Title: Leaving disturbance legacies conserves boreal conifers and maximizes net CO_2 absorption under climate change and more frequent and larger windthrow regimes

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Abstract

Context

Forest management practices that conserve biodiversity and maximize carbon sequestration under climate change are needed. Although post-windthrow salvage logging and scarification can reduce carbon dioxide (CO_2) emissions within ecosystems by removing downed logs, they can greatly affect species composition. Additionally, salvage logging may increase CO_2 emissions based on a cradle-to-grave analysis of salvaged wood.

Objectives

We aimed to assess the effects of changes in climate, windthrow regimes and post-windthrow management on aboveground biomass, species composition, and carbon balance in the forest sector by combining forest landscape simulations and life cycle assessment (LCA).

Methods

The study landscape is a 12,169 ha hemiboreal forest located in northern Japan. We simulated 115 years (2015-2130) of forest dynamics in 36 scenarios based on features of the climate, windthrow regime, and management using the LANDIS-II forest landscape model. CO_2 emissions related to management and salvaged wood were estimated by LCA.

Results

Increases in the windthrow area, which was more vulnerable to climate warming, caused a shift to temperate broadleaved forests and a decrease in aboveground biomass. These were accelerated by the removal of advanced seedlings and dead wood, which greatly reduced the recruitment of *Picea* species. The 115-year cumulative net CO_2 absorption of the forest sector, including carbon balance within ecosystems and CO_2 emissions estimated by LCA, greatly decreased due to salvage logging (maximum 81%) and scarification (maximum 114%).

Conclusions

Leaving downed logs and advanced seedlings is recommended to conserve boreal conifers and carbon sinks and maximize net CO_2 absorption under climate change.

Keywords

Disturbance regime; Species composition; Carbon balance; Forest landscape model; LANDIS-II; Life cycle assessment

Introduction

Climate change, including temperature rise and precipitation change, and climate-driven changes in disturbance regimes have the potential to alter tree species composition and carbon balance in forests. Climate change affects the physiological responses of trees (i.e., seedling establishment, growth, and mortality). This can lead to changes in tree species composition from boreal conifer-dominant forests to temperate broadleaved tree-dominant forests that adapt to warmer climates (Hiura et al. 2019). Temperature rise and the lengthening of the growing season result in an increase in the decomposition rates of dead wood and soil organic matter, as well as gross primary production (Herrmann and Bauhus 2013; Mayer et al. 2017). Natural disturbances are major factors determining forest structures, which contribute to maintaining the biodiversity and environmental diversity of a landscape (Swanson et al. 2011). Although forest ecosystems have adapted to historical disturbance regimes, increases in disturbance frequency and size, which have already been observed on a global scale, can damage forests to such a great extent that the original forest attributes (e.g., aboveground biomass and species composition) cannot recover (Johnstone et al. 2016). In particular, windthrows are a major natural disturbance in Europe, along the east coast of North America, and in East Asia, but studies of the effects of changes in windthrow regimes on forests have been limited (e.g., Wu et al. 2019; Hlásny et al. 2021; Hotta et al. 2021) compared to studies focusing on wildfire or insect outbreaks. Among the different types of natural disturbances, windthrow activity is predicted to increase the most in warmer and wetter climates (Seidl et al. 2017); therefore, the effects of changes in the windthrow regime on forest ecosystems in humid climate zones should be examined.

The balancing of climate change mitigation by maintaining carbon sinks and biodiversity conservation is indispensable for achieving social and environmental goals (IPBES 2019) such as the United Nations' Sustainable Development Goals (UN 2015), the Convention on Biological Diversity's Kunming-Montreal 2030 Global Targets (CBD Secretariat 2022), and the Paris Agreement (UNFCCC 2015) objectives. The importance of forest management to support climate change adaptation is growing (Millar et al. 2007; Gustafson et al. 2020), but an alternative goal of management is to conserve tree species that are threatened by the effects of warmer climate brought about by climate change. Therefore, forest management strategies to maintain both biodiversity and carbon balance under these novel environmental conditions should be considered. For instance, conventional post-windthrow management, such as salvage logging and scarification, destroys disturbance legacies (i.e., advanced seedlings and dead wood) that are starting points for forest recovery, therefore affecting the species composition and carbon balance of the subsequently established forests (Taeroe et al. 2019; Hotta et al. 2020, 2021). Salvage logging is a management practice that removes disturbance-affected trees, prevents subsequent wildfire and insect outbreaks and compensates for economic losses (Lindenmayer et al. 2008). Scarifications are sometimes conducted after salvaging to destroy forest floor grasses and shrubs that inhibit tree regeneration and to remove the organic-rich surface soil layer that contains pathogens (Yoshida et al. 2005). However, these management practices destroy advanced seedlings, which delays forest recovery (Greene et al. 2006; Donato et al. 2006; Morimoto et al. 2011) and increases the ratio of early-successional species to late-successional species (Ilisson et al. 2007; Prévost et al. 2010; Fischer and Fischer 2012). The removal of dead wood due to salvage logging would decrease the regeneration of tree species that require dead wood as a regeneration site, e.g., *Picea jezoensis* (Nakagawa et al. 2001; Hotta et al. 2021), *Picea rubens* (Weaver et al. 2009), and *Tsuga canadensis* (Weaver et al. 2009). In addition, the removal of dead wood would somewhat decrease carbon dioxide (CO_2) emissions within ecosystems. However, conventional post-windthrow management practices may increase CO_2 emissions when a cradle-to-grave analysis (e.g., Hudiburg et al. 2019) of salvaged wood, including management practices, manufacturing, and wood product pool storage and decay, is considered together with heterotrophic respiration (Rh) in ecosystems.

Comprehensive assessments (e.g., life cycle assessment: LCA), including assessments of CO_2 emissions due to activities such as salvaging and making products from downed logs, are required for developing post-windthrow management plans that maximizes net CO_2 absorption, as well as the cases of normal harvesting and post-outbreak salvaging (Hudiburg et al. 2019; Gunn et al. 2020). LCA is a method for evaluating the environmental aspects associated with a product over its life cycle (Muralikrishna and Manickam 2017). The usefulness of considering LCA in landscape management is becoming increasingly recognized (Eddy and Gergel 2015; Wu et al. 2022). Considering carbon balance within ecosystems and LCAs together can realize the equal comparison of the effects of management strategies on carbon balance. However, previous studies that evaluated the effects of post-windthrow management on carbon balance did not include an LCA of salvaged wood (Dobor et al. 2018, 2020a).

No study has evaluated the effects of post-windthrow management on tree species composition and carbon balance with an LCA under climate change and novel windthrow regimes, although the continuation of conventional post-windthrow management may induce changes in tree species composition (Hotta et al. 2021) and carbon balance which is evaluated with an LCA (Suzuki et al. 2019). The decrease in or loss of disturbance legacies (e.g., due to post-windthrow management) may accelerate shifts in species composition, resulting in communities that are different from the original one (Johnstone et al. 2016), such as a shift to those more adapted to warmer climates (Liang et al. 2018). In addition, the increase in the number of times post-windthrow management is applied and the amount of dead wood salvaged due to changes in windthrow regime (Lindenmayer et al. 2008) may induce the degradation of carbon sinks in the forest sector, as determined by both ecosystem analysis and a cradle-to-grave dead wood analysis. In this study, we aimed to reveal the effects of climate change, changes in windthrow regimes, and post-windthrow management on the total aboveground biomass and tree species composition in forest landscapes. We also analyzed the carbon balance in the forest sector by simulating changes in the forest landscape under several climate, windthrow regime, and management scenarios using LANDIS-II (Scheller et al. 2007), a widely used process-based forest landscape model, and LCA.

Materials and Methods

Study landscape

The study landscape is a 12,169 ha hemiboreal forest located in the University of Tokyo Hokkaido Forest (UTHF; 43°10′-21′N, 142°23′-41′E; 315-1,051 m above sea level (a.s.l); Fig. 1). The annual mean temperature and the annual total precipitation at the Rokugo meteorological observatory (43°18′6″N, 142°31′18″E, 315 m a.s.l.), which is the closest site to the study landscape, are 5.5°C and 972.6 mm, respectively (representing the averages from 1981-2010) (Japanese Meteorological Agency 2012). The study landscape is covered by hemiboreal mixed forests dominated by conifers such as *Abies sachalinensis* (F. Schmidt) Mast. and *Picea jezoensis* (Siebold et Zucc.) Carriére var. *jesoensis*; deciduous broadleaves such as *Tilia japonica* (Miq.) Simonk. and *Betula ermanii* Cham.; and herbaceous species such as *Sasa senanensis* (Franch. et Sav.) Rehder. The dominant soil type is mostly Andosols (parent material: andesite, rhyolite, volcanic ash, or dacite) with some Cambisols (parent material: rhyolite or dacite) (IUSS Working Group WRB 2015). The dominant natural disturbance of the study landscape is stand-replacing windthrow. There are records of windthrow caused by Typhoon Marie in 1954 and Typhoon Thad in 1981 in the UTHF (Watanabe et al. 1990). Notably, 8,735 ha (38.9% of the UTHF) in area and 807,000 m^3 in timber volume were damaged by Typhoon Thad in 1981 (Takada et al. 1986).

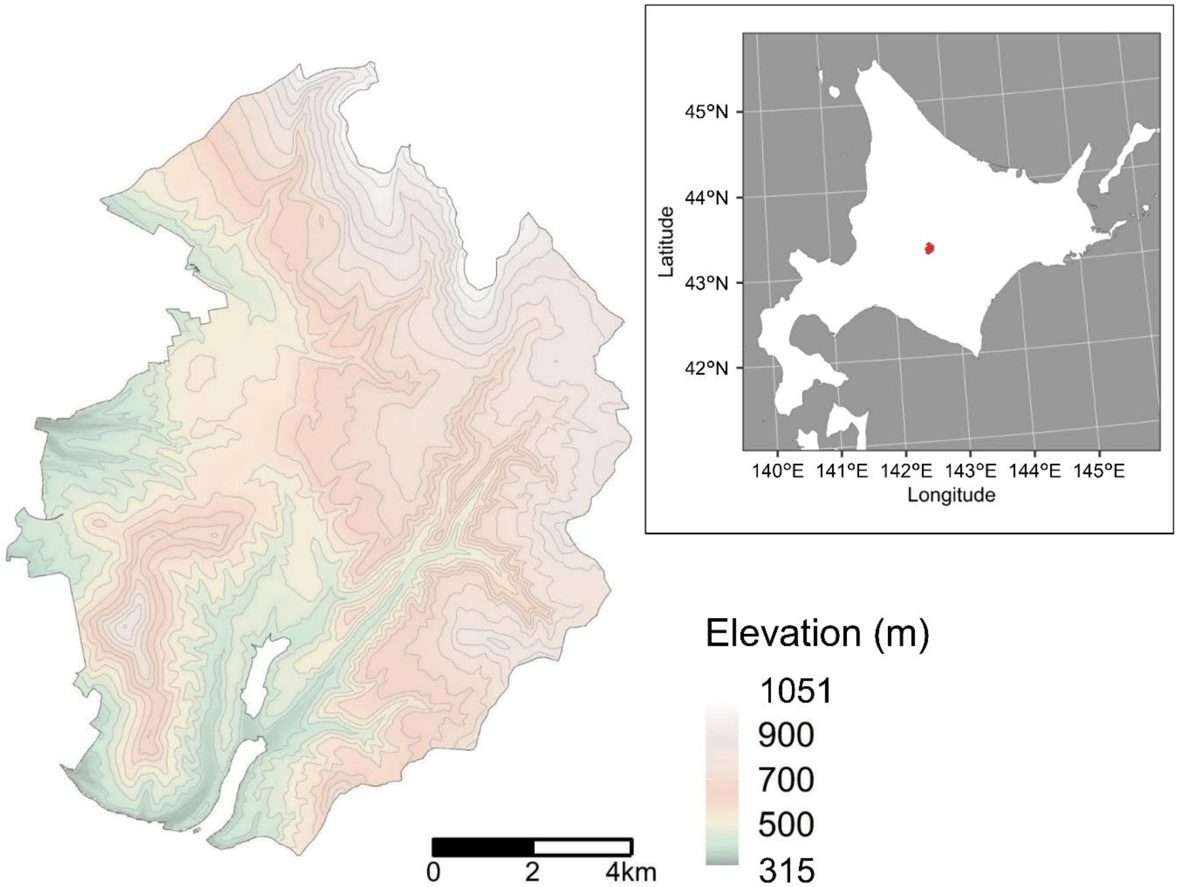

Fig. 1

Study landscape map. Right: Map of northern Japan. The red area indicates the location of the study landscape. Left: Topographical map of the study landscape.

Simulation model and its application in this study

In this study, we applied LANDIS-II (Scheller et al. 2007), a forest landscape model, to project the forest dynamics associated with climate change, changes in windthrow regimes, and post-windthrow management at the landscape scale. The landscape in LANDIS-II was represented as a collection of uniformly sized grid cells that contain the data for vegetation, climate, and soil properties. In this study, the size of a grid cell was defined as 1 ha. The vegetation data were represented as species-age cohorts, and each grid cell could contain multiple cohorts. The vegetation and environment influenced other surrounding grid cells through seed dispersal. LANDIS-II requires a single succession extension and can include multiple disturbance or output extensions.

The improved version of LANDIS-II Net Ecosystem Carbon and Nitrogen succession v6.3 (NECN succession) (Scheller et al. 2011) with tree-grass competition (Haga et al. 2022) and the regeneration process on downed logs (Hotta et al. 2021) was used as the succession extension to simulate the dynamics of forest species composition and carbon balance. In the NECN succession, biomass growth and seedling establishment were calculated based on the environmental conditions in each grid cell. The biomass growth of each cohort was calculated as the difference between monthly aboveground net primary production (NPP) and monthly mortality. Monthly aboveground NPP was calculated by multiplying the maximum value of monthly aboveground NPP (user-defined parameter for each species) by coefficients related to environmental limitation factors, such as monthly mean temperature, plant-available soil nitrogen, soil water content, the leaf area index (LAI) of the cohort itself, and the LAI of the other cohorts within the grid cell. Regarding cohort establishment, the establishment probabilities of each species in each grid cell were calculated based on the following two categories: (1) minimum January temperature (the minimum temperature of the coldest month in a year), growing degree days, and soil moisture content of each region; and (2) light availability at the site. If the two designated requirements were satisfied (i.e., the product of establishment probabilities based on two categories is larger than the random number assigned to each site), cohorts were established in the grid cell. Additionally, tree species requiring dead wood for regeneration could be established only in grid cells that had well-decayed downed logs (Hotta et al. 2021). Many field-based studies have reported that some *Picea* species largely depends on dead wood for their establishment sites because seedlings can avoid pathogens, light competition, and aridity on dead wood (e.g., Harmon and Franklin 1989; Takahashi et al. 2000; Nakagawa et al. 2001). Therefore, two species of *Picea* spp., *P. jezoensis* and *P. glehnii*, were set as dead wood-dependent species in this study. The decomposition rates of dead wood and soil organic matter were controlled by the soil temperature and moisture content. The decomposition rate of dead wood was calculated according to the amount of dead wood of each tree species in the dead wood pool using the parameters of dead wood decomposition rates of each species (user-defined parameter; WoodDecayRate). The decomposition rate of soil organic matter was calculated based on the decomposition rate parameters of the four soil pools (user-defined). Both decomposition rates were calculated to reflect the environmental conditions of each grid cell through soil temperature and moisture contents (Scheller et al. 2011).

LANDIS-II has been applied to various landscapes and ecosystems in North America, East Asia, Europe, and so on (Shifley et al. 2017; Lucash et al. 2019; Haga et al. 2020; Hotta et al. 2021). We conducted various calibrations and validations to guarantee the model performance in the study landscape. In summary, the decomposition rates of dead wood were parameterized by calibrating WoodDecayR to match the time required for reaching decay class 3 for dead wood (18 years in our study landscape) (Hotta et al. 2021). Forest recovery after each post-windthrow management effort (dead wood left intact, salvage logging, and scarifications) was validated by comparing simulation results with empirical aboveground biomass and tree species composition data from 32 years after each post-windthrow management event in UTHF (Hotta et al. 2021). In addition, the following calibration and validation in this study landscape have already been reported by Hotta et al. (2021): the calibration of aboveground biomass growth and litterfall of each species, the LAI and NPP in a grid cell, the aboveground biomass and LAI of *Sasa* (an herbaceous species), the inhibition of tree regeneration by *Sasa*, and the decomposition rate of soil. Furthermore, the dynamics of aboveground biomass and tree species composition in undisturbed forests, the carbon stocks of dead wood and soils, and the net ecosystem production (NEP) over several decades were validated in this study. The calibration, validation, and input data of the model are described in detail in Hotta et al. (2021), Supplementary materials S1 and S2 in the report by Hotta et al. (2021), and Online Resource 1 in this study (with the LANDIS-II input files available in the Supporting data (Hotta 2023)).

Landscape initialization

We focused on the tree species that accounted for 90% of the cumulative biomass in the study landscape, and the most dominant herbaceous species which were as follows: *A. sachalinensis*, *P. jezoensis*, *P. glehnii*, *T. japonica*, *Acer pictum* Thunb., *B. ermanii*, *Betula maximowicziana* Regel, *Quercus crispula* Blume var. *crispula*, *Kalopanax septemlobus* (Thunb.) Koidz., *Fraxinus mandshurica* Rupr., *Ulmus laciniata* (Trautv.) Mayr ex Schwapp., and *S.*

senanensis. Regarding tree species, the initial communities as of 2015, that is, the input data of vegetation, were created based on forest inventory data of the UTHF. Regarding herbaceous species, the input data were created by estimating the aboveground biomass of *Sasa* using the *Sasa* distribution model developed by Tatsumi and Owari (2013) and tree input data. We input the uniform value of 3,100 g m^{-2} for the initial amount of dead wood in the study landscape, as this is the mean value of the dead wood data from Hotta et al. (2020). All initial dead wood was assumed to be mostly undecomposed because the data of the amounts of dead wood in each decay class were unavailable. Additionally, the amount of dead wood cannot be input by decay classes in the NECN succession extension due to technical constraints, and it is highly challenging to estimate the amount of dead wood in stands that have different management histories due to the lack of empirical data. The absence of well-decayed dead wood at the start of the simulation would cause the underestimation of tree regeneration on downed logs in the first twenty years of the simulations. Soil property data were input based on the data from Asahi (1963), which described the soils in the UTHF in detail.

Windthrow regime scenarios

Biomass Harvest extension Ver 4.3 (Gustafson et al. 2000) was used to represent various frequencies and sizes of stand-replacing windthrow. In this study, we cannot consider the temporal randomness of windthrow event occurrences because disturbances cannot be initiated randomly in the Biomass Harvest extension. However, using Biomass Harvest extension is essential to represent the three post-windthrow management practices investigated in this work (leaving downed logs; salvage logging; and salvage logging and subsequent scarification).

(1) Historical windthrow regime scenario (Historical)

The scenario in which stand-replacing windthrow occurred with historical frequency (twice in 100 years) and size (20% of the study landscape area) (Table 1). The ratio of the windthrow area of each windthrow event to the study landscape area (20%) was determined based on the record of windthrow caused by Typhoon Thad in 1981 (Watanabe et al. 1990). The frequency and interval of windthrow (occurring in 2030 and 2080) were determined based on the data from Abe et al. (2006) (Table 1).

(2) Increased windthrow frequency scenario (Frequent)

The scenario in which stand-replacing windthrow occurred with twice the historical frequency (Table 1). The ratio of the windthrow area of a single windthrow event to the study landscape area was defined as 20%, which was the same as the Historical scenario. The frequency of windthrow was defined as four times in 100 years (occurring in 2030, 2055, 2080, and 2105).

(3) Increased windthrow size scenario (Large)

The scenario in which the stand-replacing windthrow occurred with twice the size of historical windthrow events (Table 1). The ratio of the windthrow area of a single windthrow event to the study landscape area was defined as 40%. The frequency of windthrow was defined as twice in 100 years (occurring in 2030 and 2080), which was the same as the frequency in the Historical scenario.

(4) Increased windthrow frequency and size scenario (Frequent & Large)

The scenario in which the stand-replacing windthrow occurred with twice the historical frequency and size (Table 1). The ratio of the windthrow area of a single windthrow event to the study landscape area was defined as 40%. The frequency of windthrow was defined as four times in 100 years (occurring in 2030, 2055, 2080, and 2105).

All the live trees within grid cells where windthrow occurred except for advanced seedlings and *Sasa* were assumed to be destroyed when windthrow occurred because we focused on the stand-replacing windthrow, which is the dominant natural disturbance in the studied landscape. The destruction ratios of advanced seedlings were dependent on post-windthrow management scenarios, which are described later. Whether the cohorts contained advanced seedlings was determined by the cohort age, and the threshold age was determined by the tree species based on the field data from the windthrow sites in the UTHF caused by Typhoon Thad in 1981 (see Supplementary materials S5 in Hotta et al. (2021)). The initiation grid cells where windthrow occurred were randomly selected within the grid cells where the stand age was over 50 years because the windthrow risk increases with the stand age (Foster 1988; Everham and Brokaw 1996) (Online Resource 2). The windthrow was set to spread from the initiation grid cell to a maximum of 10 ha by using the Biomass Harvest extension. The grid cells where the windthrow spread reached were also required to have a stand age over 50 years.

Table 1 The year when windthrow occurs and the ratio of windthrow areas to the study landscape area in each windthrow regime scenario

Windthrow regime scenarios	2030 (Year 15)	2055 (Year 40)	2080 (Year 65)	2105 (Year 90)
Historical	20%	—	20%	—
Frequent	20%	20%	20%	20%
Large	40%	—	40%	—
Frequent & Large	40%	40%	40%	40%

Post-windthrow management scenarios

We considered the following three post-windthrow management practices: (a) dead wood left undisturbed (windthrow only); (b) salvage logging; and (c) salvage logging and scarification. Notably, these are the same scenarios as those used in Hotta et al. (2021).

(a) Dead wood left undisturbed (windthrow only: WT)

All dead wood generated by windthrow was left undisturbed, and 20% of advanced seedlings were destroyed due to fallen trees (Table 2). The destruction ratio of advanced seedlings was determined based on the data from the windthrow sites in the UTHF caused by Typhoon Thad in 1981 (Kurahashi et al. 1984).

(b) Salvage logging after windthrow (SL)

All dead wood generated by windthrow was salvaged and removed from forest ecosystems, and 60% of advanced seedlings were destroyed due to salvaging (Table 2). The destruction ratio of advanced seedlings was determined based on the data of the ratio of forest floor area disturbed by logs that were removed (Ohsato et al. 1996).

(c) Salvage logging and scarification after windthrow (SLSC)

All dead wood generated by windthrow was salvaged and removed from the forest ecosystems, and the forest floor in all windthrow areas was scarified after salvaging. All advanced seedlings were destroyed due to scarification (Table 2). The destruction ratio of *Sasa* due to scarification was set as 99% (Table 2). Because a small percentage of *Sasa* survive scarification (Yoshida et al. 2005), we applied the maximum destruction ratio, which allowed some *Sasa* to survive.

Table 2 Settings of post-windthrow management scenarios (the same scenarios used in Hotta et al. (2021))

Post-windthrow management scenarios	Dead wood generated by windthrow	Advanced seedlings	*Sasa* (dwarf bamboo)
Windthrow (WT)	Left intact	20% destroyed	Undestroyed
Salvage logging (SL)	100% salvaged	60% destroyed	Undestroyed
Salvage logging and scarification (SLSC)	100% salvaged	100% destroyed	99% destroyed

Climate scenarios

To consider tree physiological responses to climate change, the current climate and two future climate scenarios were used for simulations. Regarding the current climate scenario (Current), the 1 km mesh climate data (an average from 1981–2010) (Japanese Meteorological Agency 2012) in the study area landscape were used for the climate data. We selected the following two extreme scenarios as future climate scenarios: (1) the representative concentration pathway (RCP) 2.6 scenario calculated by the CSIRO-Mk3-6-0 model (hereafter referred to as the RCP2.6 scenario; approximately 1℃ increase in mean annual temperature and almost no change in precipitation by 2100); and (2) the RCP8.5 scenario calculated by the GFDL-CM3 model (hereafter referred to as the RCP8.5 scenario; approximately 6.5℃ increase in mean annual temperature and 10% increase in precipitation by 2100) (Nishimori et al. 2019). In humid climate zones, temperature rise has a greater impact than precipitation changes (Feeley et al. 2012). In addition, future drought risk is expected to be low in this region (Dai 2011). To primarily evaluate the impact of temperature increase, this study adopted the future climate scenarios of RCP2.6 and RCP8.5, which have a small range of variability in precipitation and a large range of variability in temperature. The details of each climate scenario and the reasons for selecting them are described in Online Resource 3.

Simulation and evaluation indicators

We simulated 36 scenarios that were combinations of the four windthrow regime scenarios, three post-windthrow management scenarios, and three climate scenarios. The simulations were replicated five times for each scenario due to the stochasticity and uncertainties related to seed dispersal, cohort establishment, and windthrow area selection. The duration of the simulations was 115 years, from 2015 to 2130.

We evaluated the species composition in the forest landscape using the aboveground biomass of each species. Additionally, the number of cohorts successfully established for each species was evaluated to determine the effects of climate, windthrow regime, and post-windthrow management on the cohort establishment of each species. The net forest sector carbon balance (Hudiburg et al. 2019; hereafter referred to as NFCB) was calculated to evaluate the difference in the carbon balance between the following two cases: the case when dead wood generated by windthrow was decomposed within the forest ecosystem (WT scenario) and the case when dead wood generated by windthrow was salvaged and used as timber and paper products (SL and SLSC scenarios). LCAs of these scenarios were conducted to calculate the NFCB (Online Resource 4). NEP, NPP, and Rh were used to understand the factors that explain the dynamics of the NFCB. Rh is defined as the process of releasing CO_2 to the atmosphere by the decomposition of dead wood and soil organic matter. Additionally, we conducted three-way factorial analysis of variance (ANOVA; n = 5 per scenario) in which climate, windthrow regime, post-windthrow management, and their two-term interactions (climate × windthrow regime, windthrow regime × post-windthrow management, climate × post-windthrow management) were considered as factors. Then, we assessed the effect size of each factor by calculating omega-squared values (ω^2) (following the guide of White et al. 2014 and an example reported by St-Laurent et al. 2022) using the *effectsize* package (Ben-Shachar et al. 2020). ω^2 represents how much variance in the response variables is accounted for by the explanatory variables. Values larger than 0.01, 0.06, and 0.14 were interpreted as small, medium, and large effect size, respectively (Field 2013). The response variables were the total aboveground biomass in 2130, the aboveground biomass of each species in 2130, the total number of newly established cohorts in the entire simulation, the number of newly established cohorts of each species in the entire simulation, the NEP in 2130, the NPP in 2130, the Rh in 2130, the NFCB in 2130, and the cumulative NFCB in 2130 for all the scenarios. The summary and analysis of the simulation results were conducted in R ver. 3.6.2 (R Core Team 2019).

NFCB is one of the indicators of carbon balance that considers CO_2 emissions related to harvesting, transportation, manufacturing, the disposal of the product, and so on (Hudiburg et al. 2019). In this study, we defined the forest sector as shown in Fig. 2. The NFCB was calculated using Equation 1 after estimating the CO_2 emissions related to salvage logging, scarification, the manufacturing of products, and the disposal of products by LCA (Fig. 2, Online Resource 4). The CO_2 emissions related to the transportation of dead wood were excluded because they were smaller than the CO_2 emissions related to the other processes (Owari et al. 2011).

$$\mathrm{NFCB}_t = \mathrm{NEP}_t - \mathrm{CE}_{Salvage\ t} - \mathrm{CE}_{Scarification\ t} - \mathrm{CE}_{ManufactureLong\text{-}lived\ t} - \mathrm{CE}_{ManufactureShort\text{-}lived\ t} - \mathrm{CE}_{ManufactureWoodenBoard\ t} - \mathrm{CE}_{WoodProductsDecomposed\ t} \qquad \text{Eq. 1}$$

t: the simulation year; NFCB_t: net forest sector carbon balance in year t; NEP_t: net ecosystem production in year t; $\mathrm{CE}_{Salvage\ t}$: CO_2 emissions related to salvage logging (e.g., use of heavy machinery) in year t; $\mathrm{CE}_{Scarification\ t}$: CO_2 emissions related to scarification (e.g., use of heavy machinery) in year t; $\mathrm{CE}_{ManufactureLong\text{-}lived\ t}$: CO_2 emissions related to manufacturing of long-lived products (timber products used for several decades such as building materials and furniture) in year t; $\mathrm{CE}_{ManufactureShort\text{-}lived\ t}$: CO_2 emissions related to manufacturing of short-lived products (products to be disposed of in a few years such as wood chips and paper) in year t; $\mathrm{CE}_{ManufactureWoodenBoard\ t}$: CO_2 emissions related to the manufacturing of wooden boards (such as particle boards) in year *t*; and $CE_{WoodProductsDecomposed\ t}$: CO_2 emissions (flux to outside of the forest sector) related to the disposal of products made from dead wood generated by the windthrow in year *t*.

The detailed calculations of each CO_2 emission are described in Online Resource 4. The CO_2 emissions related to salvage logging, scarification, and the manufacturing of long- and short-lived products and wooden boards were assumed to occur in the year when windthrow occurred. Regarding the WT scenario, the NFCB was equal to the NEP because all dead wood generated by windthrow was left intact in the forest ecosystem. In this study, scrap wood generated by sawing was used as raw material for wooden boards to utilize dead wood generated by windthrow as products with the longest possible life. In addition, we analyzed the sensitivity of the NFCB to the usage of scrap wood, and Online Resource 5 indicated the result in the case when scrap wood was used for paper pulp and chip production, which was the scenario utilizing dead wood generated by windthrow as products with the shortest possible life.

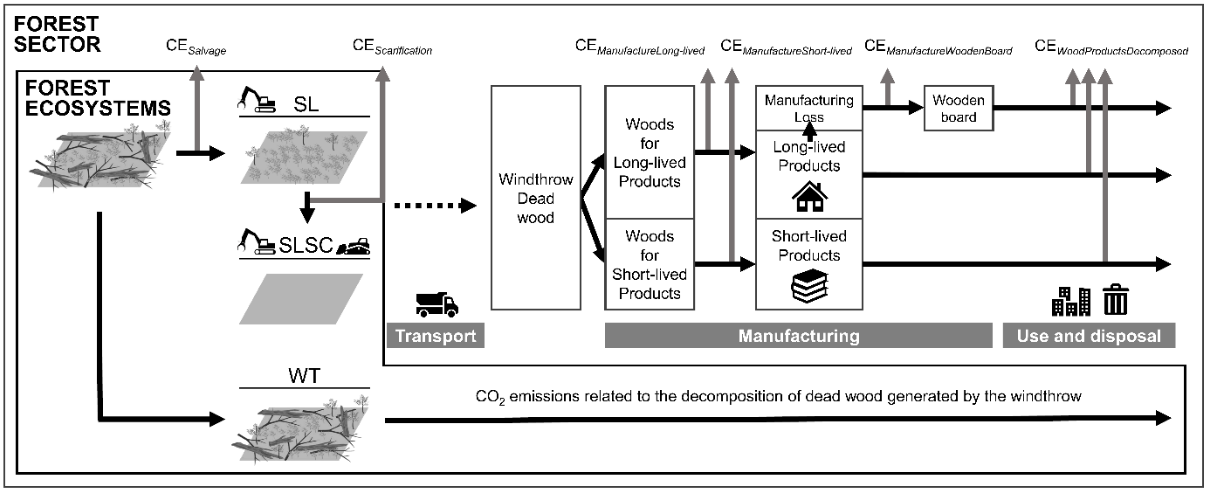

Fig. 2

The system boundary of the life cycle assessment in this study and the differences in the forest sector and forest ecosystem. Gray arrows indicate CO_2 emissions by each factor. Dark gray boxes indicate stages in the life cycle. The part indicated by a dotted arrow was cut off in the life cycle assessment. WT: windthrow only; SL: salvage logging; SLSC: salvage logging and scarification. $CE_{Salvage}$: CO_2 emissions related to salvage logging (e.g., use of heavy machinery); $CE_{Scarification}$: CO_2 emissions related to scarification (e.g., use of heavy machinery); $CE_{ManufactureLong\text{-}lived}$: CO_2 emissions related to manufacturing of long-lived products (timber products used for several decades such as building materials and furniture); $CE_{ManufactureShort\text{-}lived}$: CO_2 emissions related to manufacturing of short-lived products (products to be disposed of in a few years such as wood chips and paper); $CE_{ManufactureWoodenBoard}$: CO_2 emissions related to the manufacturing of wooden boards (such as particle boards); $CE_{WoodProductsDecomposed}$: CO_2 emissions related to the disposal of products that were made from dead wood generated by windthrow.

Results

Total aboveground biomass and species composition

Regarding total aboveground biomass in 2130, the effect sizes of windthrow regime ($\omega^2 = 0.741$) and post-windthrow management ($\omega^2 = 0.183$) were large, and those of climate ($\omega^2 = 0.037$), windthrow regime × post-windthrow management ($\omega^2 = 0.021$), and climate × windthrow regime ($\omega^2 = 0.015$) were small. The effect size of climate × post-windthrow management ($\omega^2 = 0.002$) was very small (Online Resource 9 Table S9.1). The total aboveground biomass in 2130 was only slightly different among the post-windthrow management scenarios; however, the species composition in 2130 was different between the SLSC and the other two management practices under the current climate and historical windthrow regime (Figs. 3 and 4 and Online Resource 6). In the SLSC, the aboveground biomass of *Betula* spp. was 77% larger, and those of *A. sachalinensis* and *Picea* spp. were 54 and 22% smaller, respectively, compared to the WT (Online Resource 7 Fig. S7: *Betula* spp., *A. sachalinensis*, *Picea* spp).

The total aboveground biomass in 2130 decreased as the windthrow frequency and size increased. The decreasing ratio of the total aboveground biomass to that under the Historical scenario and the effects on species composition increased as the windthrow frequency and size increased with salvage logging and scarification (Figs. 3 and 4 and Online Resource 6). The total aboveground biomass under the Frequent & Large scenario in WT, SL, and SLSC was 69%, 60%, and 46% of that under the Historical scenario, respectively (Fig. 3). In the SLSC, the aboveground biomass of *Betula* spp. showed little difference under the Historical and Frequent & Large scenarios (Online Resource 7 Fig. S7: *Betula* spp.), but the ratio of *Betula* spp.-dominant forest area to the study landscape area under the Frequent & Large scenario was twice as large as that under the Historical scenario (Fig. 4: Current; and Online Resource 6). In SL, the difference in species composition from WT was small under the Frequent or the Large scenarios. However, the aboveground biomass of *Picea* spp. in SL was lower than that in WT under the Frequent & Large scenario (Fig. 3; Online Resource 7 Fig. S7: *Picea* spp.). The ratio of *Picea* spp.-dominated forests to the study landscape area was approximately 66% of that in WT under the Frequent & Large scenario (Fig. 4: Current; and Online Resource 6). The aboveground biomass of *Sasa* increased as the windthrow frequency and size increased, regardless of post-windthrow management. The ratios of *Sasa*-dominant grid cells to the study landscape area under the Frequent & Large scenario were approximately three times as large in SL as those in WT and approximately five times as large in SLSC as those in WT (Fig. 4: Current; Online Resource 6 and 7 Fig. S7: *S. senanensis*).

The effects of temperature increase on the total aboveground biomass and species composition were more apparent as windthrow frequency and size increased and salvage logging and scarification were conducted. The total aboveground biomass and species composition under historical conditions were only slightly different among the climate scenarios. Under the Frequent & Large scenario, the total aboveground biomass was slightly different between the current climate and RCP 2.6. However, the total aboveground biomass in RCP8.5 was 64% (SLSC) – 77% (WT) of that in the current climate scenario (Fig. 3). The aboveground biomass and the percentages of dominance in the study landscape area of *A. sachalinensis* and *Betula* spp. decreased with increasing temperature (Figs. 4 and Online Resources 6 and 7 Fig. S7: *A. sachalinensis* and *Betula* spp.), regardless of post-windthrow management. Those of *Q. crispula* and *S. senanensis* increased with increasing temperature (Fig. 4 and Online Resources 6 and 7 Fig. S7: *Q. crispula* and *S. senanensis*) in the SLSC. These effects were larger as the windthrow frequency and size increased. Changes in species composition with increasing temperature were largest in the SLSC scenario. In the SLSC scenario under the Frequent & Large scenario, the aboveground biomass of *Betula* spp. was 95% smaller, and those of *Q. crispula* and *S. senanensis* were 85% and 38% larger, respectively, under RCP 8.5 than those of the Current scenario (Online Resource 7 Fig. S7: *Betula* spp., *Q. crispula*, and *S. senanensis*). Under RCP8.5 and the Frequent & Large scenario, the ratios of *Sasa*-dominated grid cells to the study landscape area were 22%, 37%, and 57% in WT, SL, and SLSC, respectively (Fig. 4).

The total number of newly established cohorts during the entire simulation period and the species composition of newly established cohorts were greatly influenced by the climate and post-windthrow management scenarios, but they were only slightly influenced by the windthrow regime (Fig. 5). Regarding the total number of established cohorts, the effect size of climate ($\omega^2 = 0.774$) was large, that of post-windthrow management ($\omega^2 = 0.102$) was medium, and the effect sizes of windthrow regime × post-windthrow management ($\omega^2 = 0.050$), climate × post-windthrow management ($\omega^2 = 0.032$), windthrow regime ($\omega^2 = 0.019$), and climate × windthrow regime ($\omega^2 = 0.018$) were small (Online Resource 9 Table S9.2). The number of established cohorts of temperate tree species such as *Q. crispula*, *F. mandshurica*, and *K. septemlobus* increased as the temperature increased (Fig. 5). However, the numbers of newly established cohorts of *A. sachalinensis* and *Betula* spp. in RCP2.6 and RCP8.5 and those of *Picea* spp. in RCP8.5 were less than those in the Current scenario (Fig. 5). The numbers of *Picea* spp. cohorts established in the SL and SLSC were lower than those established in the WT (Fig. 5). The difference in the total number and species composition of newly established cohorts among post-windthrow management increased as the windthrow frequency and size increased.

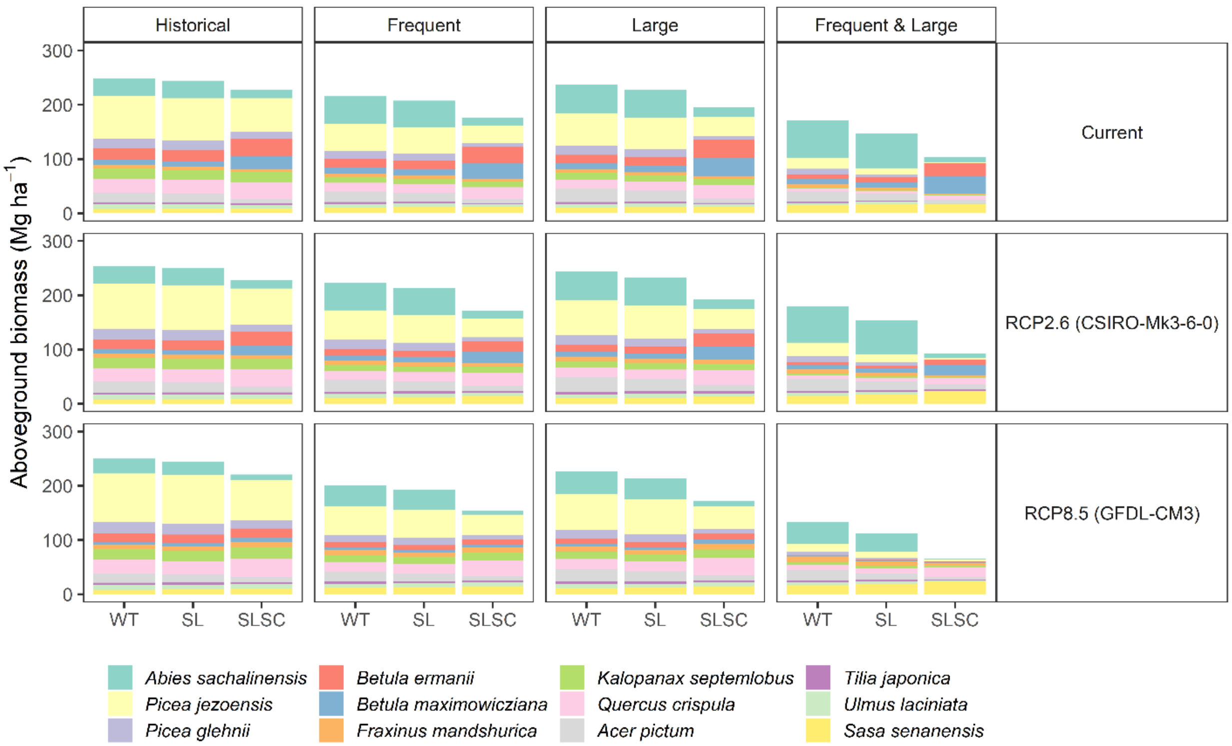

Fig. 3

Aboveground biomass of each species in 2130 (the last year of simulations). Rows and columns indicate climate scenarios and windthrow regime scenarios, respectively. The horizontal axis indicates post-windthrow management scenarios. WT: windthrow only; SL: salvage logging; SLSC: salvage logging and scarification. The mean values and standard deviations of the aboveground biomass of each species and total aboveground biomass are available in Online Resource 10.

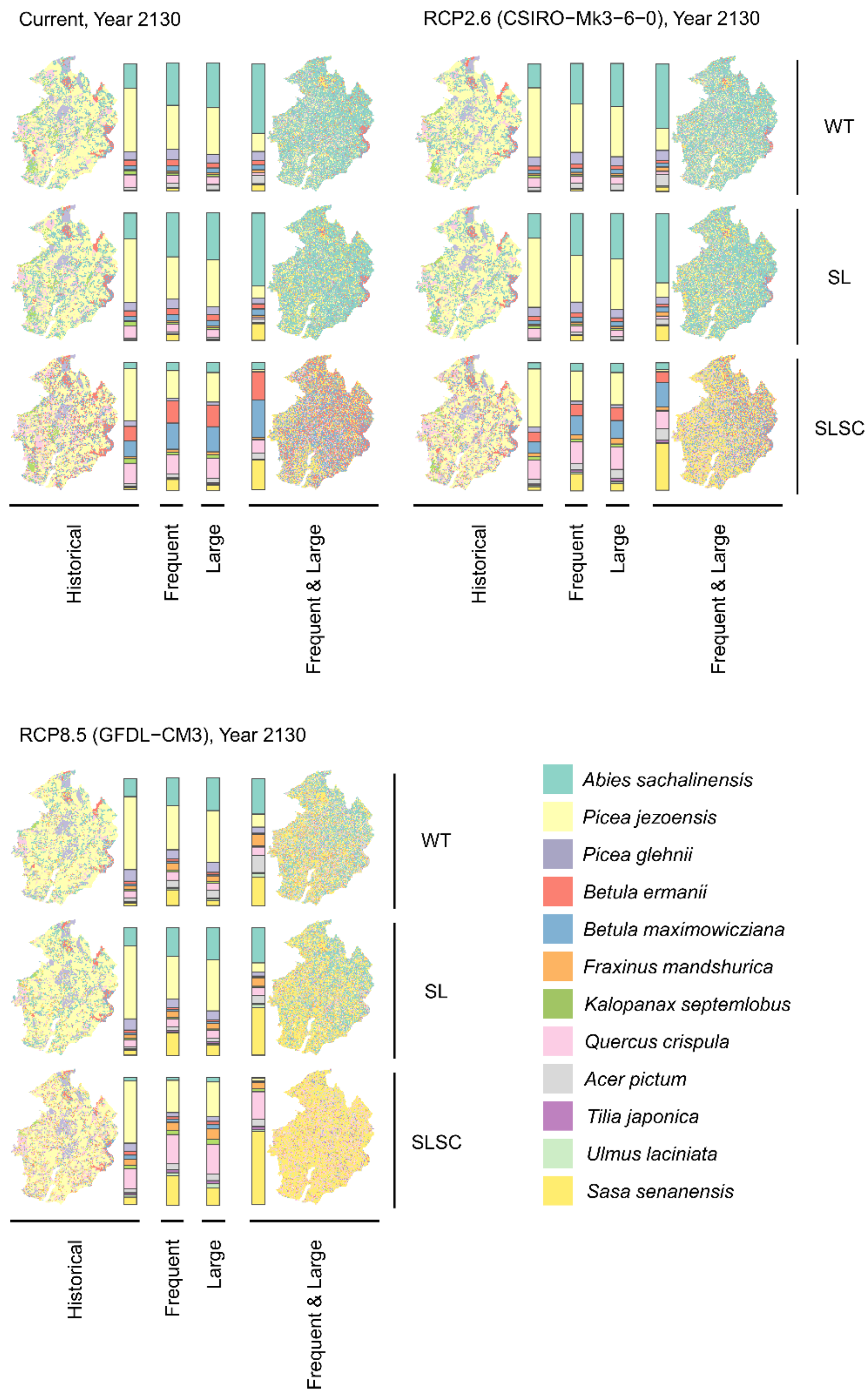

Fig. 4

The spatial distributions of forests dominated by each species and the ratio of grid cells dominated by each species in 2130 (dominance based on aboveground biomass). The raster indicates the dominant species in each grid cell.

Only the Historical and the Frequent & Large scenarios are shown. The raster of all scenarios is presented in Online Resource 6. The bar graphs indicate the ratio of grid cells dominated by each species to the study landscape. Species with the largest aboveground biomass in the grid cell were defined as the dominant species. Rows and columns indicate post-windthrow management scenarios and windthrow regime scenarios, respectively. WT: windthrow only; SL: salvage logging; SLSC: salvage logging and scarification

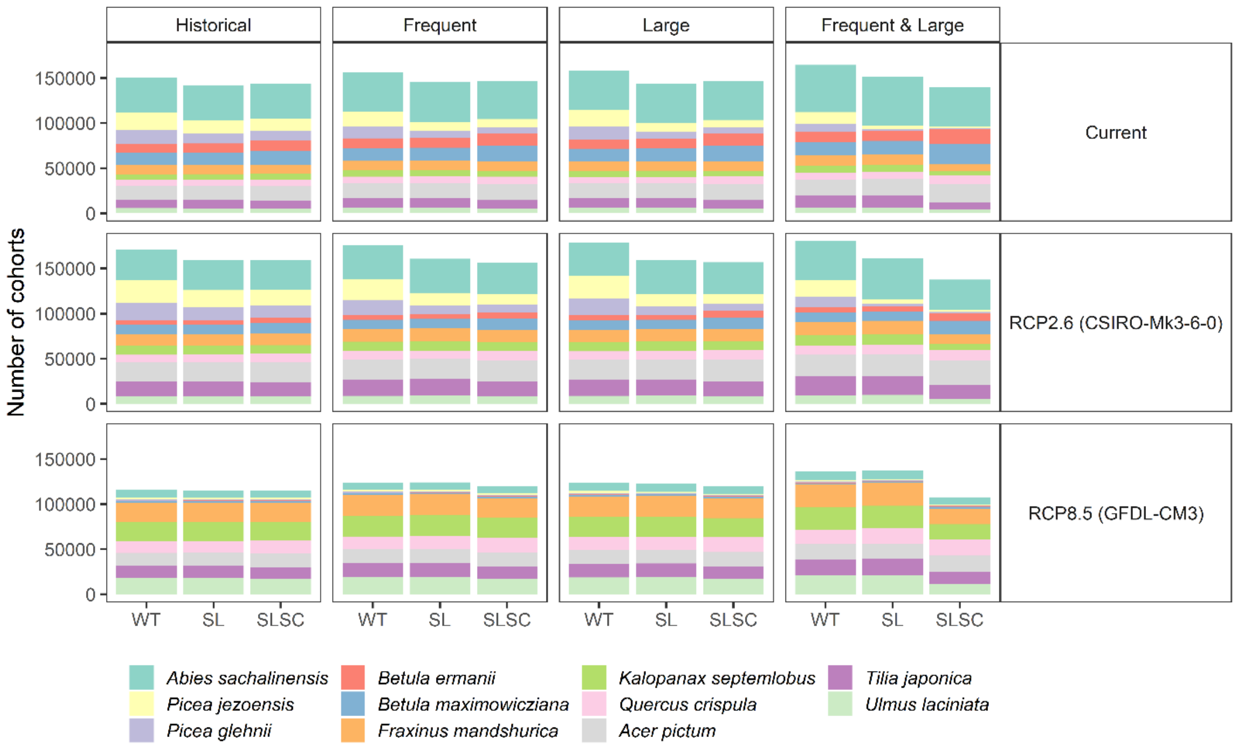

Fig. 5

The number of cohorts newly established in the entire simulation in the study landscape. Rows and columns indicate climate scenarios and windthrow regimes, respectively. The horizontal axis indicates post-windthrow management scenarios. WT: windthrow only; SL: salvage logging; SLSC: salvage logging and scarification. The mean values and standard deviations of the number of cohorts of each species and the total number of cohorts are available in Online Resource 11.

Carbon balance

The NPP in 2130 became larger in WT and SL than in SLSC, regardless of the windthrow regime scenario (Fig. 6a). The NPP in 2130 in the WT and SL increased, but that in the SLSC decreased as the windthrow frequency and size increased (Fig. 6a). The NPP in 2130 in the WT and SL under the Frequent & Large scenario was 87.54 (SL) and 107.6 (WT) gC m^{-2} $year^{-1}$ larger than that under the Historical scenario, respectively. That in SLSC under the Frequent & Large scenario was slightly lower than that under the Historical scenario. Rh was the largest in WT followed by SL and SLSC, regardless of the windthrow regime scenario (Fig. 6a). Rh increased in WT and decreased in SL and SLSC as the windthrow frequency and size increased (Fig. 6a). The Rh in 2130 under the Frequent & Large scenario was 48.39 gC m^{-2} $year^{-1}$ larger in WT, 36.03 gC m^{-2} $year^{-1}$ smaller in SL, and 74.81 gC m^{-2} $year^{-1}$ smaller in SLSC than that under the Historical scenario. As a result, the NEP in 2130 became largest in the SL, regardless of the windthrow regime scenario, because of considerable recovery of NPP and slight increase in Rh (Fig. 6a).

The CO_2 emissions related to manufacturing products from dead wood generated by windthrow ($CE_{ManufactureLong\text{-}lived}$, $CE_{ManufactureShort\text{-}lived}$, and $CE_{ManufactureWoodenBoard}$) were the largest among the CO_2 emissions related to post-windthrow management in the year when windthrow occurred (Fig. 6b). The CO_2 emissions related to post-windthrow management in the year when windthrow occurred reached a maximum of 1,563 gC m^{-2} $year^{-1}$ (under the Frequent & Large scenario in SLSC; 2055). In addition, the CO_2 emissions related to post-windthrow management in SL were only slightly different from those in SLSC because the CO_2 emissions related to scarification ($CE_{Scarification}$) were extremely low.

The NFCB in SL and SLSC became much lower just after windthrow than that in WT due to CO_2 emissions related to post-windthrow management, and the forest sector was temporally converted to a net CO_2 source (Fig. 6c). The reduction in the NFCB per single windthrow event was larger in the Large scenario and the Frequent & Large scenario than in the Historical and the Frequent scenarios because it was proportional to the amount of dead wood salvaged. The NFCB remained negative for several years after a windthrow; thereafter, the NFCB became positive after a maximum of 9 years in WT, 12 years in SL, and 16 years in SLSC. The cumulative NFCB was largest in WT followed by SL and SLSC throughout the entire simulation period, regardless of the windthrow regime scenario (Fig. 6c). The effect sizes of post-windthrow management ($\omega^2 = 0.543$) and windthrow regime ($\omega^2 = 0.222$) were large, those of climate ($\omega^2 = 0.112$) and windthrow regime × post-windthrow management

(ω^2 = 0.104) were medium, and the effect size of climate × windthrow regime (ω^2 = 0.017) was small. The effect size of climate × post-windthrow management (ω^2 = 0.001) was very small (Online Resource 9 Table S9.3). In SL and SLSC, the cumulative NFCB decreased as the windthrow frequency and size increased. The reduction in the cumulative NFCB under the other windthrow regime scenarios compared to the Historical scenario was larger in SLSC than in SL. Particularly under the Frequent & Large scenario, the cumulative NFCB in 2130 was 78% lower in SL and 119% lower in SLSC than those under the Historical scenario and became negative in SLSC under warmer climates. Although the cumulative NFCB in the WT became slightly lower as the windthrow frequency and size increased, the cumulative NFCB in the WT in 2130 among the windthrow regime scenarios had little difference. In addition, the uncertainties in the cumulative NFCB due to climate scenarios were larger as windthrow frequency and size increased, regardless of post-windthrow management.

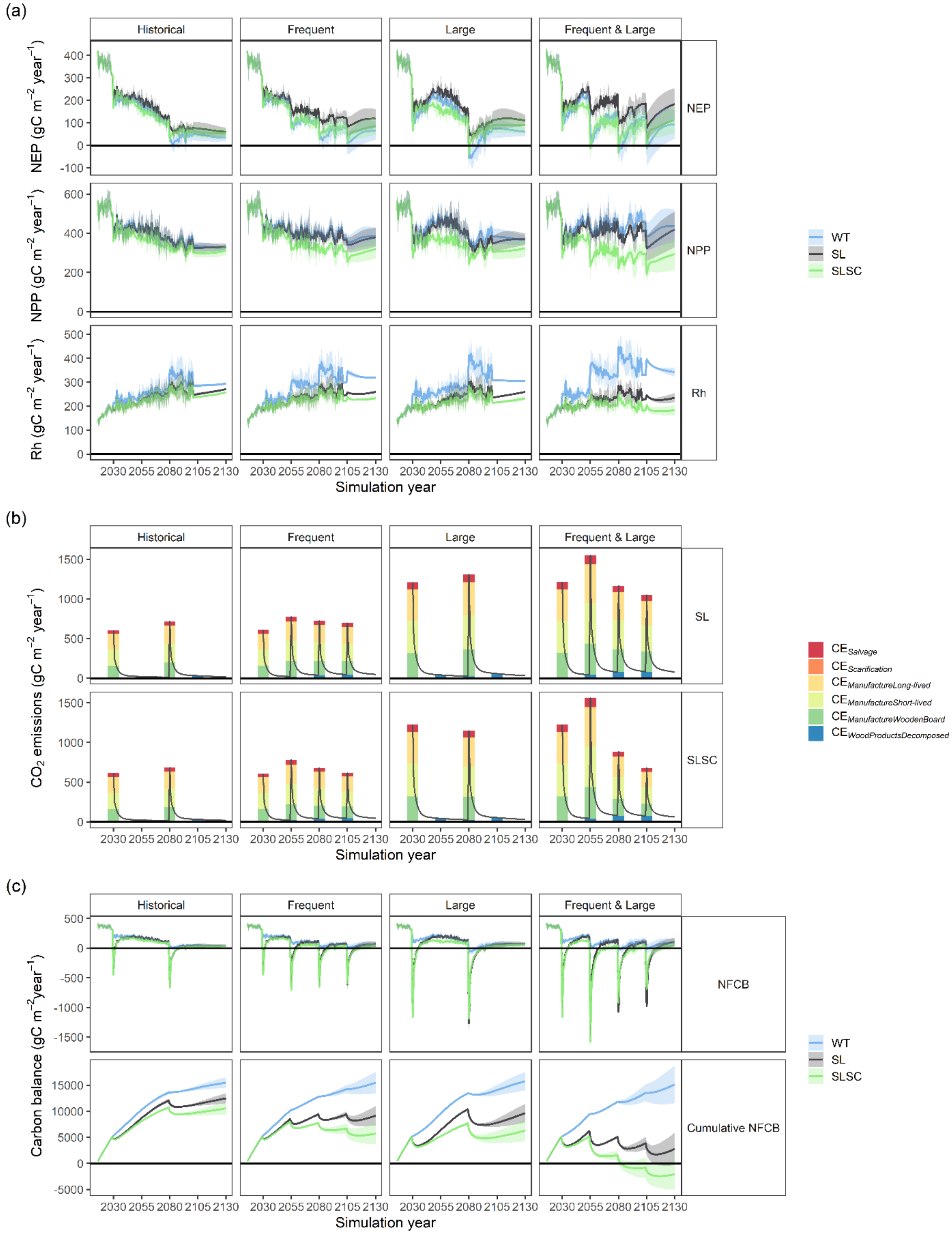
(a)
Historical
Frequent
Large
Frequent & Large
NEP
NPP
Rh
NEP (gC m−2 year−1)
NPP (gC m−2 year−1)
Rh (gC m−2 year−1)
Simulation year
WT
SL
SLSC
(b)
SL
SLSC
CO2 emissions (gC m−2 year−1)
CE Salvage
CE Scarification
CE ManufactureLong-lived
CE ManufactureShort-lived
CE ManufactureWoodenBoard
CE WoodProductsDecomposed
(c)
NFCB
Cumulative NFCB
Carbon balance (gC m−2 year−1)
2030 2055 2080 2105 2130

Fig. 6

The dynamics of carbon balance during simulations. (a) The chronological changes in net ecosystem production (NEP), net primary production (NPP), and heterotrophic respiration (Rh). (b) CO_2 emissions related to post-windthrow management practices, manufacturing, and the disposal of products. Bar graphs indicate CO_2 emissions related to post-windthrow management in 2030, 2055, 2080, and 2105. Solid lines indicate chronological changes in CO_2 emissions related to post-windthrow management (all emissions in years except for 2030, 2055, 2080, and 2105 were $CE_{WoodProductsDecomposed}$). Colors indicate causes of CO_2 emissions. (c) The chronological changes in the net forest sector carbon balance (NFCB) and the cumulative NFCB. Regarding the vertical axis, negative and positive values indicate net CO_2 sources and sinks, respectively. Solid lines and shaded areas in (a) and (c) indicate mean values and standard deviations among climate scenarios, respectively. Columns indicate windthrow regime scenarios. WT: windthrow only; SL: salvage logging; SLSC: salvage logging and scarification. $CE_{Salvage}$: CO_2 emissions related to salvage logging (e.g., use of heavy machinery); $CE_{Scarification}$: CO_2 emissions related to scarification (e.g., use of heavy machinery); $CE_{ManufactureLong\text{-}lived}$: CO_2 emissions related to manufacturing of long-lived products (timber products used for several decades such as building materials and furniture); $CE_{ManufactureShort\text{-}lived}$: CO_2 emissions related to manufacturing of short-lived products (products to be disposed of in a few years such as wood chips and paper); $CE_{ManufactureWoodenBoard}$: CO_2 emissions related to the manufacturing of wooden boards (such as particle boards); $CE_{WoodProductsDecomposed}$: CO_2 emissions related to the disposal of products that were made from dead wood generated by windthrow. The mean values and standard deviations of NEP, NPP, Rh, NFCB, and cumulative NFCB in 2130 are available in Online Resource 12.

Discussion

Leaving downed logs and advanced seedlings was the most suitable post-windthrow management action to conserve boreal conifers and carbon sinks in the forest landscape and maximize net CO_2 absorption under a warmer climate and a more frequent and larger windthrow regime. The aboveground biomass of species that use well-decayed dead wood as regeneration sites decreased due to salvage logging. Moreover, the CO_2 emissions related to salvage logging and the manufacturing and the disposal of products made from dead wood in the salvaged scenario were larger than the CO_2 emissions from the decomposition of dead wood in the unsalvaged scenario when the dead wood generated by windthrow was decomposed in the forest ecosystem. In the case of scarification, the forest landscape became dominated by early successional broad-leaved and herbaceous species due to the destruction of advanced seedlings of trees, and the effect of temperature increase on species composition was more apparent than that in the other cases.

Effects of climate and windthrow regimes on the total aboveground biomass and species composition

The total aboveground biomass decreased, and the species composition changed into one with temperate broadleaf dominance, which is more suitable for the warmer climate due to the increase in windthrow area under the warmer climate. The total aboveground biomass and species composition changed more significantly due to stand-replacing windthrow than due to natural mortality. The total aboveground biomass and species composition in the study landscape were only slightly different among the climate scenarios under the historical windthrow regime (Fig. 3). However, the species composition of the newly established cohorts changed with a warmer climate regardless of the windthrow regime, which caused net decreases in the total number of newly established cohorts under a warmer climate (Fig. 5). At windthrow sites, canopy trees fell, followed by the growth of advanced seedlings, and consisted of the forest canopy. On the other hand, seedlings established on the forest floor in remnant forests were generally suppressed by canopy trees for several decades and could only grow up when gaps formed due to natural mortalities. Therefore, the effects of temperature increase on the total aboveground biomass and species composition would become more quickly apparent in windthrow sites than in remnant forests. LANDIS-II NECN succession, which was used in this study, does not simulate the effects of climate change on natural mortality but simulates these effects on establishment probabilities and growth rate. Indeed, adult trees have resilience to a wider range of environmental conditions (Svenning and Sandel 2013) and are less likely to be affected by climate, including temperature increases, than are seedlings and saplings (Woodall et al. 2009; Zhu et al. 2012; Fei et al. 2017). A field-based study also suggested that there would be a decrease in the establishment of boreal tree species and an increase in that of temperate tree species due to a temperature increase in the transition zone of temperate and boreal forests (Fisichelli et al. 2014), and these results were also reported in a study that was conducted in the same region as the present study (Hiura et al. 2019). Moreover, the aboveground biomass of *Sasa* and the ratio of *Sasa*-dominated grid cells to the study landscape became larger with the increase in windthrow frequency and size and temperature; therefore, tree aboveground biomass would decrease due to the prevention of the growth of tree seedlings and saplings by *Sasa* for a longer time.

Effects of post-windthrow management on the total aboveground biomass and species composition under future climate and windthrow regimes

The removal of windthrow legacies such as advanced seedlings and dead wood due to post-windthrow management promoted changes in the total aboveground biomass and species composition with the increase in windthrow frequency and size and temperature. The range of decrease in the total aboveground biomass was larger due to the destruction of advanced seedlings caused by salvage logging and scarification (Fig. 3).

In particular, the increase in the ratio of sites damaged by multiple windthrows would cause a major decrease in the aboveground biomass of *Picea* spp. due to salvage logging, which is one of the main causes of differences in the total aboveground biomass between the WT and SL. *Picea* spp. considered in the present study rarely regenerate without well-decayed dead wood (Takahashi et al. 2000; Nakagawa et al. 2001). Two species of *Picea* spp., including *P. jezoensis* and *P. glehnii*, were set as dead wood-dependent species in this study; therefore, *Picea* spp. rarely regenerated in salvaged sites where the dead wood generated by windthrow was removed. These effects were suggested to be more apparent after multiple windthrows occurred (Hotta et al. 2021). Indeed, the proportion of sites damaged by multiple windthrows was approximately 15% in the Frequent scenario and the Large scenario; however, it was 63% in the Frequent & Large scenario. Therefore, these effects of salvage logging became more apparent when both the frequency and size of windthrow increased. *Picea* spp. rarely established under the RCP 8.5 scenario in the study landscape (Fig. 5); thus, the importance of *Picea* spp. conservation should increase under a warming climate. Salvage logging is not suitable for the conservation of *Picea* spp. under a warming climate.

The destruction of advanced seedlings due to scarification caused the development of early-successional species-dominated forests and a decrease in the total aboveground biomass and thus promoted changes in species composition with increasing temperature. In the WT and SL, advanced seedlings established before the windthrow grew and composed regenerated stands because a certain number of advanced seedlings were left intact. However, in SLSC, the seedlings established just after the windthrow grew and composed regenerated stands because stand development restarted from the "bare land" state as a result of scarification, which thoroughly destroyed advanced seedlings and removed *Sasa*. Therefore, a species composition reflecting a warmer climate was formed more easily in the SLSC than in the WT and SL, which indicated that scarification promoted changes in species composition with increasing temperature.

In addition, the destruction of advanced seedlings and changes in dominant tree species caused the extension of the time required for the forest canopy to be closed. This would lead to a greater *Sasa* aboveground biomass and further decrease in tree aboveground biomass due to the suppression of tree growth by dense *Sasa*. The aboveground biomass and the ratio of the dominance of *Sasa* increased with increasing temperature and windthrow frequency and size, particularly in SLSC (Figs. 3, 4, and Online Resources 6 and 7). Under the warmer climate in the SLSC, *Q. crispula*, which grows relatively slowly (Watanabe 1994), mainly regenerated, instead of *Betula* spp., which grows rapidly. Therefore, tree seedlings were suppressed by *Sasa* (which recovered more quickly than trees) for longer under a warmer climate than under the current climate. Indeed, it was reported that it was difficult for trees to regenerate once *Sasa* densely covered the forest floor at the sites where logging and past windthrow event took place in northern Japan (Noguchi and Yoshida 2004). Previous studies have reported that tree regeneration dynamics and species composition have been affected by herbaceous species densely covering the forest floor in various regions (Royo and Carson 2006). Therefore, the greater predominance of *Sasa* under the warmer climate in the SLSC would not be unrealistic.

The decrease in dead wood due to salvage logging made the regeneration of dead wood-dependent species difficult, and the destruction of advanced seedlings due to scarification led to stand development reflecting a warmer climate and local conversion from forests to grasslands. Therefore, post-windthrow management, which destroys legacies left after windthrow, such as salvage logging and scarification, would promote changes in the forest landscape caused by increases in temperature and windthrow frequency and size.

Effects of post-windthrow management on the carbon balance within the forest sector under future climate and windthrow regimes

The differences in NPP recovery among post-windthrow management scenarios became larger with the increase in windthrow frequency and size (Fig. 6a). Young to mature, fast-recovering stands generally had a larger NPP than old stands (Goulden et al. 2011). Therefore, the NPP in the WT and SL, where the forest recovered well, became larger by rejuvenating the forest landscape due to the increase in windthrow frequency and size. On the other hand, leaving dead wood caused an increase in CO_2 emissions due to decomposition; thus, Rh was the largest in the WT. As a result, the carbon balance within ecosystems (i.e., NEP) was the largest in SL characterized by considerable recovery of NPP and low Rh, regardless of windthrow regime scenarios. In addition, the CO_2 emissions related to post-windthrow management increased due to the increase in the frequency of management practices and the amount of dead wood that was salvaged (Fig. 6b), which increased the difference in the cumulative NFCB among post-windthrow management scenarios under increased windthrow frequency and size. Particularly, in SL, the increase in CO_2 emissions related to salvaging was larger than the increase in NPP (Fig. 6); therefore, the cumulative NFCB decreased with increased windthrow frequency and size. In the SLSC, these effects of increased windthrow frequency and size on the cumulative NFCB were caused by the increase in CO_2 emissions related to post-windthrow management and the decrease in NPP (Fig. 6c). Previously, the short-term ecosystem carbon balance after windthrow and/or post-windthrow management at the stand scale (Lindroth et al. 2009; Lindauer et al. 2014) and the long-term effects on carbon stocks (Suzuki et al. 2019; Dobor et al. 2020a; Hotta et al. 2020) have been reported. However, the carbon balance considering CO_2 emissions related to post-windthrow management and through the production and discard of products made from windthrown wood has never been discussed, although the importance of this has been recognized in the context of salvaging after other disturbances (e.g., Gunn et al. 2020). In this study, we compared the carbon balance between the different post-windthrow management scenarios by incorporating the CO_2 emissions related to post-windthrow management and the utilization of windthrown wood as a product. Although the effects of post-windthrow management on forest carbon stocks were limited in the long term (Hotta et al. 2020), we revealed that salvage logging and scarification strongly reduced the net CO_2 absorption of the forest sector in the long term under climate change according to the evaluation of carbon balance, including LCA. Our approach, which includes LCA when evaluating carbon balance, would also be useful to discuss the effects of the other management practices on carbon balance.

Although our results showed that the CO_2 emissions from the salvaging and utilization of windthrown wood outside a forest ecosystem exceeded those from their decomposition in the forest ecosystem, the latter may still be underestimated. The allocation ratios of long-lived products ($AR_{Long\text{-}lived}$) and short-lived products ($AR_{Short\text{-}lived}$) were set to reflect the case of undamaged timber. However, the quality of dead wood generated by natural disturbances is generally much worse than that of normal timber because trees develop many cracks, breaks, and scratches when they fall, and they are invaded rapidly by wood decaying fungi (Thorn et al. 2018). Hence, much salvaged wood could be used for manufacturing short-lived products rather than long-lived products. Therefore, this study might underestimate the CO_2 emissions related to salvage logging, and the effects of salvage logging on the carbon balance in the forest sector might be larger than the estimation provided in this study.

There were two limitations to scenarios of the manufacturing process of the forest sector and the social demands of salvaged wood (Fig. 2). First, this study used the constant greenhouse gas (GHG) emission factors for each anthropogenic emission until 2130, i.e., it was assumed that the local forest sector will not take any climate change mitigation action for manufacturing processes even in the RCP2.6 scenario. Second, our analysis assumed the current demand for woody products: long- and short-lived products and wooden boards. Regarding the former assumption, even if the GHG emission factors become zero, our sensitivity analysis showed that salvage logging and scarification also significantly degrade the carbon sinks of the forest sector (Online Resource 8). Local biomass resource use in social systems, such as energy use, is gaining more attention as a climate change mitigation strategy both locally and nationally (Furano city 2011; Agency for Natural Resources and Energy 2021). Therefore, further study is needed to examine scenarios of changes in societal systems that are in line with local plans and global sustainability scenarios.

We excluded the normal harvest (i.e., timber harvest other than salvage logging) from our simulations to focus on the effects of post-windthrow management. Because our results showed that post-windthrow management changed forest ecosystems, normal harvest strategies should be varied depending on post-windthrow management scenarios. These decision-making processes related to management strategies are highly complicated and beyond the scope of this study; thus, we did not include the normal harvest in our analyses and simply evaluated the effects of post-windthrow management. However, the normal harvest would interact with the spatial patterns of windthrow or landslide risks (Tang et al. 1997). Forest carbon stocks and species compositions are also affected by the normal harvest (Boucher et al. 2009; Scheller et al. 2011). Therefore, future studies should be encouraged to incorporate these factors to support the development of more realistic projections of future forest landscape.

Conclusions

Leaving dead wood generated by windthrow was the most suitable post-windthrow management practice for conserving boreal conifers, conserving carbon sinks, and maximizing net CO_2 absorption in the hemiboreal forest landscape under a warmer climate and a more frequent and larger windthrow regime. Therefore, salvage logging and scarification, which remove windthrow legacies, should be avoided as much as possible to conserve biodiversity and carbon balance. To develop more practical management measures that meet the needs of diverse stakeholders, future studies should consider the mixed scenarios of multiple management practices and spatial configurations of areas where management practices are applied (e.g., Dobor et al. 2020b). Additionally, there are other desirable futures of forest landscape (e.g., accelerating the adaptation of species composition to climate change), and these are dependent on local communities, parties, or regions. Future studies also need to incorporate various desirable futures and comprehensively discuss how forest landscapes should be managed for an uncertain future.

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Competing interests

The authors declare that there are no conflicts of interest.

Author contributions

WH conceived of and administered the study. WH and CH conducted the modeling and formal analyses. SS and TO provided field data for model validation. JM, TM, and FN supervised the study. WH wrote the first manuscript draft. All authors contributed to reviewing and editing the manuscript.

Data availability

The simulation datasets are available at https://doi.org/10.5281/zenodo.7824916 (Hotta 2023). The LANDIS-II model is available at https://www.landis-ii.org/. The source code for our improved version of the LANDIS-II NECN succession is available at https://github.com/hagachi/Extension-NECN-Succession/tree/feature-initdecayrate (see also Hotta et al. 2021).

References

Abe T, Kanno M, Tsushima T (2006) The damage caused by typhoon No. 18 (2004) to forests in Hokkaido (Windthrow) - damage assessment and factor analysis. Trans Meet Hokkaido Branch Japanese For Soc 54:151–155. https://doi.org/https://doi.org/10.24494/jfsha.54.0_151

Agency for Natural Resources and Energy (2021) The basic plan for energy use. https://www.meti.go.jp/press/2021/10/20211022005/20211022005-1.pdf. Accessed 5 May 2023

Asahi M (1963) Studies on the Classification of Forest Soils in the Tokyo University Forest, Hokkaido. Bull Univ Tokyo For 58:1–132

Ben-Shachar M, Lüdecke D, Makowski D (2020) effectsize: Estimation of effect size indices and standardized parameters. J Open Source Softw 5:2815. https://doi.org/10.21105/joss.02815

Boucher Y, Arseneault D, Sirois L, Blais L (2009) Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. Landsc Ecol 24:171–184. https://doi.org/10.1007/s10980-008-9294-8

CBD Secretariat (2022) Decision adopted by the conference of the parties to the Convention on Biological Diversity. Kunming-Montreal Global Biodiversity Framework CBD/COP/DEC/15/4

Dai A (2011) Drought under global warming: A review. Wiley Interdiscip Rev Clim Chang 2:45–65. https://doi.org/10.1002/wcc.81

Dobor L, Hlásny T, Rammer W, et al (2018) Post-disturbance recovery of forest carbon in a temperate forest landscape under climate change. Agric For Meteorol 263:308–322. https://doi.org/10.1016/j.agrformet.2018.08.028

Dobor L, Hlásny T, Rammer W, et al (2020a) Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks? J Appl Ecol 57:67–76. https://doi.org/10.1111/1365-2664.13518

Dobor L, Hlásny T, Rammer W, et al (2020b) Spatial configuration matters when removing windfelled trees to manage bark beetle disturbances in Central European forest landscapes. J Environ Manage 254:109792. https://doi.org/10.1016/j.jenvman.2019.109792

Donato DC, Fontaine JB, Campbell JL, et al (2006) Post-Wildfire Logging Hinders Regeneration and Increases Fire Risk. Science 311:352–352. https://doi.org/10.1126/science.1122855

Eddy IMS, Gergel SE (2015) Why landscape ecologists should contribute to life cycle sustainability approaches.

Landsc Ecol 30:215–228. https://doi.org/10.1007/s10980-014-0135-7

Everham EM, Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. Bot Rev 62:113–185. https://doi.org/10.1007/BF02857920

Feeley KJ, Malhi Y, Zelazowski P, Silman MR (2012) The relative importance of deforestation, precipitation change, and temperature sensitivity in determining the future distributions and diversity of Amazonian plant species. Glob Chang Biol 18:2636–2647. https://doi.org/10.1111/j.1365-2486.2012.02719.x

Fei S, Desprez JM, Potter KM, et al (2017) Divergence of species responses to climate change. Sci Adv 3:e1603055. https://doi.org/10.1126/sciadv.1603055

Field AP (2013) Discovering statistics using IBM SPSS statistics, 4th edn. Sage Publications Ltd, London

Fischer A, Fischer HS (2012) Individual-based analysis of tree establishment and forest stand development within 25 years after wind throw. Eur J For Res 131:493–501. https://doi.org/10.1007/s10342-011-0524-2

Fisichelli NA, Frelich LE, Reich PB (2014) Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography (Cop) 37:152–161. https://doi.org/10.1111/j.1600-0587.2013.00197.x

Foster DR (1988) Species and stand response to catastrophic wind in central New England, U.S.A. J Ecol 76:135. https://doi.org/10.2307/2260458

Furano city (2011) Furano city action plan for global warming countermeasures. https://www.city.furano.hokkaido.jp/fs/2/8/6/8/4/_/ondankataisaku.pdf. Accessed 5 Apr 2023

Goulden ML, Mcmillan AMS, Winston GC, et al (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Glob Chang Biol 17:855–871. https://doi.org/10.1111/j.1365-2486.2010.02274.x

Greene DF, Gauthier S, Noë J, et al (2006) A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. Front Ecol Environ 4:69–74. https://doi.org/10.1890/1540-9295(2006)004[0069:AFETDT]2.0.CO;2

Gunn JS, Ducey MJ, Buchholz T, Belair EP (2020) Forest carbon resilience of eastern spruce budworm (*Choristoneura fumiferana*) salvage harvesting in the Northeastern United States. Front For Glob Chang 3:1–13. https://doi.org/10.3389/ffgc.2020.00014

Gustafson EJ, Kern CC, Miranda BR, et al (2020) Climate adaptive silviculture strategies: How do they impact growth, yield, diversity and value in forested landscapes? For Ecol Manage 470–471:118208. https://doi.org/10.1016/j.foreco.2020.118208

Gustafson EJ, Shifley SR, Mladenoff DJ, et al (2000) Spatial simulation of forest succession and timber harvesting using LANDIS. Can J For Res 30:32–43. https://doi.org/10.1139/x99-188

Haga C, Hotta W, Inoue T, et al (2022) Modeling tree recovery in wind-disturbed forests with dense understory species under climate change. Ecol Modell 472:110072. https://doi.org/10.1016/j.ecolmodel.2022.110072

Haga C, Maeda M, Hotta W, et al (2020) Scenario analysis of renewable energy–biodiversity nexuses using a forest landscape model. Front Ecol Evol 8:1–15. https://doi.org/10.3389/fevo.2020.00155

Harmon ME, Franklin JF (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70:48–59. https://doi.org/10.2307/1938411

Herrmann S, Bauhus J (2013) Effects of moisture, temperature and decomposition stage on respirational carbon loss from coarse woody debris (CWD) of important European tree species. Scand J For Res 28:346–357. https://doi.org/10.1080/02827581.2012.747622

Hiura T, Go S, Iijima H (2019) Long-term forest dynamics in response to climate change in northern mixed forests in Japan: A 38-year individual-based approach. For Ecol Manage 449:117469. https://doi.org/10.1016/j.foreco.2019.117469

Hlásny T, Augustynczik ALD, Dobor L (2021) Time matters: Resilience of a post-disturbance forest landscape. Sci Total Environ 799:149377. https://doi.org/10.1016/j.scitotenv.2021.149377

Hotta W (2023) Leaving disturbance legacies conserves boreal conifers and maximizes net CO2 absorption under climate change and more frequent and larger windthrow regimes [Data set]. In: Zenodo. https://doi.org/10.5281/zenodo.7824916

Hotta W, Morimoto J, Haga C, et al (2021) Long-term cumulative impacts of windthrow and subsequent management on tree species composition and aboveground biomass: A simulation study considering regeneration on downed logs. For Ecol Manage 502:119728. https://doi.org/10.1016/j.foreco.2021.119728

Hotta W, Morimoto J, Inoue T, et al (2020) Recovery and allocation of carbon stocks in boreal forests 64 years after catastrophic windthrow and salvage logging in northern Japan. For Ecol Manage 468:118169. https://doi.org/10.1016/j.foreco.2020.118169

Hudiburg TW, Law BE, Moomaw WR, et al (2019) Meeting GHG reduction targets requires accounting for all forest sector emissions. Environ Res Lett 14:095005. https://doi.org/10.1088/1748-9326/ab28bb

Ilisson T, Köster K, Vodde F, Jõgiste K (2007) Regeneration development 4–5 years after a storm in Norway spruce dominated forests, Estonia. For Ecol Manage 250:17–24. https://doi.org/10.1016/j.foreco.2007.03.022

IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn

IUSS Working Group WRB (2015) World reference base for soil resources 2014, update 2015. International soil classification system for naming soils and creating legends for soil maps. FAO, Rome

Japanese Meteorological Agency (2012) Mesh climate data 2010. National land numerical information. https://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html. Accessed 23 Mar 2022

Johnstone JF, Allen CD, Franklin JF, et al (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378. https://doi.org/10.1002/fee.1311

Kurahashi A, Ogasawara S, Kaji M, Hamaya T (1984) A survey on the advanced seedlings at the site damaged by typhoon No. 15 in 1981 in the University of Tokyo Hokkaido Forest. Trans Meet Hokkaido Branch Japanese For Soc 32:40–42. https://doi.org/https://doi.org/10.24494/jfshc.32.0_40

Liang Y, Duveneck MJ, Gustafson EJ, et al (2018) How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. Glob Chang Biol 24:e335–e351. https://doi.org/10.1111/gcb.13847

Lindauer M, Schmid HP, Grote R, et al (2014) Net ecosystem exchange over a non-cleared wind-throw-disturbed upland spruce forest—Measurements and simulations. Agric For Meteorol 197:219–234. https://doi.org/10.1016/j.agrformet.2014.07.005

Lindenmayer D, Burton P, Franklin J (2008) Salvage logging and its ecological consequences. Island Press, Washington

Lindroth A, Lagergren F, Grelle A, et al (2009) Storms can cause Europe-wide reduction in forest carbon sink. Glob Chang Biol 15:346–355. https://doi.org/10.1111/j.1365-2486.2008.01719.x

Lucash MS, Ruckert KL, Nicholas RE, et al (2019) Complex interactions among successional trajectories and climate govern spatial resilience after severe windstorms in central Wisconsin, USA. Landsc Ecol 34:2897–2915. https://doi.org/10.1007/s10980-019-00929-1

Mayer M, Sandén H, Rewald B, et al (2017) Increase in heterotrophic soil respiration by temperature drives decline in soil organic carbon stocks after forest windthrow in a mountainous ecosystem. Funct Ecol 31:1163–1172.

https://doi.org/10.1111/1365-2435.12805

Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: Managing in the face of uncertainty. Ecol Appl 17:2145–2151. https://doi.org/10.1890/06-1715.1

Morimoto J, Morimoto M, Nakamura F (2011) Initial vegetation recovery following a blowdown of a conifer plantation in monsoonal East Asia: Impacts of legacy retention, salvaging, site preparation, and weeding. For Ecol Manage 261:1353–1361. https://doi.org/10.1016/j.foreco.2011.01.015

Muralikrishna I V., Manickam V (2017) Life Cycle Assessment. In: Environmental Management. Elsevier, pp 57–75

Nakagawa M, Kurahashi A, Kaji M, Hogetsu T (2001) The effects of selection cutting on regeneration of *Picea jezoensis* and *Abies sachalinensis* in the sub-boreal forests of Hokkaido, northern Japan. For Ecol Manage 146:15–23. https://doi.org/10.1016/S0378-1127(00)00445-X

Nishimori M, Ishigooka Y, Kuwagata T, et al (2019) SI-CAT 1km-grid square Regional Climate Projection Scenario Dataset for Agricultural Use (NARO2017). J Japan Soc Simul Technol 38:150–154

Noguchi M, Yoshida T (2004) Tree regeneration in partially cut conifer–hardwood mixed forests in northern Japan: roles of establishment substrate and dwarf bamboo. For Ecol Manage 190:335–344. https://doi.org/10.1016/j.foreco.2003.10.024

Ohsato S, Kurahashi A, Yamamoto H, et al (1996) The influence of large-sized wheel-type forestry machines on the residual forest land. A case study of selection cutting operations on a natural forest in Hokkaido. Bull Tokyo Univ For 96:1–26

Owari T, Kamata N, Tange T, et al (2011) Effects of silviculture treatments in a hurricane-damaged forest on carbon storage and emissions in central Hokkaido, Japan. J For Res 22:13–20. https://doi.org/10.1007/s11676-011-0118-3

Prévost M, Raymond P, Lussier J-M (2010) Regeneration dynamics after patch cutting and scarification in yellow birch – conifer stands. Can J For Res 40:357–369. https://doi.org/10.1139/X09-192

R Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna

Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can J For Res 36:1345–1362.

https://doi.org/10.1139/x06-025

Scheller RM, Domingo JB, Sturtevant BR, et al (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol Modell 201:409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009

Scheller RM, Hua D, Bolstad P V., et al (2011) The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. Ecol Modell 222:144–153. https://doi.org/10.1016/j.ecolmodel.2010.09.009

Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. Nat Clim Chang 7:395–402. https://doi.org/10.1038/nclimate3303

Shifley SR, He HS, Lischke H, et al (2017) The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. Landsc Ecol 32:1307–1325. https://doi.org/10.1007/s10980-017-0540-9

St-Laurent M-H, Boulanger Y, Cyr D, et al (2022) Lowering the rate of timber harvesting to mitigate impacts of climate change on boreal caribou habitat quality in eastern Canada. Sci Total Environ 838:156244. https://doi.org/10.1016/j.scitotenv.2022.156244

Suzuki SN, Tsunoda T, Nishimura N, et al (2019) Dead wood offsets the reduced live wood carbon stock in forests over 50 years after a stand-replacing wind disturbance. For Ecol Manage 432:94–101. https://doi.org/10.1016/j.foreco.2018.08.054

Svenning J-C, Sandel B (2013) Disequilibrium vegetation dynamics under future climate change. Am J Bot 100:1266–1286. https://doi.org/10.3732/ajb.1200469

Swanson ME, Franklin JF, Beschta RL, et al (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front Ecol Environ 9:117–125. https://doi.org/10.1890/090157

Taeroe A, de Koning JHC, Löf M, et al (2019) Recovery of temperate and boreal forests after windthrow and the impacts of salvage logging. A quantitative review. For Ecol Manage 446:304–316. https://doi.org/10.1016/j.foreco.2019.03.048

Takada N, Nihara K, Sato Y, et al (1986) A case of the natural forests damaged by the typhoon No. 15 in 1981 in the Tokyo University Forest in Hokkaido. Trans Meet Hokkaido Branch Japanese For Soc 35:25–27

Takahashi M, Sakai Y, Ootomo R, Shiozaki M (2000) Establishment of tree seedlings and water-soluble nutrients in coarse woody debris in an old-growth *Picea-Abies* forest in Hokkaido, northern Japan. Can J For Res

30:1148–1155. https://doi.org/10.1139/cjfr-30-7-1148

Tang SM, Franklin JF, Montgomery DR (1997) Forest harvest patterns and landscape disturbance processes. Landsc Ecol 12:349–363. https://doi.org/10.1023/A:1007929523070

Tatsumi S, Owari T (2013) Modeling the effects of individual-tree size, distance, and species on understory vegetation based on neighborhood analysis. Can J For Res 43:1006–1014. https://doi.org/10.1139/cjfr-2013-0111

Thorn S, Bässler C, Brandl R, et al (2018) Impacts of salvage logging on biodiversity: A meta-analysis. J Appl Ecol 55:279–289. https://doi.org/10.1111/1365-2664.12945

UN (2015) Transforming our world: the 2030 agenda for sustainable development. United Nations, New York

UNFCCC (2015) Adoption of The Paris Agreement. http://unfccc.int/resource/docs/2015/cop21/eng/l09r01.pdf

Watanabe S (1994) Tree sociology. University of Tokyo Press, Tokyo

Watanabe S, Shibata S, Kawahara S, et al (1990) A memoir on the actual situation of the forest wind-damaged by the typhoon No.15 in 1981 in the Tokyo University Forest in Hokkaido. Misc Information, Univ Tokyo For 27:79–221

Weaver JK, Kenefic LS, Seymour RS, Brissette JC (2009) Decaying wood and tree regeneration in the Acadian Forest of Maine, USA. For Ecol Manage 257:1623–1628. https://doi.org/10.1016/j.foreco.2009.01.023

White JW, Rassweiler A, Samhouri JF, et al (2014) Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123:385–388. https://doi.org/10.1111/j.1600-0706.2013.01073.x

Woodall CW, Oswalt CM, Westfall JA, et al (2009) An indicator of tree migration in forests of the eastern United States. For Ecol Manage 257:1434–1444. https://doi.org/10.1016/j.foreco.2008.12.013

Wu L, Kato T, Sato H, et al (2019) Sensitivity analysis of the typhoon disturbance effect on forest dynamics and carbon balance in the future in a cool-temperate forest in northern Japan by using SEIB-DGVM. For Ecol Manage 451:117529. https://doi.org/10.1016/j.foreco.2019.117529

Wu SR, Liu X, Wang L, et al (2022) Integrating life cycle assessment into landscape studies: a postcard from Hulunbuir. Landsc Ecol 37:1347–1364. https://doi.org/10.1007/s10980-021-01396-3

Yoshida T, Iga Y, Ozawa M, et al (2005) Factors influencing early vegetation establishment following soil scarification in a mixed forest in northern Japan. Can J For Res 35:175–188. https://doi.org/10.1139/x04-156

Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change.

Glob Chang Biol 18:1042–1052. https://doi.org/10.1111/j.1365-2486.2011.02571.x