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**The impact of non-structural carbohydrate production on the forest
dynamics under climate change estimated by spatially explicit individual-based
global dynamic vegetation model**

(空間明示的個体ベース動的全球植生モデルを用いた気候変動下における
非構造的炭水化物の生産が森林構造に与える影響の将来予測)

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ABSTRACT

Forest dynamics need to be considered when estimating the global carbon budget. The alteration of forest structure and function under a changing climate and expanding human activity could lead to a reduction of forest canopy cover and a spread of lower-biomass ecosystems in warm and dry regions. A non-structural carbohydrate (NSC) acts as a storage buffer between carbon supplied by assimilation and carbon consumed by respiration, reproduction, and pests. Estimation of NSC concentrations in a tree is very important for accurate projection of future forest dynamics.

I developed a new NSC module for incorporation into a spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM) to validate the simulated NSC dynamics with observations. NSC pools were simulated in three plant organs: leaves, trunk, and roots. The seasonal dynamics of the NSCs varied among plant species, and the sizes of the NSC pools inferred from observations differed between the boreal, temperate, and tropical climates. The NSC models were therefore validated for each of the three climatic regions at both point and global scales to assess the performance of the models. The modeled NSCs showed good agreement in seasonality with the observed NSCs at four sites – Canada (boreal), Austria and Switzerland (temperate), and Panama (tropical) – and in mean values for three climate zones derived from the global NSC dataset.

I compared forest composition and biome type percentages in Asia, Europe, and North America under SSP scenarios between the new and previous models. In the new model, taller trees accumulate more NSCs, which slows their growth, resulting in lower mean tree height and DBH. Unlike the previous model, where taller trees dominated, the new model allows shorter trees to outcompete taller ones, creating a broader range of tree sizes, including more near-zero values. The new model also incorporates a carbon starvation mortality process.

When carbon starvation is "switched on," tree density decreases, favoring taller tree growth while shortening tree lifespans due to increased vulnerability of shorter trees. The SEIB-DGVM-NSC improves simulations of vegetation distribution, GPP, and forest composition caused by the changes in NSC dynamics at global scales. This research advances understanding of NSC dynamics and their role in the terrestrial carbon cycle, particularly under climate change

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Chapter 1. General Introduction

1 Carbon fluxes from terrestrial ecosystem

Global warming has been intensifying in recent decades due to the rapid increase in atmospheric CO₂ concentrations since the Industrial Revolution. Current climate models simulate that global temperatures could increase by 2°C to 4°C if countries fail to reduce greenhouse gas emissions (IPCC, 2021). This warming exacerbates the frequency and intensity of extreme weather events such as droughts, wildfires, and typhoons. Ultimately, global warming and the associated extreme weather events can severely affect ecosystems, agriculture, and human livelihoods. Hence, it is crucial to understand global carbon cycle on the earth system to estimate the impacts of global warming,

The global carbon cycle consists of three major reservoirs: the atmosphere, oceans, and terrestrial ecosystems. Carbon is intricately connected among these domains through highly complex biological and geochemical processes. Within the Earth system, carbon reservoirs are often referred to as "pools" or "stocks," while the movement of carbon between these reservoirs is described as "fluxes" (Bruhwiler et al., 2018). Among these, the terrestrial ecosystem plays a particularly critical role in the global carbon cycle, as it accounts for the largest carbon flux of the three domains.

The exchange of carbon between the atmosphere and the terrestrial biosphere occurs primarily through photosynthesis and respiration. Plants absorb atmospheric CO₂ through photosynthesis and utilize the carbon for growth and metabolism in leaves, roots, stems, and woody biomass. At the same time, plants release CO₂ back into the atmosphere via autotrophic respiration, while heterotrophic respiration and the decomposition of plant litter and soil organic matter also contribute to CO₂ emissions. Additionally, tree mortality caused

by natural disturbances, such as wildfires and insect outbreaks, further releases CO₂ into the atmosphere. These processes could accelerate the climate change more and more. Therefore, estimating and simulating where and global distribution of biomass is essential to understanding carbon flux from the terrestrial ecosystem.

2 Various techniques to estimate carbon flux

Remote sensing technique

Remote sensing is the process of observing and analyzing the physical properties of a region by detecting the reflected and emitted radiation from a distance. Satellite remote sensing has been commonly used to research the terrestrial carbon flux, enabling the observation of ecosystem carbon fluxes and stocks. Since satellite land surface observations became available in the 1970s, they have allowed researchers to quantify the magnitude, spatial patterns, interannual variability, and long-term trends of ecosystem carbon fluxes at regional to global scales (Lees et al., 2018). The use of diverse remote sensing data to analyze and quantify the carbon cycle continues to expand and evolve.

For example, remote sensing data can be used to calculate vegetation indices (VIs), which combine spectral bands sensitive to chlorophyll, leaf, and canopy structure to estimate canopy greenness. These indices reflect key attributes such as canopy structure, chlorophyll content, plant phenology, and leaf ontogeny, as observed from space (Xiao et al., 2019). Because plant productivity is closely linked to the phenological life cycle of plants, VIs can serve as the metrics of gross primary production (GPP), net primary production (NPP). Furthermore, solar-induced chlorophyll fluorescence (SIF) is a spectral emission associated with photosynthetic activity, generated by excited chlorophyll-a molecules in the photosystem reaction centers, within the 650 to 800 nm spectral range (Xiao et al., 2019). It

is monitored by satellites such as the Greenhouse Gases Observing Satellite (GOSAT). Since SIF originates at the core of the photosynthetic processes, it is hypothesized to be a more reliable proxy for GPP than other biophysical parameters or VIs.

Eddy covariance flux measurement

Eddy covariance (EC) flux measurement is the widely utilized approach to quantify the fluxes of sensible heat, latent heat, and CO₂ between the land surface and the atmospheric boundary layer. The remote sensing data products include uncertainties due to factors such as scattering, ozone, aerosols, and cloud cover. To address these uncertainties, carbon flux estimates derived from remote sensing are often validated and calibrated using in-situ measurements of carbon fluxes obtained through EC flux measurements. These measurements provide critical insights into how plants physiologically respond to climate change at the site scale. Additionally, EC-derived flux datasets are widely used to evaluate or calibrate carbon fluxes estimated from remote sensing approaches.

Networks of EC flux measurements (e.g., AmeriFlux, EuroFlux, and AsiaFlux) have continued to grow, collectively building a significant repository of carbon flux data. Despite their importance, EC flux measurements have certain limitations. One key disadvantage is that the EC footprint covers a relatively small area compared to entire terrestrial ecosystems. Furthermore, most EC towers are located in northern temperate ecosystems, with relatively few installed in regions like the Amazon and other tropical systems (Zhu et al., 2023). This uneven distribution is partly due to the high costs associated with equipment and maintenance of EC towers (Baldocchi et al., 2003). Given their limited spatial coverage, it is essential to combine EC flux data with remote sensing data to upscale flux observations to larger regions.

Process-based ecosystem model

Process-based ecosystem models are different approaches from other approaches in their use of mechanistic methods to simulate carbon, water, and energy fluxes from terrestrial ecosystems. These models simplify complex ecosystem processes, providing insights into the current status of terrestrial ecosystems and their dynamic changes in mechanistic ways. By simulating these processes, the models help elucidate the roles of individual processes and their interactions within the ecosystem.

One key advantage of process-based models is their ability to quantify terrestrial ecosystem processes mechanistically, allowing for the simulation of global carbon stock distributions even in regions that are difficult to access. Additionally, these models can predict long-term future trends that remote sensing cannot directly observe, such as unmeasured tree responses to climate change. The process-based model has a potential to understand the intricate and long-term effects of climate change on terrestrial ecosystems.

Process-based ecosystem models can also be coupled with climate and ocean model enabling a clearer understanding of the global carbon cycle's interactions between terrestrial ecosystems, oceans, and the climate system. This integration is pivotal for developing comprehensive Earth system models that can estimate greenhouse gas emissions both in the present and for future scenarios.

To ensure accuracy, these models are validated using benchmarks such as remote sensing data and EC flux measurements. These benchmarks provide critical information on vegetation types, growth status, and environmental conditions, offering fundamental knowledge of global carbon cycling. Integrating process-based ecosystem models with observational data enhance our ability to comprehend, predict, and address the complexities of Earth's carbon dynamics.

3 Non-structural carbohydrates

The non-structural carbohydrates (NSCs) is comprised of starch and sugars, which are mobilized mainly for growth and metabolism when sink strength exceeds source activity (Gough et al., 2010; Richardson et al., 2013; Chuste et al., 2020; Herrera-Ramírez et al., 2020). During photosynthesis, freshly assimilated carbon is transported as triose phosphate from the chloroplast to the cytosol, where sucrose is synthesized from it. Some of the sucrose is then changed into starch in the chloroplast, and the starch is consumed to maintain growth and metabolism at times when recently assimilated carbon is not available to the plants (Dietze et al., 2014). Plants that seasonally shed leaves need to rely on stored carbon for maintenance during the leafless season. NSCs play an important role as substrates for the synthesis of compounds in plants and as energy sources for metabolic activities (Hartmann et al., 2018). Moreover, NSCs include key compounds that are used to buffer physiological stress when energy from photosynthesis does not satisfy metabolic demands (Gough et al., 2010; Sala et al., 2012) because carbohydrates such as starch can be easily mobilized and reallocated (Hartmann et al., 2018).

The NSCs are closely linked to tree mortality induced by climate change. As the frequency, duration, and severity of droughts are expected to increase globally, the damage to plants through rising temperatures, water vapor pressure deficit, and associated water loss will also increase (IPCC, 2014; Sevanto and Dickman, 2015). Trees can be killed directly by drought, i.e., vial desiccation, or indirectly by associated increases in insect or pathogen attacks. Indirect effects that cause tree mortality include girdling by bark beetles and defoliation events. According to multiple observational and experimental studies, the resulting imbalance between NSC demand and supply leads to carbon starvation, which is one of the mechanisms that contribute to drought-induced mortality (McDowell, 2011). Additionally, NSCs are vital for synthesizing defense compounds that protect against insect attacks. The frequency and

severity of this direct and indirect biotic disturbance from insects and insect– pathogen complexes have been increasing (McDowell et al., 2020; Seidl et al., 2017).

4 Objectives and composition of this thesis

To understand the distribution of and the future trend of these tree mortality, a process-based model is essential. Although an imbalance of the NSC pool could mechanistically trigger plant mortality, few ecological models predict tree mortality resulting from the role of NSC associated with climate change (Adams et al., 2013; McDowell, 2011). This is because there are very few models capable of simulating NSC dynamics. The aims of this study are to develop a new module to calculate the NSC accumulation process based on ground measurements in a process-based model and to simulate the effect of tree mortality induced by NSC depletion on forest composition under future climate change scenarios.

Chapter 2 focuses on the description of the new model, which is capable of calculating NSC dynamics. This chapter explains the process-based model used, the development of the new NSC compartment based on observed NSC data, the validation methods employed, and the validation results at both point and global scales. Chapter 3 examines the differences in forest composition under increasing CO₂ levels between the new model and the previous model across Asia, Europe, and North America, as well as the effects of tree mortality caused by NSC depletion using the new model. Chapter 4 summarizes the main findings of this research, discusses its limitations, and outlines prospects for future studies.

Chapter 2. Modeling of non-structural carbohydrate dynamics by the spatially explicit individual-based dynamic global vegetation model SEIB-DGVM (SEIB-DGVM-NSC version 1.0)

1 Introduction

Permanent shifts in forest vegetation dynamics have already been observed and are expected to accelerate under future changes in climate globally (McDowell et al., 2020). Forest dynamics are changing due to anthropogenic drivers, such as rising temperatures and CO₂ partial pressures, and are affected by transient disturbances such as wildfires, droughts, biotic attacks, and land-use changes. The dependence of tree recruitment and growth on anthropogenic drivers and transient disturbances could lead to an increase in tree mortality rates in warm and dry regions (Stevens-Rumann et al., 2018; Xu et al., 2017). These changes will cause forests to become shorter and younger. The result will be a net reduction of forest canopy cover and a shift toward low-biomass ecosystems. Furthermore, higher tree mortality will have a negative impact on the global ecosystem: lower biological diversity and altered hydrological and carbon cycles (Adams et al., 2013). Understanding the drivers of vegetation dynamics requires accurately simulating the effect of climate change on global terrestrial biogeochemistry.

To increase their chance of survival, trees control their carbon resources and strategically allocate them to growth, respiration, storage, reproduction, and defense (Hoch et al., 2003; Hartmann et al., 2018). When the atmospheric partial pressure of CO₂ increases, trees can allocate surplus carbon to either growth or carbon storage (Hoch et al., 2003; Huang et al., 2020). Changes in tree carbon allocation patterns have been shown to exert large effects on constituents of the terrestrial carbon cycle (Klein and Hoch, 2015). Clarification of the importance of carbon allocation has revealed that NSCs draw much from the other carbon

resources because they are the most significant carbon compounds involved in the life processes of trees (He et al., 2020).

In long-lived plants, the ability to store carbon is a key to survival at times when photosynthetic rates are low because of shade, drought, and disturbance (Martínez-Vilalta et al., 2016). As a result, the amount of NSC storage or remobilization depends on the balance between the supply and demand of assimilated carbon and accounts for a large fraction of the annual carbon budget of plants (Richardson et al., 2013). When carbon allocation patterns favor storage over growth, tree growth is limited (Wang et al., 2021). Hence, the dynamics of stored carbon pools can be considered an indicator of the carbon balance of the plant.

The decline of stomatal conductance during a drought reduces photosynthetic carbon assimilation and thus decreases the amount of NSC (McDowell et al., 2008; Adams et al., 2017). Although an imbalance of the NSC pool could mechanistically trigger plant mortality, few ecological models predict tree mortality resulting from the role of NSC associated with climate change (Adams et al., 2013; McDowell, 2011). Simulations of the NSC dynamics of plants will elucidate the effects of different drivers on forested ecosystems (Gough et al., 2010).

Dynamic global vegetation models (DGVMs) are often used to represent vegetation dynamics as well as biogeochemical cycles and to simulate the transition of the vegetation structure in response to climatic changes via modeling of competition and disturbance (Hickler et al., 2004; Krinner et al., 2005; Braakhekke et al., 2019). In DGVMs, plant species are classified into plant functional types (PFTs) based on their eco-physiological traits. However, most DGVMs oversimplify individual plant competition by using average values of traits for each PFT (Smith et al., 2001). Most of such models miss the effects of local competition for light, which must be considered when modeling gap population dynamics among individual trees (Sato et al., 2007). In contrast, the spatially explicit individual-based

dynamic global vegetation model (SEIB-DGVM; Sato et al., 2007) can simulate the growth of individual trees on numerous replicate patches and enable observation of how single, large trees can influence nearby trees. Plants in different patches do not interact with each other in terms of physical resources such as light and water. In each patch, the growth and mortality of each tree as well as competitive interactions between individual trees are calculated based on environmental conditions. Transient changes in vegetation distribution and dynamics can therefore be examined (Sato et al., 2007). Because the amount of stored NSC depends on the size of individual trees and because the SEIB-DGVM can simulate individual trees, I chose the SEIB-DGVM to estimate the NSC dynamics of plants.

The SEIB-DGVM has been used to simulate a transient change in the distribution and function of vegetation on the African continent in conjunction with the ranges of dispersal of trees and to address factors that had a strong impact on the transient change (Sato and Ise, 2012). Use of the SEIB-DGVM has enabled reconstruction of the geographical distributions of plant productivity and thermo-hydrology based on observations in eastern Siberia and partial representation of the effect of topography on the abundance of trees in larch forests (Sato et al., 2020). The SEIB-DGVM was coupled with an earth system model (MIROC-ESM; Watanabe et al., 2011).

However, the original SEIB-DGVM lacks the ability to compute NSC levels in trees, which means it cannot simulate the plant death caused by an imbalance in the NSC pool, as well as indirect impacts like insect infestations and defoliation. This also hinders the ability to investigate the effects of various drivers on forest ecosystems, such as the intensification of drought, and limits the development of the MIROC-ESM for simulating the global carbon cycle.

The objectives of the research were to (1) incorporate a module to simulate NSC dynamics in the SEIB-DGVM and (2) validate the simulated NSC dynamics with observational data at both point and global scales. I therefore created a new function in the SEIB-DGVM to represent the NSC dynamics of individual trees. How NSC is produced, stored, and distributed among different plant organs under environmental stress is poorly understood (Jones et al., 2020; Rademacher et al., 2021; Wang et al., 2021). Our enhanced model improves the physiological simulation of the leaf life cycle and enhances understanding of how NSC affects the distribution of vegetation, gross primary production (GPP), and net primary production (NPP) as well as tree dynamics (age, height, and trunk diameter) at global scales in the future. By adjusting the NSC accumulation rates of individual trees and the threshold of NSC-induced mortality during drought, the model can simulate the timing, location, and percentage of trees that die in response to moderate drought. Furthermore, the model can increase our understanding of the role of NSCs.

2 Model

2.1 Spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM)

The SEIB-DGVM (v3.02; http://seib-dgvm.com/data/seib_code302.zip, last access: 1 April 2020; Sato et al., 2016) is a carbon budget model that simulates the establishment of individual trees, competition between trees, and the death of individual trees according to input climate data. The default settings follow the structure of a three-dimensional virtual forest on a 30 m $\times$ 30 m stand of trees with 1 m $\times$ 1 m simulation grid cells. In each grid cell, a tree belonging to 1 of 14 woody plant functional types (PFTs) is assigned depending on conditions, in addition to 1 of 2 grass PFTs. All physical and physiological processes are calculated at daily time steps, trunk growth is estimated monthly, and vegetation dynamics and disturbance such as wildfire and heat stress are assessed annually. Because of the lack of field observations at the time the model was developed, there is no mechanism to control the NSC in leaves and roots in the original SEIB-DGVM, and only the NSC in trunks is simulated after adjusting the available organic matter for reproduction and respiration. The original SEIB-DGVM therefore cannot represent NSC-induced effects on forest ecosystems realistically without accounting for the NSC in leaves and roots.

2.2 NSC components

2.2.1 NSC pool

The new NSC pools are separated into three organs of an individual tree: leaves, trunk, and roots. In the original SEIB-DGVM, the NSC in trunks is supplemented to 250 g dry matter (DM) from the litter after seed establishment and is based on the existing leaf biomass after the first 30 d of the growing season. It is used for foliation after the dormant phase and metabolic processes such as the synthesis of a storage organ and remobilization of the

nutrients within it. In the new model, the carbon newly assimilated via photosynthesis goes into three NSC pools. The NSC pools can be later mobilized for growth and respiration as follows (Fig. 1).

$$\Delta NSC_t = NPP_t = \Delta NSC_{trunk,t} + \Delta NSC_{leaf,t} + \Delta NSC_{root,t}, \quad (1)$$

when $NSC_{trunk, t-1} < NSC_{trunk, max(t)}$, $NSC_{leaf, t-1} < NSC_{leaf, max(t)}$, and $NSC_{root, t-1} < NSC_{root, max(t)}$,

$$\begin{cases} parent\ NSC_{trunk,t} = \min(NSC_{trunk,max(t)}, \Delta NSC_t), \\ NSC_{leaf,t} = \min(NSC_{leaf,max(t)}, \Delta NSC_t - NSC_{trunk,t}), \\ NSC_{root,t} = \min(NSC_{root,max(t)}, \Delta NSC_t - NSC_{trunk,t} - NSC_{leaf,t}), \end{cases} \quad (2)$$

when $NSC_{trunk, t-1} < NSC_{trunk, max(t)}$, $NSC_{leaf, t-1} < NSC_{leaf, max(t)}$, and $NSC_{root, t-1} > NSC_{root, max(t)}$

$$\begin{cases} NSC_{trunk,t} = \min(NSC_{trunk,max(t)}, \Delta NSC_t), \\ NSC_{leaf,t} = \min(NSC_{leaf,max(t)}, \Delta NSC_t - NSC_{trunk,t}), \\ NSC_{root,t} = NSC_{root,max(t)}, \end{cases} \quad (3)$$

when $NSC_{trunk, t-1} < NSC_{trunk, max(t)}$, $NSC_{leaf, t-1} > NSC_{leaf, max(t)}$, and $NSC_{root, t-1} < NSC_{root, max(t)}$,

$$\begin{cases} \text{NSC}_{\text{trunk},t} = \min(\text{NSC}_{\text{trunk},\max(t)}, \Delta\text{NSC}_t), \\ \text{NSC}_{\text{leaf},t} = \text{NSC}_{\text{leaf},\max(t)}, \\ \text{NSC}_{\text{root},t} = \min(\text{NSC}_{\text{root},\max(t)}, \Delta\text{NSC}_t - \text{NSC}_{\text{trunk},t} - \text{NSC}_{\text{leaf},t}), \end{cases} \quad (4)$$

when $\text{NSC}_{\text{trunk}, t-1} < \text{NSC}_{\text{trunk}, \max(t)}$, $\text{NSC}_{\text{leaf}, t-1} > \text{NSC}_{\text{leaf}, \max(t)}$, and $\text{NSC}_{\text{root}, t-1} > \text{NSC}_{\text{root}, \max(t)}$,

$$\begin{cases} \text{parent NSC}_{\text{trunk},t} = \min(\text{NSC}_{\text{trunk},\max(t)}, \Delta\text{NSC}_t), \\ \text{NSC}_{\text{leaf},t} = \text{NSC}_{\text{leaf},\max(t)}, \\ \text{NSC}_{\text{root},t} = \text{NSC}_{\text{root},\max(t)}, \end{cases} \quad (5)$$

when $\text{NSC}_{\text{trunk}, t-1} > \text{NSC}_{\text{trunk}, \max(t)}$, $\text{NSC}_{\text{leaf}, t-1} < \text{NSC}_{\text{leaf}, \max(t)}$, and $\text{NSC}_{\text{root}, t-1} < \text{NSC}_{\text{root}, \max(t)}$,

$$\begin{cases} \text{NSC}_{\text{trunk},t} = \text{NSC}_{\text{trunk},\max(t)}, \\ \text{NSC}_{\text{leaf},t} = \min(\text{NSC}_{\text{leaf},\max(t)}, \Delta\text{NSC}_t), \\ \text{NSC}_{\text{root},t} = \min(\text{NSC}_{\text{root},\max(t)}, \Delta\text{NSC}_t - \text{NSC}_{\text{trunk},t} - \text{NSC}_{\text{leaf},t}), \end{cases} \quad (6)$$

when $\text{NSC}_{\text{trunk}, t-1} > \text{NSC}_{\text{trunk}, \max(t)}$, $\text{NSC}_{\text{leaf}, t-1} < \text{NSC}_{\text{leaf}, \max(t)}$, and $\text{NSC}_{\text{root}, t-1} > \text{NSC}_{\text{root}, \max(t)}$,

$$\begin{cases} \text{NSC}_{\text{trunk},t} = \text{NSC}_{\text{trunk},\max(t)}, \\ \text{NSC}_{\text{leaf},t} = \min(\text{NSC}_{\text{leaf},\max(t)}, \Delta\text{NSC}_t), \\ \text{NSC}_{\text{root},t} = \text{NSC}_{\text{root},\max(t)}, \end{cases} \quad (7)$$

when $\text{NSC}_{\text{trunk}, t-1} > \text{NSC}_{\text{trunk}, \max(t)}$, $\text{NSC}_{\text{leaf}, t-1} > \text{NSC}_{\text{leaf}, \max(t)}$, and $\text{NSC}_{\text{root}, t-1} < \text{NSC}_{\text{root}, \max(t)}$,

$$\begin{cases} \text{NSC}_{\text{trunk},t} = \text{NSC}_{t,\text{max}(t)}, \\ \text{NSC}_{\text{leaf},t} = \text{NSC}_{\text{leaf},\text{max}(t)}, \\ \text{NSC}_{\text{root},t} = \min(\text{NSC}_{\text{root},\text{max}(t)}, \Delta \text{NSC}_t), \end{cases} \quad (8)$$

when $\text{NSC}_{\text{trunk}, t-1} > \text{NSC}_{t, \text{max}(t)}$, $\text{NSC}_{\text{leaf}, t-1} > \text{NSC}_{\text{leaf}, \text{max}(t)}$, and $\text{NSC}_{\text{root}, t-1} > \text{NSC}_{\text{root}, \text{max}(t)}$,

$$\begin{cases} \text{NSC}_{\text{trunk},t} = \text{NSC}_{t,\text{max}(t)}, \\ \text{NSC}_{\text{leaf},t} = \text{NSC}_{\text{leaf},\text{max}(t)}, \\ \text{NSC}_{\text{root},t} = \text{NSC}_{\text{root},\text{max}(t)}, \end{cases} \quad (9)$$

where t is the calculation day, $t-1$ is the previous day, $\text{NSC}_{\text{organ}}$ is the amount of NSC in each organ, and $\text{NSC}_{\text{organ},\text{max}(t)}$ is the maximum amount of NSC in each organ on day t .

The NSC pools of the organs displays unique seasonality for each climatic zone. The NSC seasonality of each organ varies among tree species mainly because the climate and surrounding environment influence the capacity and utilization of NSCs in plants. To take into consideration the fact that field observations of NSC covered whole seasons and that various plant species were scarce, I classify NSC seasonality into three types: tropical, temperate, and boreal. Observations from temperate forests showed that the NSC seasonal cycles were similar among the organs and peaked around late spring–summer, although $\text{NSC}_{\text{organ}}$ differed in size (Hoch et al., 2003; Richardson et al., 2013; Woodruff and Meinzer, 2011; Gruber et al., 2012). In contrast, the NSC concentrations in the leaves of boreal trees peak in June (Sveinbjörnsson et al., 2010), and NSCs in the fine roots increase until summer and then decline toward midsummer and fall because of the initiation of root growth

(Landhäusser and Lieffers, 2003). All 14 woody PFTs of the SEIB-DGVM are sorted into one of three NSC types, and carbon assimilated via photosynthesis was allocated to the NSC pool of each organ in temperate and boreal PFTs as follows.

$$NSC_{organ, max} = (a + b \times \text{daily GPP}) \times \text{Biomass}, \quad (10)$$

where the organ is either a leaf, trunk, or root; a is the minimum value; and b is the seasonality parameter.

Tropical species have a different NSC seasonality from temperate and boreal species. The NSC of leaves display a concave upward seasonal pattern that reaches its minimum in late spring– early summer (Würth et al., 2005), which is a dry season when leaf production and flowering deplete NSC pools. Singh and Srivastava (1986) have observed that the NSC of roots is at a minimum level from July to September because the NSC pool is drained to enable survival of the rainy season during that period. The amount of NSCs then increases toward winter, when the fine-root biomass declines. Hence, Eq. (10), which is used for temperate and boreal forests, is inadequate for simulation of tropical forests because the NSC depends less on the seasonality of photosynthesis in the tropics. The size of the NSC pool of tropical species therefore accumulates as follows.

$$NSC_{organ, max} = (a + b) \times \text{Biomass} \quad (11)$$

where the organ is either the leaf, trunk, or root; a is the minimum value; and b is the seasonality parameter.

First, the surplus carbon that remains after respiration is assigned to NSC_{trunk} using Eq. (1). Once NSC_{trunk} has reached its maximum capacity, the rest of the assimilated carbon moves primarily into NSC_{leaf} and secondarily into NSC_{root} . Finally, any remaining carbon is allocated to the growth of leaves, the trunk, and roots. The sum of the NSCs in the leaves, trunk, and roots (the total NSC) is maximized in relation to total biomass for each climate region (Table 1). In cases where the total NSC exceeds this upper limit, the surplus is directly consumed for the growth of each organ.

Table 1. Maximum volume of NSC pool

Maximum of NSC pool		
Boreal	10% of total biomass	Martínez-Vilalta et al. (2016)
Temperate	5% of total biomass	Hoch et al. (2003)
Tropical	9% of total biomass	Würth et al. (2005)

2.2.2 NSC expenditure

Respiration

Normally, photosynthetically assimilated carbon is used for maintenance respiration without entering the NSC pool. When the assimilated carbon is insufficient for maintenance respiration, the NSC compensates for the shortage. The NSC loss is allocated to each organ as follows.

$$NSC_{leaf, t} = NSC_{leaf, t-1} - R_{a, t-1} \times c_{leaf}, \quad (12)$$

$$NSC_{trunk, t} = NSC_{trunk, t-1} - R_{a, t-1} \times c_{trunk}, \quad (13)$$

$$NSC_{root, t} = NSC_{root, t-1} - R_{a, t-1} \times c_{root}, \quad (14)$$

where autotrophic respiration (R_a) is the difference between assimilated carbon and maintenance respiration and c is the allocation factor for NSC utilization.

If the total NSC equals the carbon shortfall, the NSC of all organs becomes zero. If an NSC_{organ} is insufficient to provide the allocated share of R_a , the other organs will supply the difference: NSC_{leaf} is supplemented first by NSC_{trunk} , and if that is not enough, it is supplemented by NSC_{root} . Similarly, if any of the other NSC_{organ} pools is unable to cover local shortages, the NSC pools of the remaining organs will balance the supply and demand. When the total NSC is not enough to pay for the charges, a 1 % reduction in the biomass of all of the living organs occurs. The removed biomass of sapwood is transformed into heartwood, while the removed biomass of other organs is placed into the litter pool. The allocation factors of NSC utilization depend on the climatic region (Table 2) and have been adjusted to prevent the allocated share of R_a from hindering an increase in NSC_{organ} during spin-up simulations.

Table 2. Allocation ratio (c) of NSC to organs

Organ	Boreal	Temperate	Tropical
Leaf	0.20	0.05	0.01
Trunk	0.60	0.90	0.98
Root	0.20	0.05	0.01

Phenology

In SEIB-DGVM, every deciduous PFT has two phenology phases: a growth phase and a dormant phase. The NSCs are consumed for foliation after the dormant phase. The NSC is allocated at the rates shown in Table 2.

Turnover

Part of the NSC pools of leaves and roots is transformed into litter at the same fractional rates as in the turnover of general carbon pools for leaves and roots. This turnover is calculated at daily steps, regardless of the phenology phase.

Establishment

The establishment process is performed on the last day of each simulation year in the SEIBDGVM. The characteristics of the PFT are determined by five bioclimatic parameters: (1) the maximum temperature in the coldest month, (2) the maximum growing-degree day, (3) the minimum growing-degree day, (4) the minimum photosynthetically active radiation, and (5) the duration of drought. All new trees, independent of their PFT, start with a sapwood diameter of 0.01 m and heartwood diameter of 0.00 m. Initially, these new trees have no leaves or fine roots. Their carbon cycle is therefore maintained by initial values of 250 g DM

of assimilated carbon and 250 g DM of NSC ($\text{NSC}_{\text{leaf}}=10$ g, $\text{NSC}_{\text{trunk}}=190$ g, and $\text{NSC}_{\text{root}}=50$ g) from the litter pool.

2.3 Validation of NSC for point and global simulations

Observational NSC data for model validation were derived from Martínez-Vilalta et al. (2016), who reviewed 296 papers and summarized NSC dynamics in forests. Their data include total NSCs in leaves, trunks, and roots of mature terrestrial plants from observations over at least 4 months. The new model was first validated at the point scale. After confirming that the model can accurately simulate at the point scale, it was then validated at the global scale. These data were used for both point-scale and global-scale model validations. For the point-scale simulation, several field sites were selected, the NSC data of which were available for all organ. At each site, the seasonality of the NSC was measured for at least 4 months. The modeled outputs were then compared to the observed data, which were calculated using local climate data on a grid that corresponds to the field site. For the global-scale simulation, global mean NSC values were derived by using all observed data from the relevant climate zones. The modeled outputs calculated using $0.5 \times 0.5^\circ$ gridded climate data were then compared to these values.

2.3.1 Validation at a point scale

Site descriptions

Four countries were used to validate the simulated NSC content in the plant organs: boreal (Canada), temperate (Austria and Switzerland), and tropical (Panama). I used local climate data from meteorological stations gap-filled by corrected gridded climate reanalysis data as

the input at these sites. I ran the NSC module including the SEIB-DGVM with the location and climate provided and compared the model output with the observation data.

The boreal site is located near Alder Flats, Alberta, Canada (52.58' N, 114.59' W) in 2000. The site was dominated by boreal winter deciduous plants such as *Populus tremuloides* (Landhäusser and Lieffers, 2003). One of the temperate sites is located in the timberline ecotone at Mt. Patscherkofel to the south of Innsbruck, Austria (47.13' N, 11.27' E) in 2008 (Gruber et al., 2011). Temperate conifer species such as *Pinus cembra* were the dominating tree species. The other temperate site is at Mont Noble, Canton Valais, Swiss Central Alps (46.12' N, 7.30' E) and was dominated by temperate conifers (*P. cembra* L.; Hoch et al., 2003) in 2000. The tropical site is located at the Parque Natural Metropolitano near Panama City, the Republic of Panama in 1996 (85.8' N, 79.34' W; Würth et al., 2005). The site has mixed cover with 17 dominant species, including *Cecropia longipes* and *Anacardium excelsum*.

Input climate data

The SEIB-DGVM requires 10 climatic variables as environmental drivers: air temperature, soil temperature at a depth of 50 cm (soil layer 1), soil temperature at a depth of 100 cm (soil layer 2), soil temperature at a depth of 150 cm (soil layer 3), precipitation, shortwave radiation, longwave radiation, wind velocity, specific humidity, and diurnal range of air temperature. The input climate data were prepared by harmonizing a global reanalysis gridded climate dataset, the WATCH Forcing Data ERA-Interim (WFDEI, $0.5 \times 0.5^\circ$, 1979–2016, Weedon et al., 2018), and the climate generated by the SEIB generator (Tei et al., 2017), which is the monthly observation-based climatic datasets produced by Climatic Research Unit (CRU TS4.00, $0.5 \times 0.5^\circ$, 1901–2015, Harris et al., 2014) supplemented with the National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) daily climate datasets (Kalnay et al., 1996) for 1950, with local climatology recorded at meteorological stations near the sites. Local climatology in Panama is measured at the Parque

Natural Metropolitano Canopy Crane meteorological station (1995–2019). The climatology in Austria (1979–2008) and Switzerland (1979–2000) was derived from the closest meteorological station to the field site under the European Climate Assessment (Klein Tank et al., 2002, <https://www.ecad.eu>, last access: 19 November 2020). WFDEI data were used for the climatology in Canada, except for precipitation data, which are measured in the Meteorological Service of Canada (1979–1984, https://climate.weather.gc.ca/historical_data/search_historic_data_e.html, last access: 1 December 2020).

The reanalysis of daily WFDEI and SEIB climate data included daily records, which were corrected by regression models to local climate data. For temperature, humidity, and shortwave radiation values, local climatology were used directly and the daily WFDEI data were supplemented by simple linear regression. Precipitation data and wind speeds were first adjusted to monthly and then annual averages and then scaled as a correction. WFDEI precipitation data were scaled after adjusting to the annual climatological precipitation of 995 mm in 2008 for Austria and 630 mm in 2000 for Switzerland. Longwave radiation was calculated using harmonized temperatures and humidities above (Brutsaert, 1975). Missing values were estimated via linear interpolation. Because soil temperature data were unavailable for local sites and for WFDEI, soil layer temperatures were calculated using the SEIB generator by regressing soil layer 1 on atmospheric temperature, soil layer 2 on layer 1, and layer 3 on layer 2. In Austria, humidity data were available from 2005. The WFDEI data were therefore used to estimate missing data via linear interpolation. In Canada, no observational data were available, except for temperature and precipitation. Precipitation in Canada was scaled with WFDEI data after adjusting to the total climatological precipitation for 1979–1984, shortwave radiation was taken from the WFDEI, and humidity data were harmonized in the same way as the humidity data in Austria.

Simulation scheme

To reach equilibrium conditions of the biomes, plant, and soil carbon pools, a 1000-year spin-up simulation was performed by looping the climate data and atmospheric CO₂ concentrations between 1979–2000. Building on the final conditions of the spin-up simulations, continuous simulations corresponding to 1979–2001 in Canada, 1979–2008 in Austria, 1979–2000 in Switzerland, and 1979–1995 in Panama were carried out, and the NSC dynamics were compared with field data.

2.3.2 Validation at a global scale

In the global-scale simulation, the NSC seasonality in the SEIB-DGVM was validated using CRU/NCEP/MIROC integrated data ($0.5 \times 0.5^\circ$, 1850–2100, Tei et al., 2017; Watanabe et al., 2011) as climatic input. The SEIB-DGVM-NSC version 1.0 is expected to simulate on future scenarios; thus, the different climate data that cover longer period than that of section “Input climate data”. are used for validation at a global scale. The SEIB-DGVM categorizes plant species into 16 PFTs for global-scale simulations.

The outputs of the SEIB-DGVM include two boreal biome types (evergreen and deciduous forests), three temperate biome types (conifer, broad-leaved evergreen, and deciduous forests), and two tropical biome types (evergreen and deciduous forests), whereas the observations included two boreal biome types (conifer and deciduous forests), three temperate biome types (conifer, evergreen, and deciduous forests), and two tropical biome types (evergreen and deciduous forests). The model outputs and observation data were compared for each climate zone. Global climate data were available from 1850 to 2005. The first 30 years (1850–1880) were therefore looped for a 1000-year spin-up simulation. After the spin-up, simulations were

run for the period 1850–2005. The NSC dynamics from the period 1975–2005 were used for model validation.

2.4 Parameterization of NSC functions

Hoch et al. (2003) have reported that NSC_{leaf} of temperate trees sampled near the village of Hofstetten in Switzerland varies between 7 %–20 % of the total leaf DM. They determined the seasonal mean of $\text{NSC}_{\text{trunk}}$ in sapwood of temperate deciduous trees and temperate evergreen trees to be $4.7 \% \pm 0.1 \%$ of DM and $1.8 \% \pm 0.1 \%$ of DM, respectively. There were no significant seasonal differences. The mean NSC_{root} was less than 1.5 % of the root DM for forests in Austria throughout the whole season (Gruber et al., 2012), and the total NSC of temperate trees was around 4 %–5 % of the DM during the growing season (Gruber et al., 2011). For tropical trees collected in Parque Natural Metropolitano in Panama, $\text{NSC}_{\text{trunk}}$ and NSC_{root} were 8 %–10 % of their biomass, whereas NSC_{leaf} fluctuated within 5 %–9 % of leaf biomass (Würth et al., 2005). Landhäusser and Lieffers (2003) have reported that NSC_{root} of boreal trees in Canada, which is used to support leaf flush and root growth, is 3 %–4 % of their root mass. The stemwood $\text{NSC}_{\text{trunk}}$ concentration is $\sim 18 \text{ mg g}^{-1}$ of the DM for forest samples collected in the northeastern US (Carbone et al., 2013). Because of limited observational data, the parameters of the NSC processes were derived mostly from the values observed at each site used for point-scale validation, and the maximums of simulated NSCs were corrected so that they were in the range of measured NSCs.

First, the parameter a in Eq. (10) controls the base amount of photosynthetically fixed carbon mobilized for the NSC pools. The parameter b in Eq. (10) controls the seasonal fluctuations of the NSCs from the parameter a . In temperate zones, the value of b differs before and after July so that NSC peaks around mid-summer. In contrast, in tropical zones, the amount of NSC in leaves and trunks decreases throughout the spring–summer.

The same parameters a and b were basically used for global-scale validation as for point-scale validation. However, because the NSCs are influenced by environmental conditions at the field sites, the observed global mean values used for global-scale validation were different from the values used for setting parameters for point-scale validation. Therefore, some adjustments were made to certain parameters to align with the values used in the global-scale validation. Tables 3 and 4 show the parameters used for validation. Parameter values unrelated to the NSC module remain at the default values of the SEIB-DGVM (Sato et al., 2007).

Table 3. Parameters of NSC pool size function for point-scale simulation

Organ	Canada	Austria	Switzerland	Panama
Leaf	$a: 0.09, b: 0.4 \times 10^{-3}$	$a: 0.04, b: 0.065 \times 10^{-3}$ (Jul–Oct) $a: 0.04, b: 0.135 \times 10^{-3}$ (others)	$a: 0.13, b: 0.1 \times 10^{-3}$ (Jul–Oct) $a: 0.13, b: 0.7 \times 10^{-3}$ (others)	$a: 0.06, b: -0.15 \times 10^{-3}$ (Jun–Nov) $a: 0.06, b: 0.15 \times 10^{-3}$ (others)
Trunk	$a: 0.06, b: 0.03 \times 10^{-3}$	$a: 0.02, b: 0.005 \times 10^{-3}$	$a: 0.02, b: 0.01 \times 10^{-3}$	$a: 0.1, b: -0.25 \times 10^{-3}$ (Jun–Nov) $a: 0.1, b: 0$ (others)
Root	$a: 0.14, b: 0.06 \times 10^{-3}$	$a: 0.02, b: 0.01 \times 10^{-3}$	$a: 0.06, b: 0.003 \times 10^{-3}$	$a: 0.04, b: 0.5 \times 10^{-3}$

Table 4. Parameters of NSC pool size functions for global-scale simulation

Organ	Boreal	Temperate	Tropical
Leaf	$a: 0.09, b: 0.4 \times 10^{-3}$	$a: 0.13, b: 0.1 \times 10^{-3}$ (Jul–Oct) $a: 0.13, b: 0.9 \times 10^{-3}$ (others)	$a: 0.06, b: -0.15 \times 10^{-3}$ (May–Jul) $a: 0.06, b: 0.15 \times 10^{-3}$ (others)
Trunk	$a: 0.06, b: 0.03 \times 10^{-3}$	$a: 0.04, b: 0.01 \times 10^{-3}$	$a: 0.1, b: -0.13 \times 10^{-3}$ (May–Jul) $a: 0.1, b: 0$ (others)
Root	$a: 0.14, b: 0.06 \times 10^{-3}$	$a: 0.06, b: 0.003 \times 10^{-3}$	$a: 0.04, b: 0.5 \times 10^{-3}$

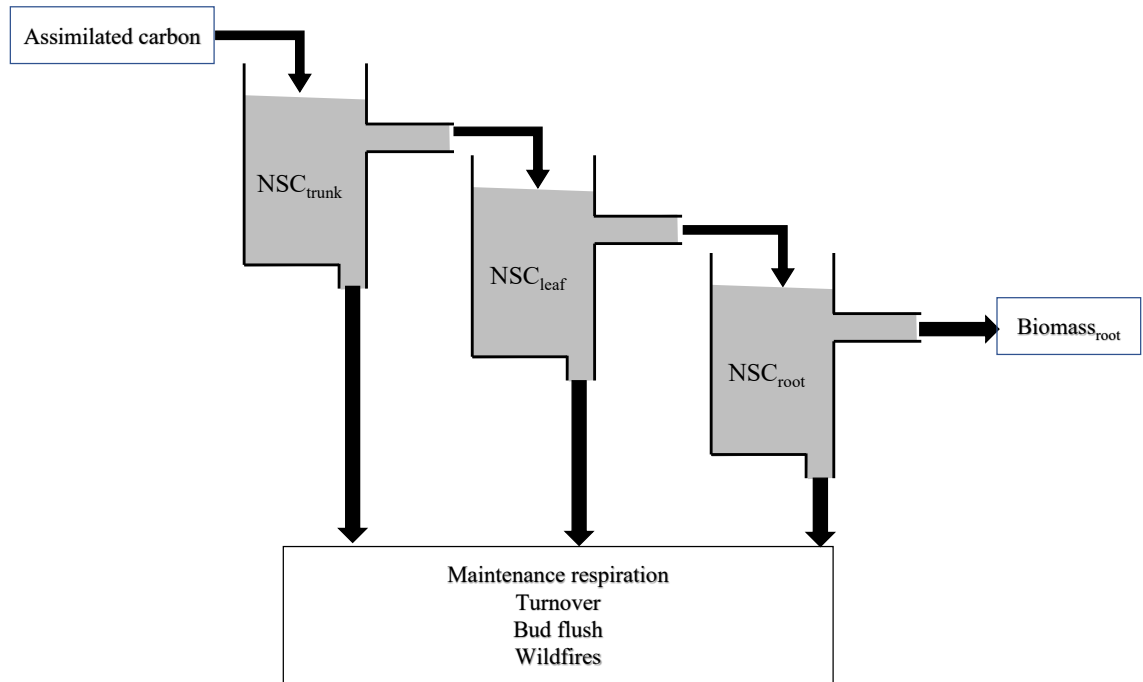


Figure 1. Schematic model structure of NSC pool. The assimilated carbon satisfies the NSC_{trunk} , and then the excess assimilated carbon satisfies the next NSC_{leaf} and NSC_{root} . The accumulated carbon in NSC pool is used to compensate for the shortage of maintenance respiration and help with bud flush, and is sometimes lost due to turnover. When the biomass of plants is lost due to wildfires, the NSC also decreases.

3 Results

3.1 Seasonality of NSC at the point scale

3.1.1 Boreal

In Canada, the fact that the dominant PFT in the simulations was boreal deciduous trees was consistent with observations at the site. The model simulated an increase in the NSC of leaves from 80 to 203 mg g⁻¹, whereas the observed NSC values were 89 mg g⁻¹ in May and 185 mg g⁻¹ in August (Fig. 2a). The modeled NSCs in leaves therefore captured the increasing trend during the growing season, but the simulations overestimated the maximum NSC a little. The observed NSCs in trunks fluctuated from 90 to 192 mg g⁻¹ during a year with no specific seasonal trend (Fig. 2e). The model outputs in trunks were in the range 56–76 mg g⁻¹. Although the observed fluctuations exceeded the modeled outputs, the modeled outputs were within

1 standard deviation of the observations. The range of the observed NSCs in roots was 97–138 mg g⁻¹, whereas the range of the modeled NSCs was 117–132 mg g⁻¹ (Fig. 2i). However, the observations peaked in August 2001 and in October 2002. The modeled NSCs of roots differed from the observed NSCs because the former peaked during August in both years. Overall, the simulated NSCs agreed well with the observed data (Fig. 3; RMSE = 69.92 mg g⁻¹, $r=0.21$).

3.1.2 Temperate

In Austria, the fact that the dominant PFT in the simulations was temperate conifer forests was consistent with observations at the site in Austria. The modeled NSCs in leaves accumulated until July with a maximum of 142 mg g⁻¹. This pattern was similar to the

observed seasonality of the NSCs, which peaked at 150 mg g^{-1} (Fig. 2b). The modeled NSCs in trunks were stable in the range $19\text{--}26 \text{ mg g}^{-1}$, and the observations were within the range $18\text{--}38 \text{ mg g}^{-1}$, with no specific seasonality (Fig. 2f). The modeled values were interspersed between the observations. The modeled NSCs in roots varied in a curvilinear manner from 18 to 26 mg g^{-1} , a range that was similar to the range of the observed NSCs, $13\text{--}32 \text{ mg g}^{-1}$ (Fig. 2j). The seasonality and magnitudes of the modeled NSCs were consistent with observations (Fig. 3; $\text{RMSE} = 9.52 \text{ mg g}^{-1}$, $r=0.95$).

In Switzerland, the dominant PFT in the simulations corresponded to the temperate conifers observed at the field site. The NSCs in the tree leaves accumulated during early spring and reached up to 222 mg g^{-1} (Fig. 2c). The decrease in the NSCs after July to a minimum of 135 mg g^{-1} was similar to the decline of the observed NSCs to a minimum of 124 mg g^{-1} . The modeled NSCs in trunks fell in the range $13\text{--}16 \text{ mg g}^{-1}$, which was overlapped with the range of the observed NSCs in trunks, $15\text{--}33 \text{ mg g}^{-1}$ (Fig. 2g), and the modeled NSCs all fell within 1 standard deviation of the observations. The modeled NSCs in roots increased gradually from 45 to 62 mg g^{-1} , which is similar to the observed range of observations, $48\text{--}64 \text{ mg g}^{-1}$ (Fig. 2k). The simulations captured the amounts and seasonal patterns of the NSCs in the different organs and produced results that compared well with observations (Fig. 3; $\text{RMSE} = 25.83 \text{ mg g}^{-1}$, $r=0.91$).

3.1.3 Tropical

In Panama, while a wide range of woody species was found at the Panama site, in the simulation the tropical evergreen PFT became dominant. The simulations showed that the NSCs in leaves were stored during winter and were then gradually consumed from July to October, when they reached a minimum of 52 mg g^{-1} (Fig. 2d). The observed NSCs in leaves likewise decreased from 69 to 48 mg g^{-1} between August and October. The model therefore followed the observed seasonality of the leaf NSCs. The modeled NSCs in trunks fell in the

range 35-73 mg g⁻¹ (Fig. 2h). The slight decrease in the modeled NSCs in trunks during the summer was not apparent in the observations. However, the simulated values fell within the range of the observed NSCs, 27-97 mg g⁻¹. The simulated NSCs in roots fell in the range 23-55 mg g⁻¹; the observed NSCs ranged from 43 to 70 mg g⁻¹ (Fig. 2l). Despite the weak correlation between simulated and observed NSCs, the model results were within the acceptable margin of error (Fig. 3; RMSE = 20.75 mg g⁻¹, $r=0.08$).

3.2 Comparison of annual mean NSC concentrations at a global scale

For validation at a global scale, the mean annual NSCs from the new model were compared with the observed mean annual NSCs in boreal, temperate, and tropical regions (Table 5). The model simulated the amounts of NSCs in forest tree trunks in all climate regions with high accuracy. The modeled NSCs in the trunks of trees in boreal forests averaged 47.48 ± 18.35 mg g⁻¹, which compared favorably with the observed average of 76.67 ± 23.68 mg g⁻¹. In temperate forests, the modeled NSCs of trunks averaged 44.78 ± 6.82 mg g⁻¹, which was close to the observed average of 51.59 ± 22.63 mg g⁻¹. The modeled NSCs of trunks in tropical forests averaged 66.68 ± 18.79 mg g⁻¹, which was close to the average of the observations, 106.23 ± 32.52 mg g⁻¹. Although the modeled NSCs in leaves of temperate and tropical forests were close to observed values, the modeled NSCs in leaves of boreal forests underestimated the observed values. Moreover, the modeled NSCs in roots of tropical forests were smaller than the observed NSCs. Overall, the simulated NSCs of all organs of forest trees in all climate regions agreed reasonably well with observations (Fig. 4; RMSE = 66.75 mg g⁻¹, $r=0.17$). The model could simulate the NSCs with high accuracy, with the exception of the NSCs of tree leaves in boreal forests and of tree roots in tropical forests (Fig. 4; RMSE = 34.15 mg g⁻¹, $r=0.71$). The original SEIB-DGVM only calculated NSCs in the trunks of trees with an average value of 63.70 ± 44.64 mg g⁻¹ in boreal forests, 20.87 ± 15.91 mg g⁻¹ in temperate forests, and 16.61 ± 10.22 mg g⁻¹ in tropical forests.

Although the NSC in trunks of boreal forests from the original SEIB-DGVM was close to observation, the old model underestimated the NSC in trunks of temperate and tropical forests. The simulated NSCs from the original SEIB-DGVM in all climate regions were found to be poorly correlated with observations (Fig. 4; RMSE = 55.37 mg g⁻¹, $r=0.01$).

Table 5. Comparison of modelled and observed annual mean NSC concentrations (mg g⁻¹) on a global scale. The observed results are represented as the mean $\pm$ 1 standard deviation.

	Boreal		Temperate		Tropical	
	Observation	Model	Observation	Model	Observation	Model
Leaf	202.80 $\pm$ 19.97	94.91 $\pm$ 42.91	127.10 $\pm$ 25.6	170.90 $\pm$ 46.54	86.42 $\pm$ 20.21	46.92 $\pm$ 16.20
Trunk	76.67 $\pm$ 23.68	47.48 $\pm$ 18.35	51.59 $\pm$ 22.63	44.78 $\pm$ 6.82	106.23 $\pm$ 32.52	66.68 $\pm$ 18.79
Root	118.49 $\pm$ 13.24	105.80 $\pm$ 40.82	67.65 $\pm$ 18.79	23.58 $\pm$ 10.57	170.40 $\pm$ 36.49	44.55 $\pm$ 15.15

3.3 Woody biomass and total NSCs on a global scale

The average of the total GPP simulated from the new model during 1976–2005 was 123 PgC yr⁻¹. The model estimated the mean total woody biomass to be 282 PgC yr⁻¹ in boreal zones, 100 PgC yr⁻¹ in temperate zones, and 337 PgC yr⁻¹ in tropical zones globally during 1976–2005. In boreal zones, the new model estimated the mean concentration of total NSCs to be 4.98 % $\pm$ 1.87 % of total woody biomass, while the original SEIB-DGVM estimated it to be 6.37 % $\pm$ 4.46 % of total woody biomass (Fig. 5). The new model's estimation of the percentage of NSCs to total woody biomass in North America and North Russia was lower than the original SEIB-DGVM. In temperate zones, the mean concentration of total NSCs was 4.67 % $\pm$ 0.54 % of total woody biomass from the new model, while it was 2.09 % $\pm$ 1.59 % from the original SEIB-DGVM. The NSCs in the temperate forests of Asia and South America accounted for a larger fraction of total biomass in the new model

compared to the original SEIB-DGVM. Total NSCs of tropical forests in South America and Africa from the new model were $6.19 \% \pm 1.66 \%$ of their total woody biomass; the original SEIB-DGVM estimated it to be $1.66 \% \pm 1.02 \%$ of the total biomass. The new model estimated a larger percentage of NSC to total biomass across tropical regions compared to the original SEIB-DGVM.

Mean values of the simulated total NSCs relative to total woody biomass from the new model were close to previous estimates for temperate and tropical forests (Table 6). The total NSCs of temperate, broad-leaved, evergreen forests from the new model were $4.63 \% \pm 0.50 \%$, which corresponded to the woody biomass reported by Smith et al. (2018). Furthermore, in the new model, the total NSCs of temperate conifer forests were $4.72 \% \pm 0.58 \%$ of total woody biomass, which was close to the figure of 4 % reported by Körner (2003), while the original SEIB-DGVM calculated the total NSCs of temperate broad-leaved evergreen forests to be $2.64 \% \pm 1.24 \%$, and the total NSCs of temperate conifer forests were $5.30 \% \pm 2.68 \%$ of the total woody biomass, which closely matched the observations. However, the original SEIB-DGVM only considered NSCs in the trunks, whereas the new model allocates the total NSC into three organs, resulting in a close match to the observed total NSC. According to Würth et al. (2005), the percentages of woody biomass contributed by NSCs are 4 %–8 % in tropical forests. The new model was calculated to be $4.66 \% \pm 1.28 \%$ in tropical deciduous forests and $7.11 \% \pm 1.08 \%$ in tropical evergreen forests. In contrast, the total NSCs of tropical deciduous forests from the original SEIB-DGVM were $1.66 \% \pm 1.35 \%$, and the total NSCs of tropical evergreen forests were $1.66 \% \pm 0.71 \%$, which were different from the observed values. These observed percentages are close to our simulated values from the new model.

Table 6. Comparison of modeled mean NSC concentrations to observed total NSC concentrations (%) for different types of biomes. The simulated results are expressed as the mean $\pm$ 1 standard deviation.

	Total NSC	Leaf	Trunk	Root	Total NSC (Original SEIB- DGVM)	Observation
Boreal deciduous	3.41 ± 1.58	0.05 ± 0.09	3.06 ± 1.23	0.30 ± 0.62	2.47 ± 3.32	
Boreal evergreen	6.06 ± 1.16	0.75 ± 0.38	4.73 ± 1.29	0.58 ± 0.37	7.24 ± 4.22	
Temperate deciduous	2.30 ± 0.33	0.02 ± 0.01	2.25 ± 0.31	0.03 ± 0.01	1.45 ± 0.93	1.0–12.5 (Gough et al., 2009)
Temperate broad-leaved evergreen	4.63 ± 0.50	0.49 ± 0.20	4.10 ± 0.56	0.04 ± 0.03	2.64 ± 1.24	2.6–4.4 (Smith et al., 2018)
Temperate conifer	4.72 ± 0.58	0.89 ± 0.38	3.77 ± 0.73	0.08 ± 0.04	5.30 ± 2.68	4.0 (Körner, 2003)
Tropical deciduous	4.66 ± 1.28	0.04 ± 0.03	4.60 ± 1.27	0.03 ± 0.02	1.66 ± 1.35	4.0–8.0 (Würth et al., 2005)
Tropical evergreen	7.11 ± 1.08	0.08 ± 0.03	7.00 ± 1.08	0.02 ± 0.01	1.66 ± 0.71	4.0–8.0 (Würth et al., 2005)

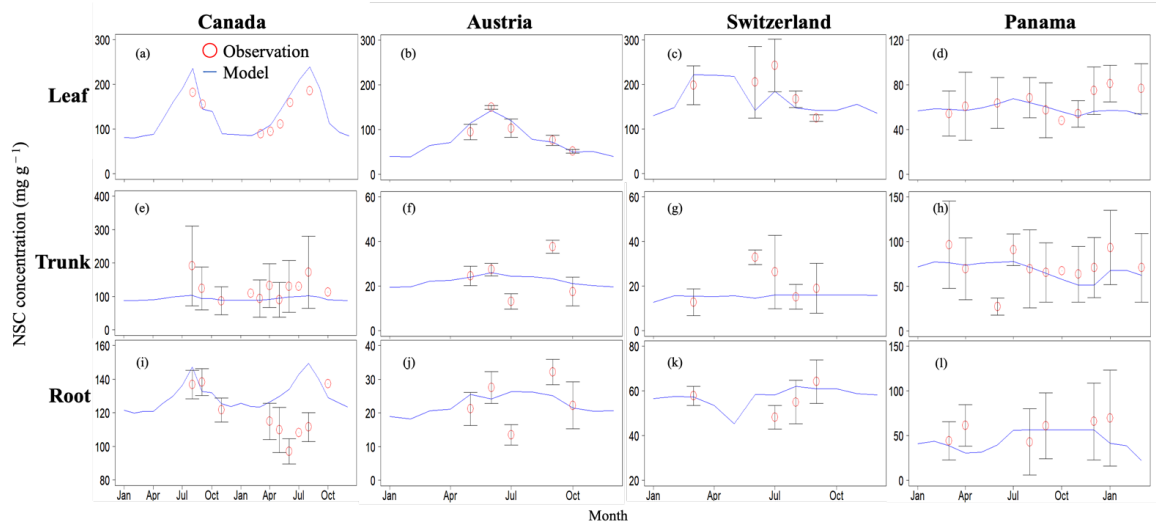


Figure 2. Validation of the modeled NSC with observed NSC data (mg g⁻¹) at sites in Canada, Austria, Switzerland, and Panama. Red circles indicate the observed data, and blue lines indicate the modeled NSC. The observed results are represented as mean $\pm$ 1 standard deviation. Observed data are derived from Martínez-Vilalta et al. (2016).

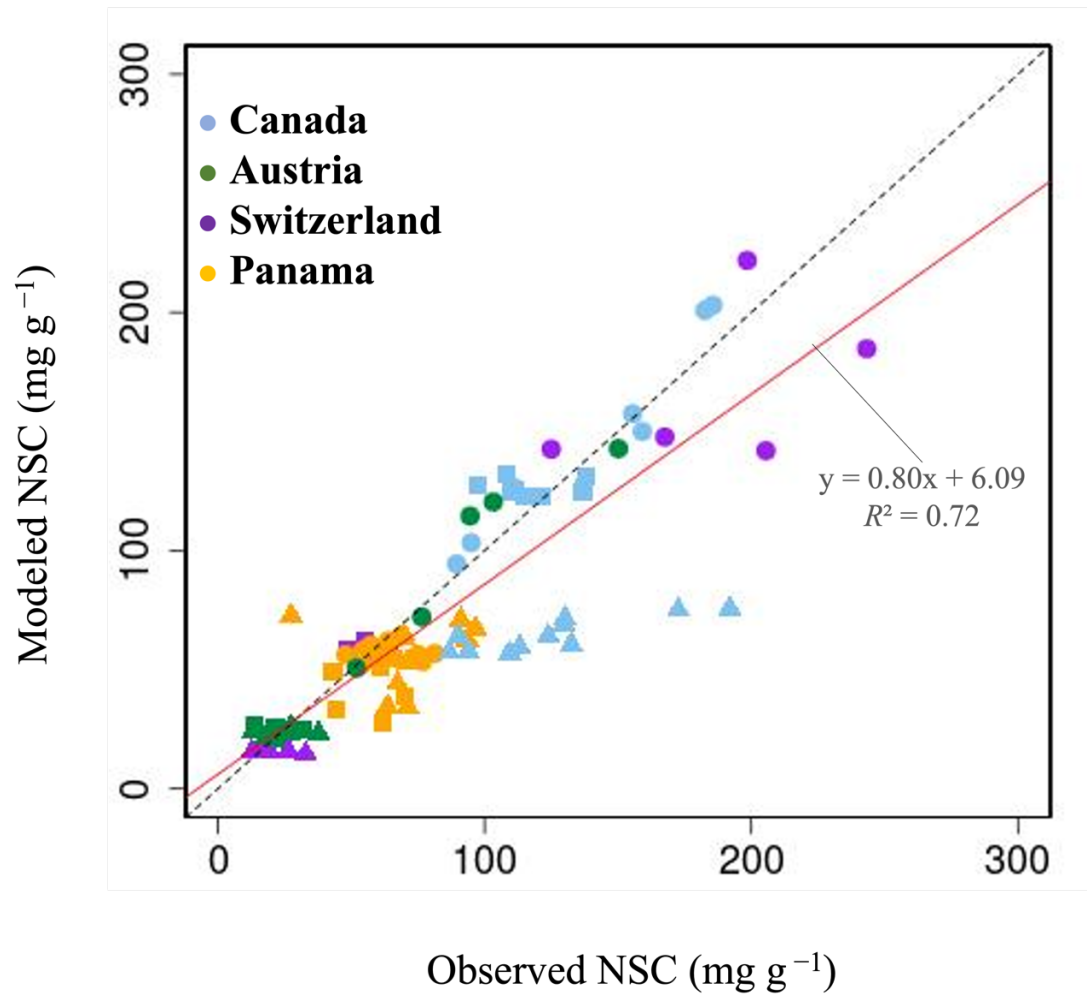


Figure 3. Plot of modeled NSC (mg g⁻¹) with observed NSC (mg g⁻¹) at a point scale. ●, leaves; ▲, trunks; ■, roots. For all data, r is 0.72, and RMSE is 29.65 mg g⁻¹.

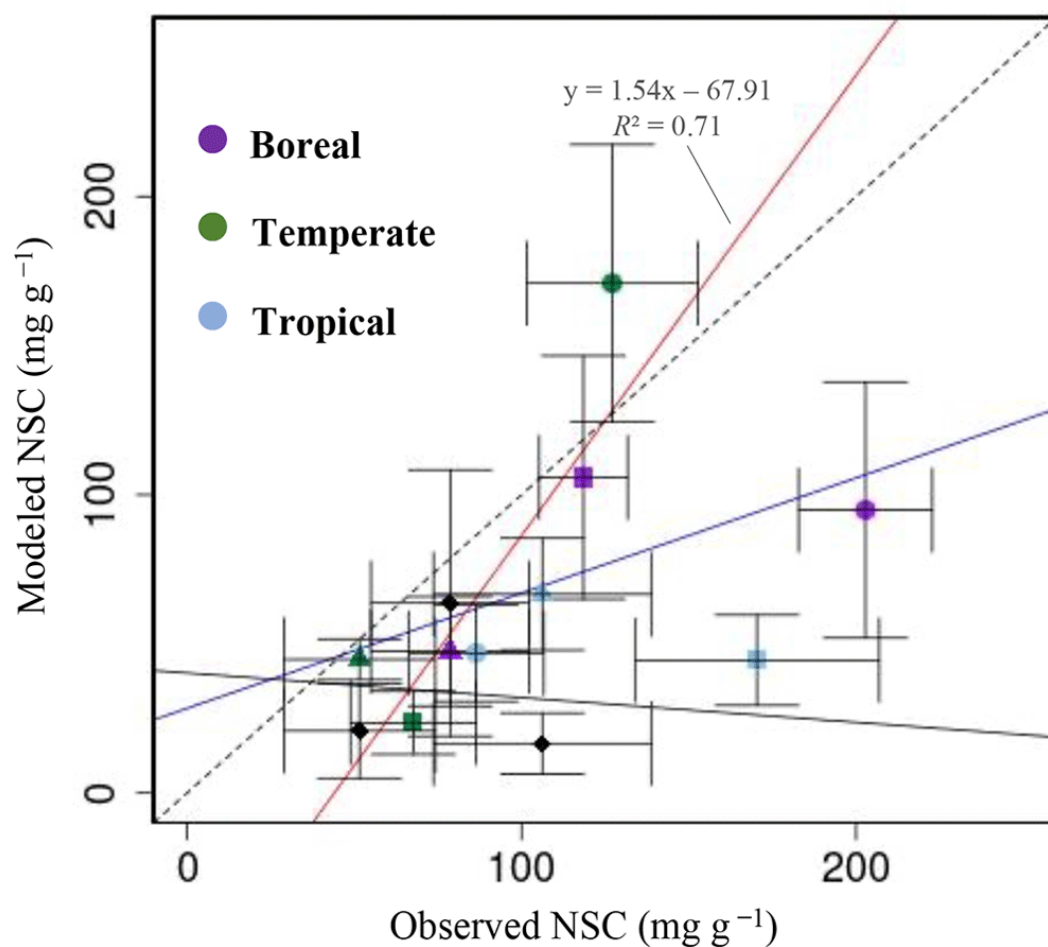


Figure 4. Plot of modeled NSC (mg g^{-1}) with observed NSC (mg g^{-1}) at a global scale. ●, leaves; ▲, trunks; ■, roots; ◆, trunks in the original SEIB-DGVM. Red line represents the regression line of the plot that compares the modeled NSC from the new model with the observed NSC, except for the NSCs of tree leaves in boreal forests and of tree roots in tropical forests. Blue line represents the regression line of all plot from the new model with the observed NSC. Black solid line represents the regression line of modeled NSC from the original SEIB-DGVM with the observed NSC.

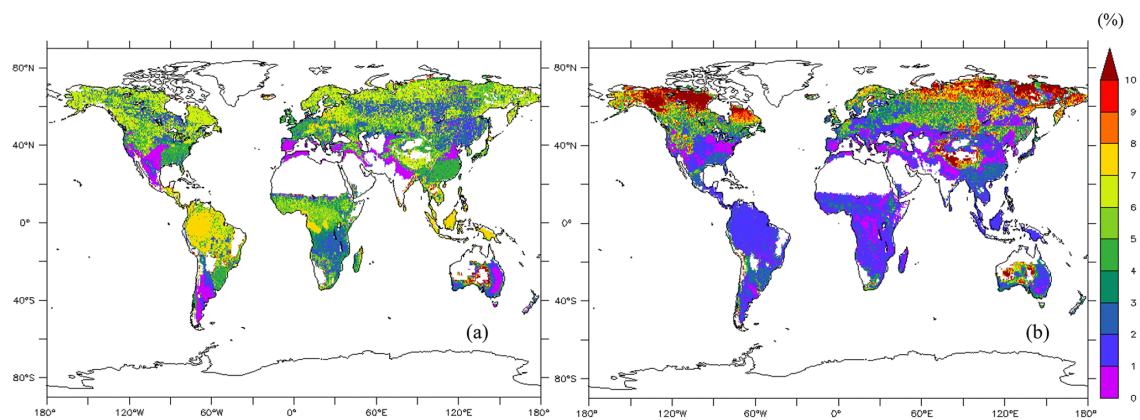


Figure 5. The global map of percentage of total NSC concentration relative to total dry woody biomass averaged during 1976–2005 (%) (a) from the new model (b) from the original SEIB-DGVM.

4 Discussion

At the point scale, the modeled NSCs for boreal forests in Canada were close to the observed NSCs. The seasonality of the modeled NSCs in leaves was consistent with observations. However, the seasonality of NSC in roots differed from the observations because there were insufficient observations in boreal regions that enabled assessment of the seasonality of NSCs in all organs. The seasonality of NSCs in roots is therefore still unclear. In temperate zones, the model simulated the observed NSCs very accurately. The simulated NSCs of temperate forests were close to observed values in Austria and Switzerland. The simulations showed that the NSCs in leaves were consumed in winter for bud flush, and the leaves accumulated NSCs during the growing season. This pattern corresponded to the seasonality reported in Asaadi et al. (2018) and Furze et al. (2019). In the tropical zones, the model also captured a seasonality of NSCs that was similar to observations. The NSC concentration in the canopy of tropical forests decreased from June to August to satisfy increased maintenance demands (Signori-Müller et al., 2022; Würth et al., 2005). The simulated NSCs in leaves followed a similar pattern from June to August, and the simulated NSCs in leaves, trunks, and roots were close to observed values.

At the global scale, the new model simulated NSC values in each organ of all climate regions that agreed with the observed data, except for the leaves of boreal forests and roots of tropical forests. As for the total NSCs of biome types, the modeled total NSCs of all temperate and tropical biomes matched the observed ranges well. In contrast, the original SEIB-DGVM only calculated NSC in trunks, and the modeled NSC in trunks of temperate and tropical forests were underestimated compared to observations. Total NSCs of tropical biomes were lower than observations, while those of temperate biomes were close to observations, but the original SEIB-DGVM did not assign the total NSC into leaves and roots. Therefore, these findings reveal that the new model can simulate NSC more accurately than

the original SEIB-DGVM. In the original SEIB-DGVM, the NSC in trunks depended on the existing leaf biomass, which could not be applied to all biome types and climate zones, especially tropical forests. In the new model, NSC_{organ} is determined by the biomass of the organ and photosynthesis in some climate zones. The new function, which was validated at the point scale, could therefore perform well on a global scale. The NSCs in trunks, which contain the greatest amounts of carbon in trees, were simulated accurately in all climate regions. The new function could therefore calculate the total NSCs in trees with great accuracy.

The model with the new function calculated the global GPP to be 123 PgC yr^{-1} , which is close to the previous estimates of $106.2 \pm 2.9 \text{ PgC yr}^{-1}$ by Zheng et al. (2020) and $130 \pm 1.6 \text{ PgC yr}^{-1}$ by Madani et al. (2020). Moreover, the simulated mean total woody biomass for boreal forests was 282 PgC yr^{-1} , which is within the range of $249\text{--}295 \text{ PgC yr}^{-1}$ reported by Pan et al. (2011). The simulated woody biomass of 100 PgC yr^{-1} for temperate forests was within the observed range of $59\text{--}139 \text{ PgC yr}^{-1}$ (Hui et al., 2017) and a little lower than the range of $113\text{--}125 \text{ PgC yr}^{-1}$ for other temperate forests (Pan et al., 2011). The calculated total woody biomass of 337 PgC yr^{-1} for tropical forests was within the range of $212\text{--}340 \text{ PgC yr}^{-1}$ reported by Hui et al. (2017) and was not very different from the estimates of $378\text{--}564 \text{ PgC yr}^{-1}$ by Pan et al. (2011) and $200\text{--}300 \text{ PgC yr}^{-1}$ by Mitchard (2018). Furthermore, the total NSCs relative to total biomass output from the new function for temperate and tropical biome types agreed with previous research. The total NSC of boreal biome types could not be compared with observations due to lack of data.

The new model allows for simulation of various biotic effects on terrestrial ecosystems by calculating the NSC dynamics within each plant organ. The NSCs stored in the trunk and roots help to compensate for the deficit of CO_2 uptake in trees under stress, and the NSC stored in roots is potentially indispensable for tree recovery after disturbances (Herrera-Ramírez et al., 2020). Therefore, the NSC changes in the trunk and roots provide better

indicators of carbon source–sink relationships under elevated CO₂ conditions and are more closely related to the carbon balance of plant bodies (Körner, 2003). While the original SEIB-DGVM was unable to simulate biotic effects due to the lack of consideration for NSCs in all organs, simulation of the dynamics of NSC in the three compartments in this research contributes to a better understanding plant growth and the response of carbon dynamics in each organ to increasing atmospheric CO₂.

Carbon starvation may also be one of the causes of plant death during drought when photosynthesis decreases and water stress increases (McDowell et al., 2008). If reduced photosynthetic rates cannot supply enough carbon for NSC accumulation during drought, there will be greater canopy dieback in the next season (McDowell, 2011; Chen et al., 2017). The new model can simulate the dieback of long-lived temperate and tropical forests during drought, because it can represent the total NSC in plant bodies at a global scale. Additionally, insect pests have a significant impact on forest ecosystems, especially in temperate biomes, and their outbreaks have increased with climate change (Canelles et al., 2021). To recover from defoliation caused by insect pests and avoid decreased growth rates and lower survival rates, plants allocate carbon for NSC defense mechanisms. The new model accurately simulates the amount of total NSCs in temperate biomes, and, therefore, it can be used to estimate the impact of insect pests on a global and future scale.

The new model introduced NSC compartments in leaves, trunk, and roots that were validated at the point and global scales. Use of the model developed here enabled simulation of the environmental effects on forests resulting from the changing amount of NSC in each organ. The simulations depicted the amount of NSC in the trunk at a global scale especially well, which constitutes a significant portion of the total NSC. The model could thus be used as an indicator of the carbon cycle in terrestrial ecosystems to understand the effect of climate change. Simulation of photosynthetic carbon allocated into NSC storage in leaves, trunks,

and roots enables a more dynamic simulation of the carbon cycle between terrestrial ecosystems and the atmosphere.

However, there were still some limitations to this research. I considered two potential limitations that could lead to some discrepancies between the modeled and measured NSC values. First, the relatively coarse spatial resolution of $0.5 \times 0.5^\circ$ gridded climate data at the global scale could not depict the details of local climates derived from observations. These differences were especially important in the case of temperature and short radiation, which play a key role in NSC dynamics. Temperature surrounding plants is a key factor for the rate of plant growth (Hatfield and Prueger, 2015). And different plant species have a specific temperature range. The short radiation is used for a calculation of the photosynthesis rate. These differences of two parameters between $0.5 \times 0.5^\circ$ gridded climate data and local climate data affect the ability of the trees to accumulate NSCs.

Second, the scarcity of ground-measured NSC seasonality prevented us from having more average information on NSC concentrations, especially in the tropical and boreal regions, where there were fewer available data. The NSC seasonality differs between biome types, but because it is difficult to measure NSC dynamics, there is a lack of long-term data for each biome type. Hence, I adjusted the new NSC process and its related parameters based on climate zones rather than biome types in our study. The fact that the NSC allocation was further influenced by environmental conditions caused the allocation patterns to change within the same biome type. The NSC allocation to roots was favored over aboveground allocations when soil resources were lacking, and tree size was considered an important determinant of carbon allocation as well as aridity (Hartmann et al., 2020). As I used data from different measurement sites for global-scale validation, I could not account for the potential influence of varying surrounding conditions on the data collected. In addition to the above factors, the number of samples and duration of observations differed between the

various studies. These differences led to no explicit NSC seasonality. These potential sources of error in the field measurements jeopardized the model performances.

5 Conclusions

In this study, a new NSC model was incorporated into the SEIB-DGVM to understand the effect of NSC allocation on global forest dynamics through competition and establishment among individual trees. The new module calculated the NSC dynamics of three organs – leaves, trunk, and roots – and the general NSC seasonality based on ground measurements was determined for biome types in three climate zones: boreal, temperate, and tropical. The NSC seasonality was validated at four sites: Canada (boreal), Austria and Switzerland (temperate), and Panama (tropical). The mean values of simulated NSC concentration agreed reasonably well with observed data on a global scale.

The model enabled me to simulate the biotic effects resulting from insufficient NSC caused by factors such as carbon starvation and insect pests that are otherwise difficult to measure in terrestrial ecosystems globally. The difference of the NSC dynamics in the organs under elevated CO₂ conditions highlighted the importance of modeling the organs separately when studying environmental stresses. As more observation data about NSC dynamics become available, the model can be further improved and can contribute to the simulations of the passive biome shifts that may occur globally.

Chapter 3. The impact of non-structural carbohydrate production on the forest composition during SSP scenarios using SEIB-DGVM-NSC

1 Introduction

The temperature has been increasing during the decades, and the following extreme weather events, such as drought and extreme precipitation events, will become more frequent and strong (IPCC, 2021). Forest productivity and species distributions are expected to be decreased by warming and shifting water availability due to increases in atmospheric CO₂ (Berner and Goetz, 2022), which in turn increase tree mortality rates and translate into changes in the global distribution of biomes (Pastor and Post, 1998; Boonman et al., 2021).

For example, in Europe, forest vulnerability to natural disturbances such as insect outbreaks and drought has also been increasing, and around 58% of the European forests are put at risk of biomass loss although global warming expands the length of the growing season in boreal forests (Romeiro et al., 2022). Moreover, the regions at high latitudes and altitudes are projected to experience drastic changes due to global warming (Antala et al., 2022). In the region a poleward shift of temperate and boreal forest, and the invasion of tropical forest into tropical grasslands are observed (Coline et al., 2021). The changes of the growth, dieback, mortality, and vegetation composition of boreal forests could suggest a shift towards an increased existence of shrublands, or grasslands. The shifts are occurring across a latitudinal gradient of broad-scale climatic patterns' which depends partly on the interaction of precipitation and temperature (Montesano. et al., 2024). The increase of presence, cover, and height of boreal forests extents may affect albedo, thereby carbon sequestration. As the high northern latitudes continue to be affected by increases in temperature, precipitation, and extreme events, the vegetation shift may persist (Montesano. et al., 2024). Biome shifts resulted from climate change have also been observed in Africa (Martens et al., 2020).

Savanna vegetation in West Africa moved southward into previously more humid areas due to change in tree density and species composition. Woody cover in savannas has been increased simultaneously at many sites across Africa, including West Africa resulted from increasing atmospheric CO₂ concentrations and changing rainfall patterns.

Plants stores carbohydrates via photosynthesis used for respiration, plant growth, reproduction, or stored carbon. Nonstructural carbohydrate (NSC) storage is important for supplying energy to plants when photosynthesis cannot produce energy due to dormant season and environmental stress (Blumstein et al., 2023). In the case of drought, the NSC could be a buffer against carbon starvation. When photosynthesis is prevented as stomata is closed to avoid water stress, NSC is gradually used as stored reserves until death. Therefore, plants that live in hotter and drier climates are believed to allocate a larger proportion of their carbon to storage than those from wetter climates as a buffer against drought stress (Blumstein et al., 2020). As the temperature and the frequency of drought will increase in the future, the NSCs play more significant role as a buffer against the drought stress. Hence, it is important to simulate the amount of NSCs and the tree mortality due to scarce of NSCs during future scenario to analyze the effects of climate change on vegetation composition and global distribution of biomes.

However, there was few process-based ecosystem model that be capable of calculating the NSC dynamics well. The spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM; Sato et al., 2007) has been developed to simulate the transient changes in vegetation distribution and dynamics. In the model, individual trees grow on numerous replicate patches, and single, large trees can influence nearby trees for water and light energy. In each grid, as a result of competitive interactions between individual trees, the model can be able to simulate the growth and mortality of each tree based on environmental conditions. We have advanced SEIB-DGVM, and developed the new ecosystem model named SEIB-

DGVM-NSC (Ninomiya et al., 2023), which can calculate the amount of NSCs in three organs (leaf, trunk, and root) of plant bodies at a global scale in SEIB-DGVM. The amount of NSCs in each organ have been validated based on observation data. Thus, in the model, individual trees possess their own NSC compartments, which influence their growth and mortality. This, in turn, impacts competition among individual trees within the environment conditions. Moreover, the model can simulate how the future production of NSC affect the global distribution of biomes, and the effect of carbon starvation on the global carbon cycle.

The objectives of the research were to simulate 1) how much the NSC will be stored with regions with increasing atmospheric CO₂, 2) how the production of NSCs affect the vegetation composition and global vegetation distribution in future scenarios, and 3) how the tree mortality resulted from decreasing NSC impact on global carbon cycle.

2 Method

2.1 Overview of SEIB-DGVM-NSC

The SEIB-DGVM-NSC is (v1.0; <https://zenodo.org/records/8080601/files/SEIB-DGVM-NSC%20ver.1.zip?download=1>, last access: 1 April 2023; Ninomiya et al., 2023) is a carbon budget model that the forest dynamics was represented in a 30 m × 30 m stand of trees with simulation grid cells. In each cell, the model simulates the establishment and death of individual trees and competition between trees based on input climate data. In each grid cell, a tree representing 1 of 14 woody plant functional types (PFTs) and 1 of 2 grass PFTs is assigned. The plants experience all physical and physiological processes at daily time steps, and trunk growth is calculated monthly. Although, the original SEIB-DGVM has no mechanism to control the NSC in leaves and roots, the SEIB-DGVM-NSC has the NSC compartments in three organs (leaf, trunk, and root) respectively. The assimilated carbon after adjusting the available organic matter for reproduction and respiration firstly satisfy three NSC compartments before being used for growth of organs. The sizes of NSC compartment are determined by the daily gross primary production (GPP) and biomass of each organ for temperate and boreal forests, and by the daily biomass for tropical forests respectively. When the photosynthetically assimilated carbon is insufficient for maintenance respiration, the NSCs in all organs compensates for the shortage.

2.2 Climate input data

The SEIB-DGVM-NSC needs 10 climatic variables: air temperature, soil temperature at a depth of 50 cm (soil layer 1), soil temperature at a depth of 100 cm (soil layer 2), soil temperature at a depth of 150 cm (soil layer 3), precipitation, shortwave radiation, longwave radiation, wind velocity, specific humidity, and diurnal range of air temperature. The input

climate data were prepared by harmonizing monthly outputs from global climate models (GCMs, <https://data.isimip.org/>, last access: 1 April 2023) with the 6-hourly CRUJra v2.2.5 dataset and the monthly CRU TS v4.0 dataset, which provides gridded time series of ten meteorological variables at a $0.5 \times 0.5^\circ$ resolution.

The preparation process involved several steps. First, the mean values of the variables (excluding relative humidity and wind velocity) during the period 1991–2000 were subtracted from the GCM data. These were then adjusted by adding the mean data for the same time range derived from CRUJra v2.2.5 for shortwave and longwave radiation, and from CRU TS v4.0 for the other parameters. For daily variations, wind velocity, relative humidity, temperature, and precipitation data were adjusted. Specifically, the daily magnitude was calculated using the 2020 daily data from CRUJra v2.2.5. This was done by subtracting the total mean daily value for precipitation and dividing by the mean annual total for other parameters. The resulting values were then multiplied by the harmonized GCM data to create the final input dataset.

To reach equilibrium conditions of the biomes, plant, and soil carbon pools, a 1000-year spin-up simulation was performed by looping the climate data and atmospheric CO₂ concentrations. The first 30 years (1850–1880) were therefore looped for a 1000-year spin-up simulation. After the spin-up, simulations were run for the historical period 1850–2014, and the future period 2015–2100. For the future period, I run the 3 different shared socio-economic pathways (SSP126, 370, and 585).

2.3 Tree mortality process related to carbon starvation

In the SEIB-DGVM-NSC, the mortality process is calculated on a yearly time step. The overall death rate for each individual tree is determined as the sum of various mortality

components, which include background mortality related to growth efficiency, heat stress, and cold stress. Additionally, a new mortality process related to NSC scarcity has been incorporated to represent carbon starvation. To simulate carbon starvation, four specific conditions must be satisfied. First, the state of water availability for each PFT, defined as a value ranging from 0.0 to 1.0, must be less than 0. Second, the state of water availability must exceed the wilting point (Table 7). Third, the photosynthetic rate must fall below 0. Finally, the ratio of total NSCs to total woody biomass must be less than 2.5%. These criteria collectively define the vulnerability threshold for carbon starvation within the model.

$$\text{Mortality}_{\text{NSC}} = -7.612 \times e^{4.506 \times \text{NSCratio}} + 8.591 \quad (15)$$

where NSCratio is the ratio of total NSCs to total woody biomass (0-0.025).

The mortality rate due to carbon starvation increases exponentially as the ratio of NSCs to total woody biomass decreases (Eq. (15)). The rates were arbitrarily defined to simulate the desired dynamics: at an NSC-to-woody biomass ratio of 2.5%, the mortality rate is set at 10%; at a ratio of 1.5%, the rate increases to 40%; and when the ratio reaches 0%, the mortality rate becomes 100%. The new mortality process allows SEIB-DGVM-NSC to simulate the effects of carbon starvation on tree mortality more effectively.

Table 7. Wilting point for different soil type

Soil type	Wilting point
Coarse loamy sand	0.029
Silty clay loam	0.119
Light clay	0.139
Coarse-medium sandy loam	0.047
Coarse-fine sandy clay	0.100
Medium-fine clay loam	0.103
Coarse-med-fine sandy clay loam	0.069
Organic loam	0.066
Glacial land ice loamy sand	0.029

3 Results

3.1. Differences of vegetation composition between SEIB-DGVM-NSC and SEIB-DGVM

Tree height

I compared tree height between SEIB-DGVM-NSC and original SEIB-DGVM that does not include NSC dynamic process. Tree height in the new model was smaller than in the original model across all regions (Figure 6). In Asia, tree height in the original model during SSP scenarios was about 1 meter higher than in historical periods, while tree height in the new model also slightly increased from the historical to SSP scenarios, but at a slower rate compared to the original model. In Europe, tree height in the original model remained consistent at around 23 meters across all scenarios, showing no growth with increasing CO₂. However, tree height in the new model decreased by about 1 meter during SSP scenarios compared to historical periods, with no significant differences observed between the three SSP scenarios. In North America, tree height did not change during SSP scenarios in either model.

The distribution of tree height also differed between the two models under SSP scenarios (Figure 7). Tree height increased in Siberia in both models, with a higher rate of increase under SSP585 compared to SSP126. The regions where tree height increased during the three SSP scenarios in the new model were more extensive than in the original model. The original SEIB-DGVM simulated a decrease in tree height in Western Asia, while SEIB-DGVM-NSC simulated a decrease in Eastern Asia under all three SSP scenarios. In Europe, the original model showed mixed regions of increasing and decreasing tree height, while the new model demonstrated a clearer pattern, with tree height decreasing in southern Europe and increasing

in northern Europe (Figure 8). The decreasing trend in southern Europe became more pronounced with rising CO₂ levels. In North America, the original model simulated a decrease in tree height in the northern regions, while the new model projected an increase. Additionally, the new model simulated a significant decline in tree height in eastern regions, which was not observed in the original model (Figure 9). The probability density of tree height across the three regions showed that the new model calculated a higher number of trees within the 0–10 meter height range compared to the original model in all regions (Figures 10–12). In Europe, the original model indicated that most regions were occupied by trees with heights of 20 meters and 25 meters. In contrast, the new model showed two dominant tree height ranges: 0–10 meters and 20–30 meters, with a wider difference between the two top densities compared to the original model.

Diameter at breast height (DBH)

I compared DBH between the new model and the original model. DBH in the new model was smaller than in the original model across all regions (Figure 13). In Asia, DBH from the original model during SSP scenarios was about 5 cm larger than in historical periods, while DBH in the new model also slightly increased from historical to SSP scenarios, but the rate of increase was smaller than in the original model. In Europe, DBH in the original model remained around 60 cm across all scenarios, showing no growth with increasing CO₂. However, DBH in the new model during the historical period was about 48 cm and decreased by 2–3 cm during SSP scenarios. In North America, DBH in the original model increased slightly by 1 cm, whereas DBH in the new model decreased by 2 cm between historical and SSP126, and by 4 cm from historical to SSP370 and SSP585.

The distribution of DBH also varied between the two models under SSP scenarios in Asia (Figure 14). In Siberia, both models simulated an increase in DBH, with a higher rate of

increase under SSP585 compared to SSP126. However, patterns of DBH decrease differed between the models. The original model predicted a decrease in DBH in the middle part of Asia, while the new model projected a decrease in Eastern Asia under all three SSP scenarios. The magnitude of the DBH changes in the original model was larger than in the new model. In Europe, the original model displayed mixed regions of increasing and decreasing DBH, while the new model showed a clearer pattern, with DBH decreasing in southern Europe (Figure 15). In North America, both models predicted an increase in DBH in northern regions, but the new model projected a significant decrease in eastern regions, while the original model showed a decrease in western regions (Figure 16). The probability density of DBH across the three regions revealed that the new model estimated a higher number of trees within the 0–10 cm DBH range compared to the original model (Figures 17–19). In Asia, the range of 0–50 cm DBH in the new model became flatter from historical to SSP scenarios compared to the original model. In Europe, the original model showed two peaks during historical scenarios (25–50 cm and 75–100 cm), but with increasing CO₂, the 75–100 cm peak diminished, resulting in a single peak at 25–50 cm. However, the new model histogram did not show significant differences between historical and SSP scenarios. In North America, both models showed a shift of the peak toward lower DBH values from historical to SSP scenarios.

Percentage of biome types occupied

In Asia, the percentage of temperate deciduous forests in the new model was lower compared to the previous model (Figure 20). The total percentage of deserts and grasslands in the new model was higher than in the original model by about 5%. The future trend of increasing desert and grassland coverage was similar in both models, with deserts and grasslands occupying more area over time and intensifying with rising CO₂ levels. In Europe, temperate deciduous forests occupied a larger area in the original model, and their percentage

remained stable across the three SSP scenarios (Figure 21). In contrast, the new model projected a larger increase in the percentage of deserts and grasslands during SSP370 and SSP585. The trend of biome type percentages in North America resembled that in Asia (Figure 22). Temperate deciduous forests occupied more area in the original model, while deserts and grasslands occupied more area in both models as CO₂ levels rose.

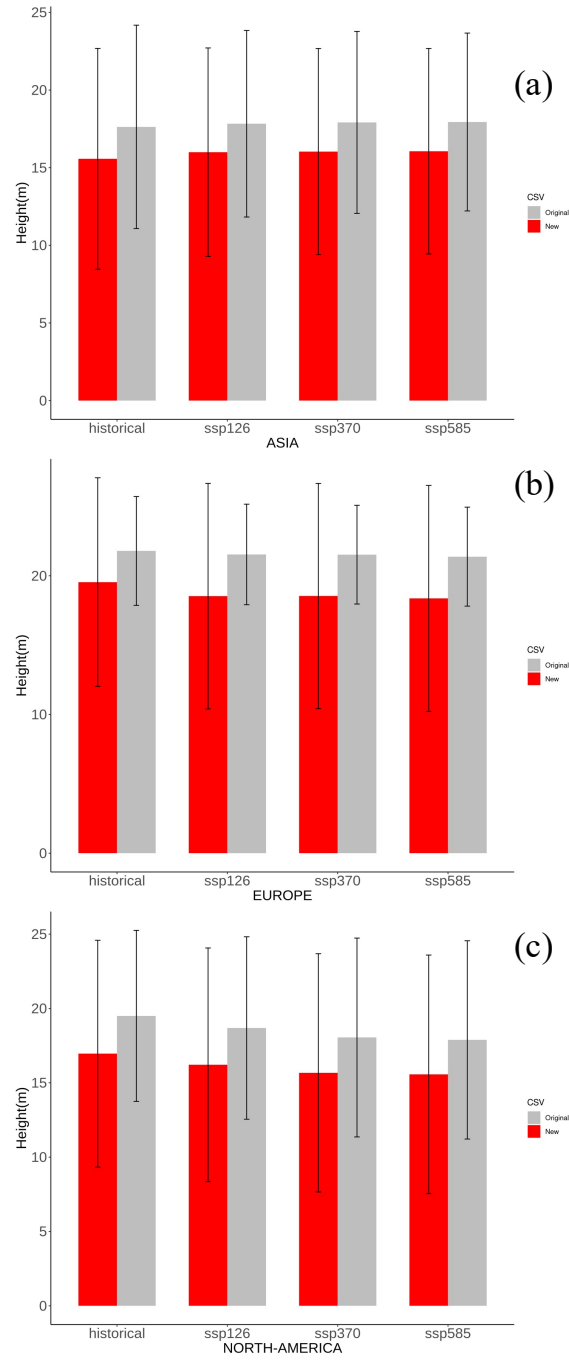


Figure 6. Changes in tree height, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from SEIB-DGVM-NSC, while the gray bars represent outputs from the original SEIB-DGVM.

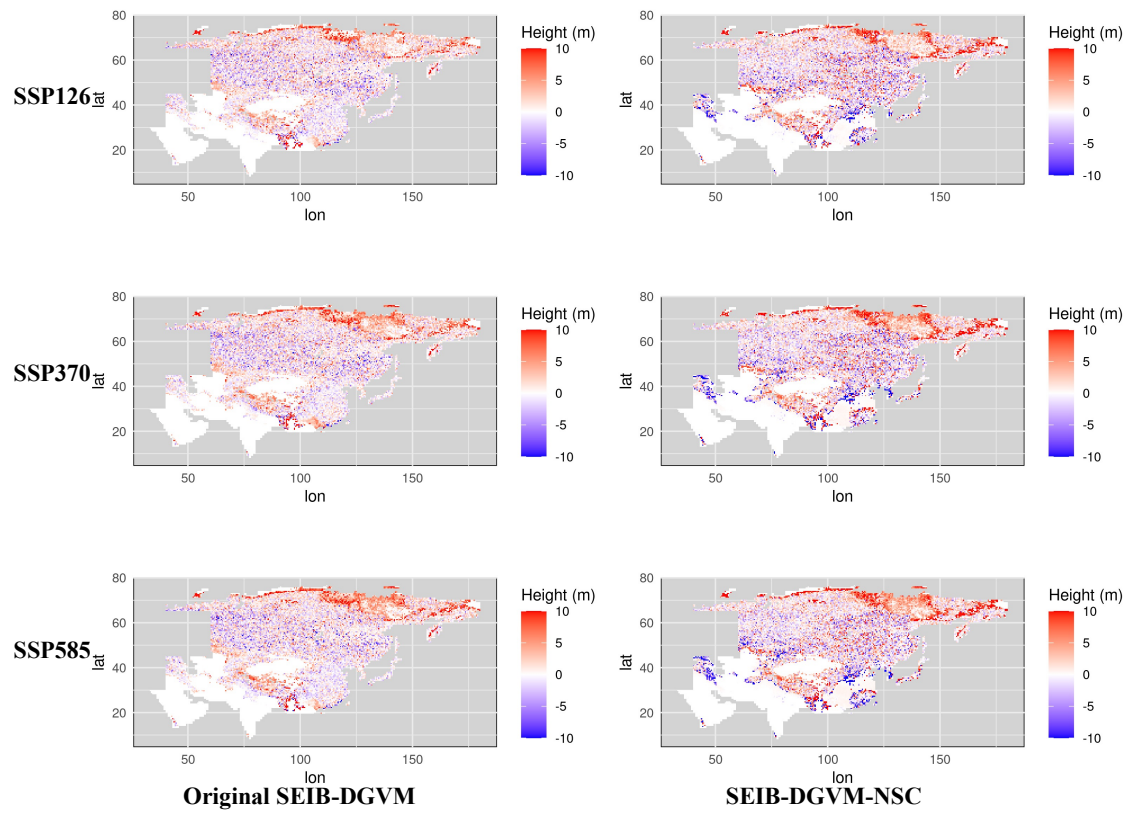


Figure 7. Distribution of differences in tree height in Asia, averaged from 1985–2014 to 2071–2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

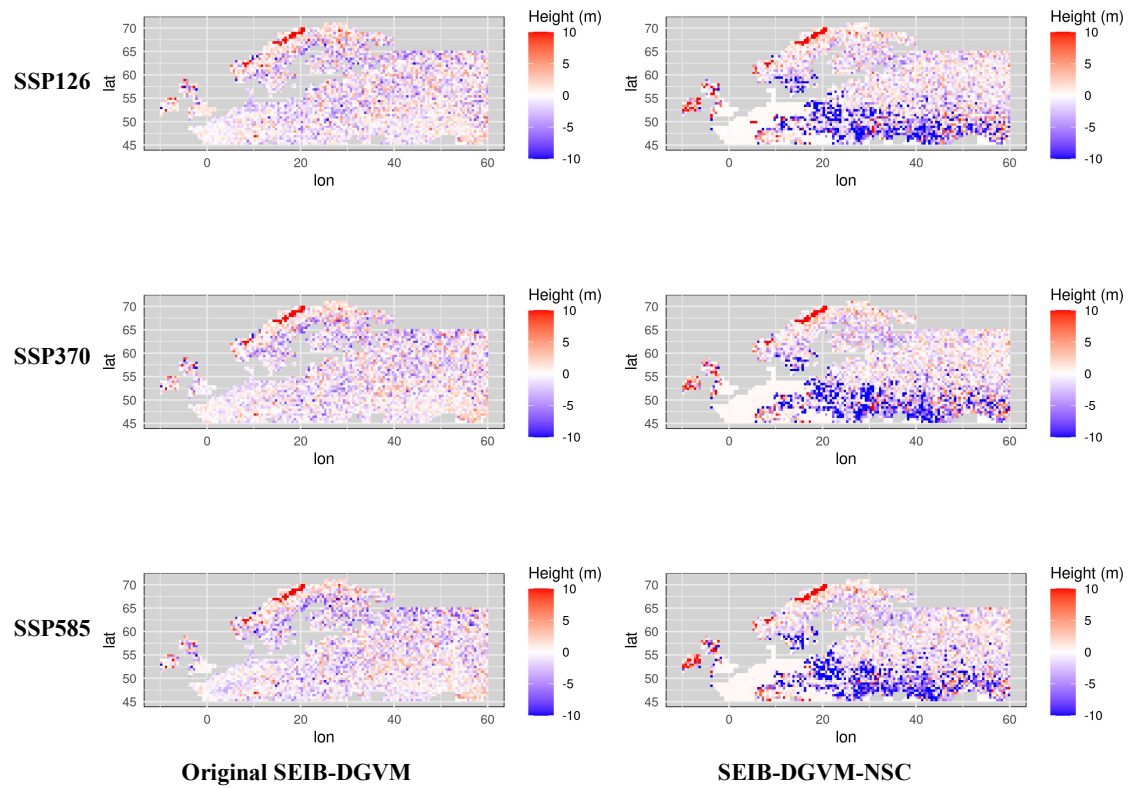


Figure 8. Distribution of differences in tree height in Europe, averaged from 1985–2014 to 2071–2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

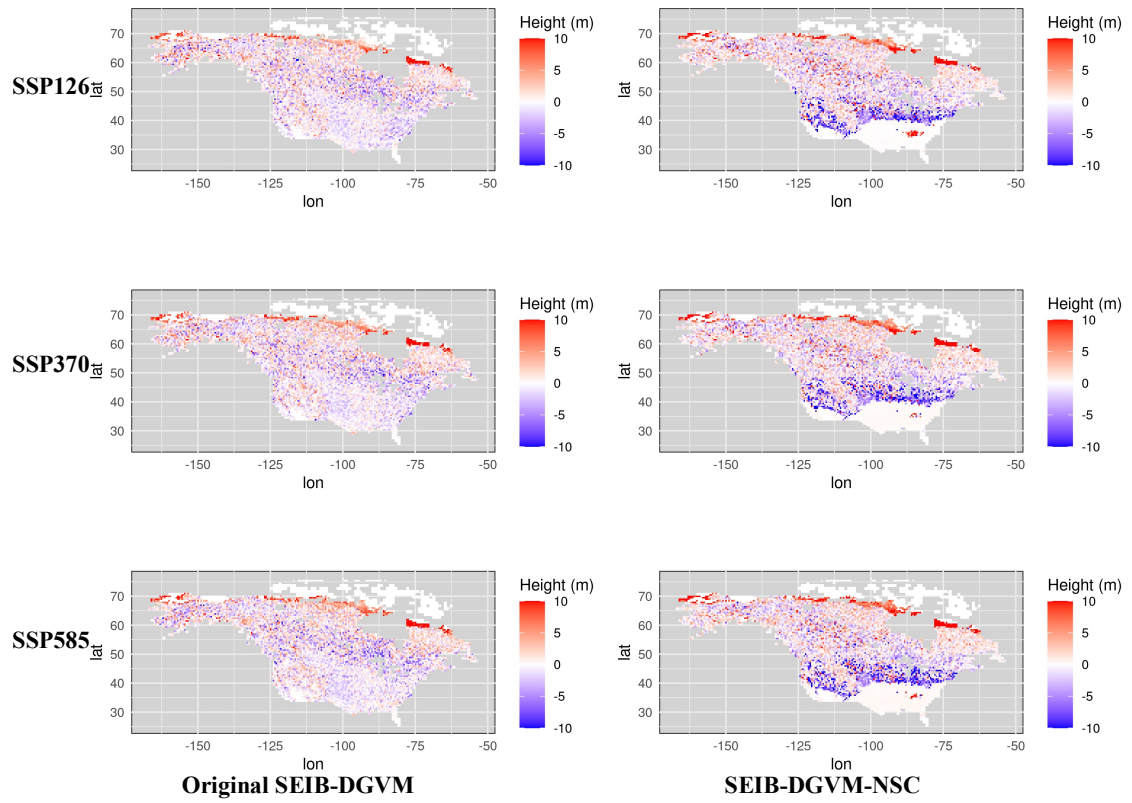


Figure 9. Distribution of differences in tree height in North America, averaged from 1985–2014 to 2071–2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

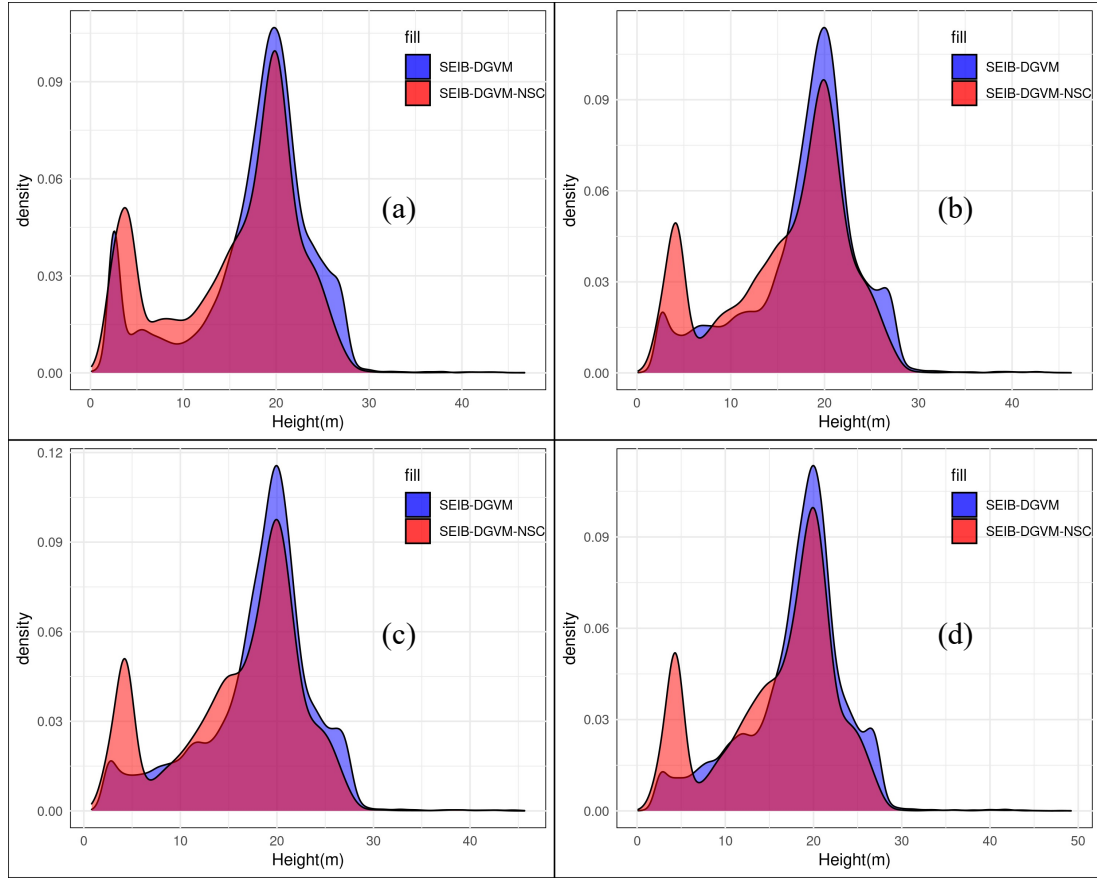


Figure 10. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in Asia. The red areas represent outputs from SEIB-DGVM-NSC, while the blue areas represent outputs from the original SEIB-DGVM.

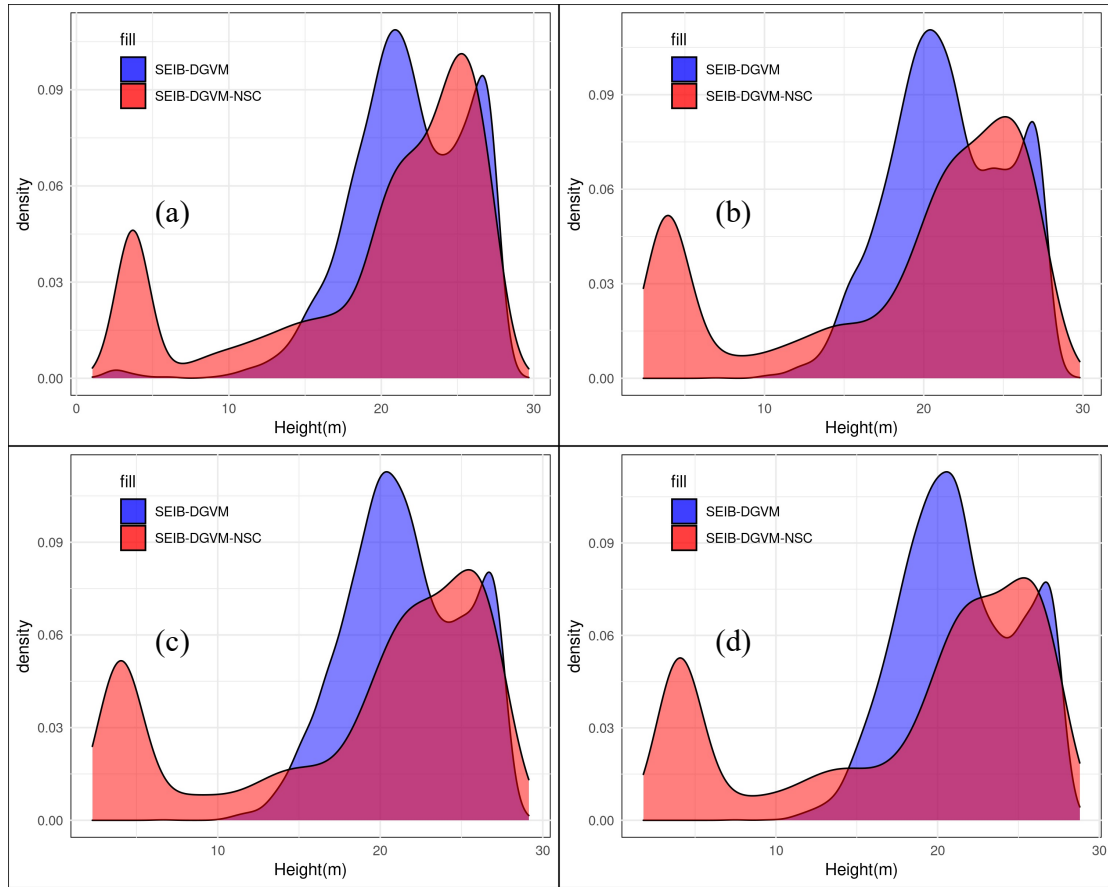


Figure 11. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in Europe. The red areas represent outputs from SEIB-DGVM-NSC, while the blue areas represent outputs from the original SEIB-DGVM.

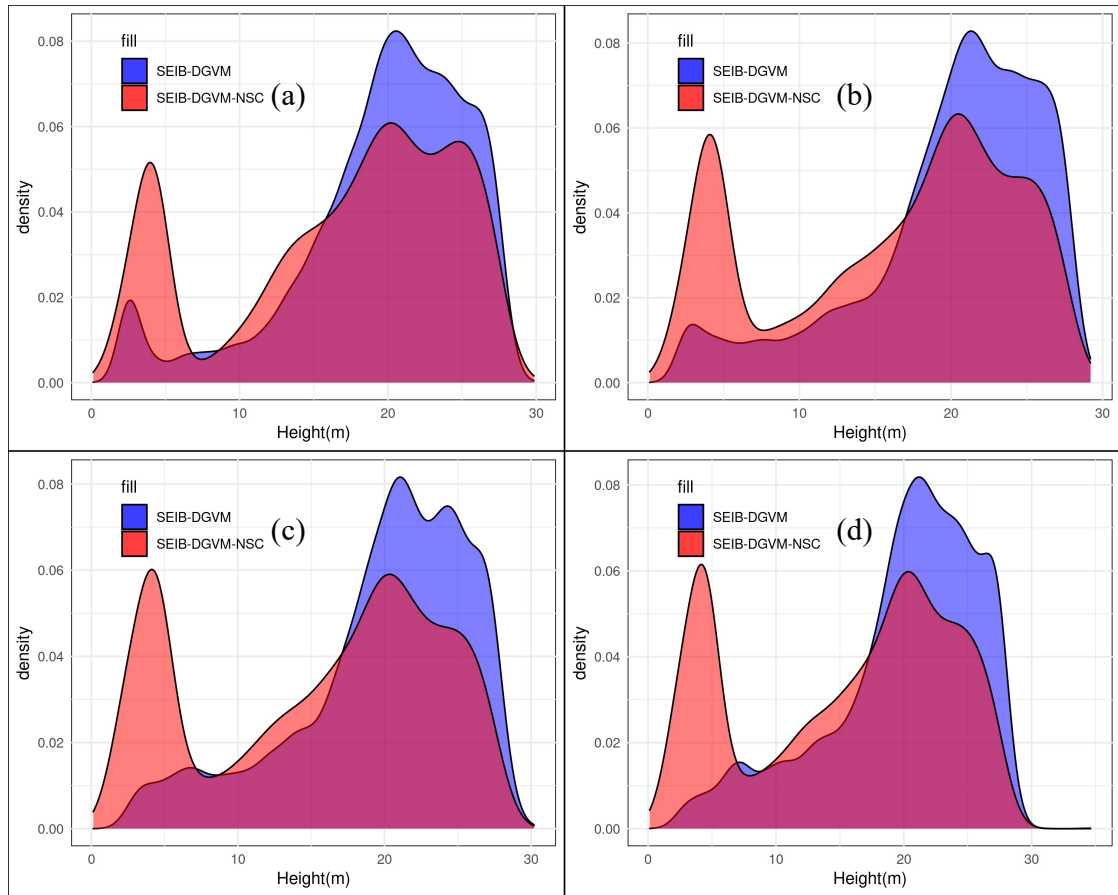


Figure 12. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in North America. The red areas represent outputs from SEIB-DGVM-NSC, while the blue areas represent outputs from the original SEIB-DGVM.

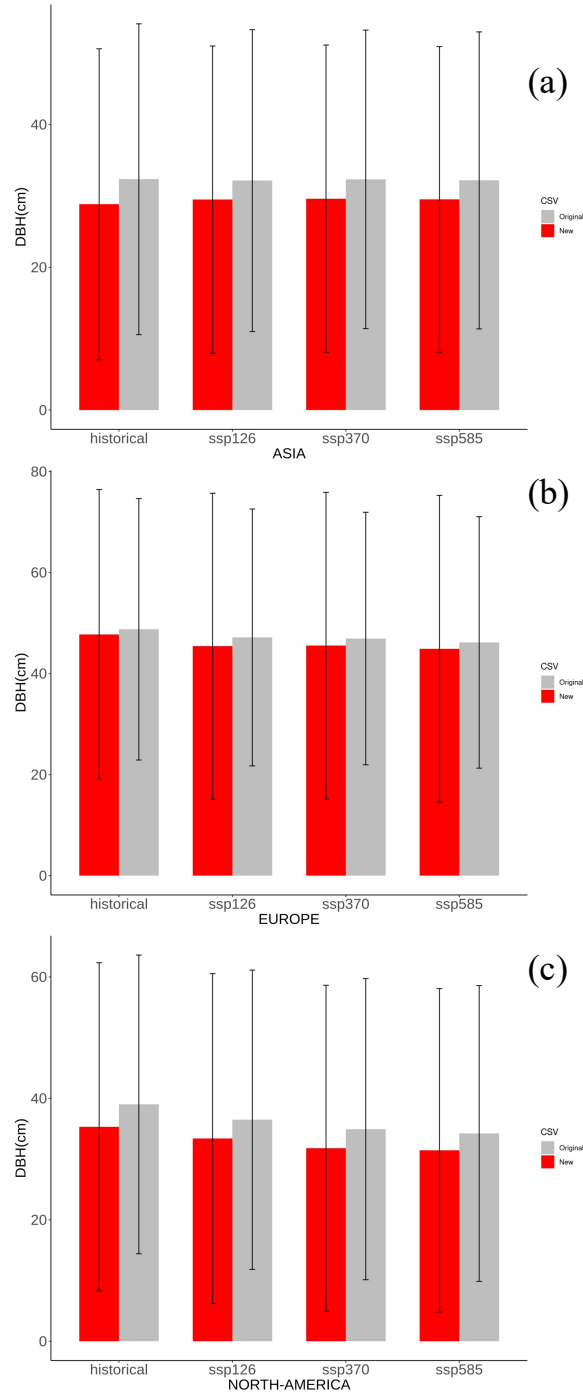


Figure 13. Changes in DBHs, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from SEIB-DGVM-NSC, while the gray bars represent outputs from the original SEIB-DGVM.

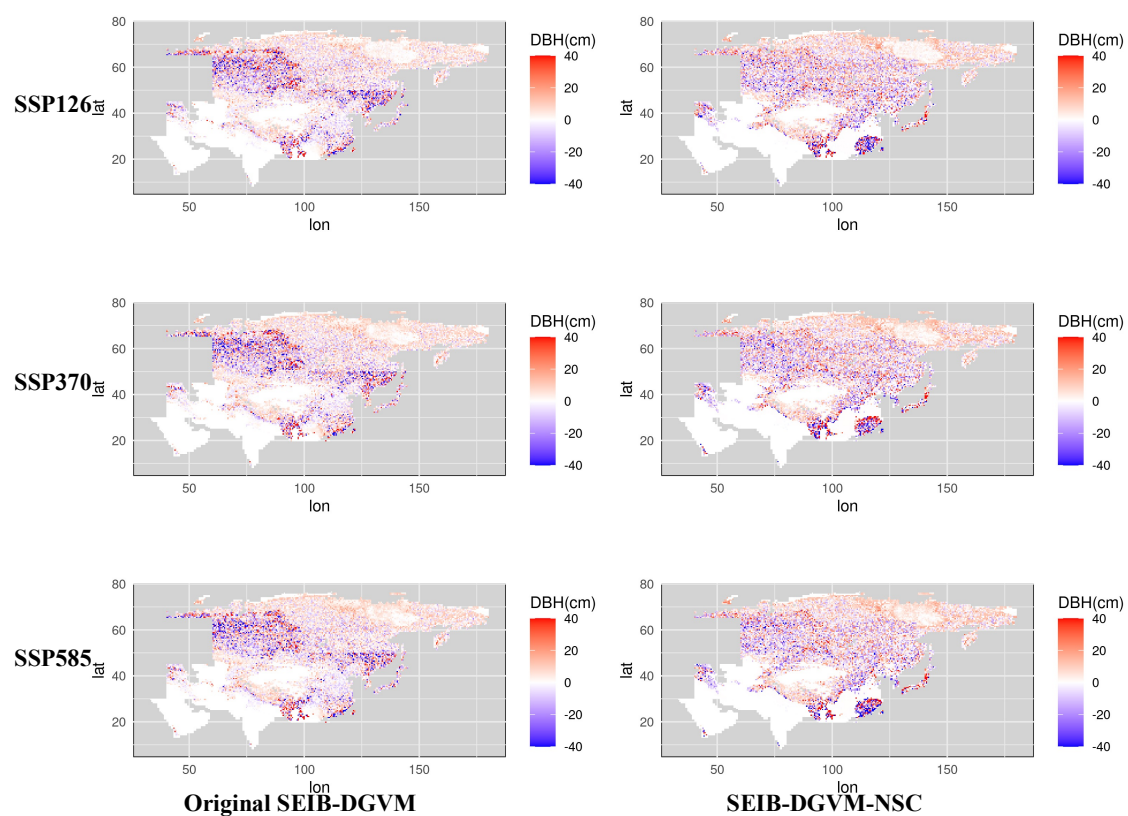


Figure 14. Distribution of differences in DBH in Asia, averaged from 1985–2014 to 2071–2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

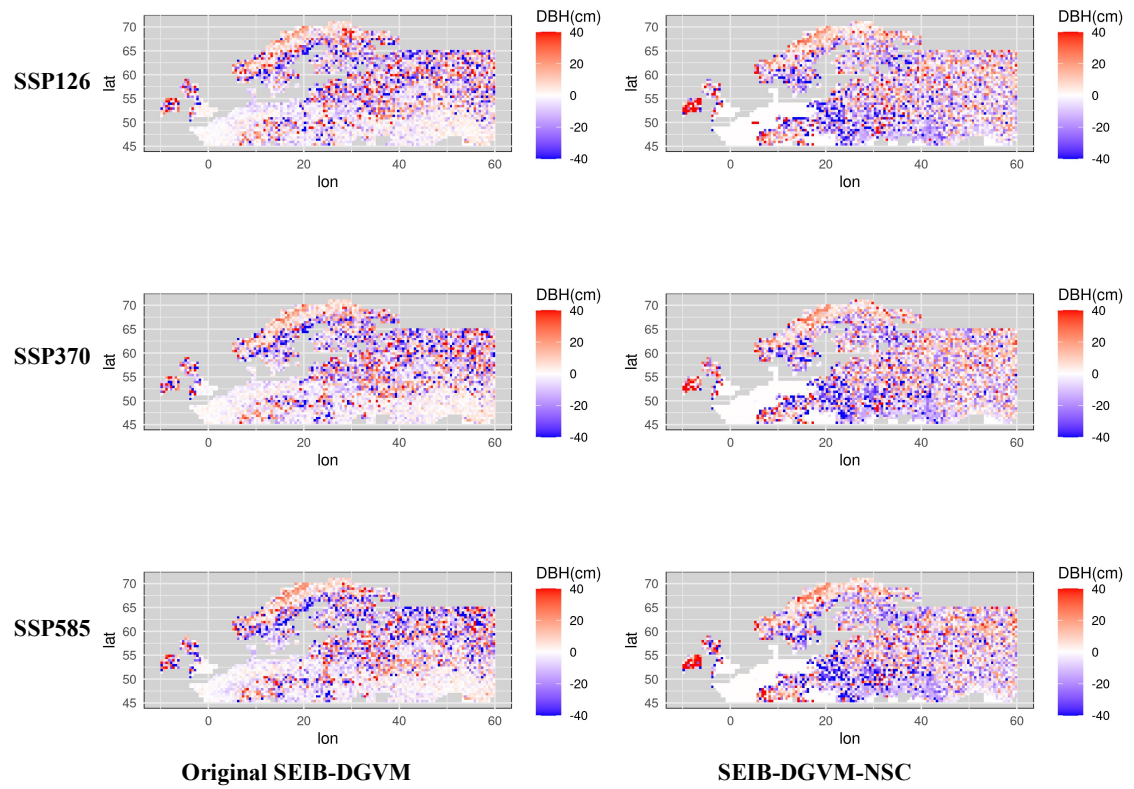


Figure 15. Distribution of differences in DBH in Europe, averaged from 1985–2014 to 2071–2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

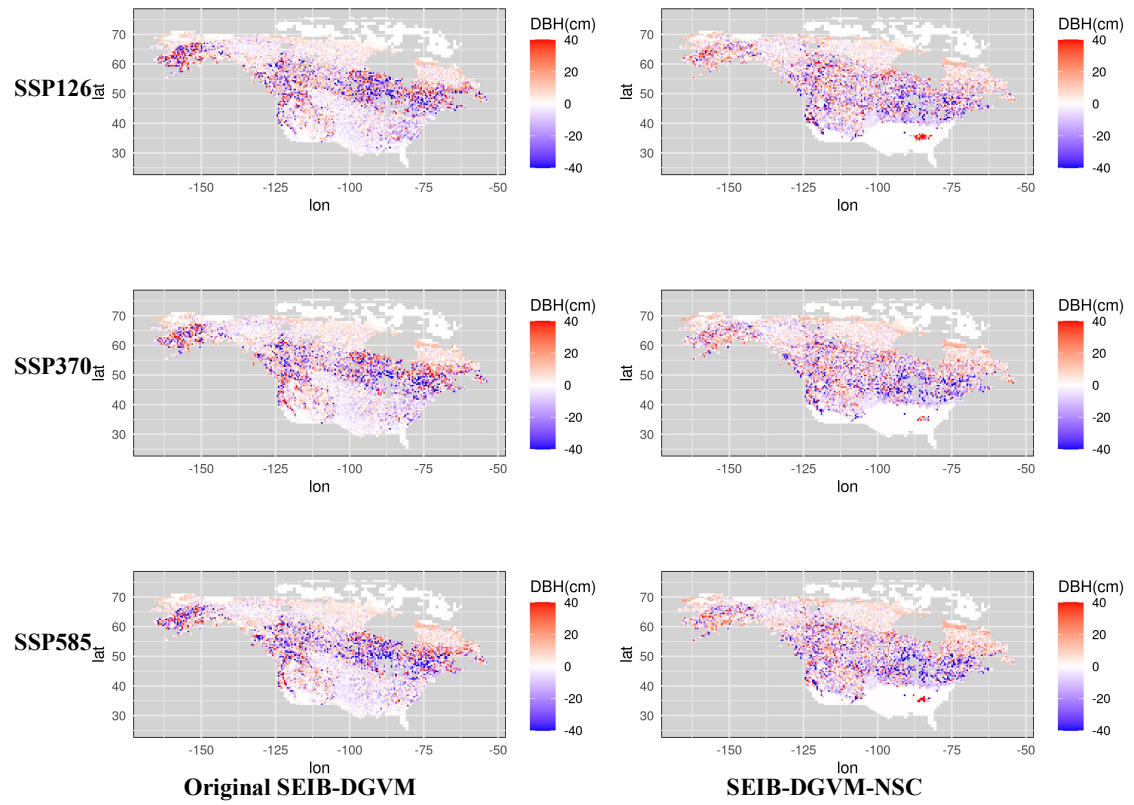


Figure 16. Distribution of differences in DBH in North America, averaged from 1985–2014 to 2071–2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

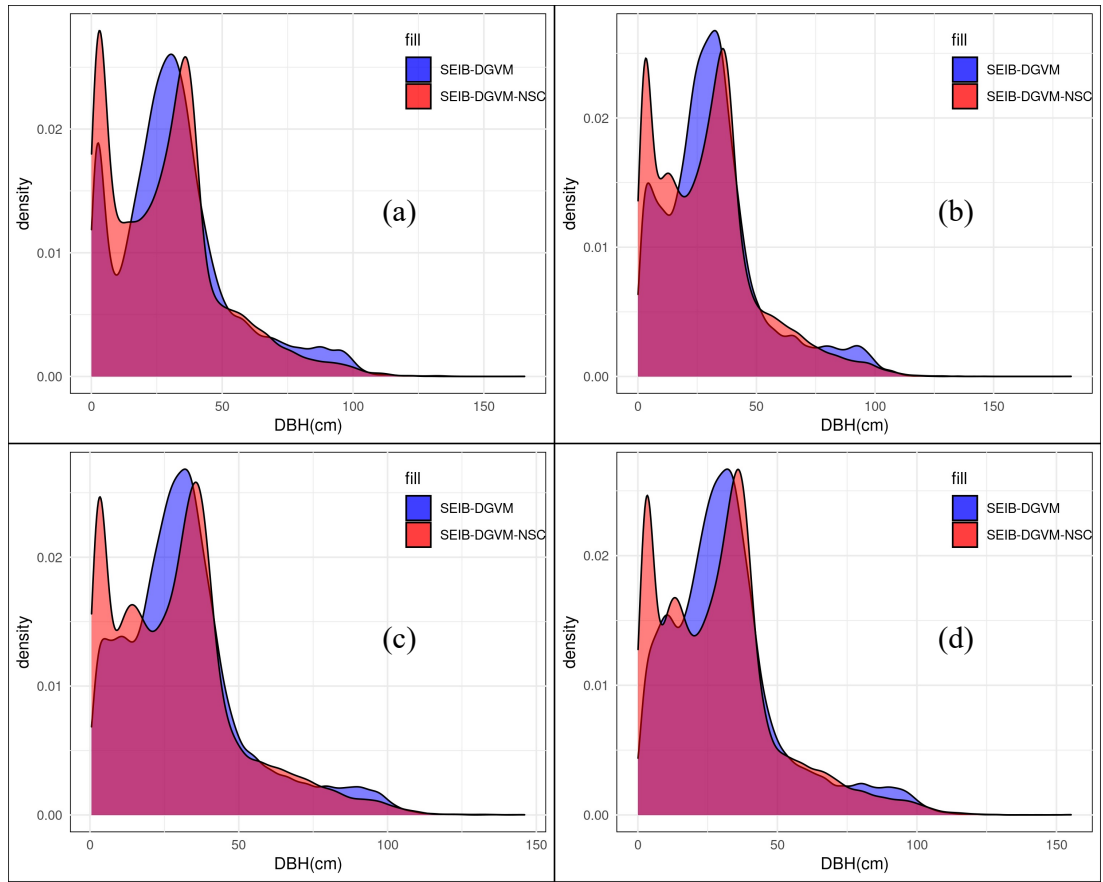


Figure 17. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in Asia. The red areas represent outputs from SEIB-DGVM-NSC, while the blue areas represent outputs from the original SEIB-DGVM.

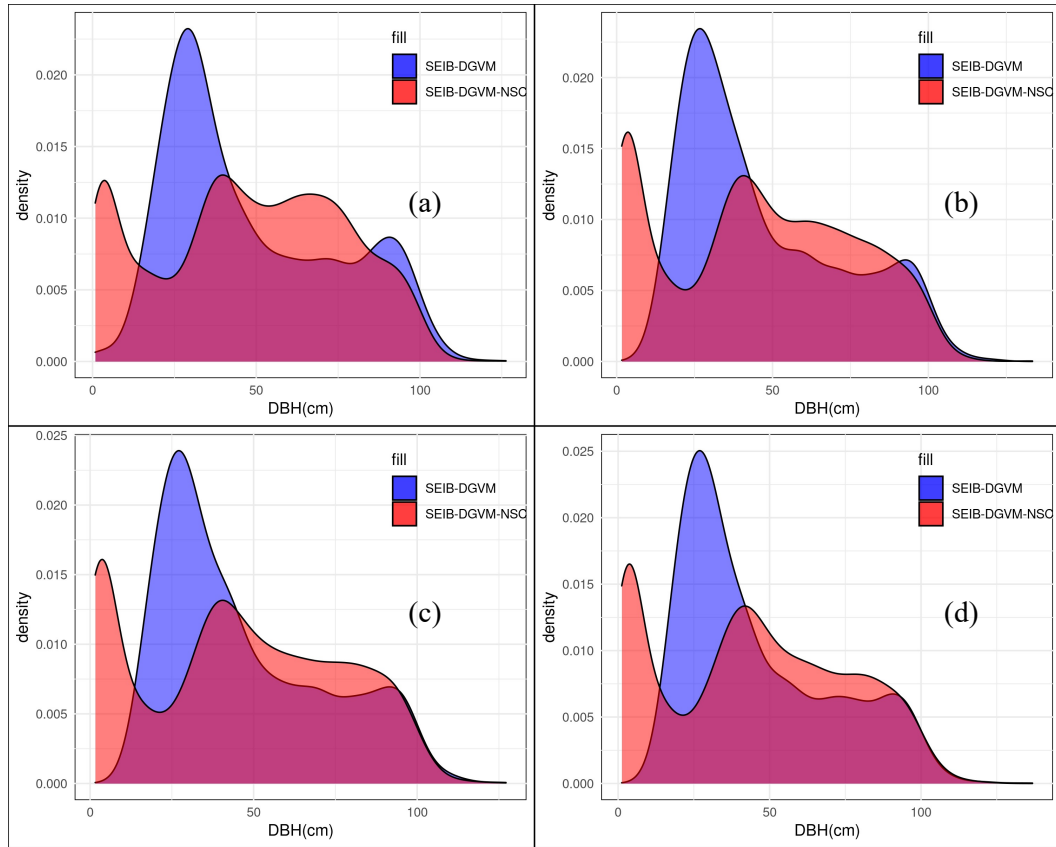


Figure 18. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in Europe. The red areas represent outputs from SEIB-DGVM-NSC, while the blue areas represent outputs from the original SEIB-DGVM.

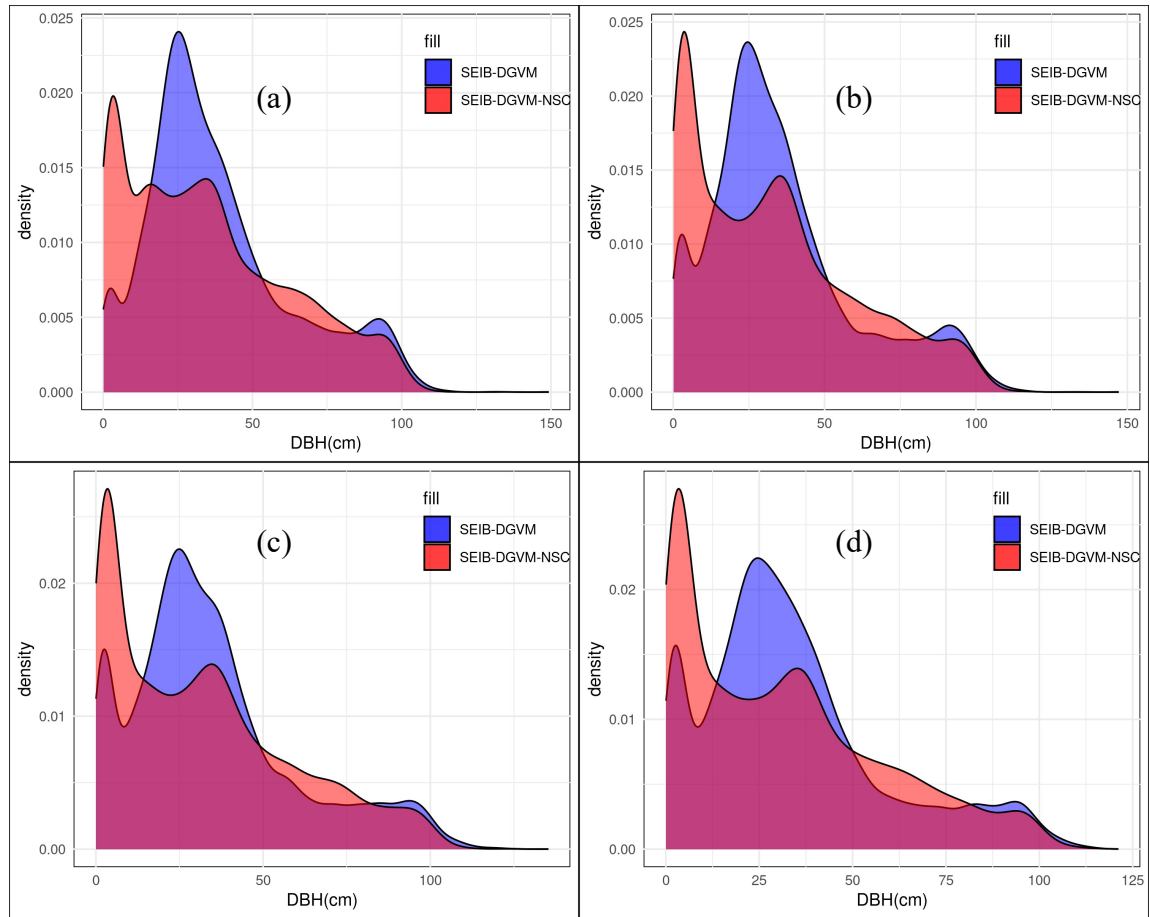


Figure 19. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in North America. The red areas represent outputs from SEIB-DGVM-NSC, while the blue areas represent outputs from the original SEIB-DGVM.

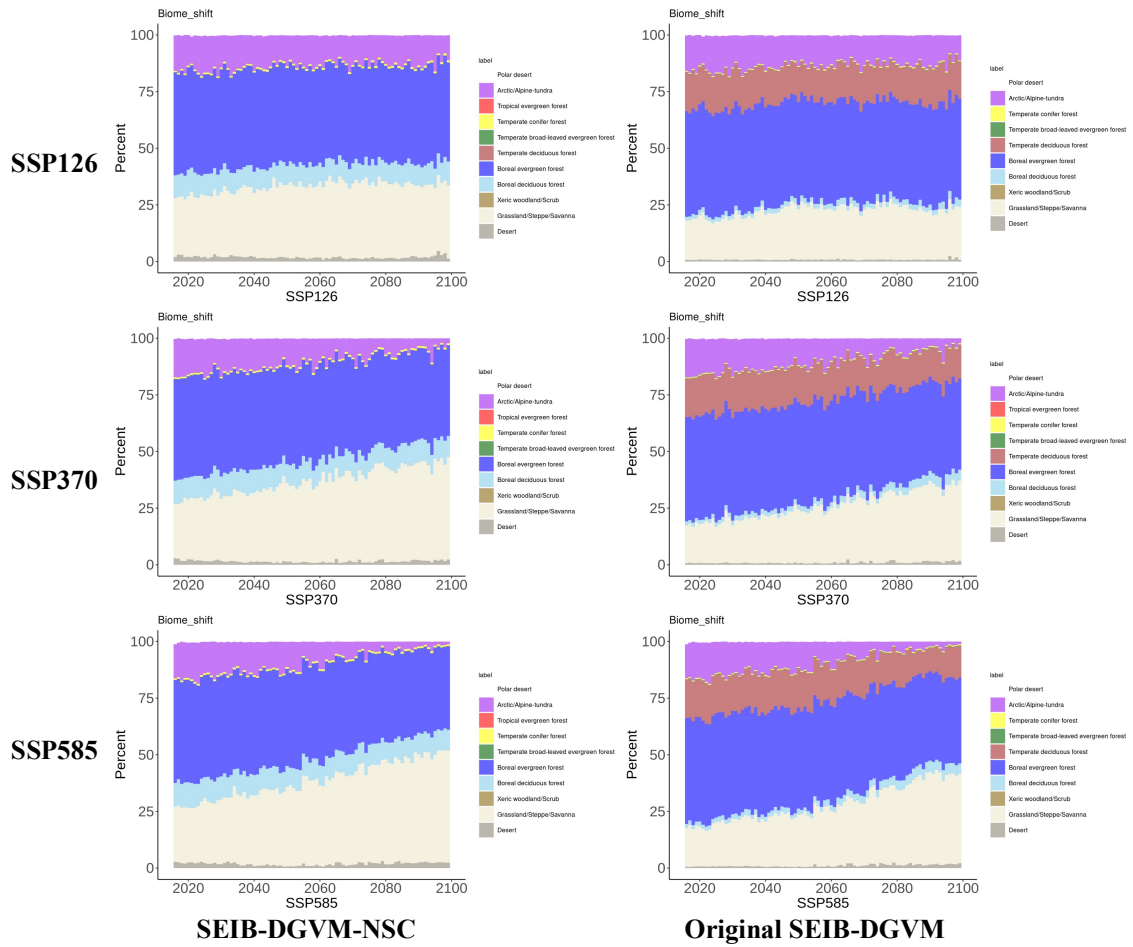


Figure 20. Percentage of biome types occupied in Asia from 2015 to 2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

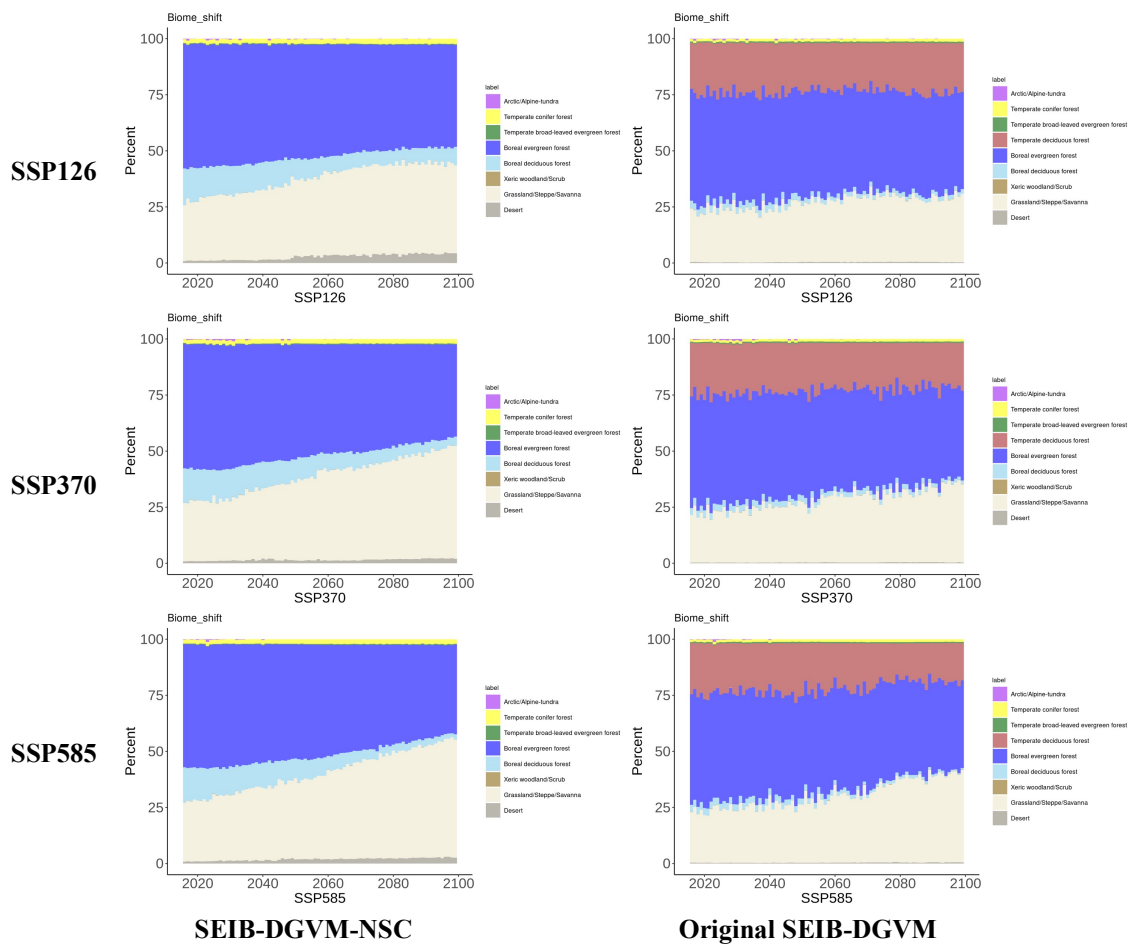


Figure 21. Percentage of biome types occupied in Europe from 2015 to 2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

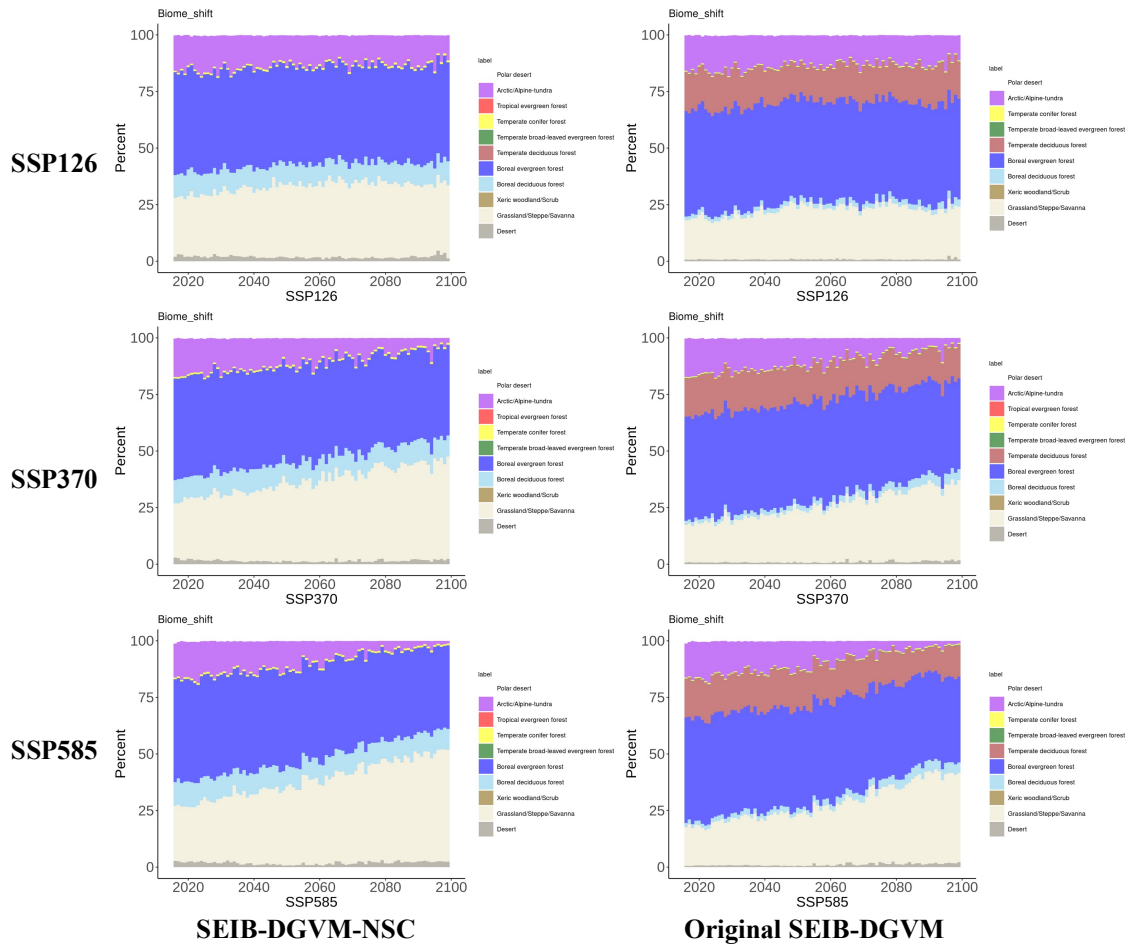


Figure 22. Percentage of biome types occupied in North America from 2015 to 2100, under SSP126, SSP370, and SSP585 scenarios, as calculated by the original SEIB-DGVM and SEIB-DGVM-NSC.

3.2 Carbon starvation effect on vegetation composition

The number of trees

I simulated the SEIB-DGVM-NSC model with carbon starvation switched on and off. First, I analyzed the decrease in tree numbers under different SSP scenarios (Figure 23). In Asia, the decrease in tree numbers was pronounced under SSP126 and gradually increased under SSP370 and SSP585 with both settings (Figure 23(a)). In Europe, the decrease in tree numbers was observed under all three SSP scenarios compared to historical periods (Figure 23(b)). When the carbon starvation switch was turned on, the magnitude of the decrease became progressively larger with increasing CO₂ levels compared to when the switch was off across all scenarios. In North America, tree numbers gradually increased with rising CO₂ levels, and the magnitude of the increase was greater when the switch was on than when it was off (Figure 23(c)).

In the probability density analysis, the highest density of tree numbers in Europe remained the same regardless of whether the carbon starvation switch was turned on or off. However, in Asia and North America, the highest density shifted to lower tree numbers (Figures 24–26). When the switch was on, the density in the 0–100 range was higher than when the switch was off across all regions and SSP scenarios. In Asia, approximately 100 trees existed in most regions with the switch off during historical and SSP scenarios, but with the switch on, the density decreased to about 75 trees during historical periods and near 50 trees in most regions during SSP scenarios (Figure 24). In Europe, the probability density remained unchanged during historical scenarios regardless of whether the switch was on or off. However, with rising CO₂ levels, the regions with a smaller number of trees increased when the switch was on compared to when it was off (Figure 25). In North America, the histogram of tree numbers with the switch on was flatter than with the switch off. Regions with fewer trees were more prevalent due to the effects of carbon starvation when the switch was on (Figure 26).

Tree age

I compared tree age between the switched-on and switched-off settings. The mean tree age, averaged across regions, slightly decreased under SSP scenarios compared to historical scenarios for both settings (Figure S1). When the switch was turned on, the mean tree age was about 5 years younger than when the switch was turned off across all three regions. When I focused on regions where carbon starvation occurred, the difference between the switched-on and switched-off settings became more pronounced (Figure 27). In Asia, tree age remained similar under all three SSP scenarios compared to historical scenarios for both settings (Figure 27(a)). However, with the switch turned on, the mean tree age was about 10 years younger than with the switch turned off. In Europe, when the switch was turned off, tree age slightly decreased consistently across the three scenarios, and the same trend was observed when the switch was turned on (Figure 27(b)). In North America, the decreasing trend in tree age was similar for both settings. However, the difference in tree age between the switched-on and switched-off settings was smaller during SSP126 than during SSP585 (Figure 27(c)).

In the probability density analysis, which included all regions (whether or not carbon starvation occurred), there was no strong difference in tree age across scenarios and regions (Figures S2–S4). Therefore, the overall effect of carbon starvation on tree age was not significant. Even when focusing only on regions where carbon starvation occurred, there was no substantial difference between the switched-on and switched-off settings (Figure 28–30). In Asia and North America, the number of trees aged less than 100 years slightly decreased with the switch turned on compared to when it was turned off.

Tree height

I compared tree height between the switched-on and switched-off settings. Tree height did not show a strong difference between the two settings across all scenarios and regions (Figure S5). In the analysis focusing only on regions where carbon starvation occurred, tree height in Asia was similar during SSP scenarios compared to historical scenarios for both settings (Figure 31). When the switch was turned on, tree height was about 0.5 m higher than when the switch was turned off.

In Europe, tree height slightly decreased during SSP scenarios by approximately 1 m compared to historical periods. The difference between the switched-on and switched-off settings gradually increased during SSP scenarios. In North America, tree height during SSP126 was about 0.5 m shorter than in historical scenarios. During SSP370 and SSP585, tree height further decreased compared to historical scenarios, with a slightly larger decline as CO₂ levels increased. When the switch was turned on, tree height slightly decreased during SSP585 and SSP370 compared to SSP126, following a similar trend as when the switch was turned off.

In the probability density analysis across all regions, the histogram did not show significant differences between the switched-on and switched-off settings across all scenarios and regions (Figure S6–S8). When analyzing only regions where carbon starvation occurred, the 20–30 m range of tree height under the switched-on setting was larger than under the switched-off setting in Asia (Figure 32). However, the size of this range gradually decreased from SSP126 to SSP370 and SSP585. In Europe, the range of trees taller than 20 m was larger under the switched-on setting compared to the switched-off setting, and it further increased during SSP scenarios compared to historical scenarios (Figure 33). In North America, the number of trees taller than 20 m was higher when the switch was turned on compared to when it was turned off (Figure 34). However, the difference between the switched-on and switched-off settings became smaller during SSP370 and SSP585 compared to historical scenarios and SSP126.

DBH

I compared DBH between the switched-on and switched-off settings. DBH did not show a significant difference between the two settings across all scenarios and regions (Figure S9). In the analysis focusing only on regions where carbon starvation occurred, DBH in Asia was similar during historical, SSP126, and SSP370 scenarios for both settings but decreased by 3 cm during SSP585 (Figure 35(a)). The difference between the switched-on and switched-off settings was about 3 cm, and this difference remained consistent across different scenarios. In Europe, DBH decreased by approximately 5 cm during SSP126 and 7 cm during SSP370 compared to historical

periods (Figure 35(b)). DBH slightly decreased across SSP scenarios up to SSP370, with no additional change during SSP585 compared to SSP370. The difference between the switched-on and switched-off settings was about 1 cm for historical scenarios but increased to approximately 2 cm across the three SSP scenarios. In North America, DBH during SSP126 was approximately 2 cm shorter than in historical scenarios (Figure 35(c)). During SSP370 and SSP585, DBH further decreased compared to historical scenarios, with a slightly larger decrease observed as CO₂ levels increased. When the switch was turned on, DBH slightly decreased during SSP585 and SSP370 compared to SSP126, following the same trend as when the switch was turned off. The difference between the switched-on and switched-off settings was about 4 cm during historical scenarios and SSP126 but decreased to 2 cm during SSP370 and SSP585, indicating a slightly smaller difference under higher CO₂ scenarios.

In the probability density analysis across all regions, the histogram did not show a significant difference between the switched-on and switched-off settings across all scenarios and regions (Figure S10–S12). When focusing only on regions where carbon starvation occurred, the 50–100 cm range of DBH under the switched-on setting was larger than under the switched-off setting in Asia (Figure 36). In Europe, the range of trees with DBH over 50 cm was larger under the switched-on setting compared to the switched-off setting, with an even greater difference observed during SSP scenarios compared to historical scenarios (Figure 37). In North America, the range of trees with DBH over 50 cm was slightly larger under the switched-on setting than under the switched-off setting (Figure 38). The difference between the two settings did not vary significantly during SSP370 and SSP585 compared to historical scenarios and SSP126.

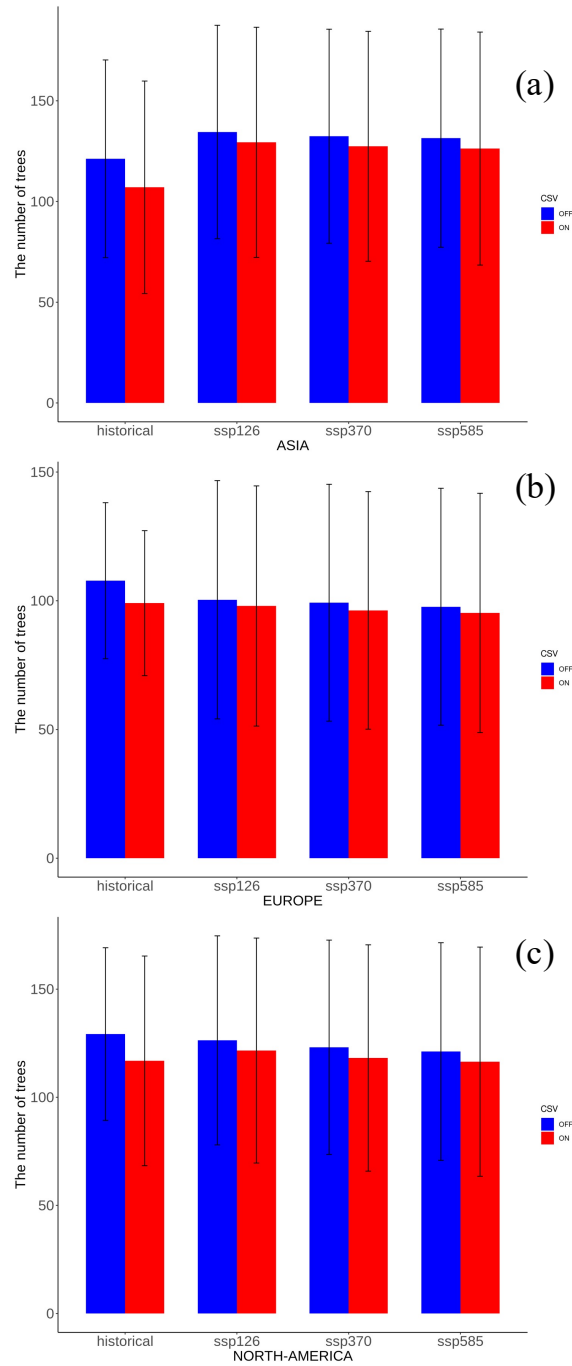


Figure 23. Changes in tree numbers, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in regions where carbon starvation occurs: (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from the "switch on" condition, while the blue bars represent outputs from the "switch off" condition.

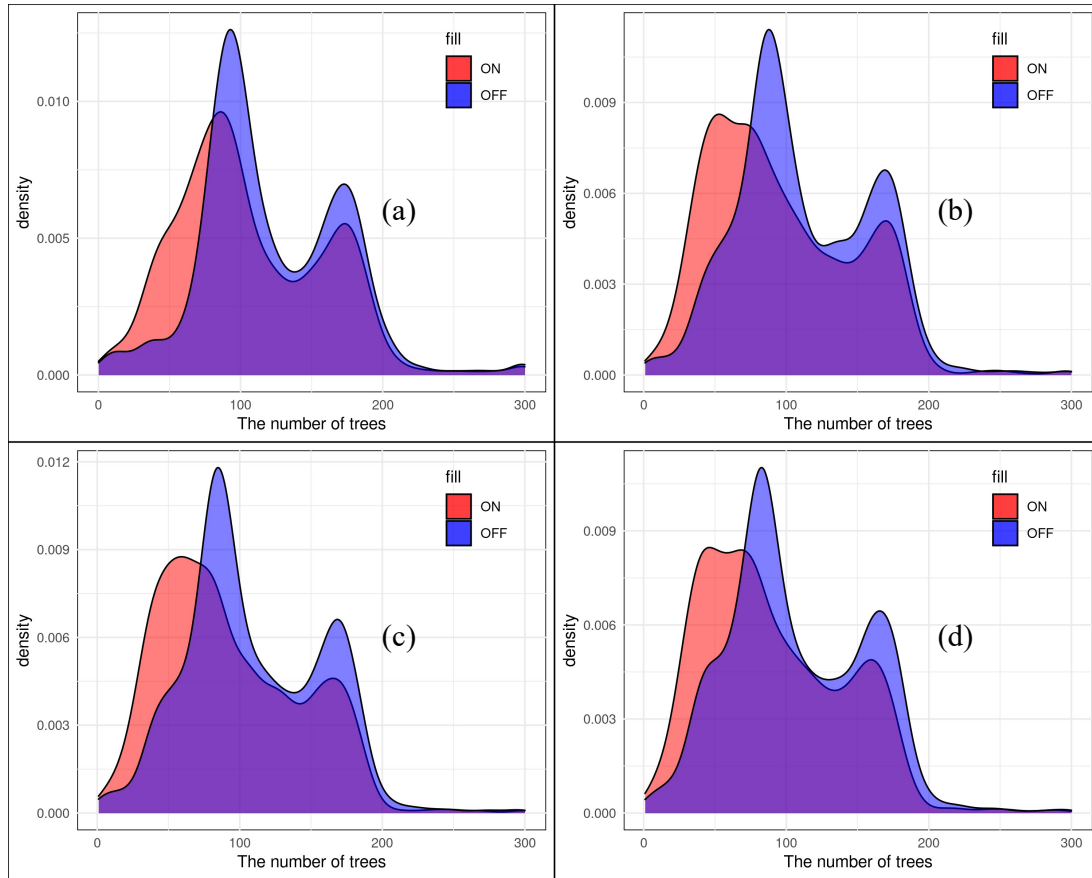


Figure 24. Probability density of tree numbers averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Asia where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

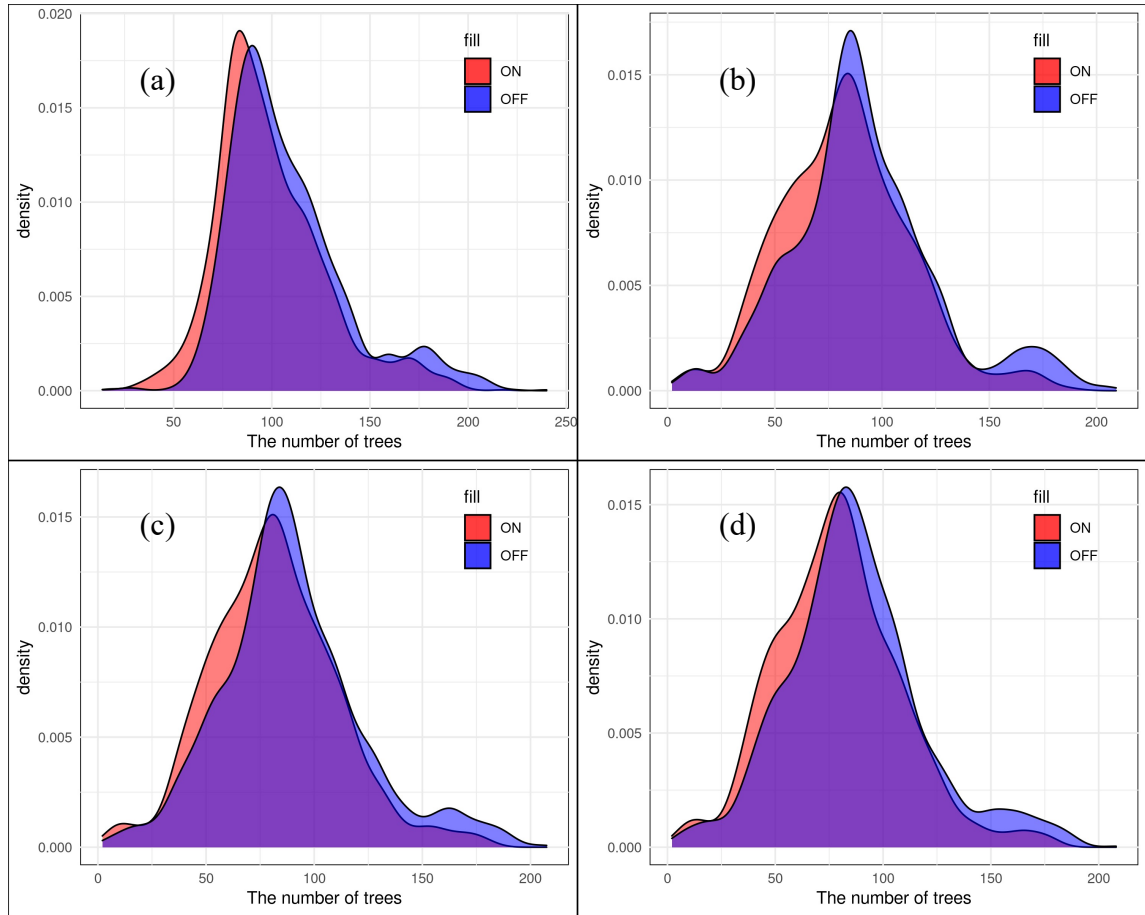


Figure 25. Probability density of tree numbers averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Europe where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

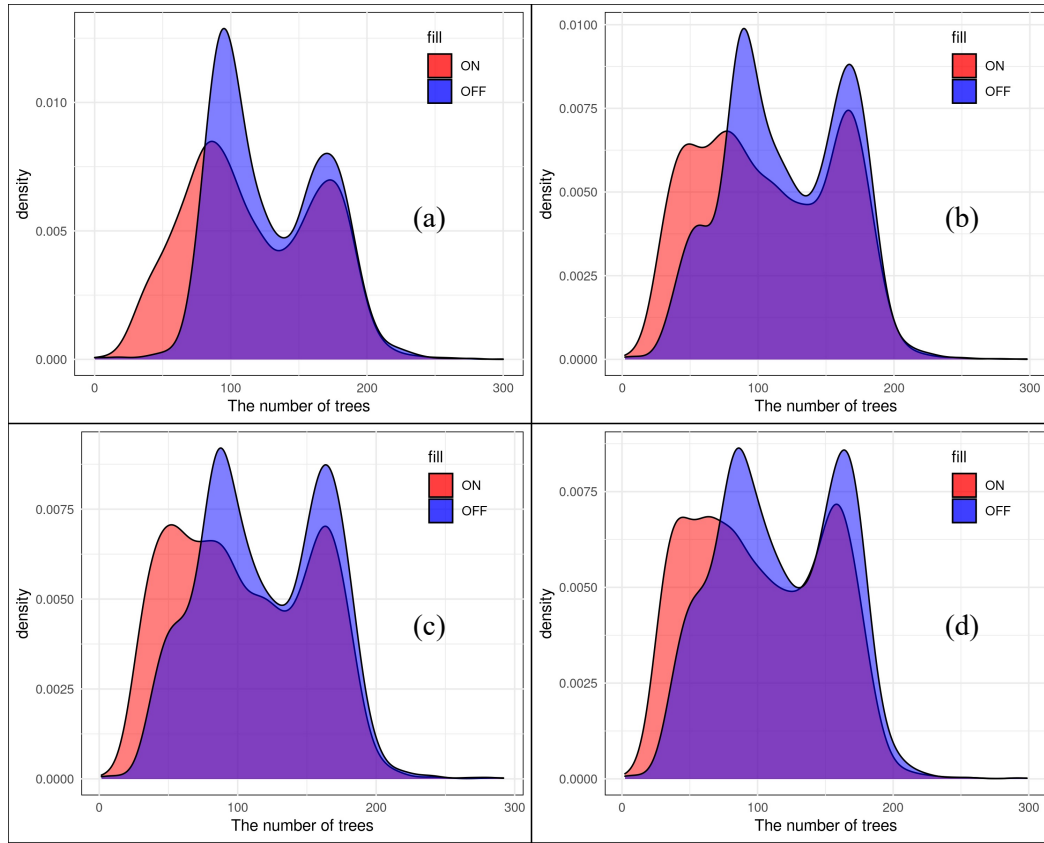


Figure 26. Probability density of tree numbers averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of North America where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

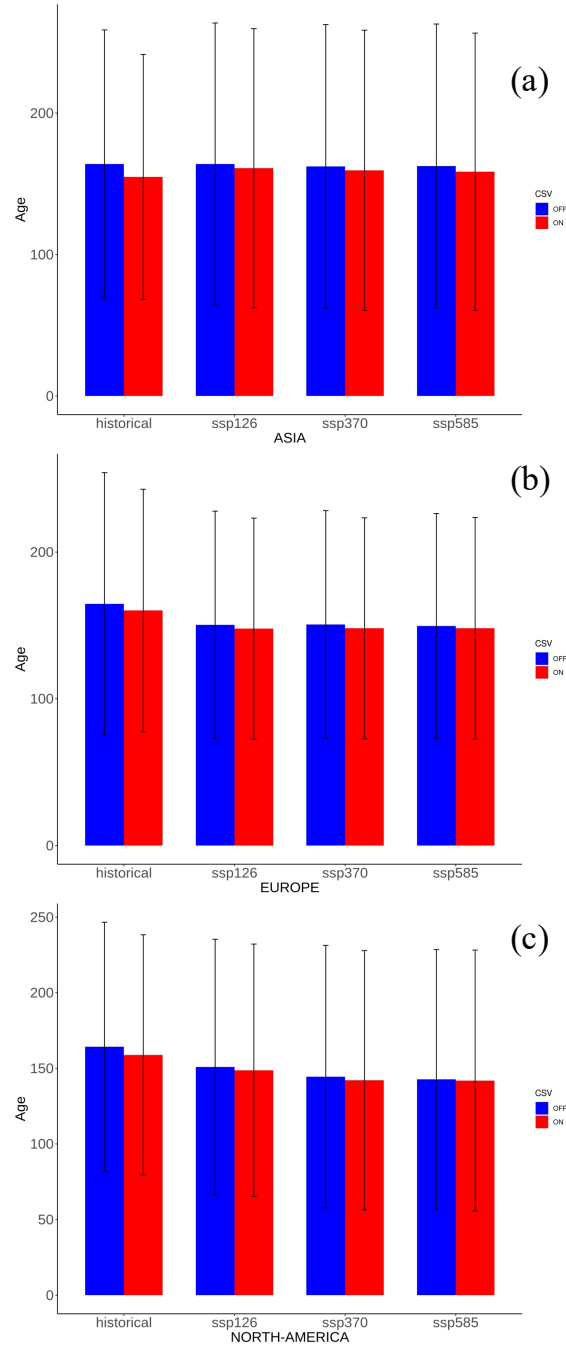


Figure 27. Changes in tree ages, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in regions where carbon starvation occurs: (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from the "switch on" condition, while the blue bars represent outputs from the "switch off" condition.

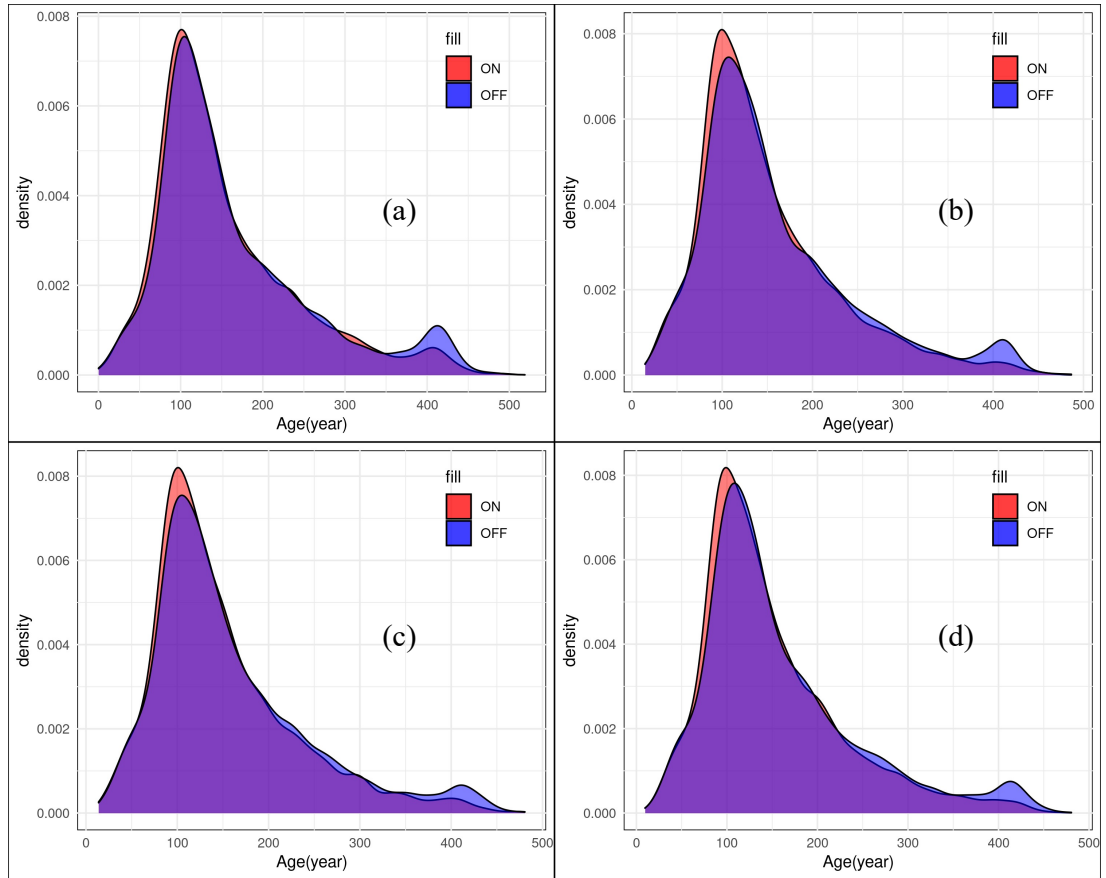


Figure 28. Probability density of tree ages averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Asia where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

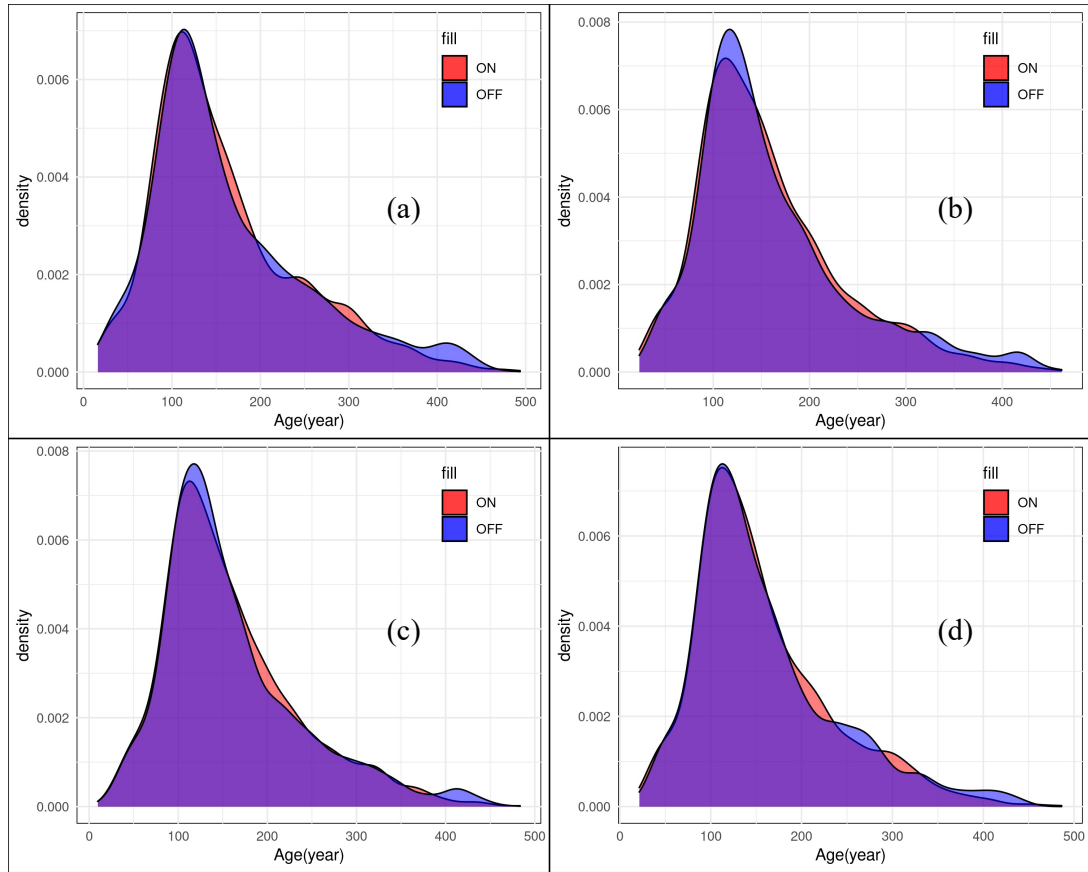


Figure 29. Probability density of tree ages averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Europe where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

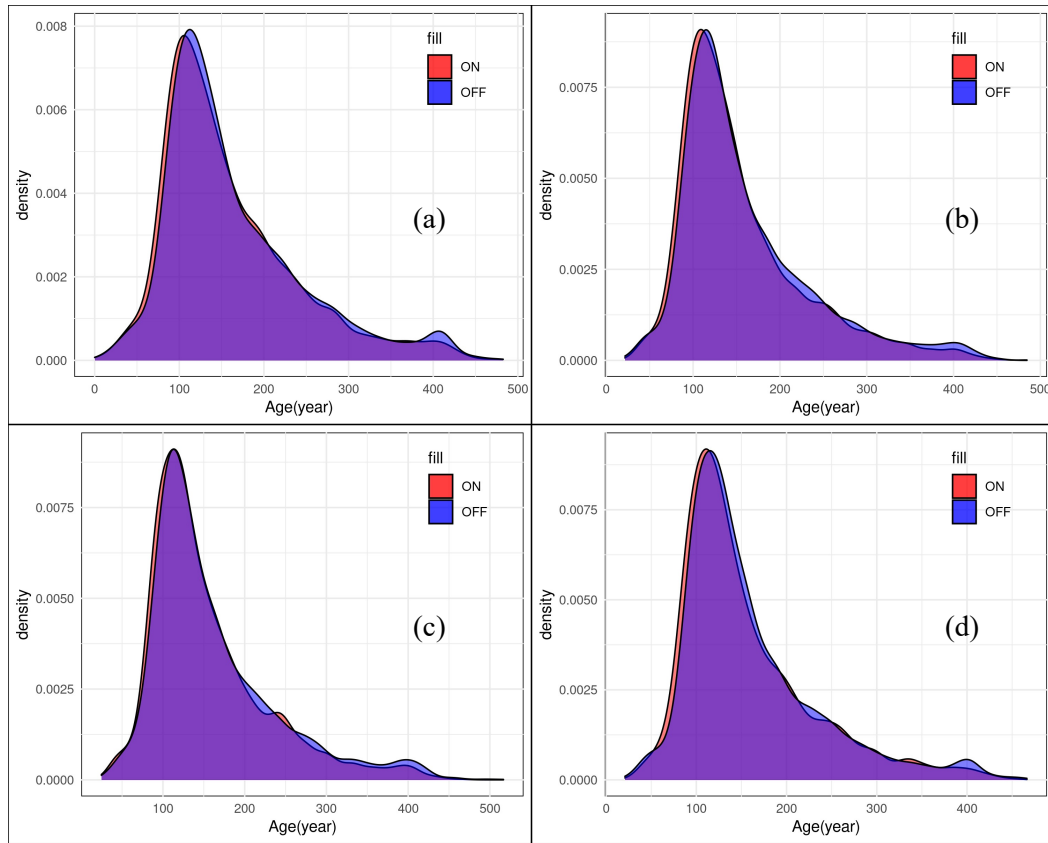


Figure 30. Probability density of tree ages averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of North America where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

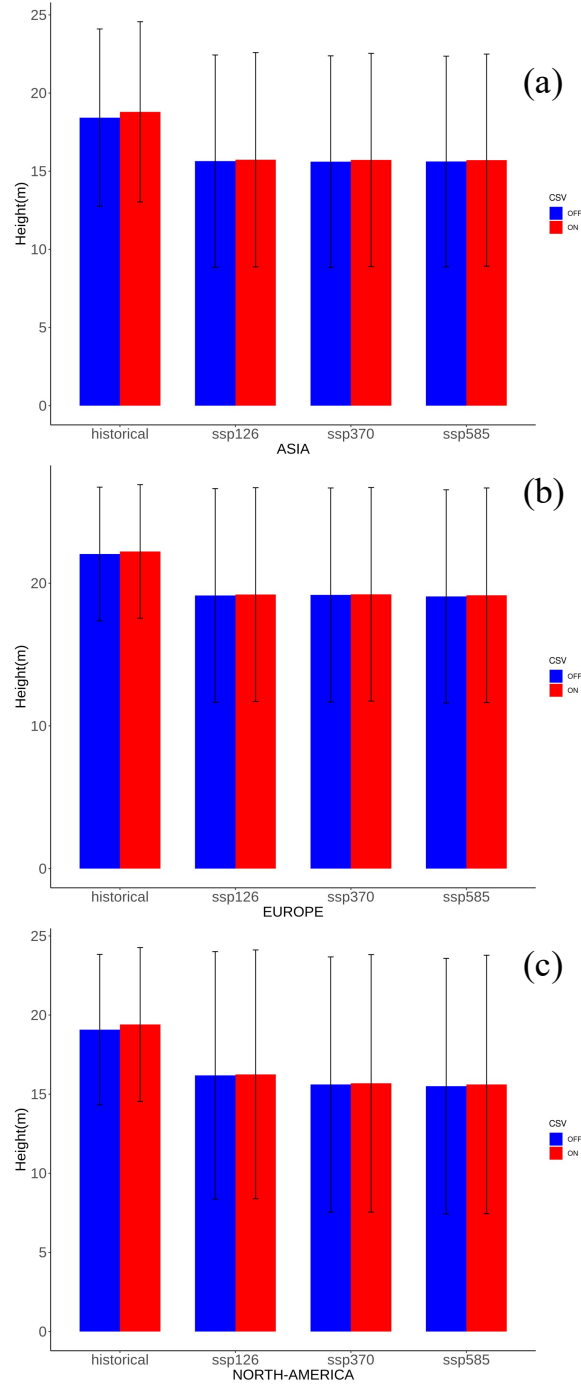


Figure 31. Changes in tree height, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in regions where carbon starvation occurs: (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from the "switch on" condition, while the blue bars represent outputs from the "switch off" condition.

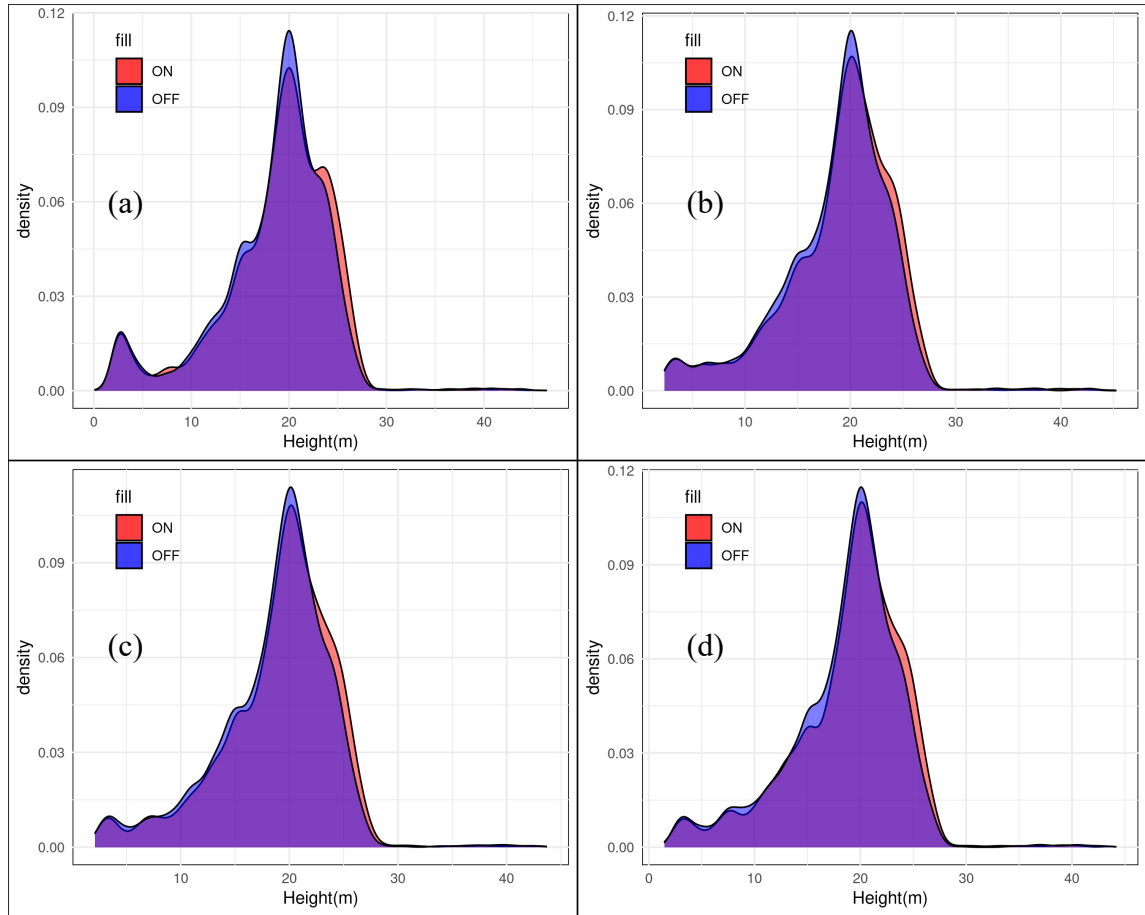


Figure 32. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Asia where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

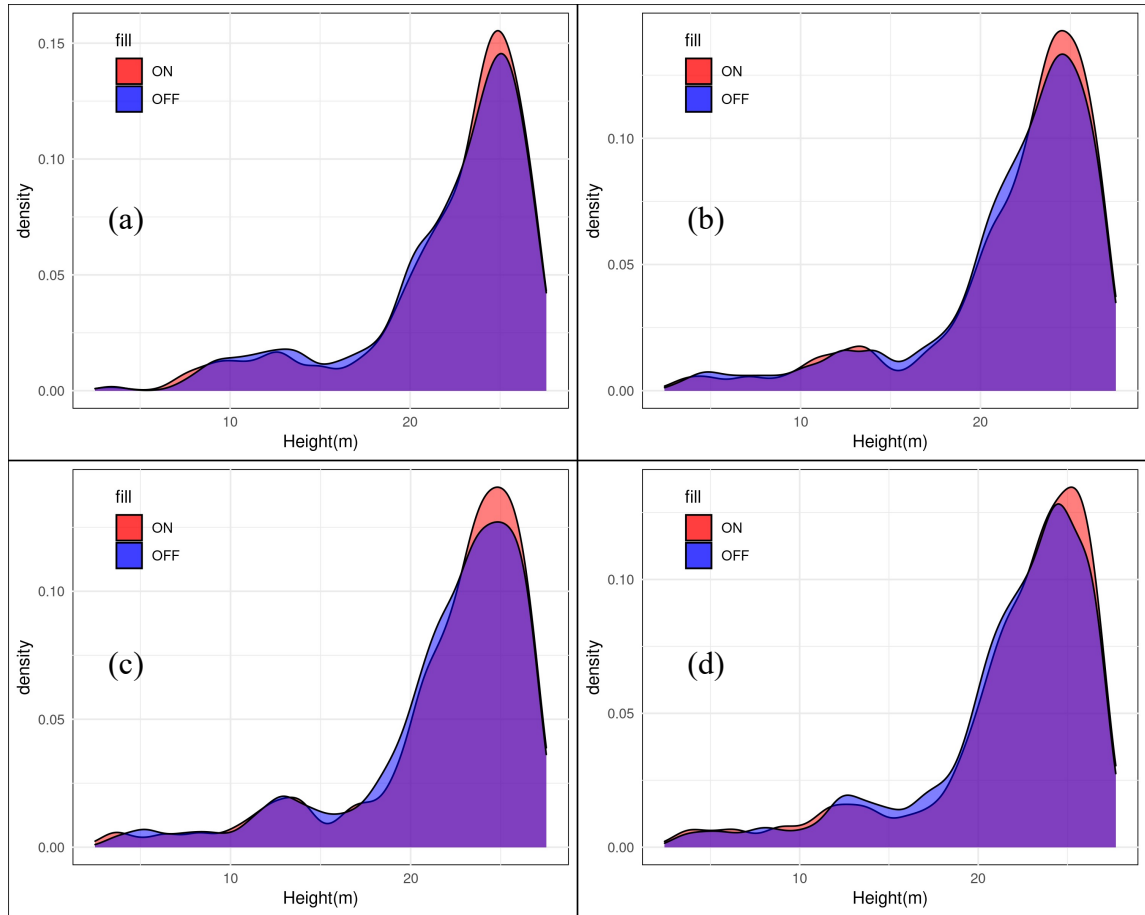


Figure 33. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Europe where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

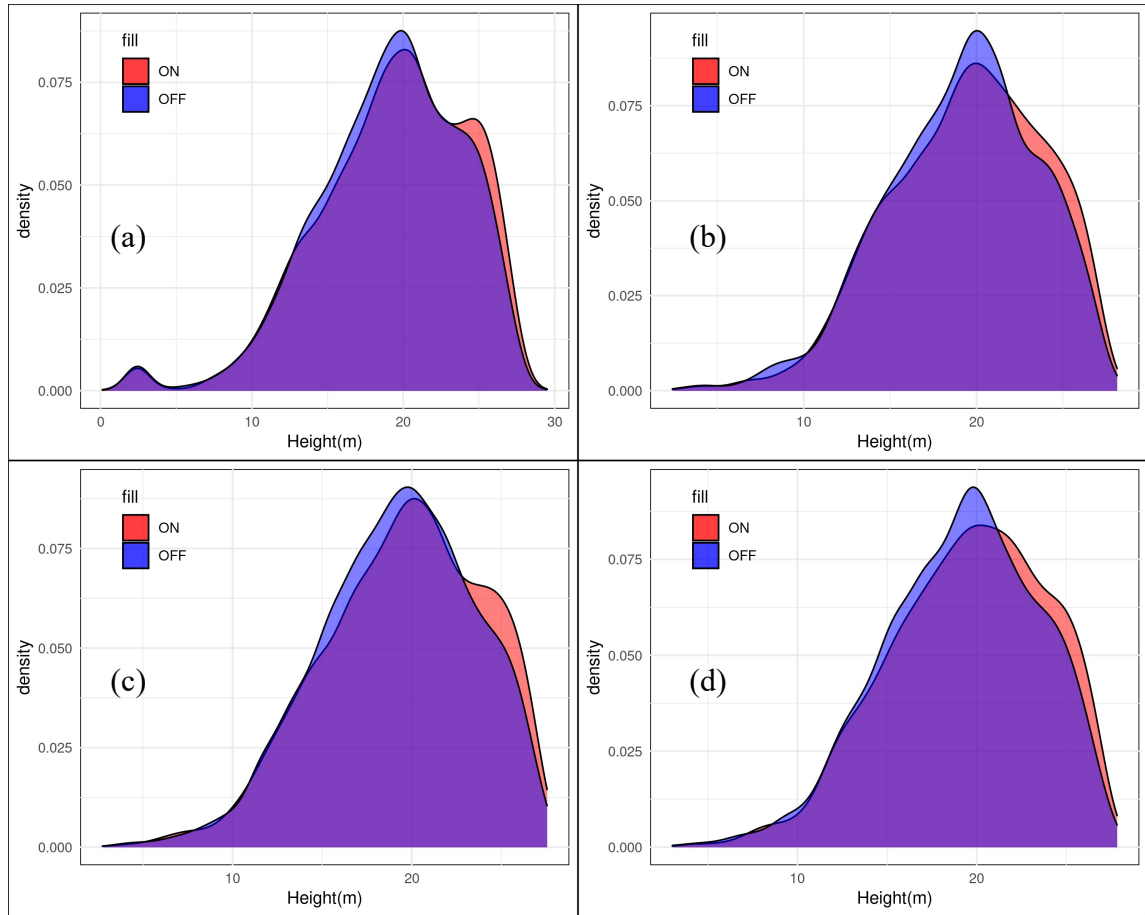


Figure 34. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of North America where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

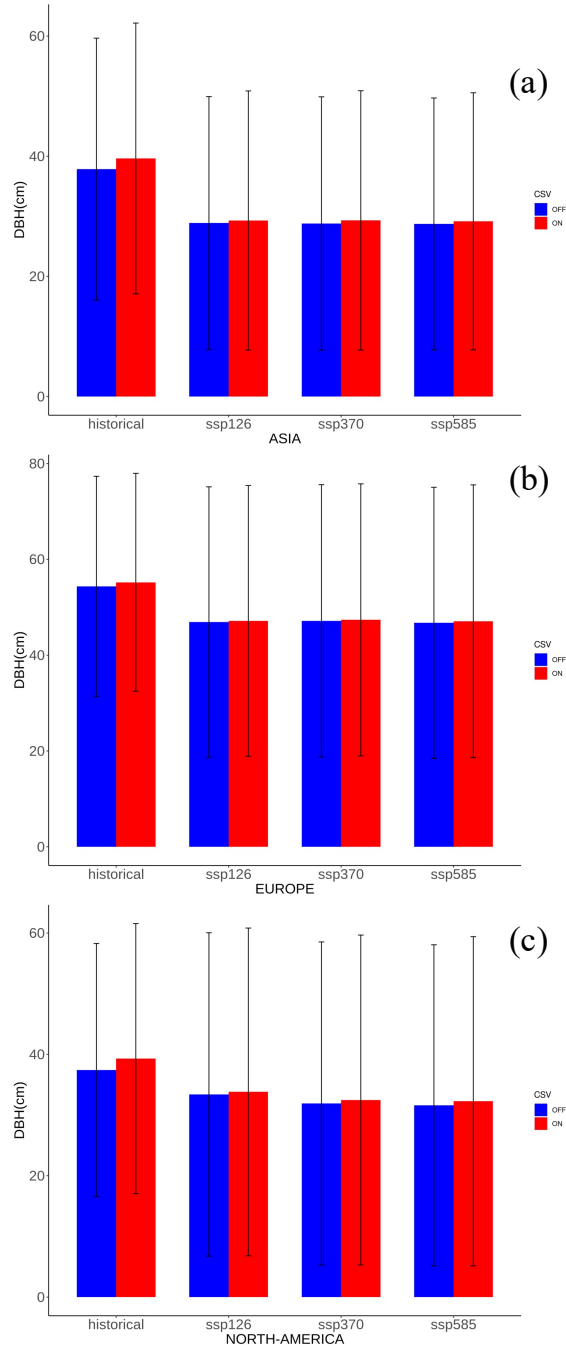


Figure 35. Changes in DBH, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in regions where carbon starvation occurs: (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from the "switch on" condition, while the blue bars represent outputs from the "switch off" condition.

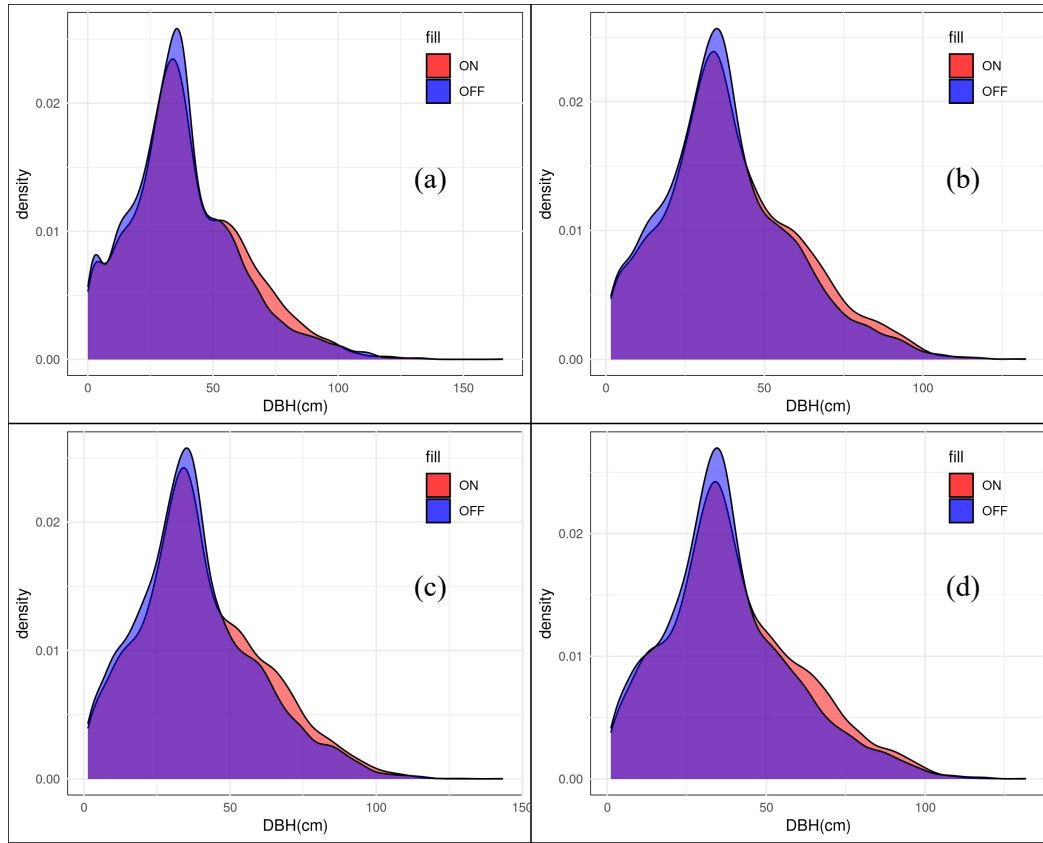


Figure 36. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Asia where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

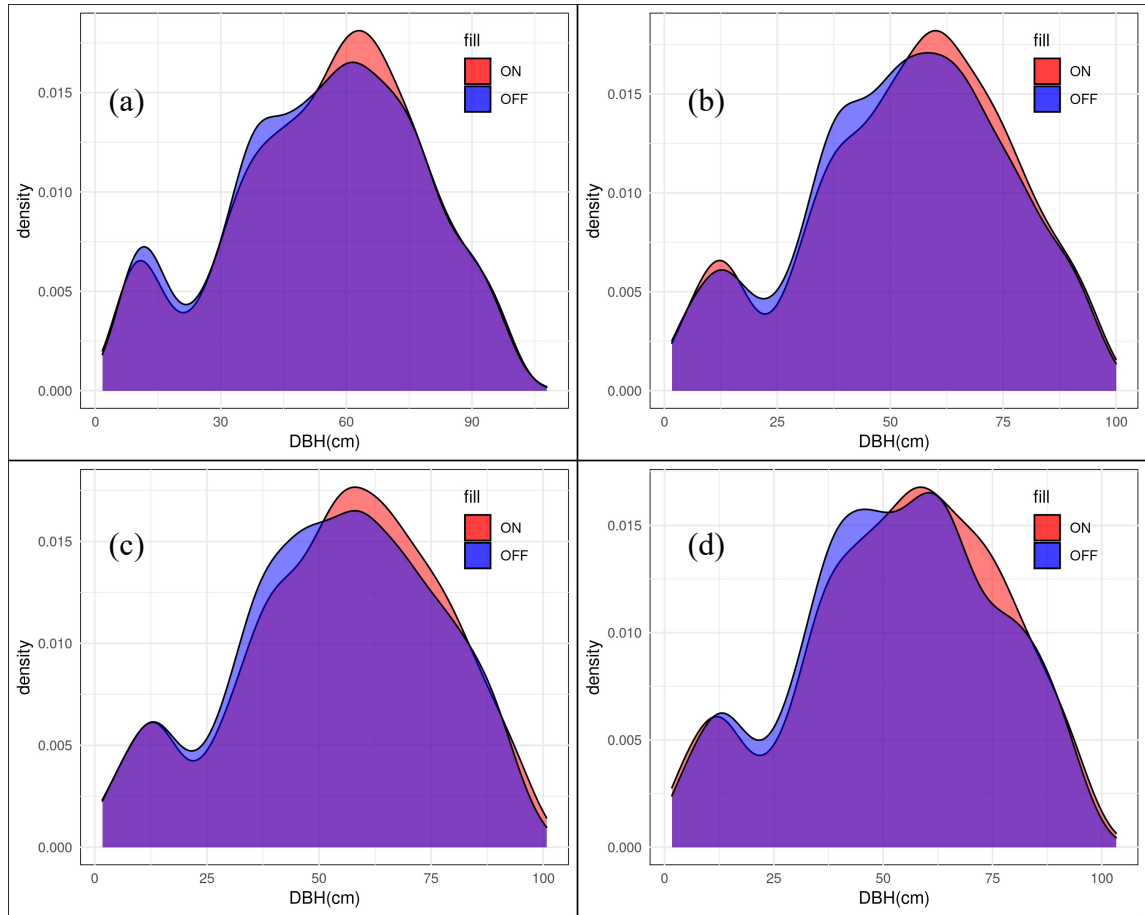


Figure 37. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of Europe where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

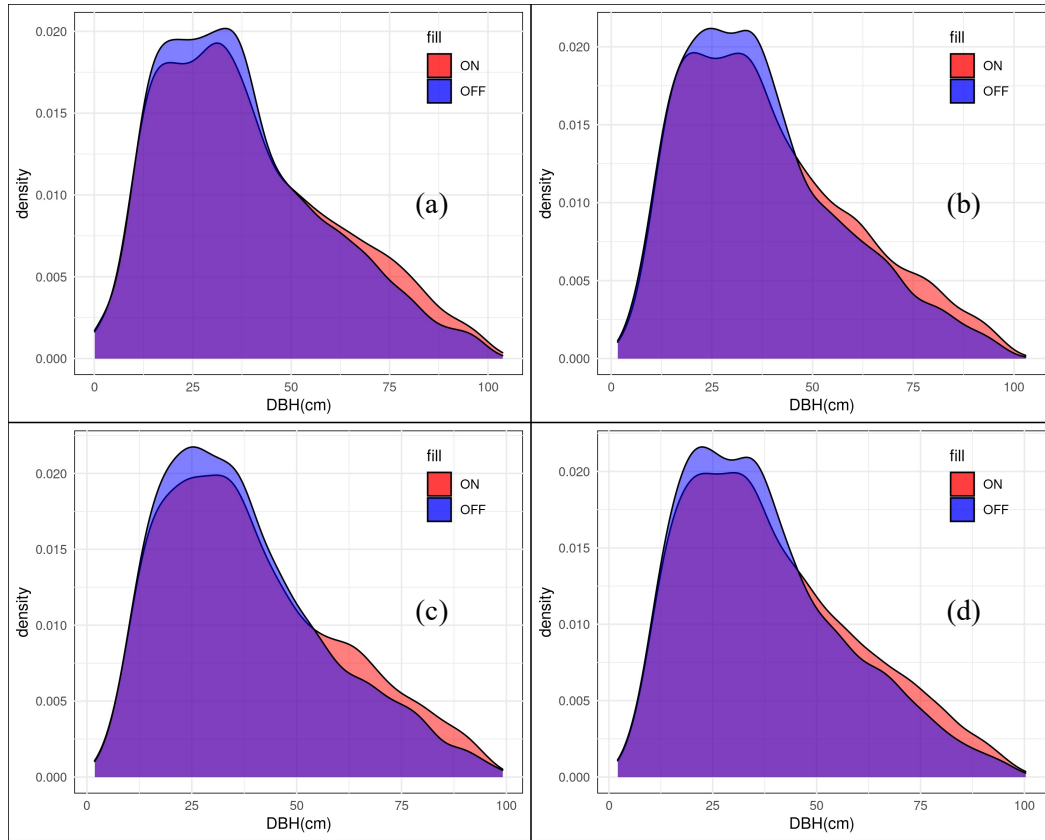


Figure 38. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in regions of North America where carbon starvation occurs. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

3.3 Time series of carbon starvation effect with climate change

The change in the number of grids where carbon starvation occurred from 1900 to 2100 was analyzed across all regions. In Asia, the number of grids continued to fluctuate during historical scenarios, then gradually increased until 2050 during all SSP scenarios, followed by a slight decrease by 2100 (Figure 39(a)). No significant differences were observed between SSP scenarios. In Europe, the number of grids remained stable during historical scenarios, except for an abnormal increase around 2000, and then gradually decreased during SSP scenarios (Figure 39(b)). The magnitude of the decrease was largest during SSP585 compared to the other SSP scenarios. In North America, the number of grids remained stable during historical scenarios, but increased significantly by 2100. The rate of increase was greater with rising CO₂ levels (Figure 39(c)).

The changes in the relative ratio of total NSCs to total woody biomass from 1900 to 2100 were also analyzed. In Asia, the ratio of total NSCs to woody biomass continued to increase from 2060 and then stabilized by 2100 for both settings (Figure 40(a)). Although no significant differences in the rate of increase were observed between the SSP scenarios, plants tended to accumulate more NSCs in Asia during SSP scenarios. When the carbon starvation switch was turned on, the rate of increase was slightly lower than when it was turned off, indicating that carbon starvation prevented plants from accumulating NSCs. In Europe, the ratio of total NSCs to total woody biomass remained stable during historical scenarios but began to increase significantly by 2100 for both settings (Figure 40(b)). The rate of increase was higher with rising CO₂ levels. When the carbon starvation switch was turned on, the rate of increase was slightly lower than when it was turned off, similar to the trend observed in Asia. In North America, the ratio continued to increase during historical scenarios but gradually decreased during SSP scenarios for both settings (Figure 40(c)). No significant differences were observed between the SSP scenarios. When the switch was turned on, the ratio was slightly higher than when it was turned off.

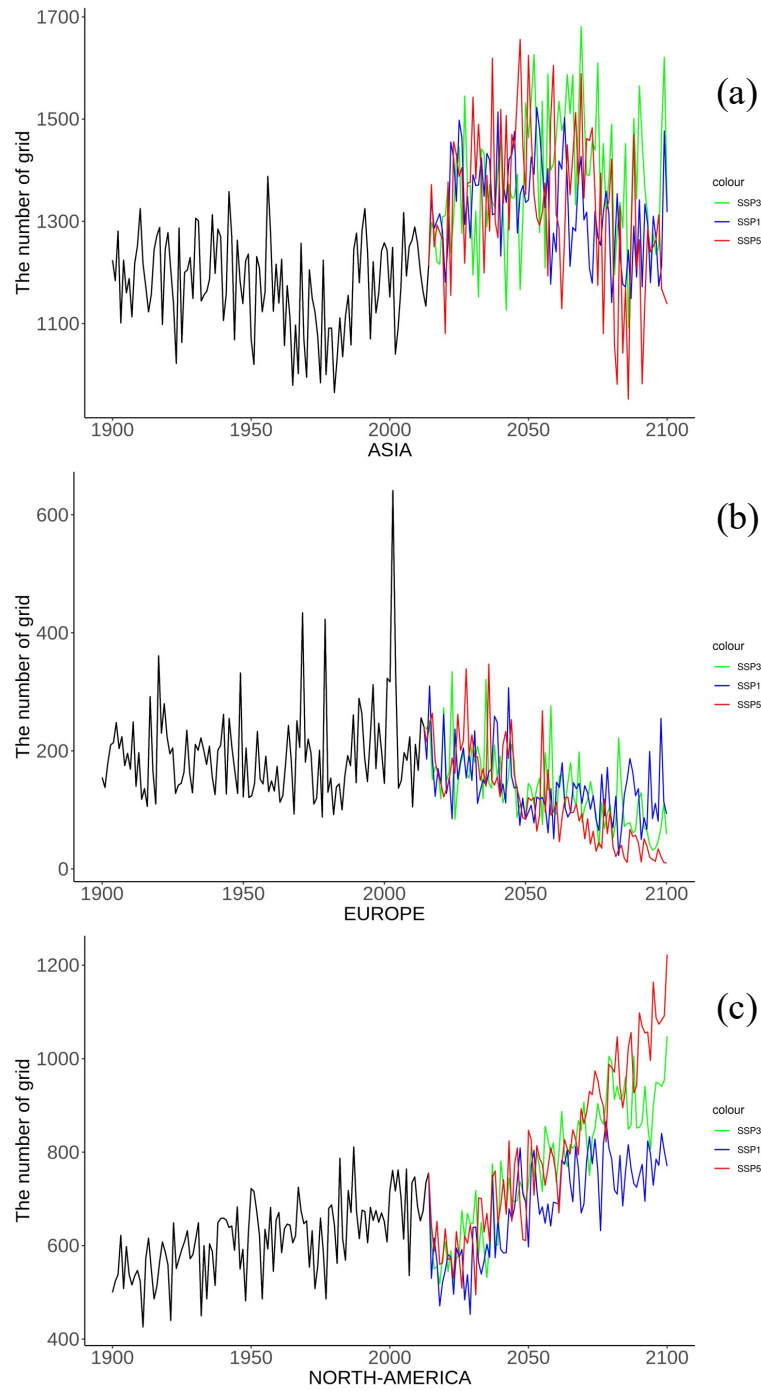


Figure 39. Changes in the number of grids where carbon starvation occurs from 1900 to 2100 in (a) Asia, (b) Europe, and (c) North America. The black line represents historical scenarios, the blue line represents SSP126, the green line represents SSP370, and the red line represents SSP585.

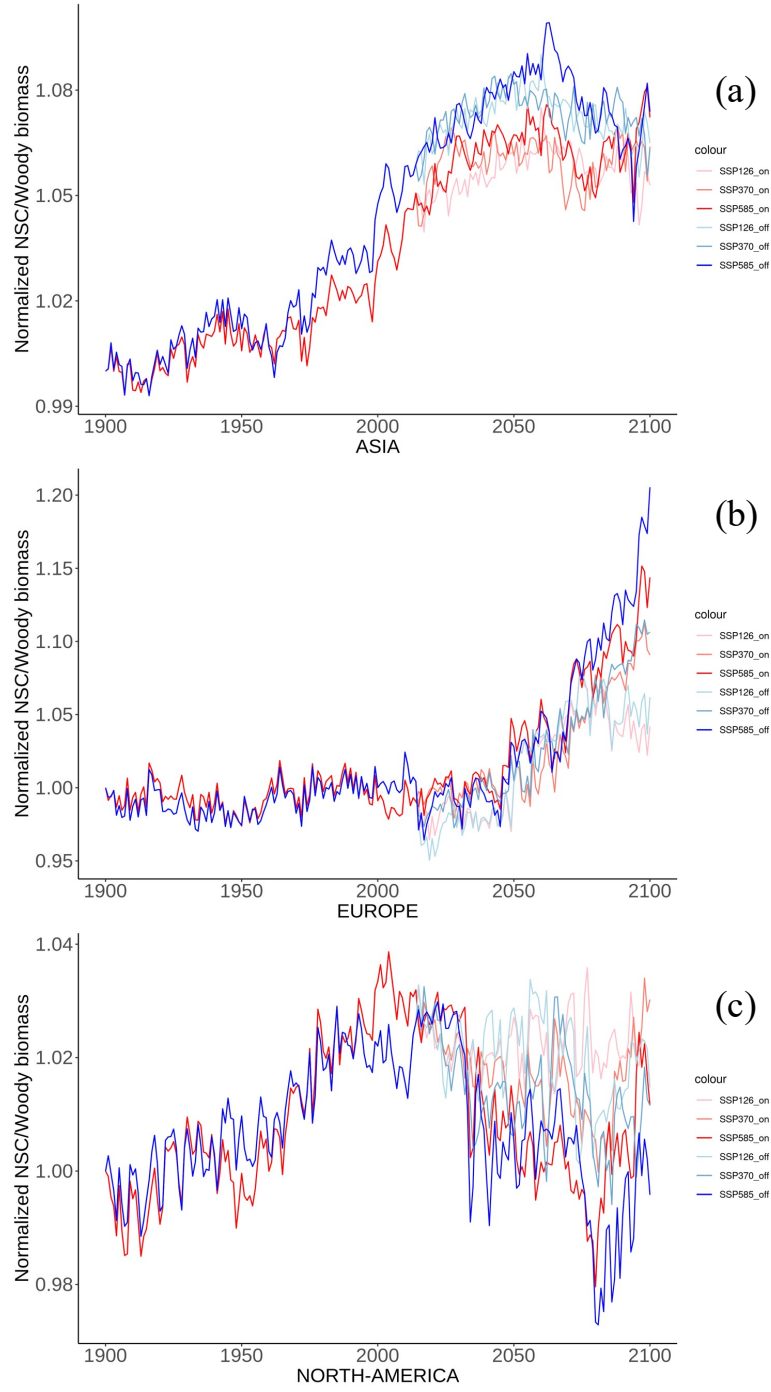


Figure 40. Changes in relative ratio of total NSCs to woody biomass from 1900 to 2100 in regions where carbon starvation occurs: (a) Asia, (b) Europe, and (c) North America.

4 Discussions

4.1. The effect of the NSC accumulation on vegetation composition under climate change

The SEIB-DGVM-NSC simulates that tree height and DBH in Asia and North America increase less than in the original model. In SEIB-DGVM-NSC, the NSC concentration increases, leading taller trees to accumulate more assimilated carbon. However, this also results in fewer trees compared to the original model. The presence of NSC components in the new model may restrict the growth of taller trees. In the forest competition within each grid, smaller trees in SEIB-DGVM-NSC occupy the space, resulting in slower growth rates for tree height and DBH compared to the original model. With rising atmospheric CO₂ levels, the growth rates of tree height and DBH show little difference between the models. The mean vegetation composition in the regions decreases with the inclusion of NSC components, although this effect is not directly linked to the intensity of climate change. This pattern is also reflected in the probability density maps, where the range of tree heights (0–10 m) and DBH (0–15 cm) is more prominent in SEIB-DGVM-NSC than in the original model. However, the probability density maps show no significant differences among the three SSP scenarios.

The distribution of tree height and DBH indicates that these variables are generally higher in the northern parts of the regions, irrespective of the SSP scenario. This suggests that trees in northern areas grow taller and thicker. For example, in Siberia, projected warming is most pronounced over the vast Siberian Plateau, characterized by boreal and sub-boreal climates and biomes, including taiga forests and tundra. Warming in these areas is especially evident during the winter season. Boreal forest vegetation is naturally influenced by periodic disturbances such as insect outbreaks and windthrow (Nurrohman et al., 2024). SEIB-DGVM-NSC simulates an increase in NSC accumulation, which supports greater tree height

and DBH compared to the original model. The results suggest that this accumulation of NSCs may enhance the trees' resilience to disturbances. Additionally, Siberian boreal forests are advancing their early phenology stages (e.g., leaf-out and flowering) and mid-season stages (e.g., fruiting) while delaying senescence onset (Rosbakh et al., 2021). These results emphasize the potential role of NSC components in supporting forest dynamics.

In Europe, the probability density of tree numbers exhibits a bimodal distribution. The number of trees also differs between the two models. In the original model, the highest probability occurs in the range of 100–150 trees, whereas the new model simulates a more uniform probability distribution of tree numbers. In the distribution, central and southern part of Europe, the number of trees decrease from the original model under SSP scenarios. Regionally, in central and southern Europe, the number of trees decreases in the new model compared to the original model under SSP scenarios. Over recent decades, growth declines have been particularly severe near the southern distribution limits in Europe (Latte et al., 2015). These trends are expected to persist as the climate continues to warm and dry. When accounting for age and size effects, significant growth declines in beech trees have been observed across southern Europe, especially at lower elevations, and these declines are now extending into central Europe (Martinez del Castillo et al., 2022). It supported that the distribution of the new model is more realistic than the original model. My results suggest that, in addition to temperature, NSCs may emerge as a key limiting factor for growth across a substantial portion of the species' distribution area.

4.2. The impact of carbon starvation effect on tree growth

The rate of change in tree height did not differ significantly between the carbon starvation switch on and switch off scenarios. However, the tallest trees were consistently taller under the "switch on" condition compared to the "switch off" condition across all regions. In terms of probability density, the number of taller trees was slightly higher in Asia under the "switch

on" condition. In Europe and North America, the increase in the number of taller trees was more pronounced. A similar trend was observed for DBH, where the rate of change was not significantly impacted by carbon starvation under the three SSP scenarios. Moreover, the number of trees decreased more under the "switch on" condition compared to the "switch off" condition across all regions and scenarios. This suggests that accounting for carbon starvation results in lower tree density within each grid, which weakens tree competition. Consequently, individual trees can grow taller and develop larger DBHs compared to the "switch off" condition.

In northeast Asia, the decline in tree numbers has been linked to warming-induced drought, which may be exacerbated by high forest stand density (Cao et al., 2021). Considering the sensitivity of trees to carbon starvation, the differences in tree height become more pronounced. Under climate change, reduced competition pressure is likely to influence tree growth dynamics. Regarding tree age, across all regions and SSP scenarios, trees were younger under the "switch on" condition compared to the "switch off" condition, indicating that carbon starvation shortens tree lifespans. This phenomenon aligns with findings in annual plants, where accelerated life cycles lead to earlier leaf and plant senescence, thereby reducing lifespan (Wingler and Henriques, 2022). The ratio of NSCs to woody biomass increases under carbon starvation, but the rate of increase is slower compared to the "switch off" condition in future scenarios. This suggests that NSCs are not effectively accumulated during carbon starvation.

In North America, water constraints on vegetation productivity increased between 1982 and 2015, and the affected area continues to expand. This trend is associated with negative drought impacts, as plants have become increasingly sensitive to drought (Jiao et al., 2021). My findings, which show an increasing number of areas experiencing carbon starvation with rising CO₂ levels, further support the notion that plants are becoming more sensitive to

drought. In these areas, plants are expected to be more vulnerable to carbon starvation, leading to reductions in tree numbers and shorter survival periods.

4.3. Model uncertainty

I aim to simulate the effects of carbon starvation on the carbon cycle, but there are several limitations in accurately modeling carbon starvation. Firstly, there is a lack of observational data on carbon starvation, which makes it impossible to validate its effects in historical scenarios. Carbon starvation typically occurs in plants that are not killed by embolism during long drought. However, distinguishing the exact cause of death in observations is challenging. Additionally, the effects of drought-induced tree mortality often result from a combination of carbon starvation and embolism. SEIB-DGVM-NSC currently cannot accurately simulate plant water potential, which prevents the model from isolating the effects of embolism. For future research, collecting sap flow data could help develop a new process to represent embolism in individual trees within SEIB-DGVM-NSC. By setting thresholds for NSC concentration and water potential for carbon starvation and embolism, it would be possible to simulate the effects of drought more accurately.

Secondly, the NSC compartment in the model is classified by climatic regions due to limited observational data. However, the NSC accumulation process differs between evergreen and deciduous forests. Because the model does not currently define NSC compartments based on PFTs, this increases uncertainty in the model outputs. In some regions, the simulated plant types differ from those observed in reality. SEIB-DGVM-NSC is the first version of the model designed to simulate NSC concentrations. With more globally distributed NSC observational data, the model can be further refined to better simulate NSC concentrations and plant phenology.

5. Conclusions

I developed SEIB-DGVM-NSC, a new version of the SEIB-DGVM model, which incorporates the dynamics of NSCs at the individual tree level. This updated model simulates greater NSC accumulation within tree organs compared to the previous version. Consequently, in tree competition scenarios within each grid cell, taller trees accumulate more assimilated carbon as NSCs, which inhibits their growth. As a result, the mean tree height and DBH are lower in the new model compared to the original version.

In the previous model, taller trees could dominate grid cells; however, in the new model, some trees struggle to grow due to excessive NSC accumulation. This allows shorter trees to outcompete taller ones and occupy the grid cells. As a result, the distribution of tree height and DBH in the new model is wider, with an increased number of trees exhibiting near-zero height and DBH. Under SSP scenarios, the new model predicts a bimodal distribution of trees, with taller and thicker trees dominating in the northern regions and shorter trees in the southern regions, particularly in Europe. This bimodal pattern is more pronounced in the new model and aligns better with observed trends. For instance, in Europe, tree growth decline is observed, especially in central Europe, where the effects are exacerbated. By including NSC dynamics, the model demonstrates that trees become more sensitive to warm and dry climate conditions.

I also incorporated a new mortality process to simulate the effects of carbon starvation. Mortality increases as the ratio of NSC to total woody biomass declines. Across all regions, tree height increases slightly when carbon starvation is "switched on," indicating that carbon starvation reduces tree density allowing trees to grow more compared to the "switched off" condition. However, the trend of height increasing does not vary significantly with rising CO₂ levels, suggesting that the carbon starvation effect does not intensify under higher CO₂ conditions. Interestingly, under all SSP scenarios, the number of trees decreases more in the

"switch on" setting than in the "switch off" setting, indicating reduced competition pressure when carbon starvation is considered. While shorter trees are more affected by carbon starvation, taller trees remain unaffected and grow more than in the "switch off" condition. Tree age is consistently younger under the "switch on" condition across all regions and SSP scenarios, demonstrating that carbon starvation shortens tree lifespan.

While SEIB-DGVM-NSC can simulate more realistic vegetation composition and offers potential for modeling carbon starvation, there are several limitations. In the current model, NSC seasonality is classified solely based on climate. However, NSC accumulation varies among PFTs. Incorporating additional classifications based on PFTs, once more validation data is available, could enhance the model's ability to simulate NSC dynamics accurately. My research contributes to a more comprehensive understanding of the role of NSC accumulation in the terrestrial carbon cycle and the impact of carbon starvation—an elusive process to observe—on global vegetation composition.

Chapter4. General Conclusion

Global warming has been occurring since Industrial Revolution, then the warming amplifies the weather extreme events such as drought, wildfire, insect outbreaks are expected to be increasing damaging significantly ecosystems, agriculture, and human lives. Understanding the global carbon cycle is important for estimating the impacts of climate change. Terrestrial ecosystems play a key role, accounting for the largest carbon flux among major carbon reservoirs. Through photosynthesis, plants absorb CO₂, utilizing it for growth and metabolism, while respiration, decomposition, and disturbances like wildfires release CO₂ back into the atmosphere. Therefore, tree mortality and permanent shifts in forest vegetation dynamics driven by rising temperatures result in shorter and younger forests, reduced canopy cover, and shifts toward low-biomass ecosystems. These changes ultimately accelerate climate change, emphasizing the importance of estimating and simulating biomass distribution to better understand carbon fluxes in terrestrial ecosystems.

Non-structural carbohydrates (NSCs) are critical in understanding the effects of tree mortality on carbon flux. NSCs serve as essential resources for growth, metabolism, storage, and defense, particularly under environmental stress. They buffer physiological stress and are vital for tree survival during droughts or disturbances. However, imbalances in NSC pools can lead to carbon starvation, contributing to drought-induced tree mortality. Current vegetation models often oversimplify these dynamics and lack mechanisms to accurately simulate NSC-driven mortality.

The aim of the research is 1) to develop new individual-based vegetation models capable of simulating NSC dynamics based on observation data, and 2) to simulate the effect of tree mortality induced by NSC depletion on forest composition under climate change.

In chapter 2, I added new module to simulate NSC dynamics into the SEIB-DGVM, a spatially explicit, individual-based dynamic global vegetation model to examine the effects of NSC allocation on global forest dynamics through competition and establishment among individual trees. The model calculates NSC dynamics for three organs—leaves, trunks, and roots—and determines NSC seasonality for boreal, temperate, and tropical biomes based on ground measurements. Validation at four sites (Canada, Austria, Switzerland, and Panama) demonstrated that the simulated NSC concentrations align well with observed data. Furthermore, global-scale validation showed that the simulated NSC concentrations are in good agreement with meta-analysis data across different biome types.

In chapter 3, forest composition and percentage of biome types occupied in Asia, Europe, and North America was analyzed during SSP scenarios between new model and previous model. In new model, taller trees accumulate more NSCs, which inhibits their growth, leading to lower mean tree height and DBH. Unlike the previous model, where taller trees dominated grid cells, the new model allows shorter trees to outcompete taller ones, resulting in a wider distribution of tree height and DBH, including more trees with near-zero values. Under SSP scenarios, the model predicts a bimodal distribution of trees, with taller, thicker trees in northern regions and shorter trees in southern regions, particularly in Europe, aligning better with observed trends. The model also incorporates a new mortality process based on carbon starvation. When carbon starvation is "switched on," tree density decreases, allowing taller trees to grow more compared to the "switched off" condition. Shorter trees are more vulnerable to carbon starvation, while taller trees remain unaffected and grow better. Tree age is consistently younger under the "switch on" condition, demonstrating that carbon starvation shortens tree lifespans. The area affected by carbon starvation is projected to expand in North America, aligning with previous research that suggests plants in this region are more sensitive to drought conditions.

This new model allows for better simulation of vegetation distribution, GPP, and forest composition (age, height, and trunk diameter) at global scales. As more observed NSC data becomes available, incorporating PFT-specific classifications, could improve the accuracy of NSC dynamics simulations. This research enhances understanding of NSC accumulation's role in the terrestrial carbon cycle and the impact of carbon starvation on global vegetation under climate change.

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APPENDIX

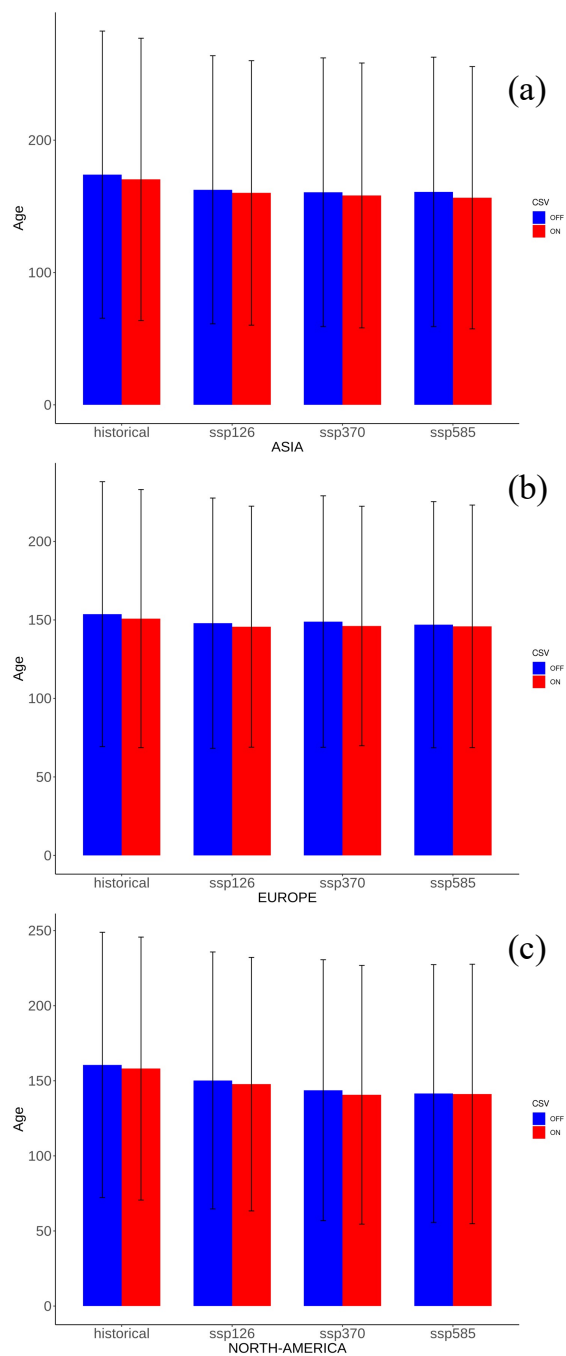


Figure S1. Changes in tree age, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in whole regions: (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from the "switch on" condition, while the blue bars represent outputs from the "switch off" condition.

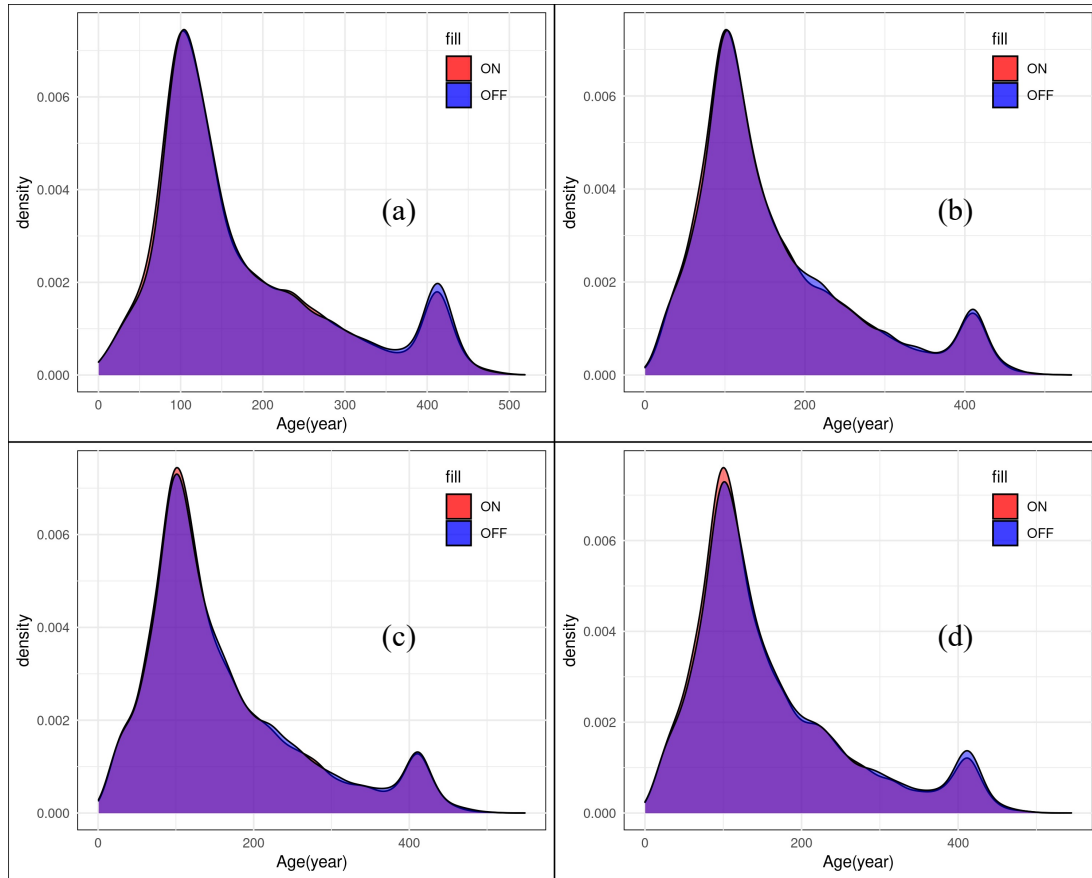


Figure S2. Probability density of tree age averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of Asia. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

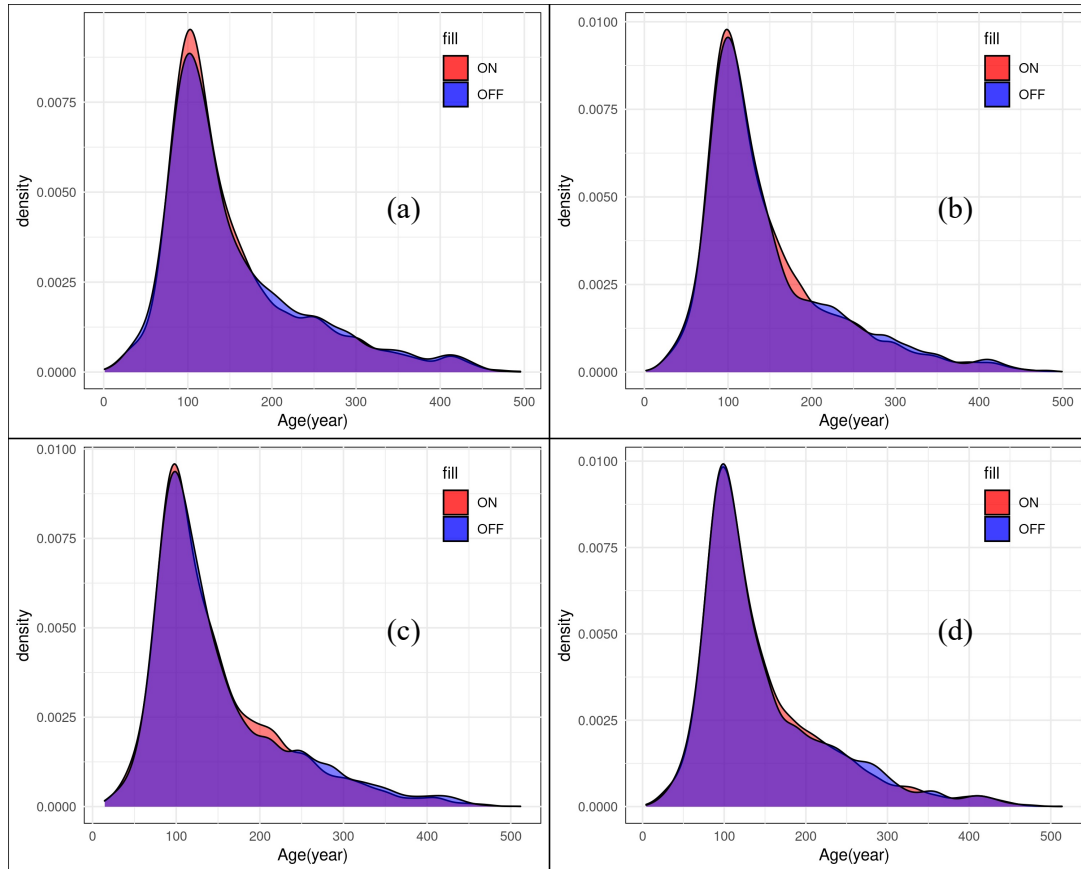


Figure S3. Probability density of tree age averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of Europe. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

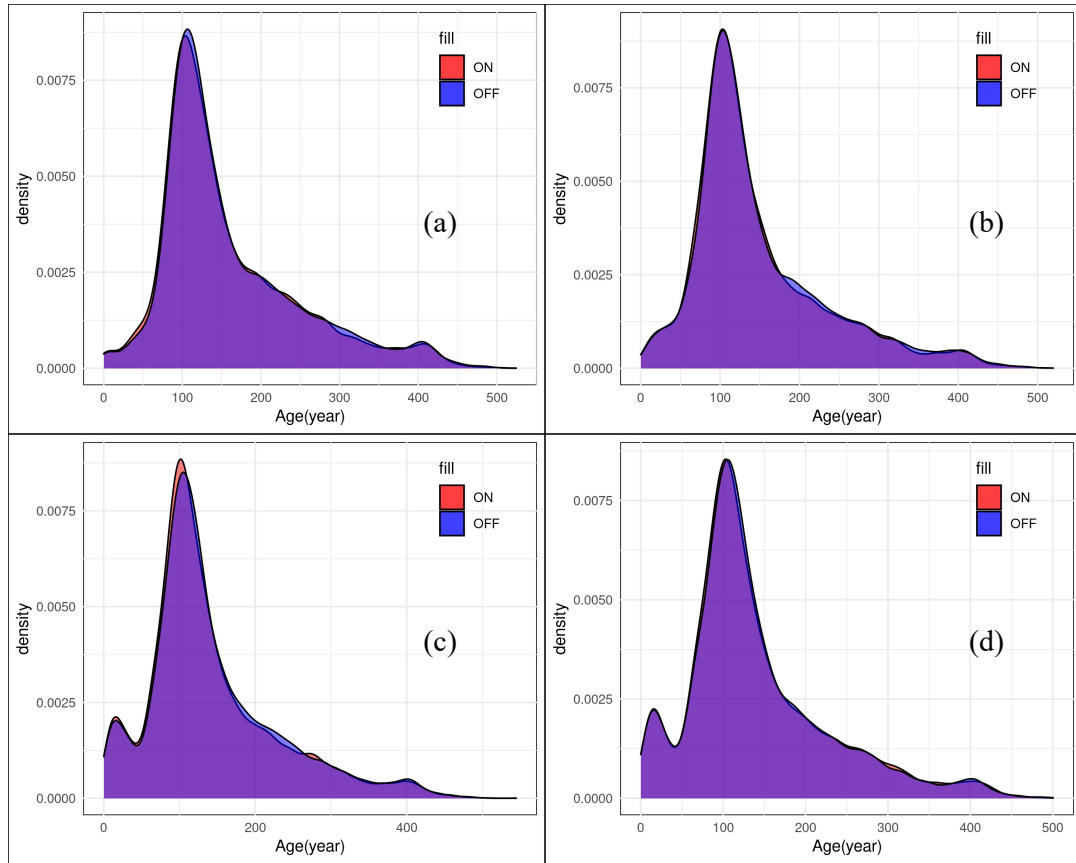


Figure S4. Probability density of tree age averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of North America. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

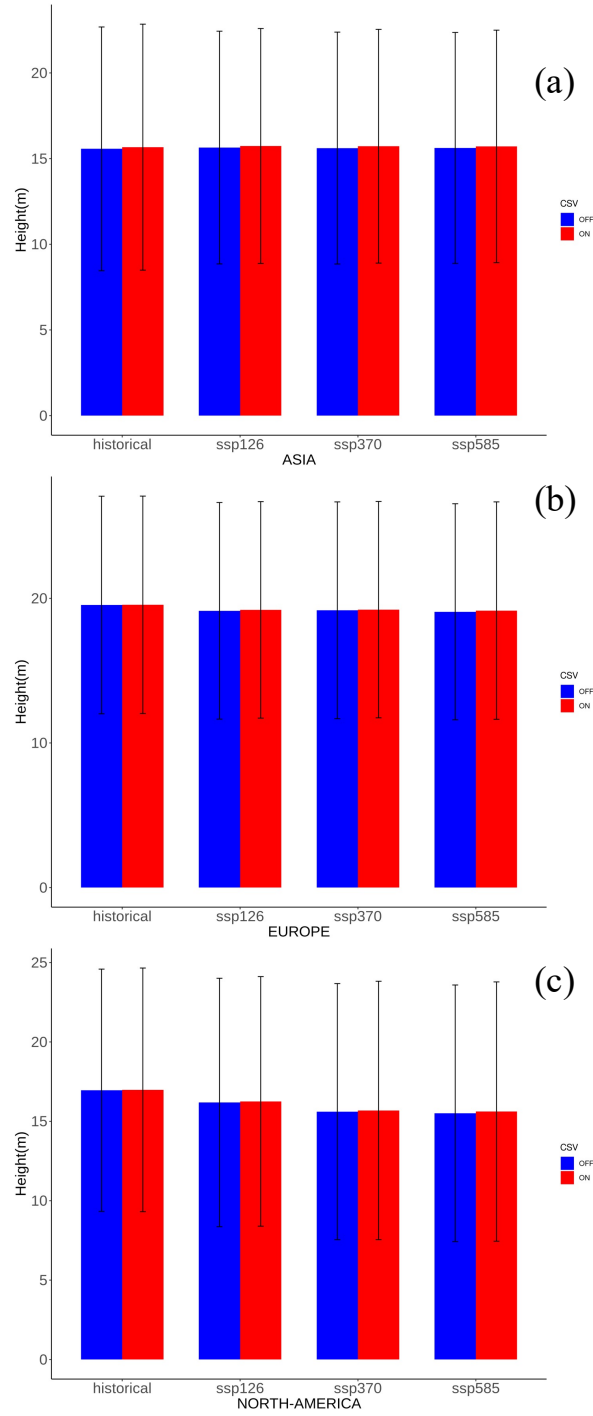


Figure S5. Changes in tree height, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in whole regions: (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from the "switch on" condition, while the blue bars represent outputs from the "switch off" condition.

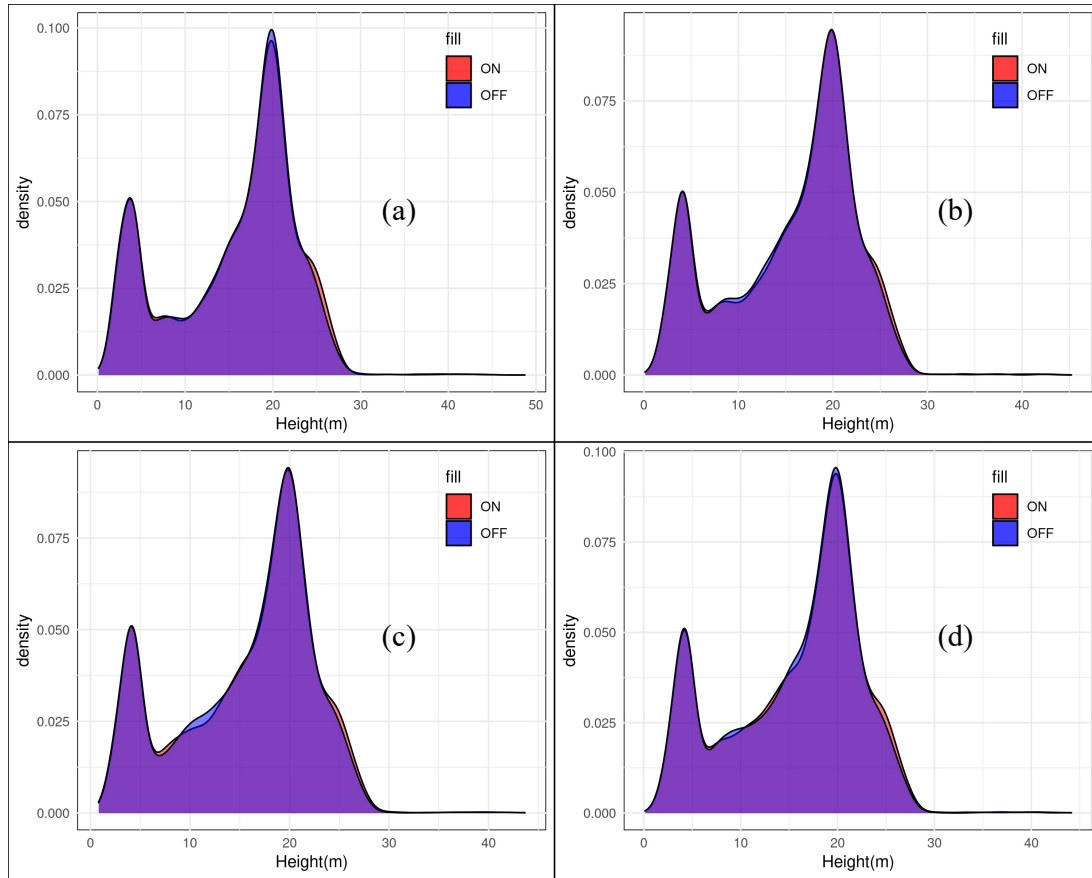


Figure S6. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of Asia. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

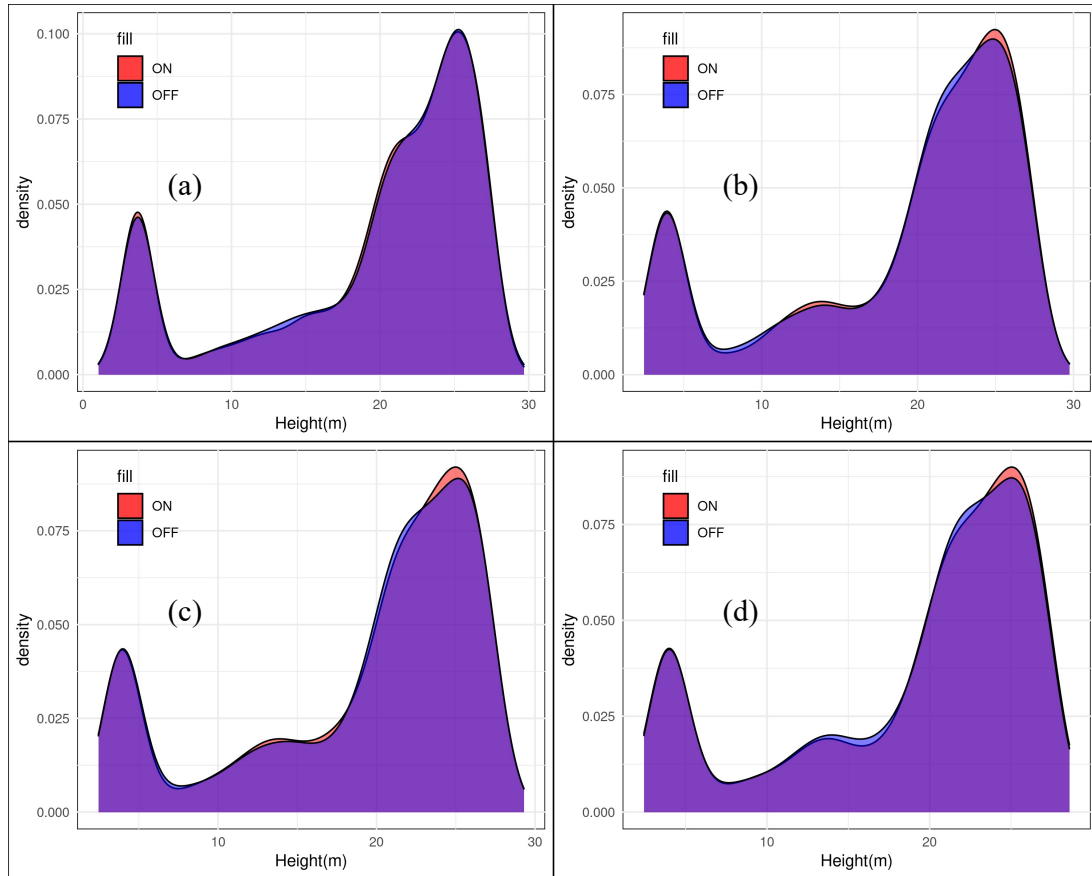


Figure S7. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of Europe. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

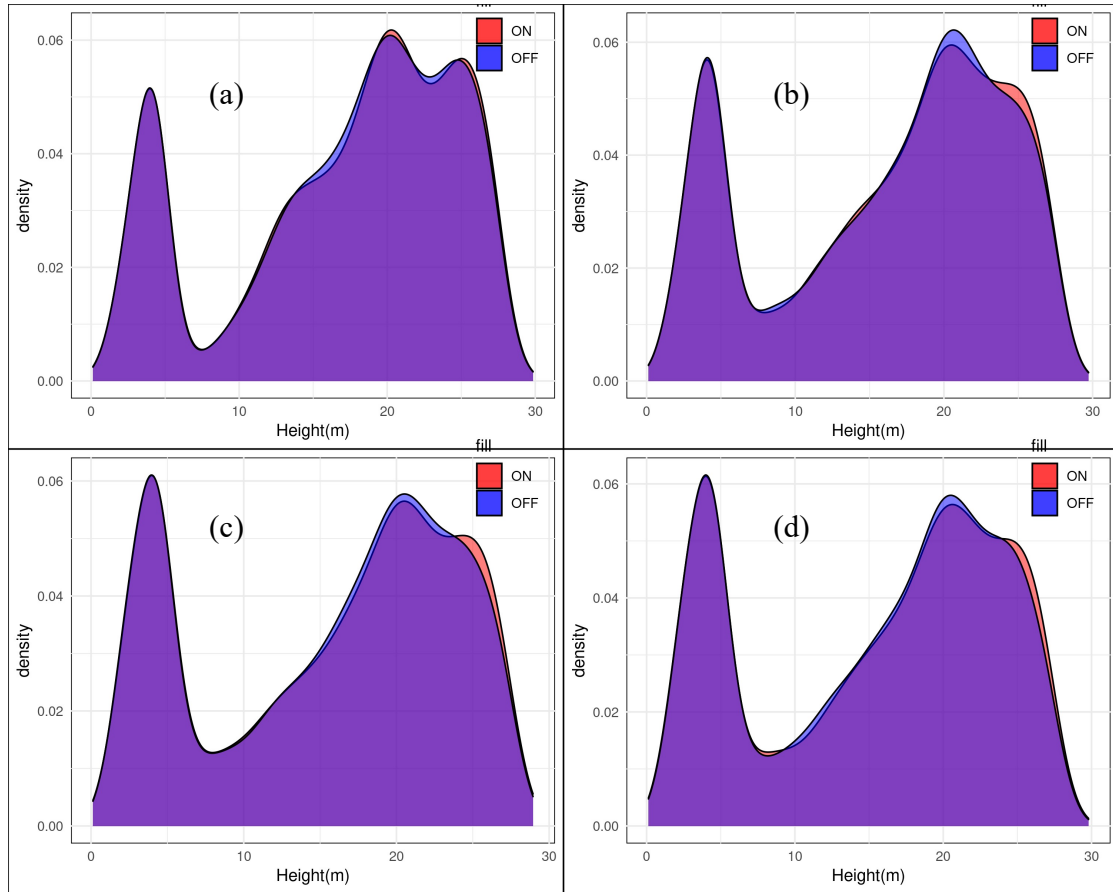


Figure S8. Probability density of tree height averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of North America. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

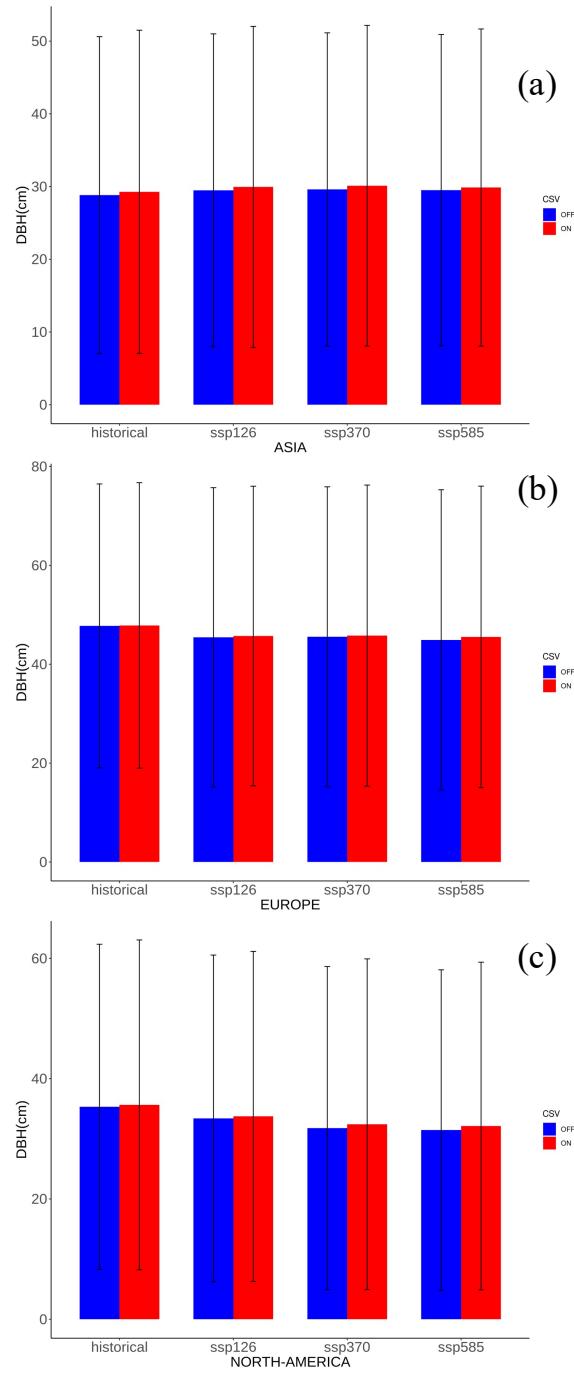


Figure S9. Changes in DBH, averaged over the periods 1985–2014 (historical scenarios) and 2071–2100 (SSP scenarios) in whole regions: (a) Asia, (b) Europe, and (c) North America. The red bars represent outputs from the "switch on" condition, while the blue bars represent outputs from the "switch off" condition.

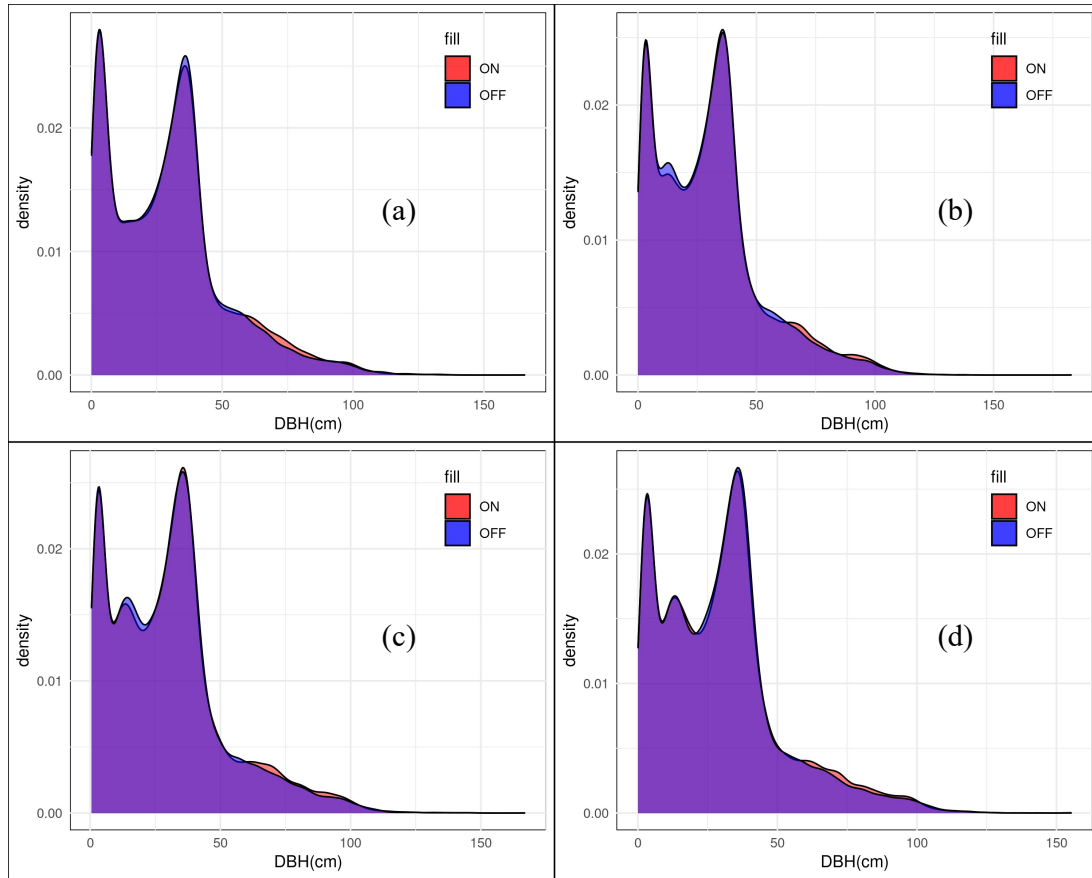


Figure S10. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of Asia. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

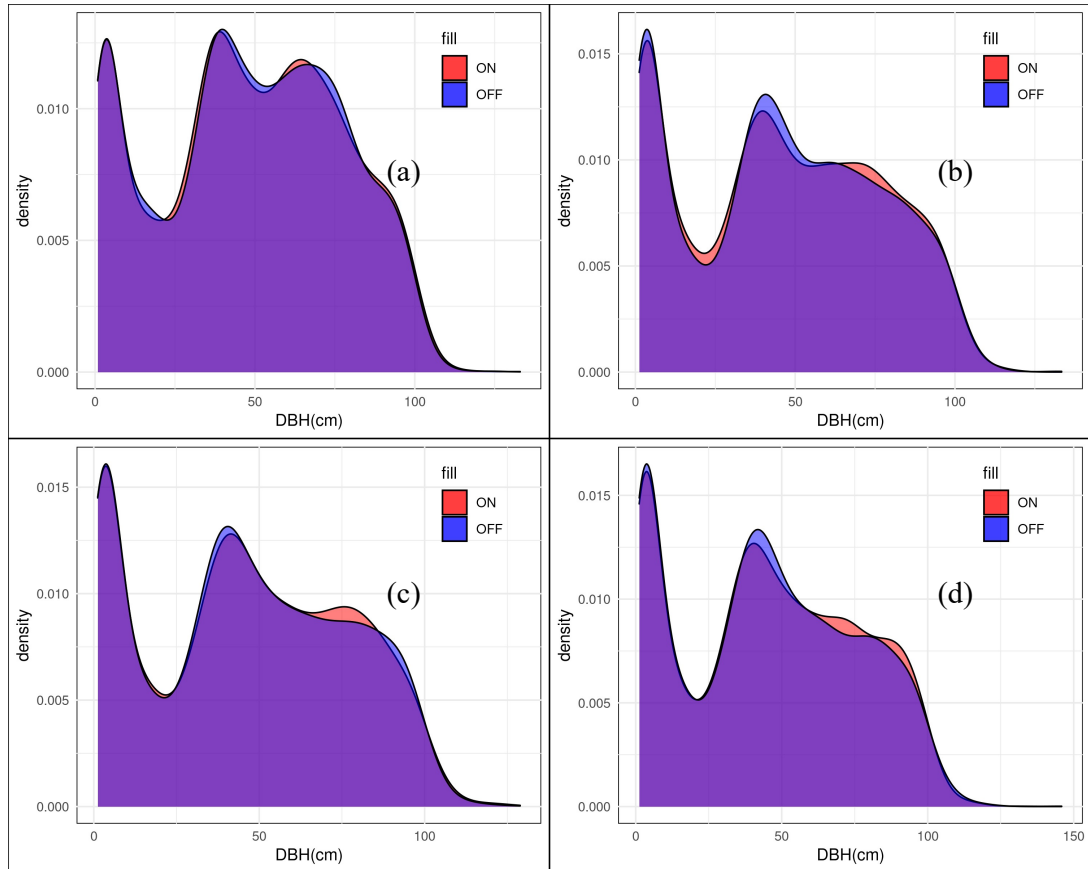


Figure S11. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of Europe. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.

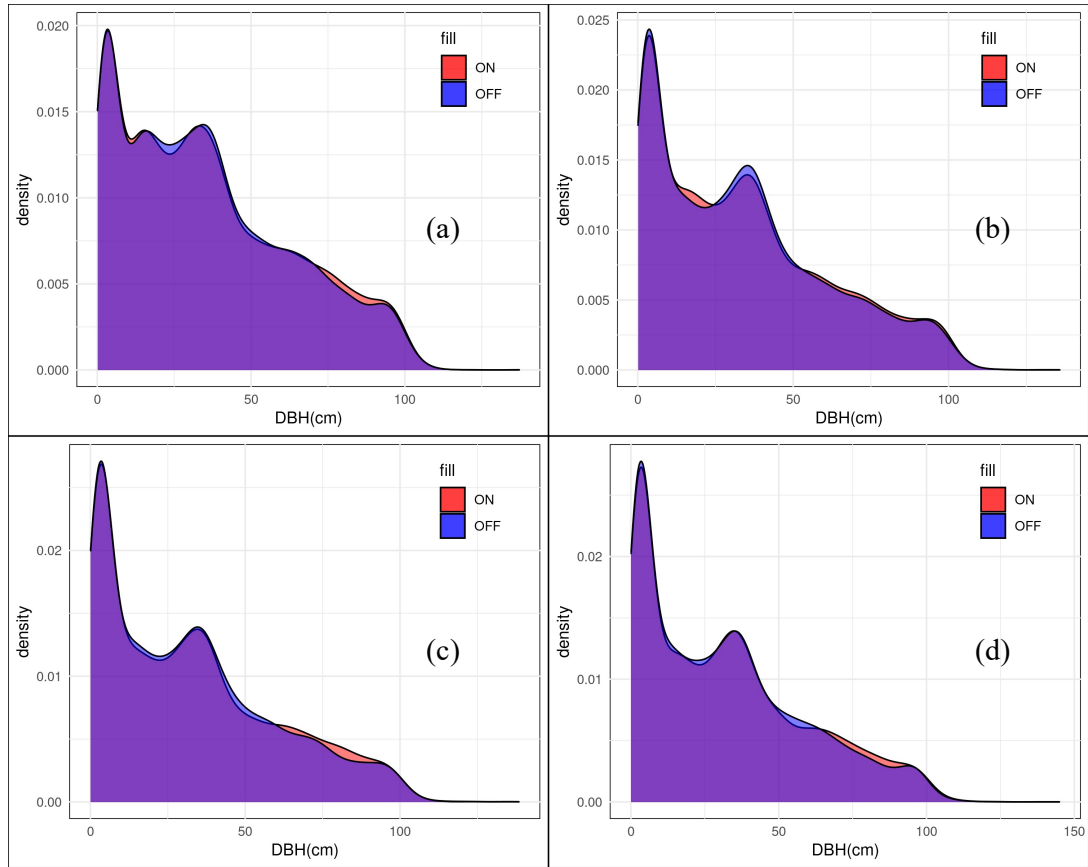


Figure S12. Probability density of DBH averaged over the last 30 years under (a) historical, (b) SSP126, (c) SSP370, and (d) SSP585 scenarios in whole regions of North America. The red areas represent outputs from the "switch on" condition, while the blue areas represent outputs from the "switch off" condition.