



Title	Leaving disturbance legacies conserves boreal conifers and maximizes net CO2 absorption under climate change and more frequent and larger windthrow regimes
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1 **Title:** Leaving disturbance legacies conserves boreal conifers and maximizes net CO₂ absorption under climate
2 change and more frequent and larger windthrow regimes

3

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26

27 **Abstract**

28 *Context*

29 Forest management practices that conserve biodiversity and maximize carbon sequestration under climate change
30 are needed. Although post-windthrow salvage logging and scarification can reduce carbon dioxide (CO₂) emissions
31 within ecosystems by removing downed logs, they can greatly affect species composition. Additionally, salvage
32 logging may increase CO₂ emissions based on a cradle-to-grave analysis of salvaged wood.

33 *Objectives*

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

37 *Methods*

38 The study landscape is a 12,169 ha hemiboreal forest located in northern Japan. We simulated 115 years (2015-
39 2130) of forest dynamics in 36 scenarios based on features of the climate, windthrow regime, and management using
40 the LANDIS-II forest landscape model. CO₂ emissions related to management and salvaged wood were estimated
41 by LCA.

42 *Results*

43 Increases in the windthrow area, which was more vulnerable to climate warming, caused a shift to temperate
44 broadleaved forests and a decrease in aboveground biomass. These were accelerated by the removal of advanced
45 seedlings and dead wood, which greatly reduced the recruitment of *Picea* species. The 115-year cumulative net CO₂
46 absorption of the forest sector, including carbon balance within ecosystems and CO₂ emissions estimated by LCA,
47 greatly decreased due to salvage logging (maximum 81%) and scarification (maximum 114%).

48 *Conclusions*

49 Leaving downed logs and advanced seedlings is recommended to conserve boreal conifers and carbon sinks and
50 maximize net CO₂ absorption under climate change.

51

52 **Keywords**

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

55 **Introduction**

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

73 The balancing of climate change mitigation by maintaining carbon sinks and biodiversity conservation is
74 indispensable for achieving social and environmental goals (IPBES 2019) such as the United Nations' Sustainable
75 Development Goals (UN 2015), the Convention on Biological Diversity's Kunming-Montreal 2030 Global Targets
76 (CBD Secretariat 2022), and the Paris Agreement (UNFCCC 2015) objectives. The importance of forest
77 management to support climate change adaptation is growing (Millar et al. 2007; Gustafson et al. 2020), but an
78 alternative goal of management is to conserve tree species that are threatened by the effects of warmer climate
79 brought about by climate change. Therefore, forest management strategies to maintain both biodiversity and carbon
80 balance under these novel environmental conditions should be considered. For instance, conventional post-
81 windthrow management, such as salvage logging and scarification, destroys disturbance legacies (i.e., advanced
82 seedlings and dead wood) that are starting points for forest recovery, therefore affecting the species composition and

83 carbon balance of the subsequently established forests (Taeroe et al. 2019; Hotta et al. 2020, 2021). Salvage logging
84 is a management practice that removes disturbance-affected trees, prevents subsequent wildfire and insect outbreaks
85 and compensates for economic losses (Lindenmayer et al. 2008). Scarifications are sometimes conducted after
86 salvaging to destroy forest floor grasses and shrubs that inhibit tree regeneration and to remove the organic-rich
87 surface soil layer that contains pathogens (Yoshida et al. 2005). However, these management practices destroy
88 advanced seedlings, which delays forest recovery (Greene et al. 2006; Donato et al. 2006; Morimoto et al. 2011) and
89 increases the ratio of early-successional species to late-successional species (Ilisson et al. 2007; Prévost et al. 2010;
90 Fischer and Fischer 2012). The removal of dead wood due to salvage logging would decrease the regeneration of
91 tree species that require dead wood as a regeneration site, e.g., *Picea jezoensis* (Nakagawa et al. 2001; Hotta et al.
92 2021), *Picea rubens* (Weaver et al. 2009), and *Tsuga canadensis* (Weaver et al. 2009). In addition, the removal of
93 dead wood would somewhat decrease carbon dioxide (CO₂) emissions within ecosystems. However, conventional
94 post-windthrow management practices may increase CO₂ emissions when a cradle-to-grave analysis (e.g., Hudiburg
95 et al. 2019) of salvaged wood, including management practices, manufacturing, and wood product pool storage and
96 decay, is considered together with heterotrophic respiration (Rh) in ecosystems.

97 Comprehensive assessments (e.g., life cycle assessment: LCA), including assessments of CO₂ emissions
98 due to activities such as salvaging and making products from downed logs, are required for developing post-
99 windthrow management plans that maximizes net CO₂ absorption, as well as the cases of normal harvesting and
100 post-outbreak salvaging (Hudiburg et al. 2019; Gunn et al. 2020). LCA is a method for evaluating the environmental
101 aspects associated with a product over its life cycle (Muralikrishna and Manickam 2017). The usefulness of
102 considering LCA in landscape management is becoming increasingly recognized (Eddy and Gergel 2015; Wu et al.
103 2022). Considering carbon balance within ecosystems and LCAs together can realize the equal comparison of the
104 effects of management strategies on carbon balance. However, previous studies that evaluated the effects of post-
105 windthrow management on carbon balance did not include an LCA of salvaged wood (Dobor et al. 2018, 2020a).

106 No study has evaluated the effects of post-windthrow management on tree species composition and carbon
107 balance with an LCA under climate change and novel windthrow regimes, although the continuation of conventional
108 post-windthrow management may induce changes in tree species composition (Hotta et al. 2021) and carbon balance
109 which is evaluated with an LCA (Suzuki et al. 2019). The decrease in or loss of disturbance legacies (e.g., due to
110 post-windthrow management) may accelerate shifts in species composition, resulting in communities that are

111 different from the original one (Johnstone et al. 2016), such as a shift to those more adapted to warmer climates
112 (Liang et al. 2018). In addition, the increase in the number of times post-windthrow management is applied and the
113 amount of dead wood salvaged due to changes in windthrow regime (Lindenmayer et al. 2008) may induce the
114 degradation of carbon sinks in the forest sector, as determined by both ecosystem analysis and a cradle-to-grave
115 dead wood analysis. In this study, we aimed to reveal the effects of climate change, changes in windthrow regimes,
116 and post-windthrow management on the total aboveground biomass and tree species composition in forest
117 landscapes. We also analyzed the carbon balance in the forest sector by simulating changes in the forest landscape
118 under several climate, windthrow regime, and management scenarios using LANDIS-II (Scheller et al. 2007), a
119 widely used process-based forest landscape model, and LCA.

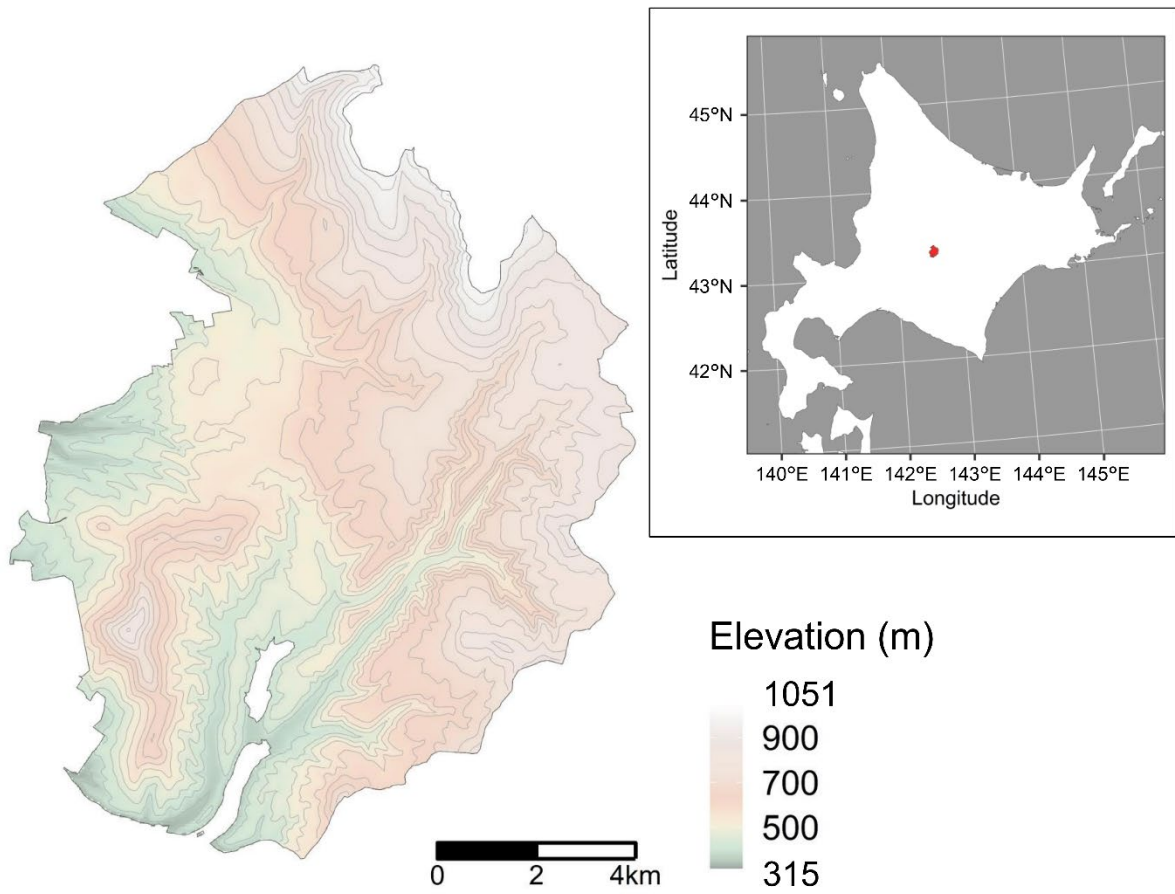
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121 **Materials and Methods**

122 **Study landscape**

123 The study landscape is a 12,169 ha hemiboreal forest located in the University of Tokyo Hokkaido Forest (UTHF;
124 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
125 annual total precipitation at the Rokugo meteorological observatory (43°18'6"N, 142°31'18"E, 315 m a.s.l.), which
126 is the closest site to the study landscape, are 5.5°C and 972.6 mm, respectively (representing the averages from
127 1981-2010) (Japanese Meteorological Agency 2012). The study landscape is covered by hemiboreal mixed forests
128 dominated by conifers such as *Abies sachalinensis* (F. Schmidt) Mast. and *Picea jezoensis* (Siebold et Zucc.)
129 Carrière var. *jezoensis*; deciduous broadleaves such as *Tilia japonica* (Miq.) Simonk. and *Betula ermanii* Cham.; and
130 herbaceous species such as *Sasa senanensis* (Franch. et Sav.) Rehder. The dominant soil type is mostly Andosols
131 (parent material: andesite, rhyolite, volcanic ash, or dacite) with some Cambisols (parent material: rhyolite or dacite)
132 (IUSS Working Group WRB 2015). The dominant natural disturbance of the study landscape is stand-replacing
133 windthrow. There are records of windthrow caused by Typhoon Marie in 1954 and Typhoon Thad in 1981 in the
134 UTHF (Watanabe et al. 1990). Notably, 8,735 ha (38.9% of the UTHF) in area and 807,000 m³ in timber volume
135 were damaged by Typhoon Thad in 1981 (Takada et al. 1986).

136



137

138 **Fig. 1**

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

140 Topographical map of the study landscape.

141

142 **Simulation model and its application in this study**

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

150 The improved version of LANDIS-II Net Ecosystem Carbon and Nitrogen succession v6.3 (NECN
151 succession) (Scheller et al. 2011) with tree-grass competition (Haga et al. 2022) and the regeneration process on
152 downed logs (Hotta et al. 2021) was used as the succession extension to simulate the dynamics of forest species
153 composition and carbon balance. In the NECN succession, biomass growth and seedling establishment were
154 calculated based on the environmental conditions in each grid cell. The biomass growth of each cohort was
155 calculated as the difference between monthly aboveground net primary production (NPP) and monthly mortality.
156 Monthly aboveground NPP was calculated by multiplying the maximum value of monthly aboveground NPP (user-
157 defined parameter for each species) by coefficients related to environmental limitation factors, such as monthly
158 mean temperature, plant-available soil nitrogen, soil water content, the leaf area index (LAI) of the cohort itself, and
159 the LAI of the other cohorts within the grid cell. Regarding cohort establishment, the establishment probabilities of
160 each species in each grid cell were calculated based on the following two categories: (1) minimum January
161 temperature (the minimum temperature of the coldest month in a year), growing degree days, and soil moisture
162 content of each region; and (2) light availability at the site. If the two designated requirements were satisfied (i.e.,
163 the product of establishment probabilities based on two categories is larger than the random number assigned to each
164 site), cohorts were established in the grid cell. Additionally, tree species requiring dead wood for regeneration could
165 be established only in grid cells that had well-decayed downed logs (Hotta et al. 2021). Many field-based studies
166 have reported that some *Picea* species largely depends on dead wood for their establishment sites because seedlings
167 can avoid pathogens, light competition, and aridity on dead wood (e.g., Harmon and Franklin 1989; Takahashi et al.
168 2000; Nakagawa et al. 2001). Therefore, two species of *Picea* spp., *P. jezoensis* and *P. glehnii*, were set as dead
169 wood-dependent species in this study. The decomposition rates of dead wood and soil organic matter were

170 controlled by the soil temperature and moisture content. The decomposition rate of dead wood was calculated
171 according to the amount of dead wood of each tree species in the dead wood pool using the parameters of dead wood
172 decomposition rates of each species (user-defined parameter; WoodDecayRate). The decomposition rate of soil
173 organic matter was calculated based on the decomposition rate parameters of the four soil pools (user-defined). Both
174 decomposition rates were calculated to reflect the environmental conditions of each grid cell through soil
175 temperature and moisture contents (Scheller et al. 2011).

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

192

193 **Landscape initialization**

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

198 *senanensis*. Regarding tree species, the initial communities as of 2015, that is, the input data of vegetation, were
199 created based on forest inventory data of the UTHF. Regarding herbaceous species, the input data were created by
200 estimating the aboveground biomass of *Sasa* using the *Sasa* distribution model developed by Tatsumi and Owari
201 (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
202 study landscape, as this is the mean value of the dead wood data from Hotta et al. (2020). All initial dead wood was
203 assumed to be mostly undecomposed because the data of the amounts of dead wood in each decay class were
204 unavailable. Additionally, the amount of dead wood cannot be input by decay classes in the NECN succession
205 extension due to technical constraints, and it is highly challenging to estimate the amount of dead wood in stands
206 that have different management histories due to the lack of empirical data. The absence of well-decayed dead wood
207 at the start of the simulation would cause the underestimation of tree regeneration on downed logs in the first twenty
208 years of the simulations. Soil property data were input based on the data from Asahi (1963), which described the
209 soils in the UTHF in detail.

210

211 **Windthrow regime scenarios**

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

217 (1) Historical windthrow regime scenario (Historical)

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

223 (2) Increased windthrow frequency scenario (Frequent)

224 The scenario in which stand-replacing windthrow occurred with twice the historical frequency (Table 1).
225 The ratio of the windthrow area of a single windthrow event to the study landscape area was defined as 20%, which

226 was the same as the Historical scenario. The frequency of windthrow was defined as four times in 100 years
227 (occurring in 2030, 2055, 2080, and 2105).

228 (3) Increased windthrow size scenario (Large)

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

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

234 The scenario in which the stand-replacing windthrow occurred with twice the historical frequency and size
235 (Table 1). The ratio of the windthrow area of a single windthrow event to the study landscape area was defined as
236 40%. The frequency of windthrow was defined as four times in 100 years (occurring in 2030, 2055, 2080, and
237 2105).

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

249

250 **Table 1** The year when windthrow occurs and the ratio of windthrow areas to the study landscape area in
 251 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%

252

253 **Post-windthrow management scenarios**

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

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

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

261 (b) Salvage logging after windthrow (SL)

262 All dead wood generated by windthrow was salvaged and removed from forest ecosystems, and 60% of
263 advanced seedlings were destroyed due to salvaging (Table 2). The destruction ratio of advanced seedlings was
264 determined based on the data of the ratio of forest floor area disturbed by logs that were removed (Ohsato et al.
265 1996).

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

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

272

273 **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	<i>Sasa</i> (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

274

275 **Climate scenarios**

276 To consider tree physiological responses to climate change, the current climate and two future climate scenarios
277 were used for simulations. Regarding the current climate scenario (Current), the 1 km mesh climate data (an average
278 from 1981–2010) (Japanese Meteorological Agency 2012) in the study area landscape were used for the climate
279 data. We selected the following two extreme scenarios as future climate scenarios: (1) the representative
280 concentration pathway (RCP) 2.6 scenario calculated by the CSIRO-Mk3-6-0 model (hereafter referred to as the
281 RCP2.6 scenario; approximately 1°C increase in mean annual temperature and almost no change in precipitation by
282 2100); and (2) the RCP8.5 scenario calculated by the GFDL-CM3 model (hereafter referred to as the RCP8.5
283 scenario; approximately 6.5°C increase in mean annual temperature and 10% increase in precipitation by 2100)
284 (Nishimori et al. 2019). In humid climate zones, temperature rise has a greater impact than precipitation changes
285 (Feeley et al. 2012). In addition, future drought risk is expected to be low in this region (Dai 2011). To primarily
286 evaluate the impact of temperature increase, this study adopted the future climate scenarios of RCP2.6 and RCP8.5,
287 which have a small range of variability in precipitation and a large range of variability in temperature. The details of
288 each climate scenario and the reasons for selecting them are described in Online Resource 3.

289

290 **Simulation and evaluation indicators**

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

295 We evaluated the species composition in the forest landscape using the aboveground biomass of each
296 species. Additionally, the number of cohorts successfully established for each species was evaluated to determine the
297 effects of climate, windthrow regime, and post-windthrow management on the cohort establishment of each species.
298 The net forest sector carbon balance (Hudiburg et al. 2019; hereafter referred to as NFCB) was calculated to
299 evaluate the difference in the carbon balance between the following two cases: the case when dead wood generated
300 by windthrow was decomposed within the forest ecosystem (WT scenario) and the case when dead wood generated
301 by windthrow was salvaged and used as timber and paper products (SL and SLSC scenarios). LCAs of these
302 scenarios were conducted to calculate the NFCB (Online Resource 4). NEP, NPP, and Rh were used to understand

303 the factors that explain the dynamics of the NFCB. Rh is defined as the process of releasing CO₂ to the atmosphere
 304 by the decomposition of dead wood and soil organic matter. Additionally, we conducted three-way factorial analysis
 305 of variance (ANOVA; n = 5 per scenario) in which climate, windthrow regime, post-windthrow management, and
 306 their two-term interactions (climate × windthrow regime, windthrow regime × post-windthrow management, climate
 307 × post-windthrow management) were considered as factors. Then, we assessed the effect size of each factor by
 308 calculating omega-squared values (ω^2) (following the guide of White et al. 2014 and an example reported by St-
 309 Laurent et al. 2022) using the *effectsize* package (Ben-Shachar et al. 2020). ω^2 represents how much variance in the
 310 response variables is accounted for by the explanatory variables. Values larger than 0.01, 0.06, and 0.14 were
 311 interpreted as small, medium, and large effect size, respectively (Field 2013). The response variables were the total
 312 aboveground biomass in 2130, the aboveground biomass of each species in 2130, the total number of newly
 313 established cohorts in the entire simulation, the number of newly established cohorts of each species in the entire
 314 simulation, the NEP in 2130, the NPP in 2130, the Rh in 2130, the NFCB in 2130, and the cumulative NFCB in
 315 2130 for all the scenarios. The summary and analysis of the simulation results were conducted in R ver. 3.6.2 (R
 316 Core Team 2019).

317 NFCB is one of the indicators of carbon balance that considers CO₂ emissions related to harvesting,
 318 transportation, manufacturing, the disposal of the product, and so on (Hudiburg et al. 2019). In this study, we defined
 319 the forest sector as shown in Fig. 2. The NFCB was calculated using Equation 1 after estimating the CO₂ emissions
 320 related to salvage logging, scarification, the manufacturing of products, and the disposal of products by LCA (Fig. 2,
 321 Online Resource 4). The CO₂ emissions related to the transportation of dead wood were excluded because they were
 322 smaller than the CO₂ emissions related to the other processes (Owari et al. 2011).

$$323 \text{NFCB}_t = \text{NEP}_t - \text{CE}_{\text{Salvage } t} - \text{CE}_{\text{Scarification } t} - \text{CE}_{\text{ManufactureLong-lived } t} -$$

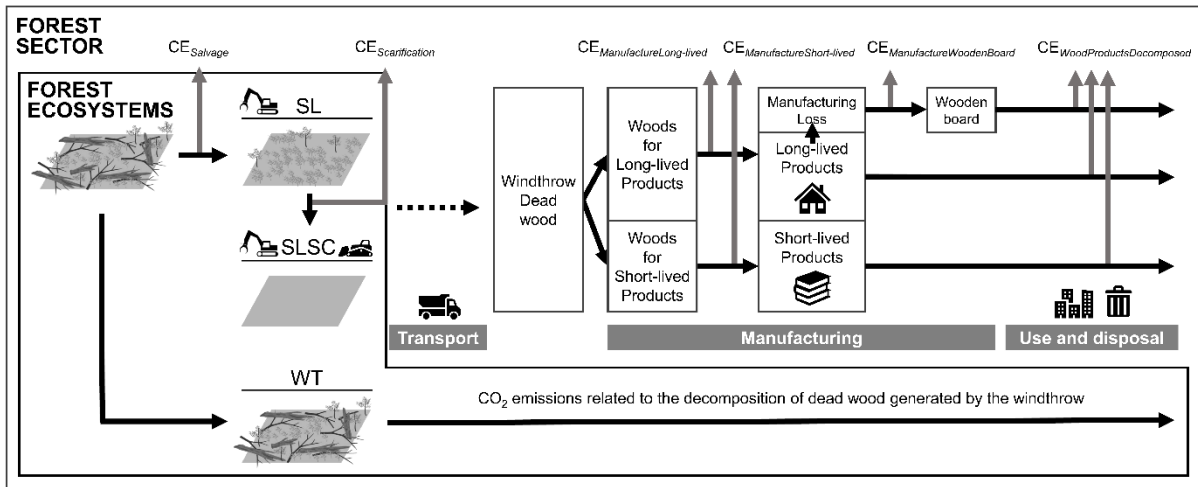
$$324 \text{CE}_{\text{ManufactureShort-lived } t} - \text{CE}_{\text{ManufactureWoodenBoard } t} - \text{CE}_{\text{WoodProductsDecomposed } t} \quad \text{Eq. 1}$$

325 t : the simulation year; NFCB_t : net forest sector carbon balance in year t ; NEP_t : net ecosystem production in year t ;
 326 $\text{CE}_{\text{Salvage } t}$: CO₂ emissions related to salvage logging (e.g., use of heavy machinery) in year t ; $\text{CE}_{\text{Scarification } t}$: CO₂
 327 emissions related to scarification (e.g., use of heavy machinery) in year t ; $\text{CE}_{\text{ManufactureLong-lived } t}$: CO₂ emissions related
 328 to manufacturing of long-lived products (timber products used for several decades such as building materials and
 329 furniture) in year t ; $\text{CE}_{\text{ManufactureShort-lived } t}$: CO₂ emissions related to manufacturing of short-lived products (products to
 330 be disposed of in a few years such as wood chips and paper) in year t ; $\text{CE}_{\text{ManufactureWoodenBoard } t}$: CO₂ emissions related

331 to the manufacturing of wooden boards (such as particle boards) in year t ; and $CE_{WoodProductsDecomposed\ t}$: CO₂ emissions
332 (flux to outside of the forest sector) related to the disposal of products made from dead wood generated by the
333 windthrow in year t .

334 The detailed calculations of each CO₂ emission are described in Online Resource 4. The CO₂ emissions
335 related to salvage logging, scarification, and the manufacturing of long- and short-lived products and wooden boards
336 were assumed to occur in the year when windthrow occurred. Regarding the WT scenario, the NFCB was equal to
337 the NEP because all dead wood generated by windthrow was left intact in the forest ecosystem. In this study, scrap
338 wood generated by sawing was used as raw material for wooden boards to utilize dead wood generated by
339 windthrow as products with the longest possible life. In addition, we analyzed the sensitivity of the NFCB to the
340 usage of scrap wood, and Online Resource 5 indicated the result in the case when scrap wood was used for paper
341 pulp and chip production, which was the scenario utilizing dead wood generated by windthrow as products with the
342 shortest possible life.

343



344 **Fig. 2**

345 The system boundary of the life cycle assessment in this study and the differences in the forest sector and forest
 346 ecosystem. Gray arrows indicate CO₂ emissions by each factor. Dark gray boxes indicate stages in the life cycle. The
 347 part indicated by a dotted arrow was cut off in the life cycle assessment. WT: windthrow only; SL: salvage logging;
 348 SLSC: salvage logging and scarification. $CE_{Salvage}$: CO₂ emissions related to salvage logging (e.g., use of heavy
 349 machinery); $CE_{Scarification}$: CO₂ emissions related to scarification (e.g., use of heavy machinery); $CE_{ManufactureLong-lived}$:
 350 CO₂ emissions related to manufacturing of long-lived products (timber products used for several decades such as
 351 building materials and furniture); $CE_{ManufactureShort-lived}$: CO₂ emissions related to manufacturing of short-lived
 352 products (products to be disposed of in a few years such as wood chips and paper); $CE_{ManufactureWoodenBoard}$: CO₂
 353 emissions related to the manufacturing of wooden boards (such as particle boards); $CE_{WoodProductsDecomposed}$: CO₂
 354 emissions related to the disposal of products that were made from dead wood generated by windthrow.

355

356 Results

357 Total aboveground biomass and species composition

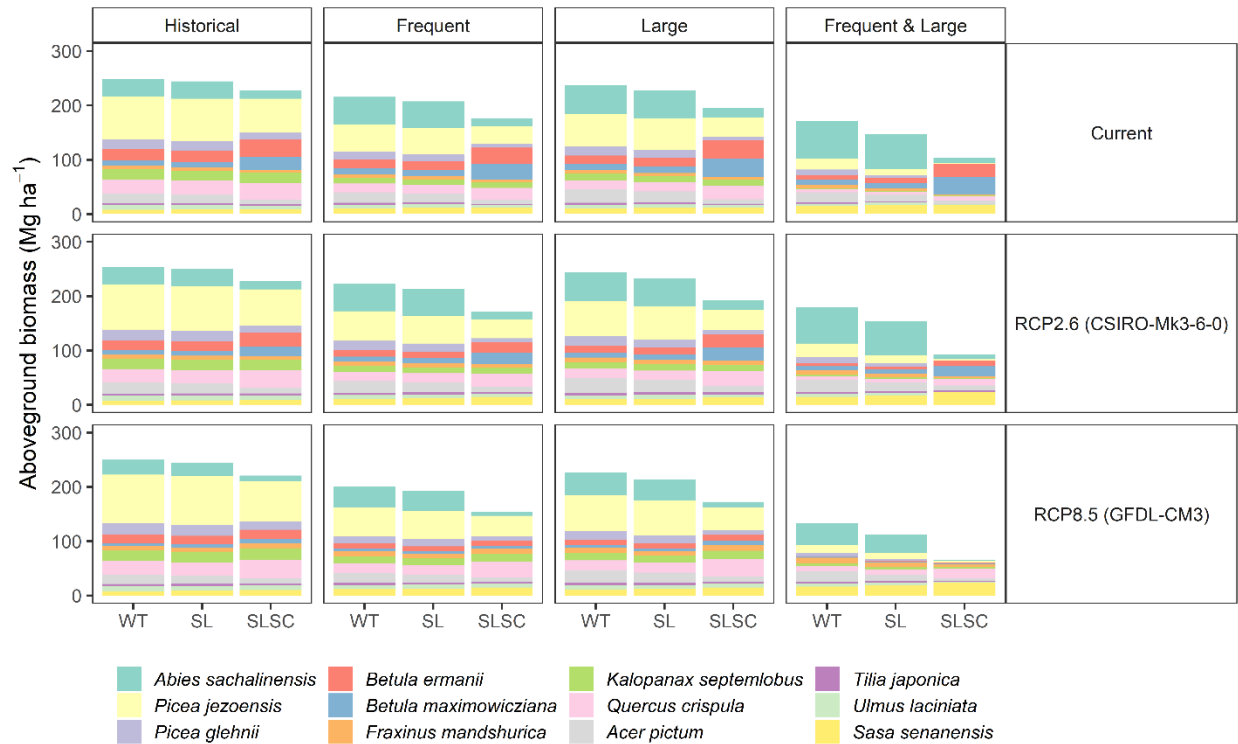
358 Regarding total aboveground biomass in 2130, the effect sizes of windthrow regime ($\omega^2 = 0.741$) and post-
359 windthrow management ($\omega^2 = 0.183$) were large, and those of climate ($\omega^2 = 0.037$), windthrow regime \times post-
360 windthrow management ($\omega^2 = 0.021$), and climate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

367 The total aboveground biomass in 2130 decreased as the windthrow frequency and size increased. The
368 decreasing ratio of the total aboveground biomass to that under the Historical scenario and the effects on species
369 composition increased as the windthrow frequency and size increased with salvage logging and scarification (Figs. 3
370 and 4 and Online Resource 6). The total aboveground biomass under the Frequent & Large scenario in WT, SL, and
371 SLSC was 69%, 60%, and 46% of that under the Historical scenario, respectively (Fig. 3). In the SLSC, the
372 aboveground biomass of *Betula* spp. showed little difference under the Historical and Frequent & Large scenarios
373 (Online Resource 7 Fig. S7: *Betula* spp.), but the ratio of *Betula* spp.-dominant forest area to the study landscape
374 area under the Frequent & Large scenario was twice as large as that under the Historical scenario (Fig. 4: Current;
375 and Online Resource 6). In SL, the difference in species composition from WT was small under the Frequent or the
376 Large scenarios. However, the aboveground biomass of *Picea* spp. in SL was lower than that in WT under the
377 Frequent & Large scenario (Fig. 3; Online Resource 7 Fig. S7: *Picea* spp.). The ratio of *Picea* spp.-dominated
378 forests to the study landscape area was approximately 66% of that in WT under the Frequent & Large scenario (Fig.
379 4: Current; and Online Resource 6). The aboveground biomass of *Sasa* increased as the windthrow frequency and
380 size increased, regardless of post-windthrow management. The ratios of *Sasa*-dominant grid cells to the study
381 landscape area under the Frequent & Large scenario were approximately three times as large in SL as those in WT
382 and approximately five times as large in SLSC as those in WT (Fig. 4: Current; Online Resource 6 and 7 Fig. S7: *S.*
383 *senanensis*).

384 The effects of temperature increase on the total aboveground biomass and species composition were more
385 apparent as windthrow frequency and size increased and salvage logging and scarification were conducted. The total
386 aboveground biomass and species composition under historical conditions were only slightly different among the
387 climate scenarios. Under the Frequent & Large scenario, the total aboveground biomass was slightly different
388 between the current climate and RCP 2.6. However, the total aboveground biomass in RCP8.5 was 64% (SLSC) –
389 77% (WT) of that in the current climate scenario (Fig. 3). The aboveground biomass and the percentages of
390 dominance in the study landscape area of *A. sachalinensis* and *Betula* spp. decreased with increasing temperature
391 (Figs. 4 and Online Resources 6 and 7 Fig. S7: *A. sachalinensis* and *Betula* spp.), regardless of post-windthrow
392 management. Those of *Q. crispula* and *S. senanensis* increased with increasing temperature (Fig. 4 and Online
393 Resources 6 and 7 Fig. S7: *Q. crispula* and *S. senanensis*) in the SLSC. These effects were larger as the windthrow
394 frequency and size increased. Changes in species composition with increasing temperature were largest in the SLSC
395 scenario. In the SLSC scenario under the Frequent & Large scenario, the aboveground biomass of *Betula* spp. was
396 95% smaller, and those of *Q. crispula* and *S. senanensis* were 85% and 38% larger, respectively, under RCP 8.5 than
397 those of the Current scenario (Online Resource 7 Fig. S7: *Betula* spp., *Q. crispula*, and *S. senanensis*). Under
398 RCP8.5 and the Frequent & Large scenario, the ratios of *Sasa*-dominated grid cells to the study landscape area were
399 22%, 37%, and 57% in WT, SL, and SLSC, respectively (Fig. 4).

400 The total number of newly established cohorts during the entire simulation period and the species
401 composition of newly established cohorts were greatly influenced by the climate and post-windthrow management
402 scenarios, but they were only slightly influenced by the windthrow regime (Fig. 5). Regarding the total number of
403 established cohorts, the effect size of climate ($\omega^2 = 0.774$) was large, that of post-windthrow management ($\omega^2 =$
404 0.102) was medium, and the effect sizes of windthrow regime \times post-windthrow management ($\omega^2 = 0.050$), climate
405 \times post-windthrow management ($\omega^2 = 0.032$), windthrow regime ($\omega^2 = 0.019$), and climate \times windthrow regime ($\omega^2 =$
406 0.018) were small (Online Resource 9 Table S9.2). The number of established cohorts of temperate tree species such
407 as *Q. crispula*, *F. mandshurica*, and *K. septemlobus* increased as the temperature increased (Fig. 5). However, the
408 numbers of newly established cohorts of *A. sachalinensis* and *Betula* spp. in RCP2.6 and RCP8.5 and those of *Picea*
409 spp. in RCP8.5 were less than those in the Current scenario (Fig. 5). The numbers of *Picea* spp. cohorts established
410 in the SL and SLSC were lower than those established in the WT (Fig. 5). The difference in the total number and
411 species composition of newly established cohorts among post-windthrow management increased as the windthrow

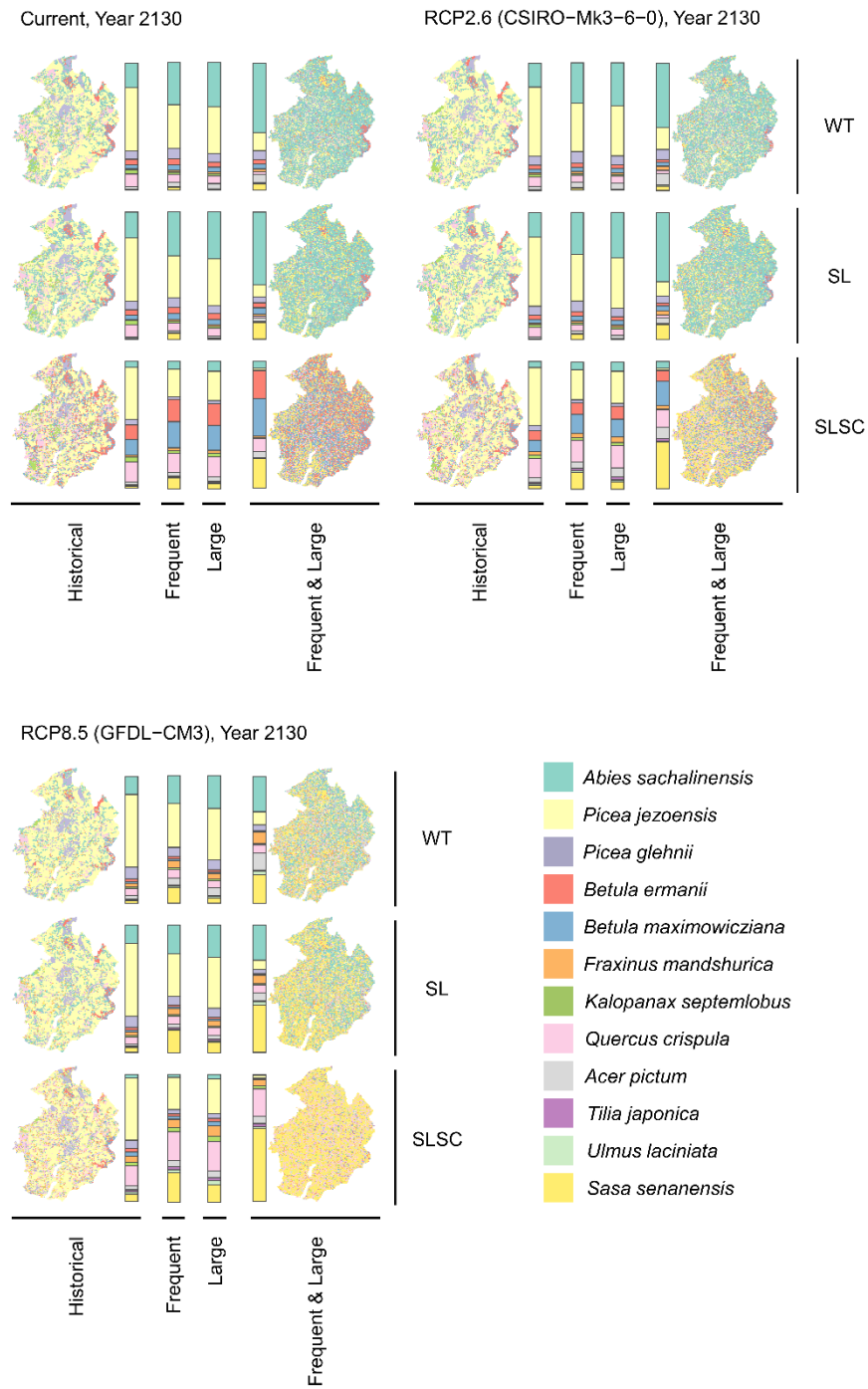
412 frequency and size increased.



413

414 **Fig. 3**

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



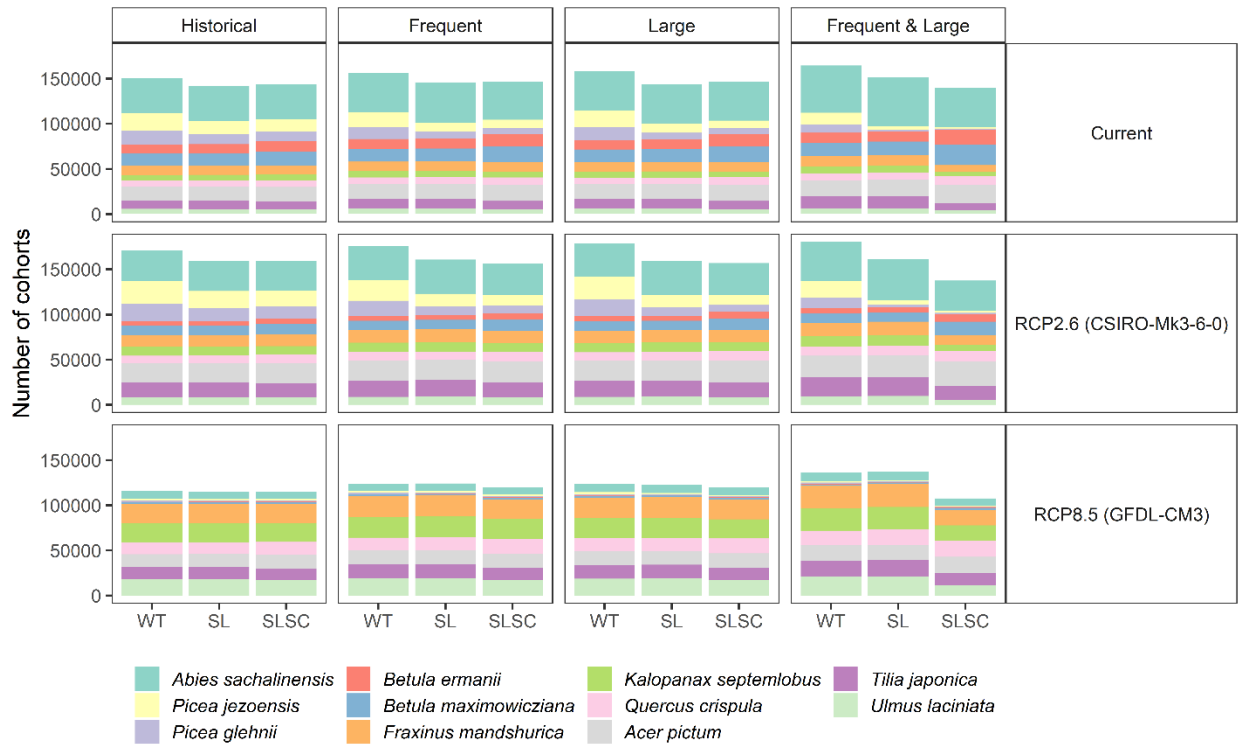
420

421 **Fig. 4**

422 The spatial distributions of forests dominated by each species and the ratio of grid cells dominated by each species

423 in 2130 (dominance based on aboveground biomass). The raster indicates the dominant species in each grid cell.

424 Only the Historical and the Frequent & Large scenarios are shown. The raster of all scenarios is presented in Online
425 Resource 6. The bar graphs indicate the ratio of grid cells dominated by each species to the study landscape. Species
426 with the largest aboveground biomass in the grid cell were defined as the dominant species. Rows and columns
427 indicate post-windthrow management scenarios and windthrow regime scenarios, respectively. WT: windthrow only;
428 SL: salvage logging; SLSC: salvage logging and scarification
429



430

431 **Fig. 5**

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

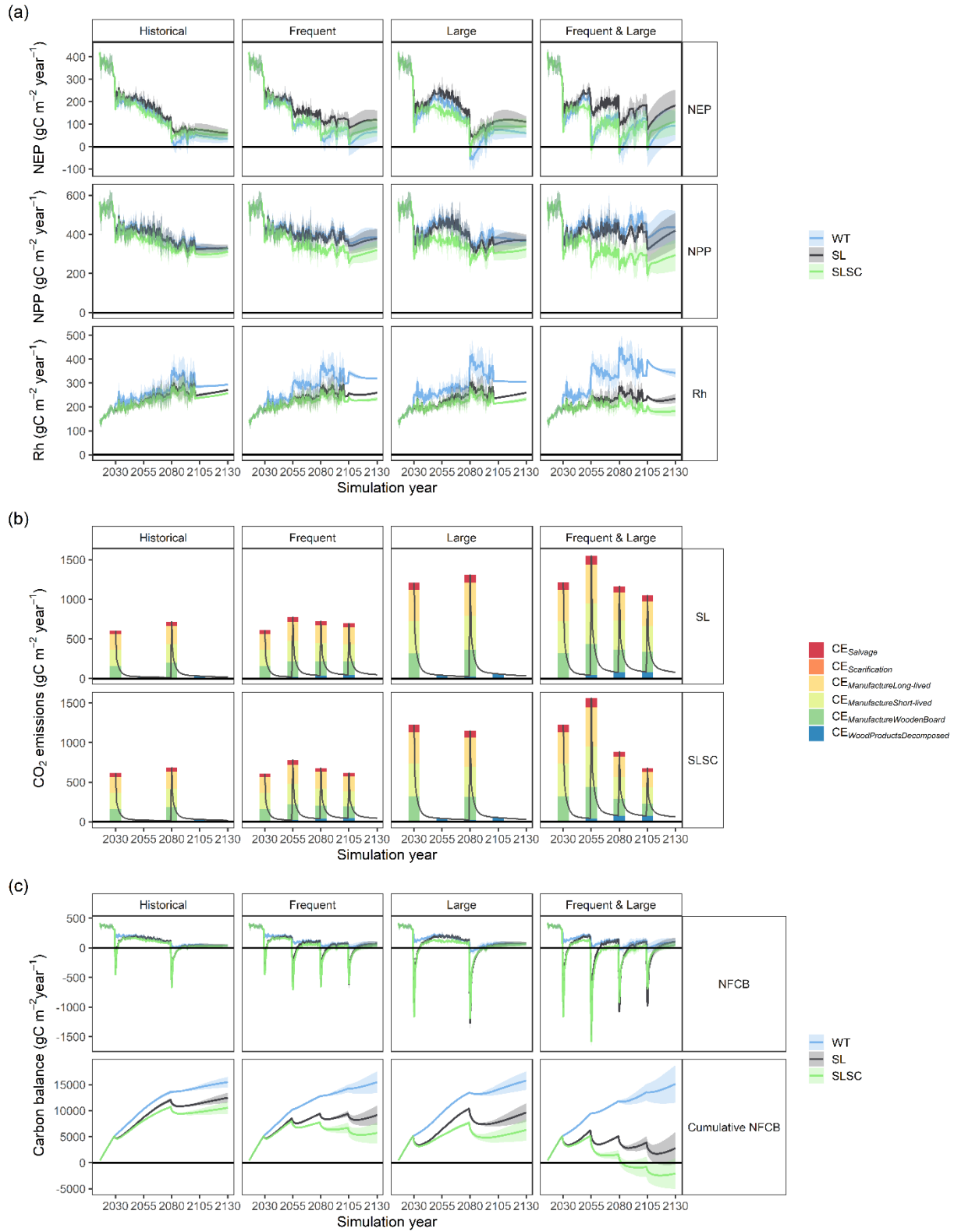
437 **Carbon balance**

438 The NPP in 2130 became larger in WT and SL than in SLSC, regardless of the windthrow regime scenario (Fig. 6a).
439 The NPP in 2130 in the WT and SL increased, but that in the SLSC decreased as the windthrow frequency and size
440 increased (Fig. 6a). The NPP in 2130 in the WT and SL under the Frequent & Large scenario was 87.54 (SL) and
441 107.6 (WT) $\text{gC m}^{-2} \text{ year}^{-1}$ larger than that under the Historical scenario, respectively. That in SLSC under the
442 Frequent & Large scenario was slightly lower than that under the Historical scenario. Rh was the largest in WT
443 followed by SL and SLSC, regardless of the windthrow regime scenario (Fig. 6a). Rh increased in WT and
444 decreased in SL and SLSC as the windthrow frequency and size increased (Fig. 6a). The Rh in 2130 under the
445 Frequent & Large scenario was 48.39 $\text{gC m}^{-2} \text{ year}^{-1}$ larger in WT, 36.03 $\text{gC m}^{-2} \text{ year}^{-1}$ smaller in SL, and 74.81 gC
446 $\text{m}^{-2} \text{ year}^{-1}$ smaller in SLSC than that under the Historical scenario. As a result, the NEP in 2130 became largest in the
447 SL, regardless of the windthrow regime scenario, because of considerable recovery of NPP and slight increase in Rh
448 (Fig. 6a).

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

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

465 ($\omega^2 = 0.104$) were medium, and the effect size of climate \times windthrow regime ($\omega^2 = 0.017$) was small. The effect
466 size of climate \times post-windthrow management ($\omega^2 = 0.001$) was very small (Online Resource 9 Table S9.3). In SL
467 and SLSC, the cumulative NFCB decreased as the windthrow frequency and size increased. The reduction in the
468 cumulative NFCB under the other windthrow regime scenarios compared to the Historical scenario was larger in
469 SLSC than in SL. Particularly under the Frequent & Large scenario, the cumulative NFCB in 2130 was 78% lower
470 in SL and 119% lower in SLSC than those under the Historical scenario and became negative in SLSC under
471 warmer climates. Although the cumulative NFCB in the WT became slightly lower as the windthrow frequency and
472 size increased, the cumulative NFCB in the WT in 2130 among the windthrow regime scenarios had little difference.
473 In addition, the uncertainties in the cumulative NFCB due to climate scenarios were larger as windthrow frequency
474 and size increased, regardless of post-windthrow management.
475



476

477 **Fig. 6**

478 The dynamics of carbon balance during simulations. (a) The chronological changes in net ecosystem production
479 (NEP), net primary production (NPP), and heterotrophic respiration (Rh). (b) CO₂ emissions related to post-
480 windthrow management practices, manufacturing, and the disposal of products. Bar graphs indicate CO₂ emissions
481 related to post-windthrow management in 2030, 2055, 2080, and 2105. Solid lines indicate chronological changes in
482 CO₂ emissions related to post-windthrow management (all emissions in years except for 2030, 2055, 2080, and 2105
483 were $CE_{WoodProductsDecomposed}$). Colors indicate causes of CO₂ emissions. (c) The chronological changes in the net forest
484 sector carbon balance (NFCB) and the cumulative NFCB. Regarding the vertical axis, negative and positive values
485 indicate net CO₂ sources and sinks, respectively. Solid lines and shaded areas in (a) and (c) indicate mean values and
486 standard deviations among climate scenarios, respectively. Columns indicate windthrow regime scenarios. WT:
487 windthrow only; SL: salvage logging; SLSC: salvage logging and scarification. $CE_{Salvage}$: CO₂ emissions related to
488 salvage logging (e.g., use of heavy machinery); $CE_{Scarification}$: CO₂ emissions related to scarification (e.g., use of
489 heavy machinery); $CE_{ManufactureLong-lived}$: CO₂ emissions related to manufacturing of long-lived products (timber
490 products used for several decades such as building materials and furniture); $CE_{ManufactureShort-lived}$: CO₂ emissions
491 related to manufacturing of short-lived products (products to be disposed of in a few years such as wood chips and
492 paper); $CE_{ManufactureWoodenBoard}$: CO₂ emissions related to the manufacturing of wooden boards (such as particle
493 boards); $CE_{WoodProductsDecomposed}$: CO₂ emissions related to the disposal of products that were made from dead wood
494 generated by windthrow. The mean values and standard deviations of NEP, NPP, Rh, NFCB, and cumulative NFCB
495 in 2130 are available in Online Resource 12.
496

497 **Discussion**

498 Leaving downed logs and advanced seedlings was the most suitable post-windthrow management action to conserve
499 boreal conifers and carbon sinks in the forest landscape and maximize net CO₂ absorption under a warmer climate
500 and a more frequent and larger windthrow regime. The aboveground biomass of species that use well-decayed dead
501 wood as regeneration sites decreased due to salvage logging. Moreover, the CO₂ emissions related to salvage
502 logging and the manufacturing and the disposal of products made from dead wood in the salvaged scenario were
503 larger than the CO₂ emissions from the decomposition of dead wood in the unsalvaged scenario when the dead wood
504 generated by windthrow was decomposed in the forest ecosystem. In the case of scarification, the forest landscape
505 became dominated by early successional broad-leaved and herbaceous species due to the destruction of advanced
506 seedlings of trees, and the effect of temperature increase on species composition was more apparent than that in the
507 other cases.

508

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

510 The total aboveground biomass decreased, and the species composition changed into one with temperate broadleaf
511 dominance, which is more suitable for the warmer climate due to the increase in windthrow area under the warmer
512 climate. The total aboveground biomass and species composition changed more significantly due to stand-replacing
513 windthrow than due to natural mortality. The total aboveground biomass and species composition in the study
514 landscape were only slightly different among the climate scenarios under the historical windthrow regime (Fig. 3).
515 However, the species composition of the newly established cohorts changed with a warmer climate regardless of the
516 windthrow regime, which caused net decreases in the total number of newly established cohorts under a warmer
517 climate (Fig. 5). At windthrow sites, canopy trees fell, followed by the growth of advanced seedlings, and consisted
518 of the forest canopy. On the other hand, seedlings established on the forest floor in remnant forests were generally
519 suppressed by canopy trees for several decades and could only grow up when gaps formed due to natural mortalities.
520 Therefore, the effects of temperature increase on the total aboveground biomass and species composition would
521 become more quickly apparent in windthrow sites than in remnant forests. LANDIS-II NECN succession, which
522 was used in this study, does not simulate the effects of climate change on natural mortality but simulates these
523 effects on establishment probabilities and growth rate. Indeed, adult trees have resilience to a wider range of
524 environmental conditions (Svenning and Sandel 2013) and are less likely to be affected by climate, including

525 temperature increases, than are seedlings and saplings (Woodall et al. 2009; Zhu et al. 2012; Fei et al. 2017). A field-
526 based study also suggested that there would be a decrease in the establishment of boreal tree species and an increase
527 in that of temperate tree species due to a temperature increase in the transition zone of temperate and boreal forests
528 (Fisichelli et al. 2014), and these results were also reported in a study that was conducted in the same region as the
529 present study (Hiura et al. 2019). Moreover, the aboveground biomass of *Sasa* and the ratio of *Sasa*-dominated grid
530 cells to the study landscape became larger with the increase in windthrow frequency and size and temperature;
531 therefore, tree aboveground biomass would decrease due to the prevention of the growth of tree seedlings and
532 saplings by *Sasa* for a longer time.

533

534 **Effects of post-windthrow management on the total aboveground biomass and species composition under** 535 **future climate and windthrow regimes**

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

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

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

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

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

580

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

583 The differences in NPP recovery among post-windthrow management scenarios became larger with the increase in
584 windthrow frequency and size (Fig. 6a). Young to mature, fast-recovering stands generally had a larger NPP than old
585 stands (Goulden et al. 2011). Therefore, the NPP in the WT and SL, where the forest recovered well, became larger
586 by rejuvenating the forest landscape due to the increase in windthrow frequency and size. On the other hand, leaving
587 dead wood caused an increase in CO₂ emissions due to decomposition; thus, Rh was the largest in the WT. As a
588 result, the carbon balance within ecosystems (i.e., NEP) was the largest in SL characterized by considerable
589 recovery of NPP and low Rh, regardless of windthrow regime scenarios. In addition, the CO₂ emissions related to
590 post-windthrow management increased due to the increase in the frequency of management practices and the
591 amount of dead wood that was salvaged (Fig. 6b), which increased the difference in the cumulative NFCB among
592 post-windthrow management scenarios under increased windthrow frequency and size. Particularly, in SL, the
593 increase in CO₂ emissions related to salvaging was larger than the increase in NPP (Fig. 6); therefore, the cumulative
594 NFCB decreased with increased windthrow frequency and size. In the SLSC, these effects of increased windthrow
595 frequency and size on the cumulative NFCB were caused by the increase in CO₂ emissions related to post-
596 windthrow management and the decrease in NPP (Fig. 6c). Previously, the short-term ecosystem carbon balance
597 after windthrow and/or post-windthrow management at the stand scale (Lindroth et al. 2009; Lindauer et al. 2014)
598 and the long-term effects on carbon stocks (Suzuki et al. 2019; Dobor et al. 2020a; Hotta et al. 2020) have been
599 reported. However, the carbon balance considering CO₂ emissions related to post-windthrow management and
600 through the production and discard of products made from windthrown wood has never been discussed, although the
601 importance of this has been recognized in the context of salvaging after other disturbances (e.g., Gunn et al. 2020).
602 In this study, we compared the carbon balance between the different post-windthrow management scenarios by
603 incorporating the CO₂ emissions related to post-windthrow management and the utilization of windthrown wood as
604 a product. Although the effects of post-windthrow management on forest carbon stocks were limited in the long term
605 (Hotta et al. 2020), we revealed that salvage logging and scarification strongly reduced the net CO₂ absorption of the
606 forest sector in the long term under climate change according to the evaluation of carbon balance, including LCA.
607 Our approach, which includes LCA when evaluating carbon balance, would also be useful to discuss the effects of
608 the other management practices on carbon balance.

609 Although our results showed that the CO₂ emissions from the salvaging and utilization of windthrown
610 wood outside a forest ecosystem exceeded those from their decomposition in the forest ecosystem, the latter may
611 still be underestimated. The allocation ratios of long-lived products ($AR_{Long-lived}$) and short-lived products (AR_{Short-}
612 *lived*) were set to reflect the case of undamaged timber. However, the quality of dead wood generated by natural
613 disturbances is generally much worse than that of normal timber because trees develop many cracks, breaks, and
614 scratches when they fall, and they are invaded rapidly by wood decaying fungi (Thorn et al. 2018). Hence, much
615 salvaged wood could be used for manufacturing short-lived products rather than long-lived products. Therefore, this
616 study might underestimate the CO₂ emissions related to salvage logging, and the effects of salvage logging on the
617 carbon balance in the forest sector might be larger than the estimation provided in this study.

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

629 We excluded the normal harvest (i.e., timber harvest other than salvage logging) from our simulations to
630 focus on the effects of post-windthrow management. Because our results showed that post-windthrow management
631 changed forest ecosystems, normal harvest strategies should be varied depending on post-windthrow management
632 scenarios. These decision-making processes related to management strategies are highly complicated and beyond the
633 scope of this study; thus, we did not include the normal harvest in our analyses and simply evaluated the effects of
634 post-windthrow management. However, the normal harvest would interact with the spatial patterns of windthrow or
635 landslide risks (Tang et al. 1997). Forest carbon stocks and species compositions are also affected by the normal

636 harvest (Boucher et al. 2009; Scheller et al. 2011). Therefore, future studies should be encouraged to incorporate
637 these factors to support the development of more realistic projections of future forest landscape.

638

639 **Conclusions**

640 Leaving dead wood generated by windthrow was the most suitable post-windthrow management practice for
641 conserving boreal conifers, conserving carbon sinks, and maximizing net CO₂ absorption in the hemiboreal forest
642 landscape under a warmer climate and a more frequent and larger windthrow regime. Therefore, salvage logging and
643 scarification, which remove windthrow legacies, should be avoided as much as possible to conserve biodiversity and
644 carbon balance. To develop more practical management measures that meet the needs of diverse stakeholders, future
645 studies should consider the mixed scenarios of multiple management practices and spatial configurations of areas
646 where management practices are applied (e.g., Dobor et al. 2020b). Additionally, there are other desirable futures of
647 forest landscape (e.g., accelerating the adaptation of species composition to climate change), and these are
648 dependent on local communities, parties, or regions. Future studies also need to incorporate various desirable futures
649 and comprehensively discuss how forest landscapes should be managed for an uncertain future.

650

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655

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661

662 **Competing interests**

663 The authors declare that there are no conflicts of interest.

664

665 **Author contributions**

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

669

670 **Data availability**

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

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