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Title: Long-term cumulative impacts of windthrow and subsequent management on tree species composition and aboveground biomass: A simulation study considering regeneration on downed logs

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Abstract

Post-windthrow management delays forest biomass recovery by altering the situation of disturbance legacies and can change the species composition. Although the short-term effects of post-windthrow management have been well studied, we do not have enough knowledge about the long-term effects of post-windthrow management on species composition and biomass recovery. Those effects associated with an increase in the windthrow frequency are also unknown. Although forest landscape models can effectively evaluate these effects, conventional models do not represent the regeneration process on downed logs, which is essential for simulating forest succession. We focused on hemiboreal forests in northern Japan and aimed to (1) incorporate the regeneration process on downed logs into LANDIS-II, which is one of the most used forest landscape models; (2) evaluate the long-term effects of post-windthrow management on tree species composition and aboveground biomass recovery; and (3) evaluate the associated long-term effects of interactions between post-windthrow management and increased windthrow frequency. We incorporated the regeneration process on downed logs into LANDIS-II by regulating the probability of the establishment of species that depend on dead wood, such as spruce, according to the availability of well-decayed dead wood. The incorporation of this process resulted in simulations of trends in species composition and aboveground biomass recovery after post-windthrow management that were more accurate than those produced by the original model. In the modified LANDIS-II simulation, reductions in dead wood and advanced seedlings due to salvage logging had little effect on the tree species composition or aboveground biomass recovery; however, the complete destruction of advanced seedlings by scarification induced a delay in aboveground biomass recovery and a shift to birch-dominated forests that continued for 100 years. In addition, the reduction in dead wood due to salvage logging decreased the number of seedlings, especially of dead wood-dependent species, that established after windthrow. When the windthrow frequency doubled, this decrease in seedlings induced a delay in aboveground biomass recovery, and a substantial decrease in dead wood-dependent species biomass occurred after a subsequent windthrow event. However, after the second windthrow event and following scarification, the forest recovered in the same way as after the first windthrow because the destruction of advanced seedlings and understory plants, namely, dwarf bamboo (*Sasa* spp.), by scarification reset the site conditions. To conserve the species composition and aboveground biomass of hemiboreal forests under climate change, which is expected to increase windthrow frequency, salvage logging and scarification should be avoided.

(398/400 words)

Keywords:

Salvage logging; Scarification; Decayed downed logs; Regeneration; LANDIS-II; Forest landscape model

1. Introduction

Windthrow is a major natural disturbance in temperate and boreal forest ecosystems in East Asia (Nakashizuka 1989; Yamamoto 1989) that causes mass deaths of live trees and temporary decreases in forest biomass. Post-windthrow managements delay the recovery of biomass by altering the situation of disturbance legacies and is likely to change species composition. Post-windthrow managements, such as salvage logging and scarification, affect forest recovery by creating additional disturbances in forests that have been damaged by windthrow (Leverkus *et al*. 2018). Salvage logging is a conventional forest management strategy used after natural disturbances and removes dead wood to compensate for economic losses and to prevent additional wildfire and insect outbreaks (Lindenmayer *et al*. 2008). Additionally, salvaged sites are sometimes scarified to destroy grasses and shrubs preventing tree regenerations and to remove the organic-rich surface soil layer, which contains pathogens (Yoshida *et al*. 2005). All fallen trees are salvaged after severe windthrows in Japanese national forests, and sites are scarified as necessary (Director-General of Japanese forest agency 2011). However, post-windthrow management has significant impacts on the species composition and recovery of aboveground biomass in forests developing after windthrow by altering situation of disturbance legacies, such as advanced regeneration and dead wood (Kurz *et al*. 2008; Taeroe *et al*. 2019).

The long-term effects of post-windthrow management on species composition and biomass recovery are unknown, although its short- and mid-term effects have been well studied. A short- and mid-term study that measured the effects of salvage logging and scarification on forests 3-40 years after windthrow reported a delay in forest regeneration (Donato *et al*. 2006; Greene *et al*. 2006; Morimoto *et al*. 2011) and an increase in the proportions of early successional species such as *Betula* spp. (Ilisson *et al*. 2007; Fischer and Fischer 2012) due to a lack of advanced regeneration. Specifically, even-aged forests of *Betula* spp. often develop after scarification (Yoshida *et al*. 2005; Prévost *et al*. 2010; Aoyama *et al*. 2011; Suzuki 2020). Long-term (over 50 years after windthrow) studies also reported an increase in broadleaved trees in salvaged stands (Morimoto *et al*. 2019a; Hotta *et al*. 2020). On the other hand, some studies reported that the species composition of the canopy layer did not differ according to whether salvage logging was performed (Sass *et al*. 2018). In addition, Fischer *et al*. (2002) simulated the long-term effects of salvage logging on tree species composition in a simplified manner and reported that *Betula* spp. are dominant in the first 30 years after windthrow and that afterward, the dominant species are gradually replaced by *Picea* spp. These results indicate that we still do not have a consensus about the effects of post-windthrow management on the long-term changes in species composition.

The effects of multiple windthrows should be considered to understand the long-term effects of post-windthrow management on forests. This is because post-windthrow management can substantially affect the quantity and species composition of advanced regeneration that develops after windthrow by altering microsite conditions and the post-windthrow canopy species composition (Waldron *et al*. 2014). In particular, salvage logging decreases the amount of dead wood in forests after windthrow (Suzuki *et al*. 2019; Morimoto *et al*. 2019a; Hotta *et al*. 2020); therefore, tree species that establish only on well-decayed dead wood could decrease in the long term. Because advanced seedlings greatly contribute to forest recovery after windthrow, differences in seedling species composition could also affect the recovery process of forests after a subsequent windthrow event.

Furthermore, hemiboreal forests are projected to experience multiple windthrows at shorter return intervals than in the past due to the increase in windthrow frequency under climate change (Usbeck *et al*. 2010; Donat *et al*. 2011; Gregow *et al*. 2017; Laapas *et al*. 2019). The effects of post-windthrow management on forests would diminish with time (Taeroe *et al*. 2019). However, when windthrow occurs before the effects of previous post-windthrow management do not completely faded, the effects of post-windthrow management could accumulate; in the worst case, this could result in the conversion of forests to completely different forest types. Thus, understanding the effects of multiple windthrows at shorter return intervals and following management is essential in considering appropriate post-windthrow management under climate change.

It is difficult to empirically evaluate the effects of forest management and the changes in the frequency of windthrow which occurs only once every few decades on forest ecosystems because it needs continuous monitoring extending over several hundred years. Only Pontailler *et al*. (1997) reported the effects of multiple windthrows and their cumulative effects on forest succession; however, the effects of management after multiple windthrows have not been assessed. Forest landscape simulations are an effective tool for evaluating the effects of various post-windthrow management and windthrow regimes on long-term forest dynamics. However, no modeling study has yet revealed the effects of multiple windthrows and subsequent management on species composition and aboveground biomass.

To evaluate the effects of post-windthrow management on species composition and the recovery of forest biomass using forest landscape models, it is essential to refine the representation of regeneration processes. The lack of detailed representation of regeneration processes is one of the problems with existing forest landscape models (Albrich *et al*. 2020). Among the various regeneration processes, tree-grass competition is represented in some models (Thrippleton *et al*. 2016; Scheller *et al*. 2021), but regeneration on downed logs has not been represented in any models. In forests in North America and Japan, many studies have reported that seedlings of certain tree species distribute only on downed logs or stumps (Harmon and Franklin 1989; Takahashi *et al*. 2000; Nakagawa *et al*. 2001). In particular, more than 90% of seedlings of *Picea* spp. and *Tsuga* spp. distribute on well-decayed downed logs or stumps (Weaver *et al*. 2009). Furthermore, downed logs and stumps function as places where seedlings can escape shading by dwarf bamboo (*Sasa* spp., hereafter referred to as *Sasa*); *Sasa* dominates the understory of forests in regions covered with snow in winter in east Asia, and downed logs and stumps are therefore essential for forest regeneration in such forests (Hiura *et al*. 1996). Thus, the incorporation of the regeneration process on downed logs into forest landscape models is essential for evaluating the effects of post-windthrow management using these models.

In this study, we focused on hemiboreal mixed forests in northern Japan and approached the following three objectives using the process-based forest landscape model LANDIS-II (Scheller *et al.* 2007):

(1) To incorporate the regeneration process on downed logs into LANDIS-II.
(2) To reveal the long-term effects of post-windthrow management on species composition and the recovery of aboveground biomass.
(3) To reveal the long-term effects of the interaction between post-windthrow management and windthrow frequency on species composition and aboveground biomass recovery.

LANDIS-II is a well-known powerful model that simulates forest dynamics and has been tested and validated by many previous studies in various regions (e.g., Scheller et al. 2011; Shifley et al. 2017; Lucash et al. 2019; Haga et al. 2020; Petter et al. 2020).

2. Materials & Methods

2.1 *Study area*

The simulated landscape was a 12,169 ha forested area in the eastern half of the University of Tokyo Hokkaido Forest (UTHF: 43°10′-21′N, 142°23′-41′E), located at 350-1,000 m a.s.l. in central Hokkaido, northern Japan (Fig. 1). The annual mean temperature and precipitation at the meteorological observatory at Rokugo (43°18′6″N, 142°31′18″E, 315 m a.s.l.; Japanese Meteorological Agency 2012, an average of 1981-2010) are 5.5 °C and 972.6 mm, respectively. The forested area is dominated by *Abies sachalinensis* (F. Schmidt) Mast., *Picea jezoensis* (Siebold et Zucc.) Carrière var. *jesoensis*, *Betula ermanii* Cham., and *Tilia japonica* (Miq.) Simonk. The dominant soil types at the study site are Cambisols (parent material: rhyolite or dacite) and Andosols (parent material: andesite, rhyolite, or dacite) (IUSS Working Group WRB 2015). The natural disturbance regime of this area is stand-replacement windthrow, and there are many records of damage by windthrow (e.g., Typhoon Marie in 1954 and Typhoon Thad in 1981; Watanabe *et al*. 1990). In particular, the damage by Typhoon Thad in 1981 accounted for 8,735 ha (38.9% of the UTHF) in the area and 807,000 m^3 in timber volume (Takada *et al*. 1986).

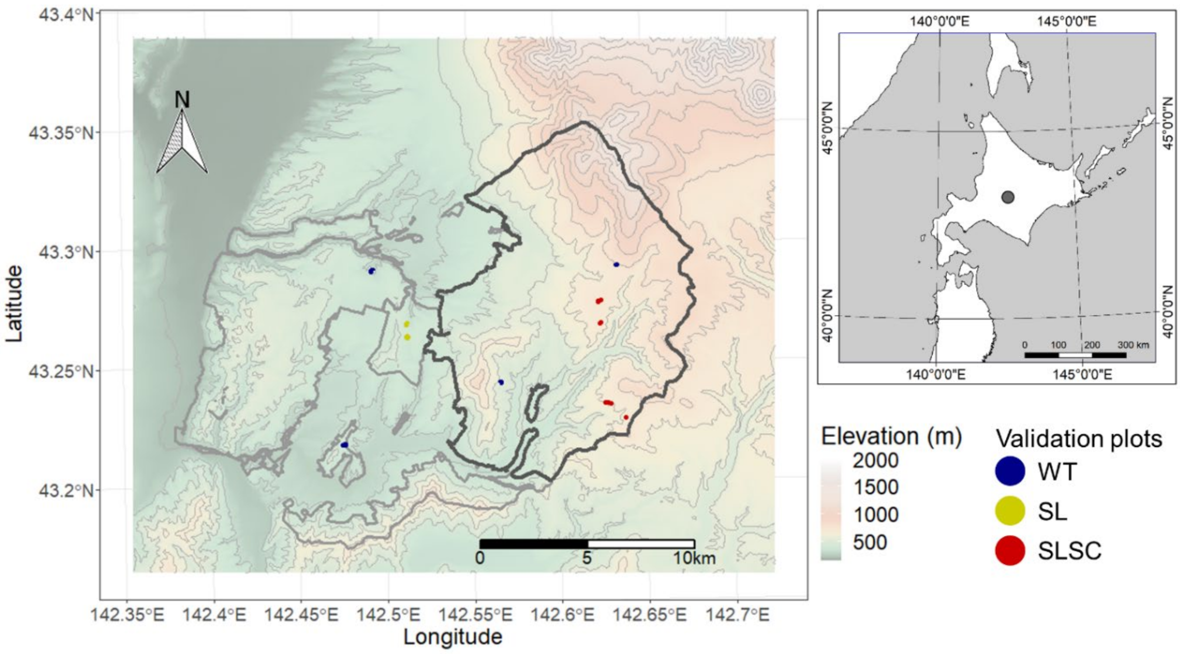


Fig. 1 Right: Map of northern Japan and its surroundings. The gray point indicates the location of the study area. Left: Detail of the study landscape. The University of Tokyo Hokkaido Forest is indicated by the light and dark gray lines, and the simulated landscape is indicated by the dark gray lines. The points indicate the locations of the plots used for validation; WT: stands where dead wood generated by the windthrow in 1981 was left intact; SL: stands where dead wood generated by the windthrow in 1981 was salvaged; SLSC: stands where dead wood generated by the windthrow in 1981 was salvaged, followed by scarification.

2.2 *LANDIS-II*

LANDIS-II, one of the forest landscape simulation models, can simulate forest dynamics and biogeochemical cycling at the landscape scale (Scheller *et al*. 2007). The landscape is represented as a collection of interconnecting uniformly sized sites (cells) that contain information about vegetation, climate, soil nutrients, and so on. In this study, the size of a site was defined as 1 ha. Vegetation is represented in the model as species-age cohorts, and any number of cohorts can be contained in each site. The vegetation and environment at each site influence other surrounding sites through seed dispersal. The seed dispersal algorithm proceeds by the following steps: (1) the conditions at each site, such as light and nutrients, are checked to determine whether seeds of each species can germinate and establish; (2) for each site, neighboring sites are searched for seed sources; (3) a neighboring site can serve as a seed source if (a) at least one cohort of the same species at the neighboring site is older than the age of maturity and (b) the distance of the neighboring site from the examined site is equal to or less than (maximum distance + cell size); (4) the probability of seed arrival is calculated based on the effective and maximum distances, which are user-defined parameters; and (5) neighboring sites, as defined by the maximum distance, are searched until the probability of seed arrival exceeds a random number. At this point, all three criteria for reproduction (light, establishment, and seeds) are met, and seed dispersal ends. Alternatively, seed dispersal ends when all neighboring sites have been checked (Scheller *et al*. 2007). LANDIS-II requires a single “succession extension” and can include optional additional extensions such as disturbance or output extensions. These features enable the effects of forest fire, windthrow, or harvest on forest ecosystems to be evaluated.

To simulate forest succession, we used the improved version of the Net Ecosystem Carbon and Nitrogen Succession extension v 6.3 (Scheller *et al*. 2011; NECN succession) in LANDIS-II. The improvements to NECN succession are explained in detail in section 2.3. In NECN succession, the growth of biomass and the establishment of seedlings are calculated based on the environmental conditions at each site. The growth of the biomass of each cohort is represented as the difference between the monthly aboveground net primary production and the monthly mortality. The monthly aboveground net primary production is calculated by multiplying the maximum value of that (maxANPP; user-defined parameter) by coefficients related to environmental limiting factors as follows: (1) limitTemperature: the coefficient calculated with soil temperature; (2) limitN: the coefficient calculated with nitrogen availability; (3) limitH_2O: the coefficient calculated with soil water content; (4) limitLAI: the coefficient calculated with the Leaf Area Index (LAI) of the cohort itself; and (5) limitCompetition: the coefficient calculated with the LAIs of the other cohorts within the site. The establishment of cohorts of each tree species at each site is determined by two criteria: (1) temperature and moisture conditions and (2) light availability. The light availability at each site is defined as one of five shade classes (ShadeClass) determined by the total LAI at the site. When these two requirements were satisfied, cohorts established at the site. The tree species parameters and their calibrations are explained in detail in supplementary materials S1 and S2.

2.3 *Improvements to LANDIS-II*

We added the regeneration process on downed logs to LANDIS-II NECN succession v 6.3 with tree-grass competition implemented (Scheller *et al*. 2021) as follows.

(1) The identification of dead wood decay classes and the calculation of the amount of dead wood in each decay class.

To calculate the amount of well-decayed dead wood at each site, NECN succession extension was modified to compute the amount of dead wood in each decay class (five levels). It is noted that "dead wood" in LANDIS-II includes dead wood of all sizes, such as fine and coarse woody debris. The decay class is an indicator of the dead wood decay advancement level, and the characteristics of dead wood in each decay class are as follows: "decay class 1 - boles with no decay, fine twigs remaining, and complete bark coverage; decay class 2 - slightly decayed boles with most of the bark present but no fine twigs; decay class 3 - moderately decayed boles with some bark present but only stubs of branches remaining; decay class 4 - boles that can no longer support themselves, with all bark gone; and decay class 5 - boles detected only by their moss outlines on the forest floor" (Graham and Cromack 1982). First, we modified the model to track dead wood and to calculate the retention rate of dead wood (the ratio of the amount of dead wood in each year (currentDeadWood) to that in the year in which each piece of dead wood was produced (originalDeadWood)). Then, we determined the decay class of the dead wood by comparing the calculated retention rate with empirical data on the retention rate of each decay class. The empirical data on the retention rate of each decay class was calculated by Eq. 2.3.1.

$$\mathrm{RR}_{\mathrm{decayClass}X} = \mathrm{WD}_{\mathrm{decayClass}X}/\mathrm{WD}_{\mathrm{decayClass1}} \quad \cdots\cdots \quad 2.3.1$$

*$\mathrm{RR}_{\mathrm{decayClass}X}$: the mass retention ratio of dead wood in decay class X relative to decay class 1; $\mathrm{WD}_{\mathrm{decayClass}X}$: the wood density of dead wood in decay class X (the empirical data provided in Ugawa *et al*. (2012)); and X: decay class (1, 2, 3, 4, 5).

Finally, NECN succession extension was modified to compute the amount of dead wood in each decay class in each year (see also, supplementary materials S3).

(2) The calculation of the area occupied by downed logs available as regeneration sites

The downed logs available as regeneration sites were those in decay classes 3, 4, and 5. In these downed logs, decay had progressed throughout the wood, the bark had been removed, and moss was attached to the surface (Takahashi *et al*. 2000). Thus, the area occupied by downed logs in decay classes 3, 4, and 5 at each site was made computable by the model. The shape of downed logs was assumed to be an elliptical column, and the area occupied by downed logs in decay classes 3, 4, and 5 was calculated by Eq. 2.3.2 using the calculated amount of downed logs in decay classes 3, 4, and 5. Finally, the ratio of the total area occupied by downed logs in decay classes 3, 4, and 5 to the site area (nurseryLogAreaRatio) was calculated.

$$\mathrm{nurseryLogArea}_{\mathrm{decayClass}X} = 4 * 2 * \mathrm{C}_{\mathrm{decayClass}X}/(\pi * \mathrm{h} * \mathrm{WD}_{\mathrm{decayClass}X}) \quad \cdots\cdots \quad 2.3.2$$

$nurseryLogArea_{decayClassX}$: the area occupied by downed logs in decay class *X*; $C_{decayClassX}$: the carbon stock of dead wood in decay class *X*; h: the average height of downed logs (0.28 m: data from Hotta *et al*. (2020)); $WD_{decayClassX}$: the wood density of dead wood in decay class *X* (data from Ugawa *et al*. (2012)); *X*: the decay class (3, 4, or 5).

The amount of dead wood is not strictly equal to the number of downed logs because dead wood includes snags, which are standing dead trees. However, almost all snags are classified as decay class 1 or 2; as decay progresses, the snags break or fall and turn into downed logs. Thus, we assumed that the amount of dead wood in decay classes 3, 4, or 5 was equal to that of downed logs in decay classes 3, 4, or 5.

(3) The improvements to the determination of cohort establishment

In NECN succession, the probability of the establishment of cohorts based on light availability is determined by comparing random numbers with “LightProbability”, which is determined by the shade tolerance of each species and the shade class of each site. In this study, the tree species were categorized into dead wood-dependent and dead wood-independent species; dead wood-dependent species required well-decayed dead wood for regeneration, while dead wood-independent species did not require dead wood for regeneration. We modified the model to change the LightProbability variable depending on the amount of well-decayed dead wood. The cohort establishment determination process was improved as follows (Fig. 2).

(A) Dead wood-dependent species

P. jezoensis and *Picea glehnii* (F. Schmidt) Mast. were defined as dead wood-dependent species (Takahashi *et al*. 2000). dead wood-dependent species require dead wood for regeneration; thus, we modified the calculation of the probability of establishment based on LightProbability as shown in Eq. 2.3.3.

$$\mathrm{LightProbability}_{\mathrm{Modified}} = \mathrm{LightProbability}_{\mathrm{Original}} * \mathrm{nurseryLogAvailability} \quad \cdots\cdots \quad 2.3.3$$

*$\mathrm{LightProbability}_{\mathrm{Modified}}$: LightProbability calculated by the modified way; $\mathrm{LightProbability}_{\mathrm{Original}}$: LightProbability calculated by the original way; nurseryLogAvailability: the adjustment coefficients calculated by nurseryLogAreaRatio ($\mathrm{nurseryLogAvailability} = 1 - (\mathrm{nurseryLogAreaRatio} - 1)^{\mathrm{nurseryLogAvailabilityModifier}}$; nurseryLogAvailabilityModifier: a tuning parameter that is an even number. In this study, 4 was the most suitable nurseryLogAvailabilityModifier according to our calibrations (supplementary materials S4).

(B) Dead wood-independent species

Dead wood-independent species were defined as species that can establish without dead wood. All tree species except for *P. jezoensis* and *P. glehnii* were defined as dead wood-independent species because previous studies suggested those species can establish on forest floor (Takahashi et al. 2000; Weaver et al. 2008). In determining the establishment of dead wood-independent species, in addition to the original determination process, we made it possible to determine the possibility of establishment on downed logs in case the site was too dark for the species to establish, as follows (Fig. 2).

(a) In the original determination method, the cohort can establish when $\text{LightProbability}_{\text{Original}}$ exceeds a random number generated for each site. If a cohort can establish in stage (a), the location of its establishment is the forest floor.

(b) If cohorts cannot establish in stage (a) and the shade class of the site is darker than the most suitable shade class for the species, the model checks whether the cohorts can establish if they are not shaded by grasses, such as *Sasa* dwarf bamboo. Specifically, the model checks whether the LightProbability calculated according to the tree species LAI exceeds the random number at each site. In stage (b), the model checks only the possibility of establishment and does not determine the establishment of the cohorts.

(c) When the LightProbability calculated according to the tree species LAI exceeds the random number in stage (b), cohorts can establish if there are sufficient amounts of downed logs in decay classes 3, 4, and 5. Specifically, cohorts can establish on downed logs when nurseryLogAvailability exceeds a random number generated for each site.

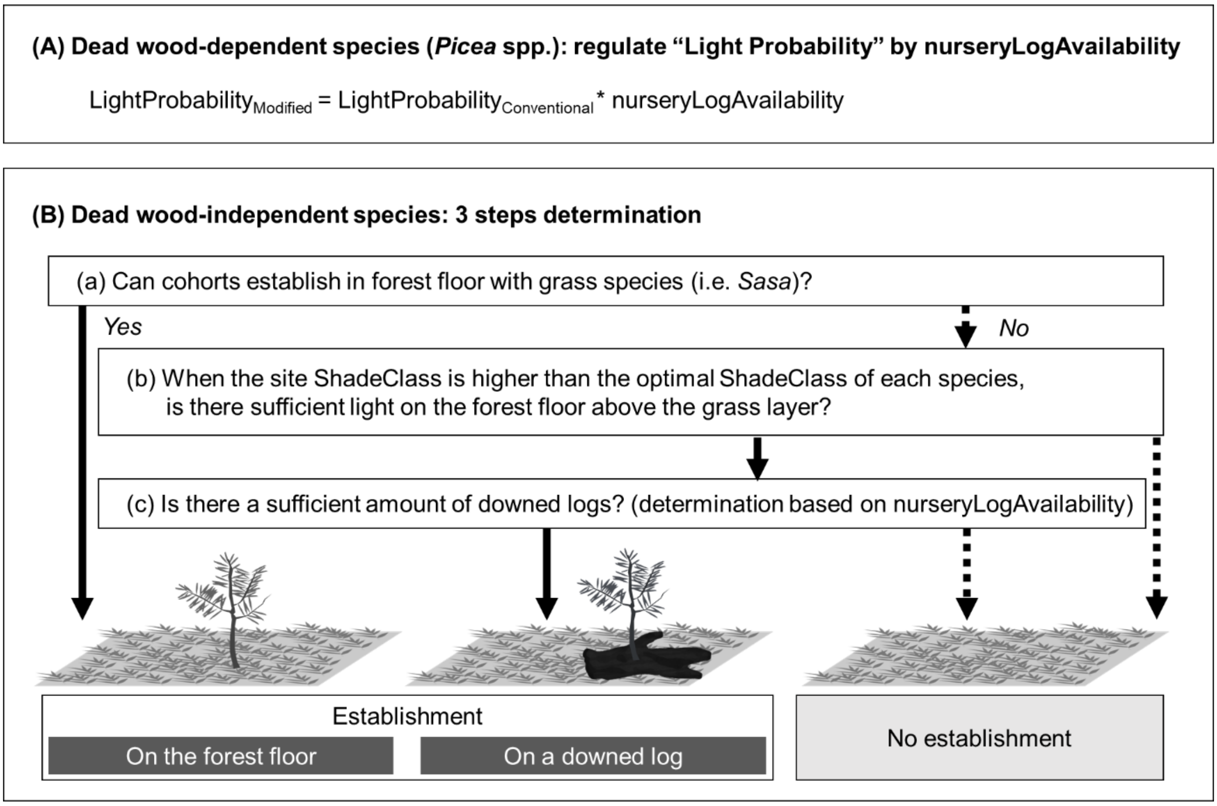


Fig. 2 Flowchart showing the determination of the establishment of seedlings in LANDIS-II NECN succession in which the process of regeneration on downed logs was implemented. A: in the case of dead wood-dependent species; B: in the case of dead wood-independent species. LightProbability: the probability of establishment determined by the shade tolerance of each species and the shade class of each site; nurseryLogAvailability: the amount of dead wood available as regeneration sites; and ShadeClass: the degree of darkness of the site, as classified into five levels.

2.4 *Input data*

2.4.1 *Initial communities*

We focused on the tree species that accounted for 90% of the total biomass and on the dominant grass species: *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 *Sasa senanensis* (Franch. et Sav.) Rehder.

The initial communities of trees were created based on forest inventory data from the UTHF. The data were acquired in three different periods in the study landscape: period 11: 1996-2005; period 12: 2006-2010; and period 13: 2011-2020. We summarized the inventory data by period, and we treated the data collected in periods 11, 12, and 13 as data collected in 2000, 2008, and 2015, respectively. Additionally, the data collected in periods 11 and 12 were simulated for 15 years and 7 years, respectively, to align all data to the same year (2015). Then, we constructed the initial communities in the study landscape in 2015.

The initial aboveground biomass of *S. senanensis* at each site was determined through an estimation from tree biomass at each site using the *Sasa* distribution model developed by Tatsumi and Owari (2013).

2.4.2 *Dead wood*

The amount of dead wood was uniformly input within the landscape to eliminate uncertainties derived from the heterogeneity of the distribution of dead wood. We used the average value of the amount of dead wood in Hotta *et al*. (2020), 3,100 g m^{-2}, as the input amount. We assumed the decay class of dead wood to be decay class 1 because the amount of dead wood in each decay class was unknown.

2.4.3 *Soil*

The input data related to soils were based on Asahi (1963), which reported the soil properties of the UTHF in detail. The following data were used as soil input data: drainage, field capacity, wilting point, sand rate, clay rate, carbon content, and nitrogen content.

2.4.4 *Climate*

The input data related to climate were configured as follows. The 1 km mesh climate data (Japanese Meteorological Agency 2012, on average over 1981-2010) in the study landscape were classified into 10 clusters with k-means clustering based on the monthly maximum temperature, monthly minimum temperature, and monthly precipitation. Each climate data was standardized before clustering. The climate data were spatially averaged and input according to climate cluster.

2.5 *Settings for windthrow and post-windthrow management scenarios*

The Biomass Harvest extension v. 4.3 (Gustafson *et al*. 2000) was used to represent stand-replacing windthrow in the study landscape. We defined stand-replacing windthrow as follows: windthrow area: 20% of the study landscape; windthrow intensity: all living trees blown down except for advanced seedlings; windthrow frequency: interval of 50 years (with windthrow occurring in years 15 and 65). The ratio of windthrow area for each windthrow event was determined based on the records of windthrow by Typhoon Thad in 1981 (Watanabe *et al*. 1990). The interval of windthrow was determined based on Abe *et al*. (2006). The sites where windthrow occurred were randomly selected from among sites where the stand age was more than 50 years. Windthrow risk is influenced not only by stand age but also by the wind direction, wind intensity, forest structures, topography, and so on. Previous studies have reported that the risk of windthrow is greater in individual trees with larger diameters at breast height or tree heights (Rich *et al*. 2007) and in stands that have homogeneous structures (Jalkanen and Mattila, 2000; Mitchell *et al*. 2001; Morimoto *et al*. 2019b). On the other hand, predicting windthrow risk is very challenging because it varies greatly among regions and among windthrow events (Dobor *et al*. 2019). Because a detailed evaluation of windthrow risk is beyond the scope of the objectives of this study, the windthrow risk was determined only by the stand age in this study.

We evaluated the following three post-windthrow management scenarios: (a) dead trees left undisturbed; (b) salvage logging; and (c) salvage logging and scarification. The proportion of advanced seedlings that are destroyed differs among scenarios. Whether the cohorts contained advanced seedlings was determined by the cohort age, and the threshold age was determined by the tree species based on data from the windthrow sites in the UTHF caused by Typhoon Thad in 1981 (supplementary materials S5).

(a) Dead trees left undisturbed (WT)

In the WT scenario, the dead wood generated by the windthrow was left intact, and 20% of advanced seedlings were destroyed (Table 1). The advanced seedling destruction ratio was determined based on data from the windthrow sites in the UTHF caused by Typhoon Thad in 1981 (Kurahashi *et al*. 1983).

(b) Salvage logging (SL)

In the SL scenario, dead wood generated by windthrow was salvaged, and 60% of advanced seedlings were destroyed (Table 1). This percentage was the most suitable for empirical data in salvaged sites, and Ohsato *et al*. (1996) also reported that the percentage of forest area disturbed by salvage logging was approximately 60%.

(c) Salvage logging and scarification (SLSC)

In the SLSC scenario, dead wood generated by windthrow was salvaged, and the forest floor was scarified after salvaging. All advanced seedlings and 99% of *Sasa* were destroyed due to scarification (Table 1).

Table 1 Post-windthrow management scenarios

Post-windthrow management scenario	**Dead wood generated by the windthrow**	**Advanced seedlings**	**Dwarf bamboo (*Sasa*)**
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

2.6 *Calibration*

To adjust the performance of the model to better fit the empirical data, some parameters were calibrated by comparing the simulation results and the empirical data. Previous studies also calibrated parameters used to calculate the biomass growth, litterfall, decomposition rate of soil organic carbon, etc. (Lucash et al. 2019; Haga et al. 2019; Haga et al. 2020). In addition to these parameters, parameters related to the calculation of the LAI, net primary production (NPP), tree–grass competition, and decomposition rate of dead wood were also calibrated in this study. The SPOTPY package (Houska et al. 2015) in Python ver. 3.10 was used to perform the calibrations.

2.6.1 *Aboveground biomass growth of trees and the litterfall, LAI, and NPP at the sites*

The mortality shape, maxANPP, maxBiomass, monthly wood mortality, and KLAI were used as tuning parameters, and the aboveground biomass growth of trees and the litterfall, LAI, and NPP at the sites were calibrated for each species. For the aboveground biomass growth, the volume table of living trees according to tree species and area (Hokkaido 2010) was used to provide empirical data. In addition, the aboveground biomass growth curves were extended to age 140 by nonlinear regression using the least squares method because data for some species were insufficient in terms of stand age. Regarding litterfall, data from deciduous broadleaved forests (Tomakomai, Uryu, Ashoro in Hokkaido, northern Japan) and evergreen coniferous forests (Otanomousdaira in Nagano, central Japan) collected in the monitoring site 1000 project (Ishihara et al. 2011) were used as empirical data. Data from Muraoka et al. (2010) and Sumida et al. (2018) were used as empirical data for the LAIs of deciduous broadleaved forests and evergreen coniferous forests, respectively. Data from Ishii (2019) were used to provide empirical data on the NPP in cool–temperate forests.

We selected the best parameter set based on the following conditions: (1) the simulated LAI and NPP at the sites were within the range of the empirical values and (2) the root mean squared errors (RMSEs) of the aboveground biomass and litterfall between ages 130 and 140 were minimal (Fig. S2.1, S2.2).

2.6.2 *Aboveground biomass and the LAI of Sasa and tree–grass competition*

We calibrated the parameters related to *Sasa* for the following three processes: (1) simulating the aboveground biomass of *Sasa* between 27 and 32 years after scarification to match the empirical data; (2) simulating the LAI of *Sasa* between 27 and 32 years after scarification to match the empirical data; and (3) simulating tree species composition 32 years after scarification to match the empirical data. The RMSE was used to evaluate the objective functions of (1) and (2), and the Bray-Curtis index of dissimilarity was used to evaluate the objective function of (3). Finally, the parameter set in which the sum of the three standardized objective functions was minimized was selected. The MaxANPP, maxBiomass, monthly wood mortality, KLAI, BTOLAI, and grass threshold multiplier were used as the tuning parameters.

2.6.3 ***Dead wood decomposition rate***

The dead wood decomposition rate was calibrated by tuning the time until dead wood reached decay class 3 using the "Wood decay rate" parameter. The actual time until dead wood reached decay class 3 was estimated by the following processes. First, the decomposition rate constant (k) in the climate of the simulated landscape was estimated using the equation in Russel et al. (2015). Second, the retention ratio of dead wood (R) was calculated by the following equation: $R = -\exp(kt)$ (t: the elapsed time since the trees died). The retention ratio of the mass of dead wood in decay class 3 was calculated by using the wood density of dead wood in each decay class provided in Ugawa et al. (2012). Finally, the actual time until dead wood reached decay class 3 was estimated from k and R.

2.6.4 ***Soil organic carbon***

We selected the parameter set in which the change in soil organic carbon in the first five years was the lowest because no data on changes in soil organic carbon over time were available. In LANDIS-II, there are four pools of soil organic carbon. We carefully avoided the decomposition rates of SOM2 and SOM3 exceeding those of the surface and SOM1, which are more active pools (Lucash et al. 2019).

2.7 ***Validation***

The results of the simulation of post-windthrow management scenarios were validated by comparison with empirical data. We used data of permanent plots for measuring forest recovery after the windthrow caused by Typhoon Thad in 1981 and following various post-windthrow managements carried out in the UTHF. The data were collected in 1982, just after the windthrow, and in 2014, and included species and diameter at breast height (DBH) and height measurements. We determined the age of each individual according to the DBH, calculated aboveground biomass by the DBH and height, aggregated the aboveground biomass of each individual into cohorts of 10-year age intervals, and constructed the initial communities based on the empirical data from 1982, simulated forest succession for 32 years in a single grid, and compared the simulated results with the empirical data from 2014. Additionally, to quantitatively evaluate the accuracy of validation, we used relative errors and the Brey-Curtis index of dissimilarity for the aboveground biomass and species composition, respectively.

2.8 *Simulation*

The simulation was replicated 10 times for each scenario to capture the stochasticity related to seed dispersal, cohort establishment, and the selection of windthrow sites. The duration of the simulation was 115 years. The results were classified into the following two categories: stands where windthrow occurred only in year 15 (1,947 sites) and stands where windthrow occurred in both year 15 and year 65 (486 sites). The 10 replicates of the mean aboveground biomass for each category and post-windthrow management scenario were ensemble-averaged. It is noted that the aboveground biomass of windthrow sites was averaged in each category.

3. Results

3.1 *Validation of and improvements in LANDIS-II*

The relative errors of the total aboveground biomass from empirical data versus LANDIS (after improvement) were in the range from -0.27 to 5.7. The Brey-Curtis index of dissimilarity in species composition between empirical data and LANDIS (after improvement) were in the range from 0.17 to 0.87. Although there were slight differences in species composition and aboveground biomass in some plots, the tree species composition and aboveground biomass in each plot coincided more with the empirical data after the incorporation of the regeneration process on downed logs than before, regardless of which post-windthrow management practice was implemented (Fig. 3, 4). Before the incorporation of this regeneration process, dead wood-dependent species such as *P. jezoensis* and *P. glehnii* were simulated to be able to regenerate under SL and SLSC, which are scenarios that leave behind little well-decayed dead wood. However, their simulated regeneration decreased after the incorporation of regeneration on downed logs into the model; accordingly, the simulated aboveground biomass was also closer to the empirical values. Additionally, the relative error and Brey-Curtis index were substantially closer to 0 and relatively lower than those of empirical data versus LANDIS (before improvement) (0.22 to 10.3 and 0.20 to 0.92, respectively). Furthermore, the RMSE of aboveground biomass growth for each species in the calibration ranged from 714 to 3,158 g m^{-2} (Fig. S2.1).

Although the differences in tree species composition and aboveground biomass between the simulated and empirical data were small after the improvement of the model, the simulated aboveground biomass was still slightly overestimated, and the simulated species composition was slightly different from that in the empirical data in some WT and SL plots (Fig. 3, 4). Under SLSC, the difference in aboveground biomass between the simulated and empirical data was minimal, and *Betula* spp. was dominant in both the simulated and empirical data (Fig. 3, 4). In particular, the differences in species composition were relatively large in plots E, G, H, I, and J under WT and in plot L under SL, and the differences in aboveground biomass were relatively large in plots F, G, H, I, and K under WT and in plot M under SL.

Trees aboveground biomass recovery 32 years after windthrow.

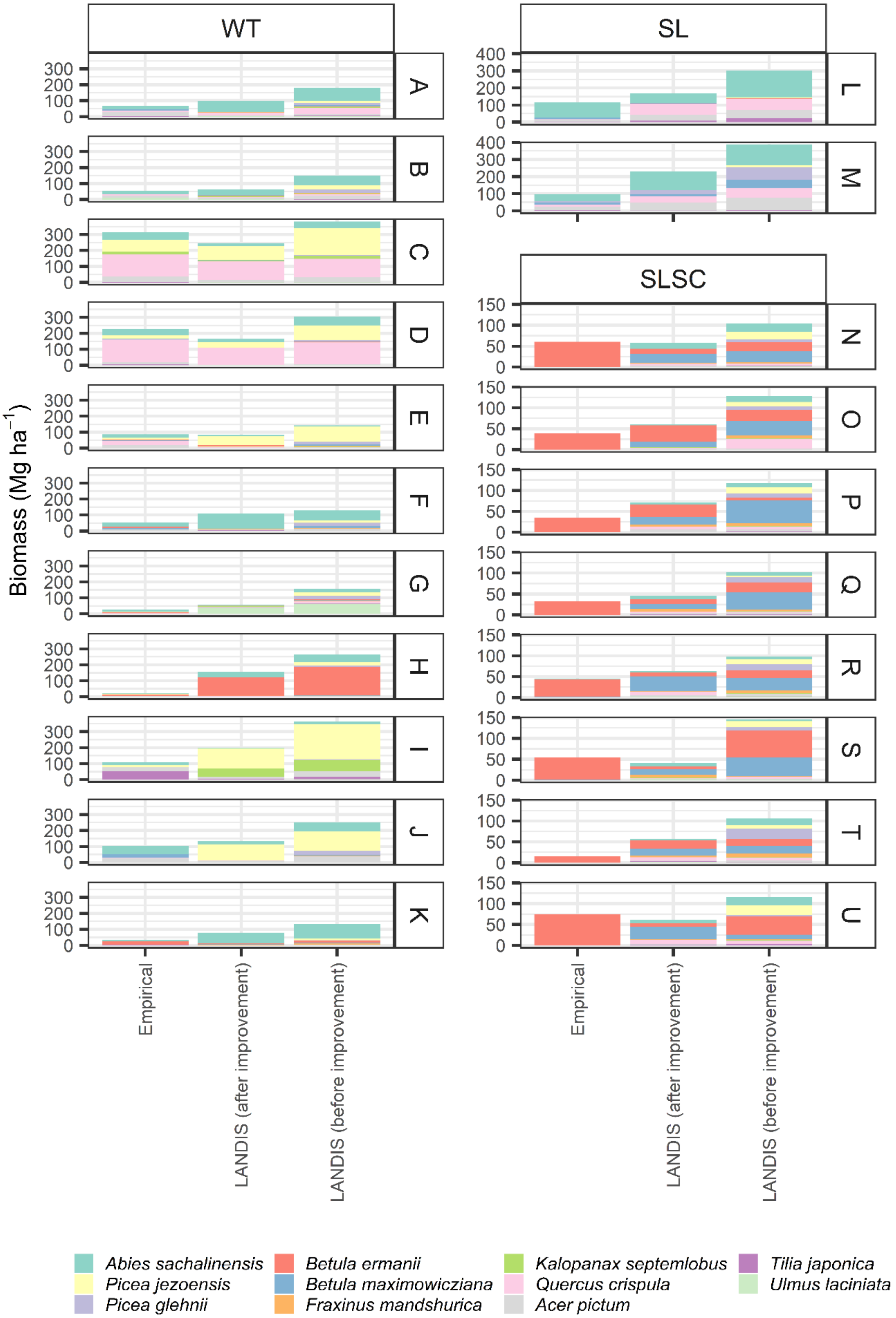


Fig. 3 The results of validations of aboveground biomass and species composition 32 years

after windthrow. Empirical: empirical aboveground biomass data for each species 32 years after windthrow and post windthrow management; LANDIS (after improvement): the results for the aboveground biomass of each species 32 years after windthrow and post windthrow management simulated by LANDIS-II NECN succession in which the process of regeneration on downed logs was implemented; LANDIS (before improvement): the results for the aboveground biomass of each species 32 years after windthrow and post windthrow management simulated by the original version of LANDIS-II with NECN succession. WT: the scenario in which dead wood generated by windthrow is left intact; SL: the scenario in which dead wood generated by windthrow is salvaged; SLSC: the scenario in which dead wood generated by windthrow is salvaged, followed by scarification. Alphabets on the right side of each figure indicate the IDs of the permanent plots.

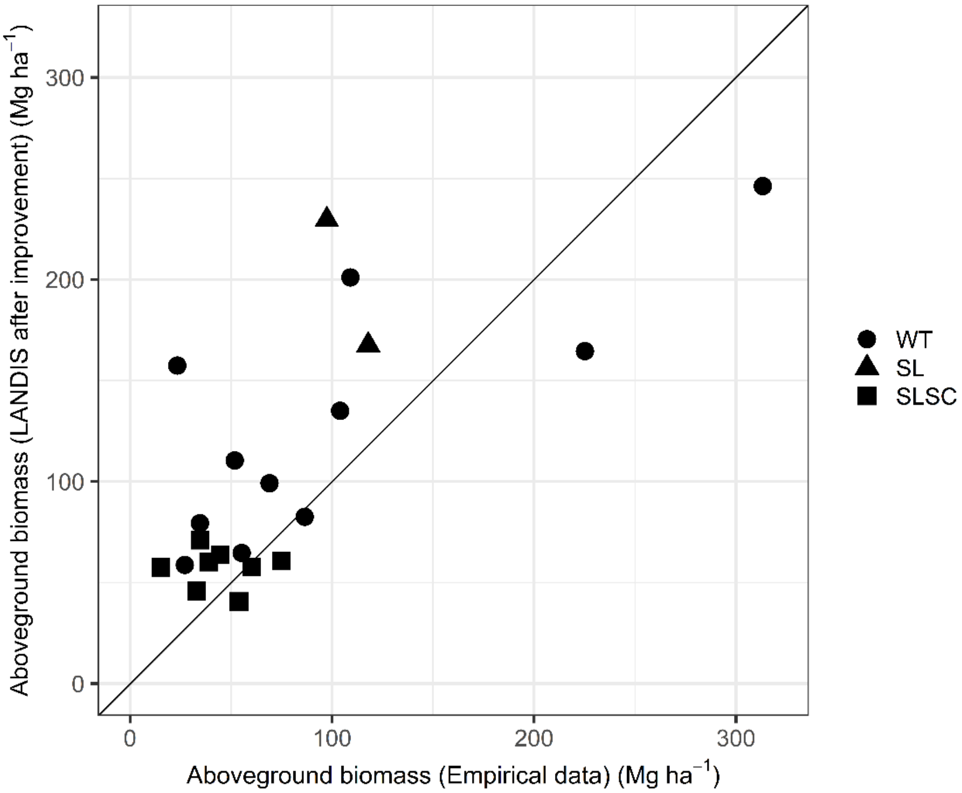
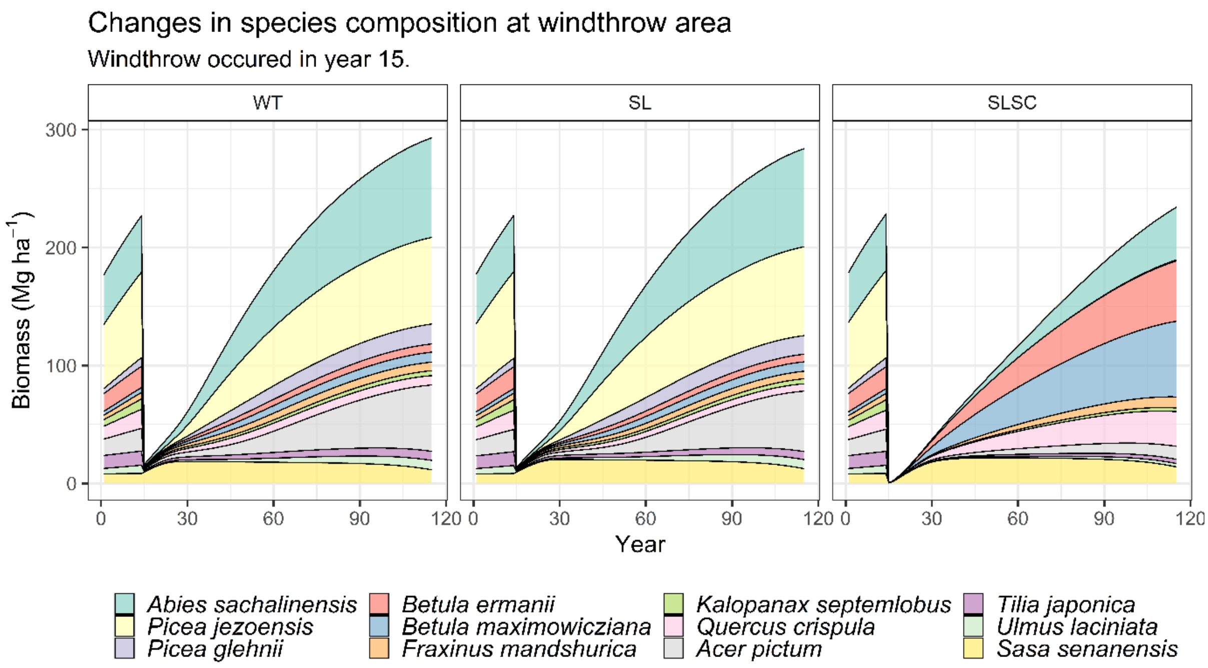


Fig. 4 Scatter plot of the tree aboveground biomass 32 years after the windthrow and following management from empirical data and LANDIS-II simulation results after improvement. WT: the scenario in which dead wood generated by windthrow was left intact; SL: the scenario in which dead wood generated by windthrow was salvaged; and SLSC: the scenario in which dead wood generated by windthrow was salvaged, followed by scarification.

3.2 *Recovery after a single windthrow and subsequent management*

In stands where windthrow occurred only in year 15, the recovery of aboveground biomass was slower under SLSC than under WT and SL (Fig.5). In the long term, the dominant species under SLSC were *B. ermanii* and *B. maximowicziana*, which are quite different from the dominant species under WT and SL (Fig.5). The species composition and aboveground biomass under SL were little different from those under WT (Fig.5). Under SLSC, the establishment of early-successional species such as *B. ermanii*, *B. maximowicziana*, and *Q. crispula* increased soon after windthrow (Fig.6). Under WT and SL, the establishment of mid-successional species such as *T. japonica* and *A. pictum* increased soon after windthrow (Fig.6). In addition, the establishment of *P. jezoensis* and *P. glehnii* increased more than 20 years after windthrow under WT; however, such an increase was not detected under SL or SLSC (Fig.6).


Changes in species composition at windthrow area
Windthrow occured in year 15.
WT
SL
SLSC
Biomass (Mg ha^{-1})
0
100
200
300
0
30
60
90
120
Year
Abies sachalinensis
Picea jezoensis
Picea glehnii
Betula ermanii
Betula maximowicziana
Fraxinus mandshurica
Kalopanax septemlobus
Quercus crispula
Acer pictum
Tilia japonica
Ulmus laciniata
Sasa senanensis

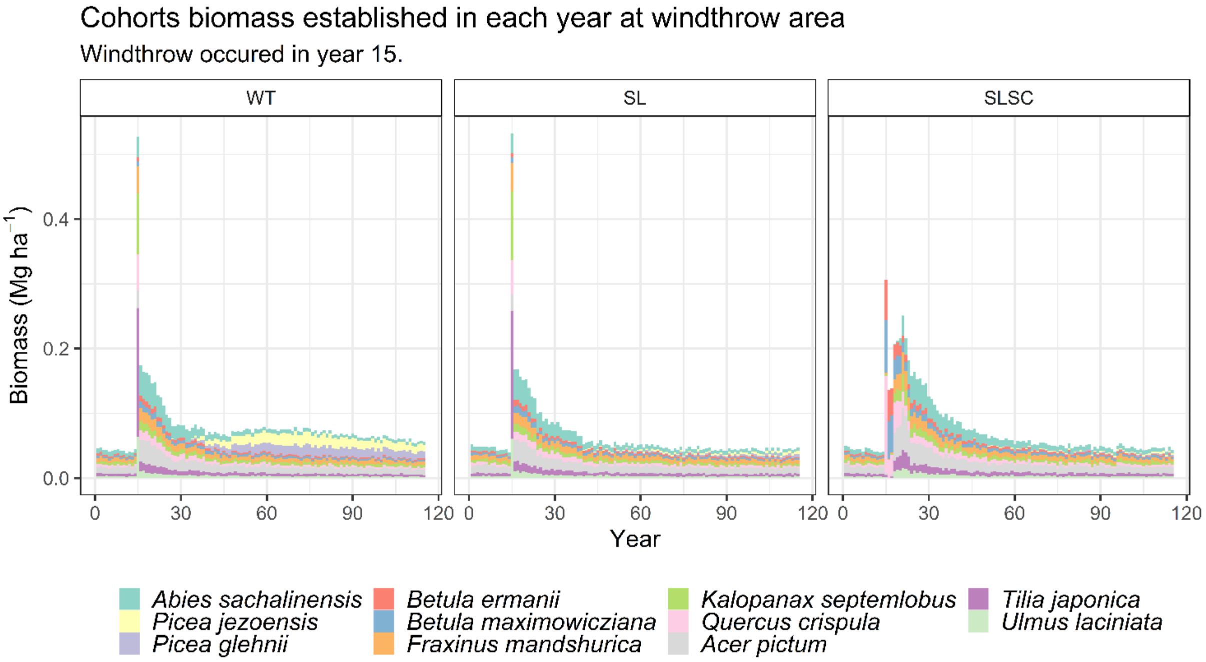
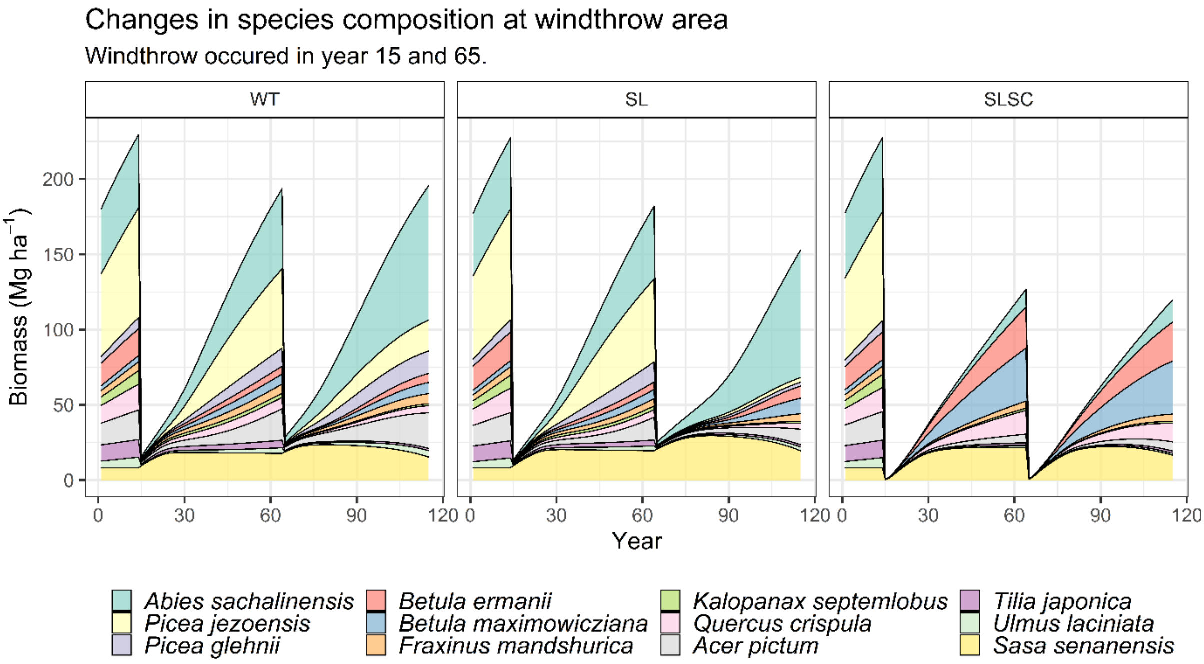


Fig.6 The species composition of cohorts established in each year in stands where windthrow occurred only in year 15. WT: the scenario in which dead wood generated by windthrow is left intact; SL: the scenario in which dead wood generated by windthrow is salvaged; SLSC: the scenario in which dead wood generated by windthrow is salvaged, followed by scarification.

3.3 *Recovery after the two windthrows and subsequent management*

In the stands where windthrow occurred in years 15 and 65, the recovery of aboveground biomass after the second windthrow (year 65) was slower under SL than under WT, and dead wood-dependent species hardly regenerated after the second windthrow under SL (Fig.7). On the other hand, there were no differences in species composition or aboveground biomass recovery after the first and second windthrow under SLSC (Fig.7). Regardless of the post-windthrow management scenario, there was also no difference between the species composition of the cohorts established after the first windthrow and that of the cohorts established after the second windthrow (Fig.8).


Changes in species composition at windthrow area
Windthrow occured in year 15 and 65.
WT
SL
SLSC
Biomass (Mg ha^{-1})
0
50
100
150
200
0
30
60
90
120
Year
Abies sachalinensis
Picea jezoensis
Picea glehnii
Betula ermanii
Betula maximowicziana
Fraxinus mandshurica
Kalopanax septemlobus
Quercus crispula
Acer pictum
Tilia japonica
Ulmus laciniata
Sasa senanensis

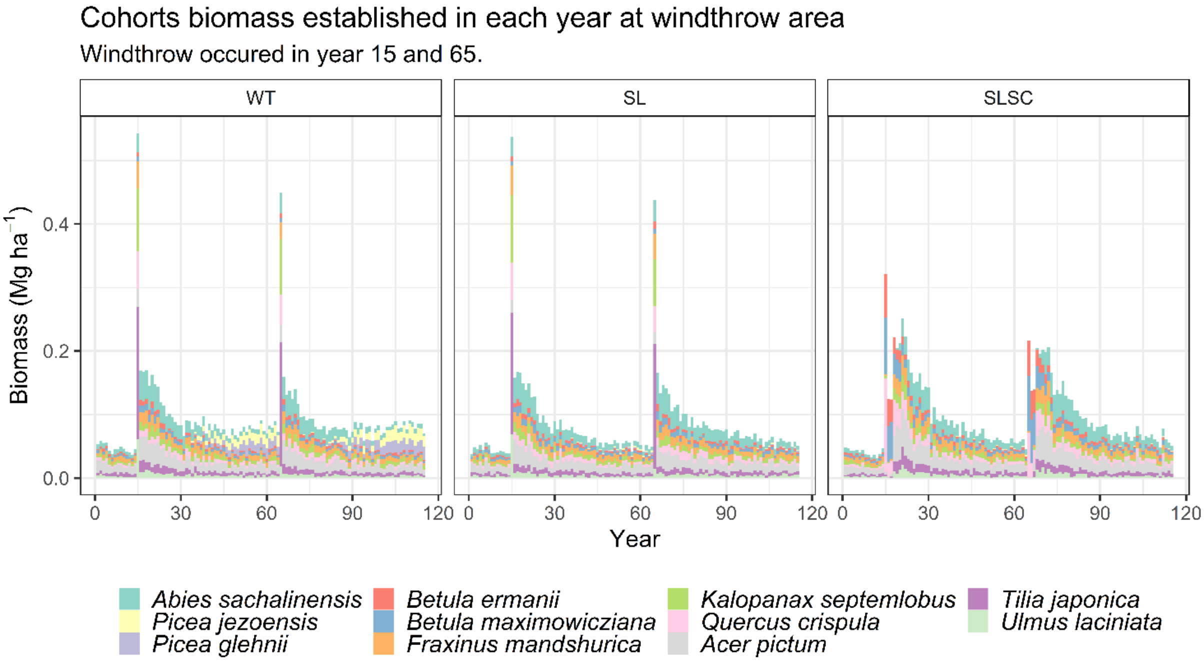


Fig.8 The species composition of cohorts established in each year in stands where windthrows occurred in years 15 and 65. WT: the scenario in which dead wood generated by windthrow is left intact; SL: the scenario in which dead wood generated by windthrow is salvaged; SLSC: the scenario in which dead wood generated by windthrow is salvaged, followed by scarification.

4. Discussion

4.1 *Improvements in LANDIS-II*

The trends in forest recovery associated with post-windthrow management were represented more precisely by LANDIS-II that incorporated the regeneration process on downed logs in addition to tree-grass competition (Scheller *et al*. 2021) than by the original LANDIS-II model (Fig. 3). Before the improvements, the simulations showed dead wood-dependent species such as *P. jezoensis* and *P. glehnii* regenerating even under SL and SLSC, which are scenarios with less well-decayed dead wood. We successfully represented the establishment process of dead wood-dependent species by limiting the establishment probabilities of dead wood-dependent species on the basis of the number of downed logs in decay classes 3, 4, and 5. This change resulted in a more precise representation of the species composition and aboveground biomass 32 years after windthrow and the subsequent management. Although multiple empirical studies have demonstrated the importance of dead wood for tree regeneration (Harmon and Franklin 1989; Takahashi *et al.* 2000; Nakagawa *et al*. 2001; Weaver *et al*. 2009), this process has not yet been implemented in forest landscape models. Forest landscape models have often been used to evaluate the effects of harvesting or various natural disturbances, and these disturbances likely also affect dead wood dynamics in forest ecosystems. Therefore, forest landscape models that incorporate the regeneration process on downed logs will contribute to improving the accuracy of predictions of forest dynamics in future research.

In this study, we tried our best to validate forest development after various post-windthrow management scenarios; however, its duration (32 years) was somewhat short relative to the duration of main simulation analysis (100 years), and the empirical data used for validation were data related to a single windthrow event due to lack of additional empirical data. Establishing permanent plots and continuous monitoring surveys in forests managed in a variety of ways would be critical for more precise validation. Evaluating biases among results from multiple simulation models would also be useful.

4.2 ***Long-term effects of post-windthrow management on species composition and aboveground biomass***

The decrease in dead wood and the destruction of advanced seedlings due to salvage logging had little effect on the species composition or aboveground biomass recovery in the stands. However, the complete destruction of advanced seedlings due to scarification resulted in a delay in the recovery of aboveground biomass and a conversion to birch-dominated forests, and these effects lasted for 100 years. In stands where windthrow occurred once, there was no difference in species composition or the recovery of aboveground biomass between WT and SL (Fig.5). Many of the surviving advanced seedlings had already exceeded the height of the *Sasa* understory just after windthrow; these seedlings grew rapidly and formed the forests that developed after windthrow (Taeroe *et al*. 2019). In this study, the advanced seedling retention rate under SL was half of that under WT. Thus, it appears that the destruction of at least half of the advanced seedlings had little effect on long-term forest recovery after windthrow and salvage logging. In contrast to these results, many empirical studies have reported delays in forest recovery and increases in early-successional species due to intensive salvage logging (Donato *et al*. 2006; Ilisson *et al*. 2007; Morimoto *et al*., 2011; Fischer and Fischer 2012). More intensive salvage logging than that we assumed in this study, i.e., the destruction of more than half of the advanced seedlings, could delay forest recovery more than our simulation predicted and result in a forest more similar to that predicted under SLSC. Although the effects of salvage logging on the species composition and aboveground biomass recovery were limited, the establishment of *P. jezoensis* and *P. glehnii* was less common under SL than under WT (Fig.6). These two species can establish only on well-decayed downed logs or stumps (Takahashi *et al*. 2000; Nakagawa *et al*. 2001), and the decrease in dead wood due to salvage logging resulted in a decrease in the establishment of these species.

Short-term empirical studies have reported that *Betula* spp., which are major pioneer species in boreal and hemiboreal zones, dominate forests that have undergone salvage logging followed by scarification (Yoshida *et al*. 2005; Prévost *et al*. 2010; Aoyama *et al*. 2011; Suzuki 2020). Our results showed that the effects of scarification remained even 100 years after scarification was performed (Fig.5). In our simulation, seedlings of *B. ermanii* and *B. maximowicziana* became established several years after *Sasa* was destroyed by scarification; these seedlings immediately grew up and dominated the canopy after scarification. However, the growth of a dense stand of *Betula* was diminished, probably due to competition with rapidly recovering *Sasa*. As a result, the recovery of aboveground biomass under SLSC was slower than that under WT and SL, and birch-dominated forests developed. Fischer *et al*. (2002) applied an individual-based stand dynamics model and predicted that birches would dominate immediately after windthrow; however, their populations gradually decreased at more than 30 years after windthrow. This may be due to the relatively short longevity of the *Betula* spp. focused on in Fischer *et al*. (2002), *Betula pendula* Roth and *Betula pubescens* Ehrh., whose longevity is 40-100 years (Jónsson 2004). On the other hand, *B. ermanii* and *B. maximowicziana*, which were focused on in this study, are known as long-lived pioneers and can live for more than 300 years (Watanabe 1994). Therefore, our predictions showed the birch-dominated forest remaining for 100 years after scarification. In the UTHF, *B. maximowicziana* has also been dominant for over 100 years at sites that burned in the 1910s (Suzuki 2020). This result suggests that the progress of forest succession can slow after long-lived pioneer species become dominant (Chazdon 2008; Donate *et al*. 2012). Seed dispersal is also one of the major factors influencing forest dynamics. Although variations in seed dispersal related to the wind direction, topography and rich versus poor seed production are not represented, fundamental processes of seed dispersal such as the effective and maximum seed dispersal distances and mature age are represented in LANDIS-II. Therefore, there could be few effects to our discussion.

4.3 *Long-term effects of the interaction between post-windthrow management and frequent windthrows on species composition and aboveground biomass*

The decrease in dead wood due to salvage logging caused a delay in the recovery of aboveground biomass and a change in species composition after windthrow occurred again. The decrease in newly established cohorts after the first windthrow, especially cohorts of *P. jezoensis* and *P. glehnii*, due to salvage logging delayed forest recovery after the second windthrow occurred 50 years after the first windthrow; these conditions resulted in a decrease in aboveground biomass, especially that of *P. jezoensis* and *P. glehnii*. Birch-dominated forests developed after the second scarification just as they did after the first scarification; this occurred because stand development restarted from the "bare land" produced by scarification, which thoroughly destroyed advanced seedlings and removed *Sasa*. The repeated windthrows and salvaging (SL) at 50-year intervals slowed the recovery of aboveground biomass and greatly reduced the biomass of *P. jezoensis* and *P. glehnii* after the second windthrow compared with those in WT stands (Fig.7). This could be attributed to the lower number of advanced seedlings, especially of *P. jezoensis* and *P. glehnii*, under SL than under WT when the second windthrow occurred. Under WT, the species composition and aboveground biomass recovery after the second windthrow were the same as those after the first windthrow because there was plenty of well-decayed dead wood after the first windthrow, and dead wood-dependent species were able to become established (Fig.8). However, fewer seedlings established between the first and second windthrows (from years 16 to 64) under SL than under WT (Fig. 8); moreover, the advanced seedlings were destroyed due to salvage logging after the second windthrow. Thus, there were much fewer surviving advanced seedlings after the second windthrow under SL than under WT. This difference explains why the recovery of aboveground biomass after the second windthrow was slower under SL than under WT. Furthermore, the seedling community without dead wood-dependent species (due to salvage logging after the first windthrow) grew into mature trees after the second windthrow; as a result, dead wood-dependent species hardly regenerated under SL after the second windthrow. Although previous studies have suggested that salvage logging may affect the long-term regeneration dynamics of dead wood-dependent species (Suzuki *et al*. 2019; Morimoto *et al*. 2019a; Hotta *et al*. 2020), these effects have not yet been directly observed due to the difficulty of performing long-term monitoring in forest ecosystems. Previous simulation studies have not evaluated these effects of salvage logging because the regeneration process on downed logs had not yet been incorporated into forest landscape models (Dobor *et al*. 2019). However, we successfully quantitatively evaluated the effects of salvage logging on the regeneration dynamics of dead wood-dependent species by using a process-based simulation model that includes the regeneration process on downed logs.

5. Implications for forest management

When windthrow occurred only once, salvage logging hardly affected the species composition and aboveground biomass of the forest within 100 years after the windthrow. However, the number of advanced seedlings decreased, and the species composition of the seedlings changed due to the decrease in dead wood caused by salvage logging. Therefore, when windthrow occurred again within a short interval, salvage logging decreased the aboveground biomass of the forest and changed its species composition after the second windthrow. To conserve the species composition and aboveground biomass of forest ecosystems under climate change, which is predicted to increase windthrow frequency (Usbeck *et al*. 2010; Donat *et al*. 2011; Gregow *et al*. 2017; Laapas *et al*. 2019), it is preferable to leave the dead wood generated by windthrow and not perform scarification after windthrow. Because this paper describes a case study in hemiboreal forests in northern Japan, forest landscapes in different climatic zones and dominated by different tree and grass species might show different results. The promotion of similar studies in various regions worldwide would be useful to obtain a more robust conclusion. Additionally, this study involved assumptions regarding scenario settings (e.g., windthrow regimes and the destruction rate of advanced seedlings). Although these assumptions were based on real situations and findings of previous studies as much as possible, examining the effects of these assumptions could also be an important topic of future studies. Besides, leaving the dead wood after windthrow could result in insect outbreaks (Mezei *et al*. 2017). However, salvage logging to prevent insect outbreaks would decrease the diversity of forest ecosystems, which can result in even more serious insect outbreaks (Hughes and Drever 2001). In addition, the simulation results of Dobor *et al*. (2019) suggest that over 95% of the dead wood generated by windthrow in the landscape must be salvaged to prevent insect outbreaks; however, this is nearly impossible, because pieces of dead wood at inaccessible sites are left in the forest. Therefore, salvage logging could not effectively prevent insect outbreaks, changes forest tree species composition and decreases the aboveground biomass of forests in the long term.

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Appendix A. Supplementary materials

Appendix B. Source code availability

The source code for our improved version of LANDIS-II NECN succession is available at https://github.com/hagachi/Extension-NECN-Succession/tree/feature-initdecayrate.

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