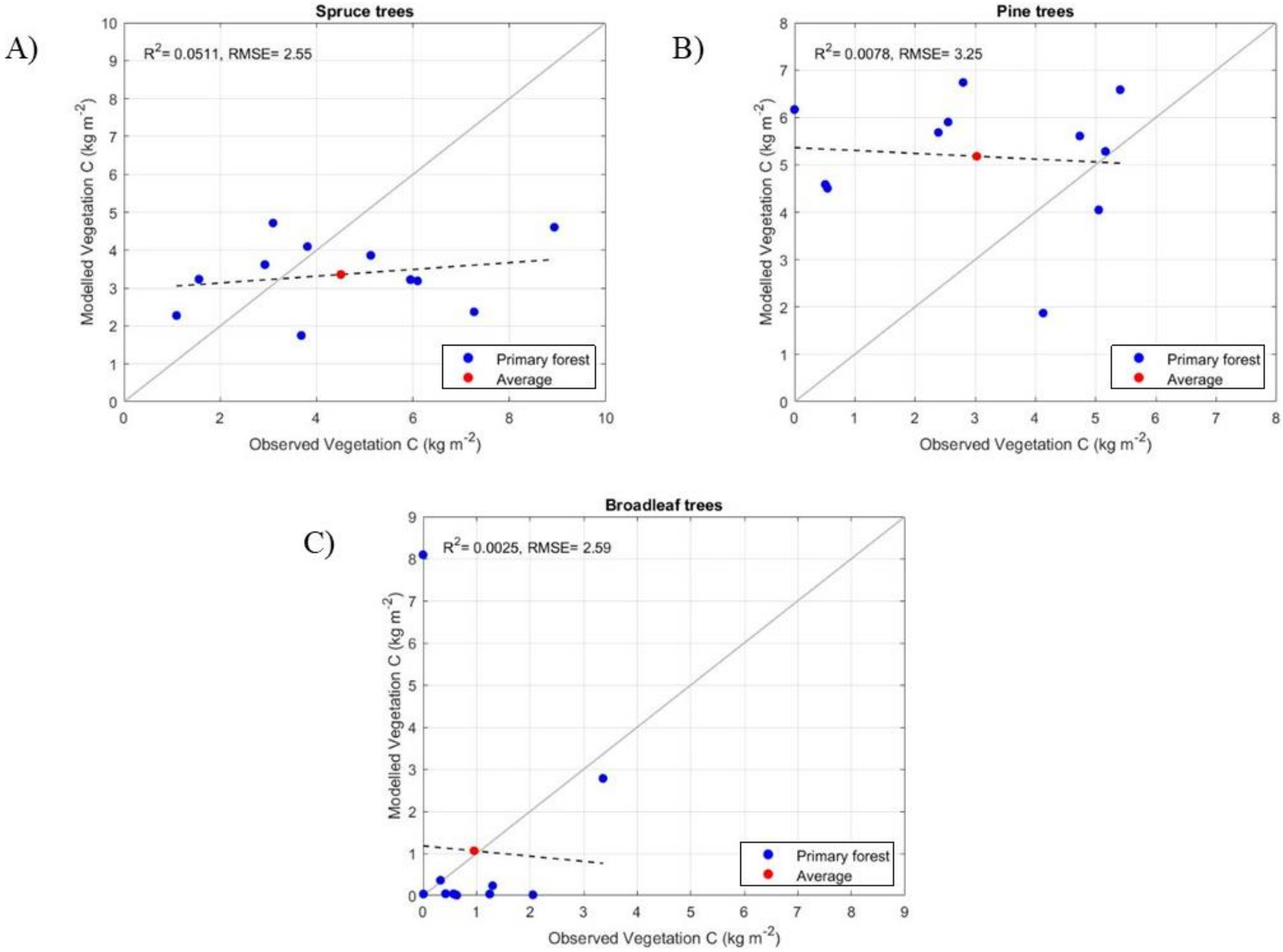


Figure 9. The Vegetation carbon storage of the 11 primary forests for the three different tree types present, compared with the modelled values. In figure A the storage in spruce trees is shown, in figure B the storage in pine trees and in figure C the storage in broadleaf trees.

3.2 Influence of naturalness

The results for vegetation carbon storage of forests with different levels of naturalness showed that the model estimated vegetation carbon storage better for forests with a higher level of naturalness, see *Figure 10*. Forests with a naturalness value of 9 were an exception, because here an increase in the overestimation of carbon storage in comparison with forests with the naturalness value 8 could be observed. The model performed the best for a Buchwald value of 8 and the worst for a Buchwald value of 6. Overall, the model tended to overestimate the vegetation carbon storage with overestimations up to 84% over the observed value.

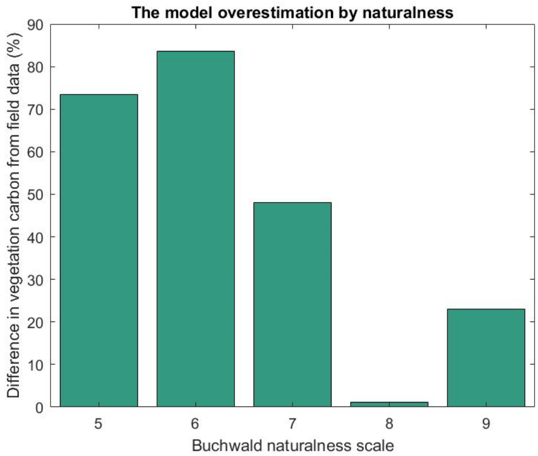


Figure 10. Bar chart showing the percentage difference between the simulated data and the observed data for vegetation carbon storage for each naturalness value with available data on the Buchwald (B) scale that falls under the term primary forest. The overestimation of B=5 was based on 14 observations, B=6 on 19, B=7 on 20, B=8 on 16 and B=9 on 6 observations.

3.3 Parameter adjustments

The parameter adjustments showed that the investigated parameters could improve the model accuracy both when it came to the R^2 and RMSE (*Table 4*). Most chosen values (coloured in green) were neighbouring, leaf longevity for pine was an exception. A leaf longevity of 6 years, had a worse influence on the R^2 and RMSE than a leaf longevity of 5 or 7 years.

Table 4. The adjusted parameters and their influence on the R2 and RMSE values for Veg C.

	Values	R^2	RMSE (kg m^{-2})
Bole height ratio	0	0.0037	3.11
	0.1	0.1934	2.8
	0.25	0.3294	2.93
	0.5	0.1126	3.01
Disturbance interval (years)	100	0.0037	3.11
	143	0.1354	3.25
	200	0.1386	4.11
	300	0.0188	4.88
Leaf longevity Pine (years)	3	0.0037	3.11
	5	0.3373	2.21
	6	0.0172	2.94
	7	0.2417	2.5
Respiration (g C g N^{-1} day^{-1} °C^{-1})	1	0.0037	3.11
	1.5	0.0266	2.99
	2	0.3095	3.39
	2.5	0.2224	4.51

In green: the chosen values for the parameters.

3.4 Model optimization

The optimization of the model, as done according to the section *2.8 Model optimization*, shows that the chosen parameters could improve the model accuracy, see *Table 5*. The highest improvement was achieved with Run 8, where the R^2 was found to be 0.3928 and the RMSE 2.26 kg m^{-2}, which was a vast improvement from the default simulation which had a R^2 of 0.0037 and a RMSE of 3.11 kg m^{-2}. Thereby, the spread and the percentages of forests that could be explained by the model improved with the optimization.

Overall, all model runs except for run 6 and 13 contributed positively. Several model runs even gave almost as good an impact on the R^2 and RMSE as Run 8, namely Run 3 and Run 7 were really close in values. The results of all these optimized runs show there are two parameter values which gave good results, the leaf longevity of pine of 7 years and a respiration value of 1 g C g N^{-1} day^{-1} $°C^{-1}$. Additionally changing the disturbance interval to 143 or the bole height ratio to 0.25 gave the best model results.

Table 5. The statistical results from the different model optimization attempts

	R2	RMSE
Run 1	0.112	2.54
Run 2	0.0494	2.89
Run 3	0.3501	2.27
Run 4	0.1897	2.52
Run 5	0.0004	2.94
Run 6	0.0897	3.06
Run 7	0.3657	2.28
Run 8	0.3928	2.26
Run 9	0.0411	3.48
Run 10	0.1908	2.67
Run 11	0.2424	3.32
Run 12	0.3318	2.77
Run 13	0.1486	3.52
Run 14	0.0007	3.26
Run 15	0.1265	3.68
Run 16	0.1394	3.03

3.5 Optimized model evaluation

The optimized model results show that the average vegetation carbon storage has not changed significantly from the default simulation, see *Figure 11*. However, the trendline has improved, it is now much closer to the 1:1 line. Furthermore, the optimized model performed a lot better when estimating carbon storage for high storage forests. The R^2 and RMSE also improved significantly.

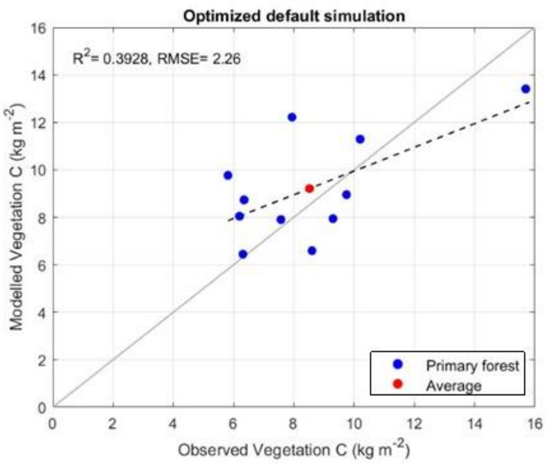


Figure 11. The simulated vegetation carbon storage of the optimized model compared with the field data.

The average maximum tree height improved greatly with the optimized model run, see *Figure 12A*. The average value is now situated on the 1:1 line, with a trendline close to the 1:1 line, but a bit steeper. The R^2 and RMSE have also improved compared to the default simulation.

The maximum tree height worsened compared to the default simulation, see *Figure 12B*. The trendline and model values are further overestimated. On top of that, the data spread and RMSE have increased, whilst the R^2 has decreased.

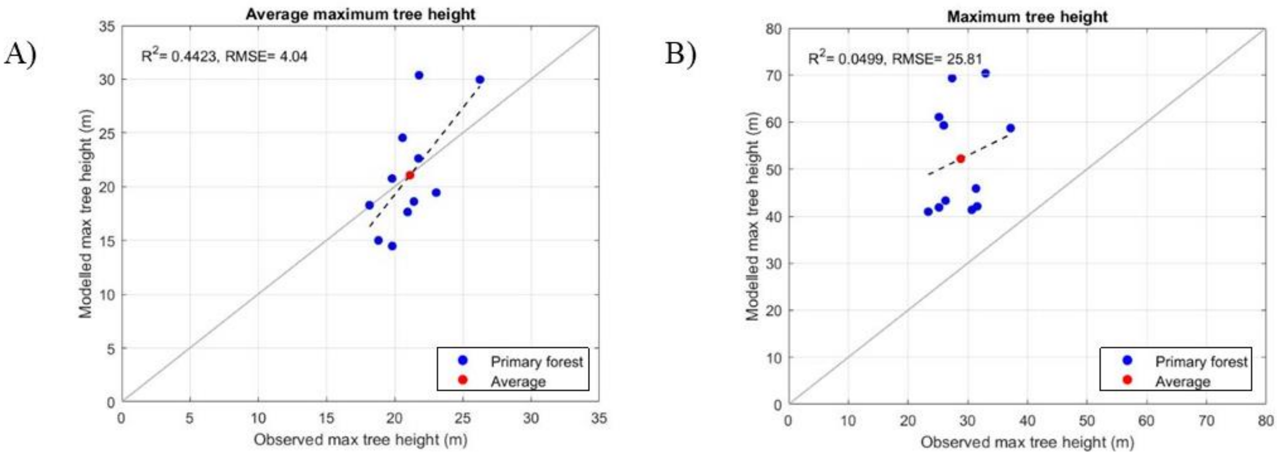


Figure 12. The average maximum tree height (A) and maximum tree height (B) based on the optimized model run, compared with the field data.

For the tree density, the results were mixed, see *Figure 13*. The average has improved a bit as has the trendline, which is now closer and more parallel to the 1:1 line. On the contrary, the R^2 has decreased and the data spread and RMSE have increased.

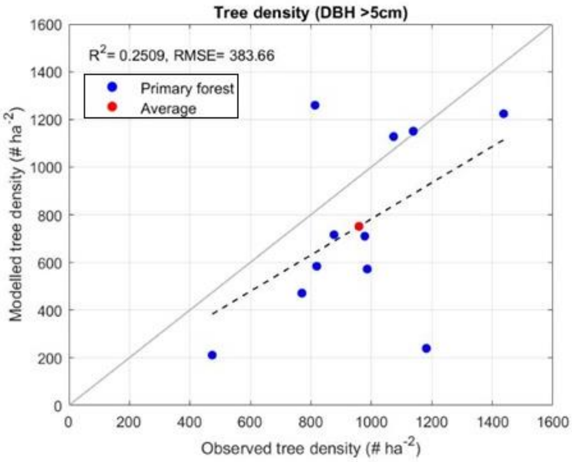


Figure 13. The tree density for the optimized model run. Only trees with a DBH over 5 cm were included.

For spruce trees, the trendline improved compared to the default simulation, as well as the previous underestimation for high carbon storage, see *Figure 14A*. Although, the model now overestimated almost all forests and the average model value was a lot higher. The R^2 improved, but the RMSE increased.

For pine trees, the model is now instead of overestimating, underestimating the carbon storage, see *Figure 14B*. The trendline is less horizontal, but instead of positive, it is negative. The R^2 improved moderately, as did the RMSE.

There were little visible changes for broad leaf trees, except for the fact that the one outlier decreased slightly in value, see *Figure 14C*. Thus resulting in a lower RMSE.

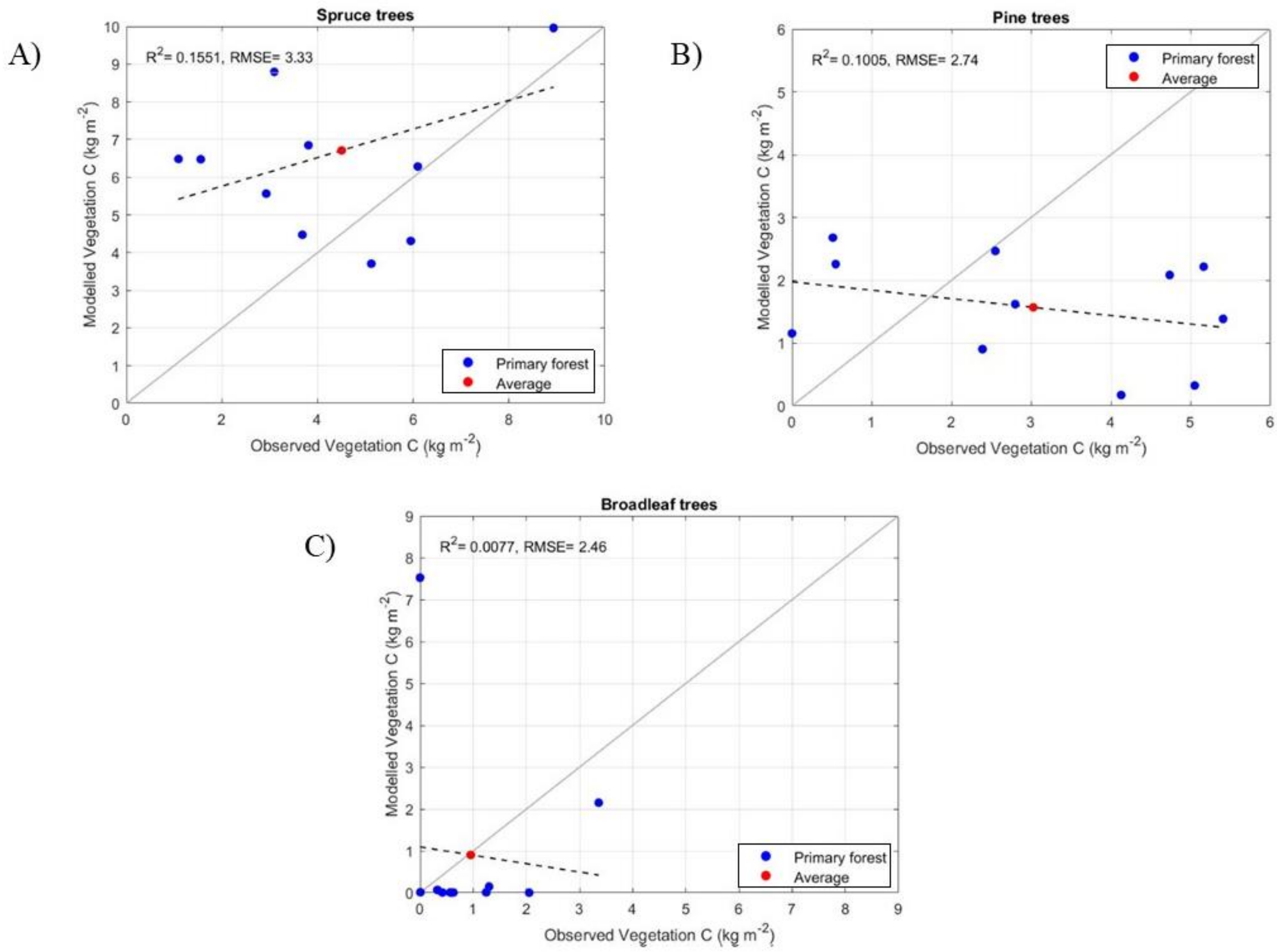


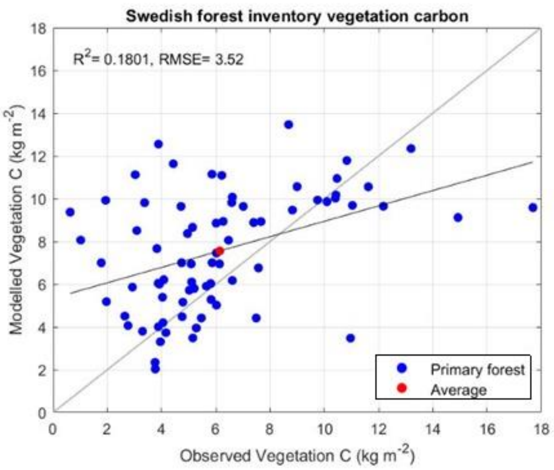
Figure 14. The Vegetation carbon storage of the 11 primary forests for the three different tree types present, compared with the optimized modelled values. In figure) the storage in spruce trees is shown, in figure B the storage in pine trees and in figure C the storage in broadleaf trees.

3.6 Optimized model and NFI data

The default model simulation for the Swedish forest inventory data gave a relatively good result, see *Figure 15A*. The data was relatively close to the 1:1 line and the R^2 was better than the R^2 for the data from the primary forests. The model did have a hard time with the higher field vegetation carbon (>11 kg m^{-2}). Overall, the model also overestimated vegetation carbon storage for this dataset.

The optimized model did not show improvements for the Swedish forest inventory data, see *FigureB*. The average and trendline were very similar to the default simulation. The R^2 was also very similar, but the RMSE increased.

A)



B)

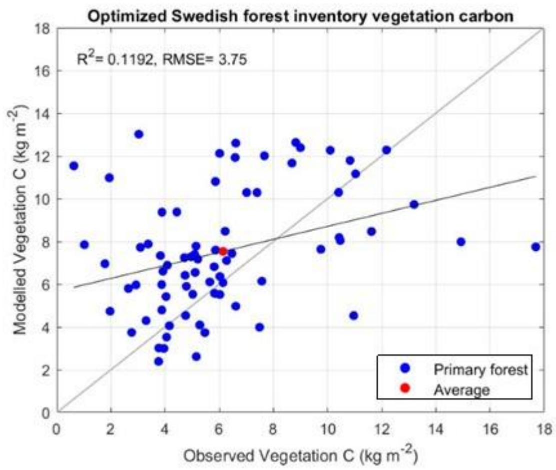


Figure 15. The vegetation carbon storage of the NFI field data compared with the model simulation. In figure A, the default simulation is shown, whilst in figure B the optimized model results are shown.

4 Discussion

In the following section, the results will be discussed. The uncertainties within the field data and model will also be discussed, as well as suggestions for future studies.

4.1 Evaluation of the default simulation

The default simulation showed a good estimation of vegetation carbon storage by the model. However, the statistics, mainly the R^2, did not reflect this. This was mainly because of a high underestimation of high carbon storage by the model, thus leading to a horizontal trendline. It can be concluded that the model had a harder time simulating a highly productive primary forest and performed better for a moderate carbon storage.

Results for the investigation into the confidence interval of the used means showed that there is 95% likelihood that the used means are within 2 kg m^{-2} of the used values. Looking at the results for the default simulation, it was found that despite this uncertainty, the model still overestimated vegetation carbon storage in primary forests. Furthermore, the highly underestimated southern forest was with a 95% confidence underestimated.

The overall overestimation that can be seen in the default simulation can be explained by the fact that LPJ-Guess was found to have many thin trees. In the model data there were on average 1876 trees with a diameter below 0.05 m per hectare. Some of these thin trees were the result of disturbances, but the majority was not, as the rest of the patch contained old trees and the thin trees were present in almost all patches. This is unrealistic as primary forests are far into the development stage and new trees rarely occur, except after disturbances (Linder & Ostlund, 1998). These trees still contribute to the carbon storage and might thus help explain why LPJ-Guess overestimates carbon storage for primary forests in Sweden. The model thus simulates trees way too thin, making the vegetation carbon storage higher than it would be in reality.

Another factor that might help explain the model overestimation is the fact that grass is also included in vegetation carbon storage, whereas this was not included in the field data. This is however only 0.037 kg m^{-2} and will have much less of an influence on the carbon storage than the presence of 1876 thin trees per hectare.

It was found that on average the model simulated smaller trees than what was found in the field data. A similar result was found by Smith et al. (2014) when looking at average tree height for needle leaf trees. Unlike the average maximum tree height, the maximum tree height was overestimated by the model. This overestimation could be simply explained by the difference in patch size and amount between the model data which had a patch size of 0.1 ha and consisted of 50 patches and the field data which had a patch size of 0.0154 ha and consisted of 15 to 26 patches, which made the likelihood of having taller trees much higher for the model.

Furthermore, the density showed a good agreement between the model and field observations. This is in agreement with Smith et al. (2014) who found that the model accurately captures mean forest density in needle leaved forests. In the forest density calculations, the thin trees were excluded, which could mean that without these thin trees LPJ-GUESS might simulate values closer to the field data.

For the different tree types, the model showed a similar storage for all forests. This was mainly seen in the almost horizontal trendline for all species. This was remarkable because the forests were spread all over Sweden. As a result, a difference between north and south was to be expected.

The differences found between the model and field data might have been more pronounced if data with a different naturalness was used for the primary forests field data. The investigation into the model accuracy for different naturalness showed that the model performs better for higher naturalness, which the used field data had (B=7 or 8). Although, a higher overestimation for forests with a naturalness value of 9 was found, thus breaking the trend. This is to be expected as these forests are often situated up in the mountains and thus have a low productivity and carbon storage. But, the estimated value for this naturalness class is also the most uncertain. To accurately estimate the overestimation for this class, further observations would be needed. The high overestimation for low naturalness forests is indicative of human influence and can thus point towards logging activities in the past, resulting in a lower carbon stock. The observed trend is indicative that perhaps the model has almost no bias for completely natural forests.

4.2 Adjusted parameters

For all chosen parameters, parameter changes gave better results when comparing observed and simulated vegetation carbon storage than the default. All of the used parameters thus seem to play a role in improving the estimations for the carbon storage of these boreal primary forests. Some parameters improved the model accuracy a lot more than others, mainly the leaf longevity and bole height ratio played important roles. Changing the respiration did not seem to have a large effect when combined with other parameters and could thus be disregarded in further studies.

Changing the disturbance interval did not help reduce the overestimation by the model, but instead increased it. However, a larger disturbance interval than 100 years still gave better results when it came to data trend. It might be more realistic to increase the disturbance interval for primary forests, as resulted from field data by (Rodrigo et al., 2022), despite the model overestimation.

The adjusted parameters showed some interesting results. The needle longevity for pine had good results for 5 and 7 years, but worse results for 6 years. This could be attributed to the location of the forests. As stated by Jankowski et al. (2017) the leaf longevity varies along the latitude of Sweden from 3 years in the South to 7 years in the North. It could thus be speculated that the latitude of the forests played a role in the worse results for 6 years. This seems relatively unlikely as the spread of the forests is quite uniform. However, the best way to represent the leaf longevity all over Sweden, might be to vary the needle longevity parameter north to south as suggested by Reich et al. (2014) and Jankowski et al. (2017). Furthermore, parameters for the respiration rate and disturbance interval were found to have a higher R2 when increased, but also a higher RMSE. Consequently, the trendline would improve, but estimations would be further from the field data. Higher respiration or disturbance interval values were thus not used in the model optimization.

It was also found that changing these parameters adjusted the tree type composition. Similar results were found by Wramneby et al. (2008), where a shift in competitive balance was found when parameters were adjusted. The main influence on the shift in this study is assumed to be the leaf longevity for pine, as this impacted the pine trees, giving less storage in this tree type and thus more competition from the other tree types.

4.3 Evaluation of the optimized model

The best model results were found when the bole height ratio was adjusted to 0.25, the disturbance interval to 143 years and the leaf longevity to 7 years. The model optimization runs showed that it was overall best to keep the respiration at 1 g C g N^{-1} day^{-1} $°C^{-1}$, as was the default in the model. Except for this parameter all other parameters could be varied and give good results. The resulting best R^2 value of 0.3928 showed that LPJ-GUESS can explain about 40% of the variance within the field data. Similar statistical values were found by Lindeskog et al. (2021) when evaluating vegetation carbon storage in managed forests. The model could thus estimate vegetation carbon storage well, with a few small adjustments.

However, the optimization did not give improvement for all investigated forest structural parameters. The accuracy of the model predictions for maximum tree height decreased and the carbon storage in spruce was more overestimated on average. However, the average maximum tree height did give a better estimation after the optimization. This is remarkable because the model was not optimized for this parameter. This result suggests that the model represents primary forests better after optimization when it comes to certain structural parameters. The choice of changing the suggested parameters thus depends on what parameters are of interest.

The NFI data did not experience the same improvements seen in the primary forest data. The default simulation performed better statistically than the default simulation for the primary forests field data. However, it could not be improved using the same parameters. This could be explained by the differences between the two field datasets. Mainly that the NFI field data had less samples per forests, sometimes only one or two, and the used vegetation carbon storage values therefore had more uncertainties.

4.4 Uncertainties in the field data

The field data that was used brought several uncertainties.

Firstly, the number of forests was relatively low, not all types of primary forests present in Sweden might thus be represented. Furthermore, the way that the vegetation carbon is calculated can give some uncertainties. The used functions have been found to underestimate belowground biomass and the dataset that the Marklund function was based on also had a slightly higher wood density than is found nowadays (Petersson & Ståhl, 2006). However, the method is considered the standard in Sweden and has been found to accurately represent carbon storage in trees all over Sweden (Finér, 1989; Fridman et al., 2014).

The NFI field data used the same sampling strategy and biomass calculations as the primary forests field data, however it was not focused particularly on primary forests. Here, primary forests were only selected based on the Buchwald value. It is unknown how these values were determined in the field and their accuracy is thus unknown. Because of the sampling strategy used by the NFI, the amount of samples per forest can also differ vastly. Thus giving different levels of accuracy in forest averages.

4.5 Uncertainties within the model

Models are a simplification of reality and thus carry uncertainties. Firstly, the climate data brings large uncertainties. Findings presented by Wu et al. (2017) show that errors in climate datasets have a higher influence on model results than the model structure shortcomings or parameterizations.

Secondly, the model does not use data on current forests, but instead estimates what trees can grow in certain areas and based on that constructs a forest. This means that little input data is necessary, but also that results can deviate from the actual forest that is being modelled. This was reflected in the difficulty that LPJ-GUESS had when estimating different values for the southernmost forests. It simulated an underestimation of carbon storage, overestimations for average tree height and carbon storage in broadleaf trees. Overall, the model seems to have difficulty in predicting forests based on latitudinal differences.

4.6 Further studies

The model contained many parameters that are of influence on the vegetation carbon storage and that could thus also be investigated. Furthermore, soil carbon storage and dead wood carbon storage could be evaluated, which are important carbon stores in primary forests (Luyssaert et al., 2008). Furthermore, the results of this study can be used to investigate the impact of land use on carbon storage or to determine the carbon storage of individual primary forests.

5 Conclusion

It was found that the default set-up of LPJ-GUESS can estimate the vegetation carbon storage, but the trend in the data is off. There is also a general overestimation, which could be explained by an abundance of thin trees that were simulated in LPJ-GUESS, which should not be present in an actual primary forest. The model performed well for tree height and density, but has difficulties in the carbon storage per tree type. Particularly the carbon storage in pine trees was overestimated. The model also had difficulties with the north-south distribution in Sweden. Furthermore, the model was found to perform better for forests with a higher naturalness on the Buchwald scale. The investigated parameters, the disturbance interval, leaf longevity and turnover, respiration coefficient and bole height ratio, were all relevant for improving the model simulation of vegetation carbon storage in primary forests. For the used field data, a combination of the adjustment of the bole height ratio to 0.25, the disturbance interval to 143 years and the leaf longevity to 7 years resulted in the best simulation of vegetation carbon storage. This resulted into the model being able to explain 40% of the variation in the field data. The same result was however not achieved when a different dataset (NFI) was used, thus the adjustments of parameters might need to be evaluated per dataset. Overall, LPJ-GUESS could be used to relatively accurately estimate carbon storage in primary forests, with a few small adjustments giving an even better result. The results have both a general relevance to users of natural vegetation within LPJ-Guess, as well as a relevance to help further our understanding of the effect of land use on carbon storage.

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A Appendix – Justification of npatch (50)

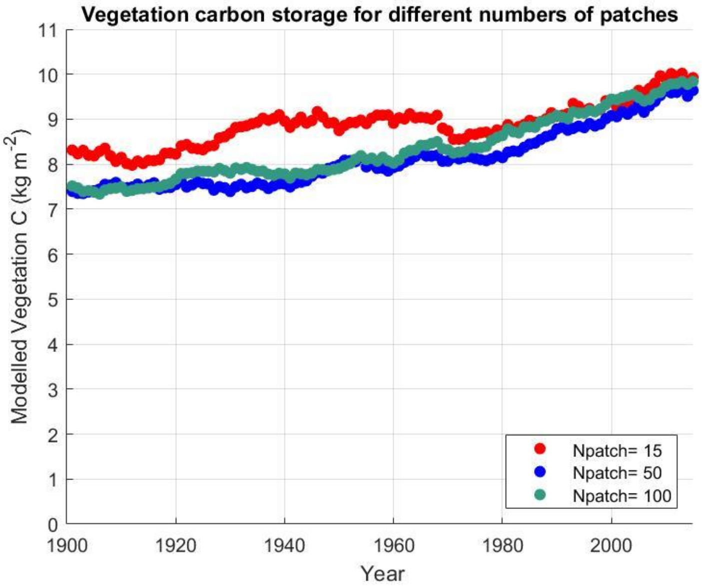

Figure A. Plot showing the vegetation carbon storage from 1900 to 2015 for different numbers of simulated patches (Npatch).