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ORIGINAL PAPER

Diversification of forest management can mitigate wind damage risk and maintain biodiversity

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Abstract

Mitigating future forest risks, safeguarding timber revenues and improving biodiversity are key considerations for current boreal forest management. Alternatives to rotation forestry likely have an important role, but how they will perform under a changing climate remains unclear. We used a boreal forest growth simulator to explore how variations on traditional clear-cutting, in rotation length, thinning intensity, and increasing number of remaining trees after final harvest (green tree retention), and on extent of continuous cover forestry will affect stand-level probability of wind damage, timber production, deadwood volume, and habitats for forest species. We used business-as-usual rotation forestry as a baseline and compared alternative management adaptations under the reference and two climate change scenarios. Climate change increased overall timber production and had lower impacts on biodiversity compared to management adaptations. Shortening the rotation length reduced the probability of wind damage compared to business-as-usual, but also decreased both deadwood volume and suitable habitats for our focal species. Continuous cover forestry, and management with refraining from thinnings, and extension of rotation length represent complementary approaches benefiting biodiversity, with respective effects of improving timber revenues, reducing wind damage risk, and benefiting old-growth forest structures. However, extensive application of rotation length shortening to mitigate wind damage risk may be detrimental for forest biodiversity. To safeguard forest biodiversity over the landscape, shortening of the rotation length could be complemented with widespread application of regimes promoting old-growth forest structures.

Keywords Boreal forests · Continuous cover forestry · Climate change · Forest management planning · Forest modeling · Habitat suitability index · Rotation forestry

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Introduction

Boreal forest management faces uncertainties caused by the complex impacts and interactions of climate change (Daniel et al. 2017), increasing biotic and abiotic disturbances (Seidl et al. 2017; Venäläinen et al. 2020; Knoke et al. 2021) and a continuous decline of forest biodiversity due to intensive forest exploitation over past decades (Kuuluvainen 2002; Felton et al. 2020). Boreal forests are the world's largest forest biome, covering about 29% of global forest area, and producing 33% of global lumber and 25% of global paper (Kayes and Mallik 2020), but are also predicted to experience the highest rate of warming under climate change over the next century (Gauthier et al. 2015; Kellomäki 2017). Adaptation of forest management is thus beneficial to address changing dynamics of boreal forest ecosystems under climate change, including an increase in tree growth rates (Matala et al. 2005; Kellomäki et al. 2008; Kellomäki 2017) and an increase in disturbance risk (Venäläinen et al. 2020). On the other hand, management that increases forest structural diversity and restores deadwood would improve biological diversity of boreal forests. Climate change, however, can complicate these goals and may reinforce the existing conflicts between economic and ecological objectives within commercial forests (Angelstam et al. 2018).

The main objective of boreal forest management over recent decades has been to obtain economic benefits (Kuuluvainen 2002), causing habitat loss and fragmentation that have led to a continuous decline of biodiversity (Kayes and Mallik 2020). Commercial forestry prioritizes rotation forest management, dominated by even-aged and monospecific stands (Huuskonen et al. 2021) of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), limiting the presence of less economically important tree species including many deciduous species. Moreover, faster growing trees under climate change are harvested at a younger age, which further reduces the forest structural diversity and presence of the old-growth forest structures, e.g., deadwood and large and old living trees (Henttonen et al. 2019). Yet these habitats provide critical substrates and resources for several endangered species (Timonen et al. 2010; Stokland et al. 2012; Jacobsen et al. 2020). In Finland, 20–25% of the forest-dwelling species are dependent on deadwood resources, including 60% of red-listed species (Tikkanen et al. 2006). Intensive rotation forestry has reduced the amount and diversity of deadwood in these forests to a small fraction of its levels in natural and unmanaged forests (Siitonen 2001; Kuuluvainen and Gauthier 2018).

To increase the structural variability and the presence of old-growth structures in commercial forests, retention forestry, i.e., retaining living standing trees after the final harvest, has become widely accepted (Ezquerro et al. 2018; Felton et al. 2020; Gustafsson et al. 2020). Yet, this management practice remains insufficient for creating adequate amounts and diversity of deadwood and lacks clear species-specific conservation objectives to safeguard biodiversity (Kuuluvainen et al. 2019). Rotation length, the amount of time between consecutive final fellings, is the defining variable of commercial rotation forestry and depends on species-specific growth potential and local site conditions (e.g., fertility, Seidl and Blennow 2012). Modification of the rotation length provides opportunities to diversify forest structures in commercial forests (Ranius and Roberge 2011; Roberge et al. 2016, 2018). Extending the rotation length (Roberge et al. 2018), combined with retention forestry (Ezquerro et al. 2018) and growing stands unthinned, e.g., promoting stand-capacity to self-thin to build up deadwood (Tikkanen et al. 2012), facilitates the creation of deadwood and forest structure resembling old-growth forest even within commercial forest landscapes.

Boreal forest management, however, requires consideration of the whole forest ecosystem context, focusing not only on economic objectives, but on safeguarding biodiversity while improving the provisioning of non-woody ecosystem services (Angelstam et al. 2018; Felton et al. 2020). Recent studies have shown that improving the multifunctionality of boreal forests would be helped by a change of current forest management approaches (Eyvindson et al. 2021; Blattert et al. 2022). Several adaptations of forest management, such as transitioning from rotation to continuous cover forestry (Pukkala 2016; Peura et al. 2018), seem to be viable tools to simultaneously improve timber- and non-timber-oriented forest ecosystem services. A diversification of forest management regimes (Duflot et al. 2021) based on landscape-level planning can allow for an efficient balance between economic and ecological objectives within the landscape (Pohjanmies et al. 2017b; Triviño et al. 2017; Eyvindson et al. 2021).

Climate change-induced disturbances introduce unexpected challenges and may limit the efficiency of planned management actions for biodiversity conservation and forest multifunctionality (Roberge et al. 2018; Zimová et al. 2020). Thus, these uncertainties warrant consideration while developing new forest management approaches that safeguard biodiversity (Arneth et al. 2020). Climate change is expected to produce major changes in boreal forest ecosystems in the next decades (Gauthier et al. 2015; Kellomäki 2017). The productivity of forests will benefit from increasing levels of carbon dioxide (CO_2) and higher temperatures (Kellomäki et al. 2008). However, more frequent and intense natural disturbances can cancel out this increased forest productivity (Reyer et al. 2017). Rising temperatures, for example, are

expected to shorten the soil frost period, which, along with increasing timber stock, could increase the likelihood and intensity of windthrow damage (Peltola et al. 2010; Seidl et al. 2011). Shortening the rotation length can be used to adapt to future climatic conditions and reduce risks of wind damage in the forests, while simultaneously allowing for the harvest of high-quality timber (Roberge et al. 2016; Kellomäki 2017). A shorter rotation length, however, bears the risk of further threatening the habitats of many species (Ranius and Roberge 2011; Roberge et al. 2018). Thus, novel climate-adaptive forest management strategies would be beneficial to sustain timber provision, halt biodiversity decline, and minimize climate-induced disturbance risks.

To address these challenges, we have performed a simulation study to understand how potential adaptations of forest management would affect timber revenues, probability of wind damage, and forest biodiversity over long-term planning horizon. Specifically, we used SIMO, an open-access, boreal forest growth simulator (Kangas et al. 2008; Rasinmäki et al. 2009) and a wind damage risk model (Suvanto et al. 2019), both developed and parametrized on Finnish forest conditions. We simulated the alternative developments of forest stands over 100 years under a reference and two climate change scenarios using the Representative Concentration Pathways (RCP4.5 and RCP8.5). RCP scenarios represent diverging trajectories of climate change based on level of emissions, concentration and land-use over next century, where RCP8.5 represents a more severe climate change scenario then RCP 4.5 (van Vuuren et al. 2011). For each climate scenario, we compared the effects of management adaptations to the currently applied rotation forestry (business-as-usual, BAU), a dominant management style in Finnish boreal forests (Äijälä et al. 2014). Specifically, we evaluated changes in economic and ecological indicators, such as harvested timber volume, wind damage probability, net present value and two complementary biodiversity indicators: deadwood volume and habitats availability for selected vertebrate species covering a wide range of habitat types. Our management adaptations included variation in rotation length, refraining from thinnings, increasing green tree retention, and adoption of continuous cover forestry. We hypothesized that (1) shortening rotation lengths would reduce wind damage probability, but at the same time would reduce deadwood volumes and the habitats of forest dwelling species. Opposingly, we predicted that (2) the extension of the rotation length, and regimes promoting diverse stand structure (e.g., continuous cover forestry, increased green tree retention), would benefit biodiversity (specifically deadwood diversity, limiting resource for species in Finnish boreal forests Vanha-Majamaa et al. (2007)), while increasing wind damage risk due to tree senescence and increasing height. For climate change, we further expected that (3) higher severity of climate change would reduce the

effectiveness of shorter rotation length on reducing wind damage probability, but that (4) would benefit biodiversity through increased tree growth and tree mortality (Mazziotta et al. 2016).

Methods

Study region

Our study area represents the entire area of Finland (Fig. 1). Finnish boreal forests are dominated by Scots pine (50%, *Pinus sylvestris*), followed by Norway spruce (30%, *Picea abies*), birch (17%, *Betula pendula*, *B. pubescens*), and other broadleaved species (3%, e.g., *Betula* sp., *Populus* sp.). The total annual increment of growing stock is 103 Mm^3, with a mean of 6.9 m^3 ha^{-1} in southern and 2.9 m^3 ha^{-1} in Northern Finland (Niinistö et al. 2021). Two-thirds of the forestry land is on mineral soil, with the remaining part on peatlands. Figure 1 illustrates our study flow.

Input data for forest development simulation

For initial forest conditions in our simulations, we used the open-access Multi-Source National Forest Inventory (MS-NFI) data of 2013 available from the National Resources Institute Finland (Luke) (http://kartta.luke.fi/index-en.html). MS-NFI represents the forest landscape in a raster format (resolution 16 m), containing basic environmental information (e.g., location, soil type) and detailed information about forest structure (e.g., tree species, age, density, height, basal area). MS-NFI combines georeferenced field data of the NFI (National Forest Inventory) with satellite images and digital map data (Makisara et al. 2019). To accurately represent Finnish forest conditions while allowing a reasonable simulation and computation time, we sampled the forest datasets along the systematic sampling grid of the 11th National Forest Inventory (http://www.metla.fi/ohjelma/vmi/vmi11-otanta-en.htm). Here, one sample point represents a forest stand condition as a mean of 3×3 (Southern Finland, average size of 0.2 ha) and 4×4 grid cells (Northern Finland, average size of 0.4 ha), corresponding to a lower density of sample points in the north (where forests are less variable) compared to the south. From the total of 48,015 collected forest stands, we have selected only stands for which initial structural characteristics (e.g., growth increment, basal area, height, age, and dominant tree species) allowed simulation of all forest management across all climate scenarios (e.g., we excluded stands with reduced growths that may not meet the threshold conditions for thinning or harvests, or stands that are currently unproductive but become productive only under more severe climate change). This resulted in a total of 25,394 stands to use for all forest management adaptation
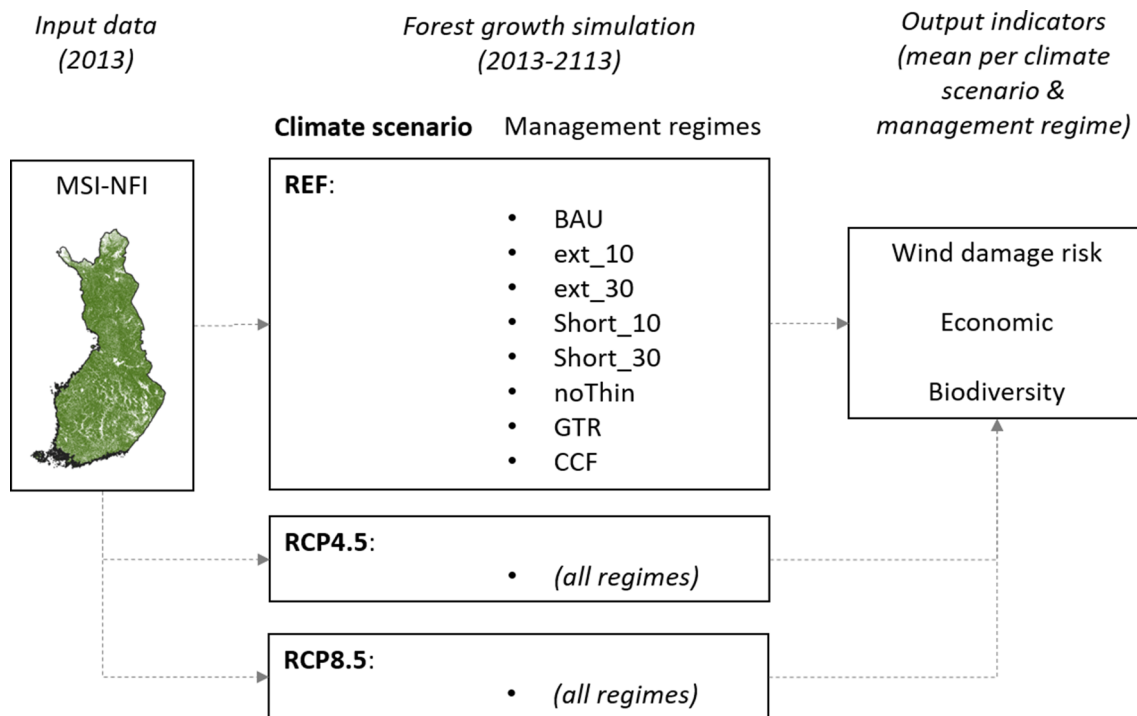
Fig. 1 Study workflow. Input data were acquired from the Multi-Source National Forest Inventory data (MSI-NFI) collected over Finland and were used to initiate forest growth simulations under respective climate scenarios and forest management regimes. Output indicators (representing forest structural characteristics) were used to further calculate wind damage risk and economic and biodiversity indicators per each stand. Climate scenarios represent a reference climate (REF), and two alternative greenhouse forcing scenarios as Representative Concentration Pathways (RCP4.5 and RCP8.5), representing moderate and high levels of warming, respectively. CCF—Continuous Cover Forestry, GTR—Green Tree Retention, ext_30 and ext_10 are extension of rotation length by 30 or 10 years, respectively, noThin—no thinning, short_10 and short_30 are shortening of rotation length by 10 and 30 years, respectively. For full regime descriptions, refer to Table 2

regimes and simulated climate change scenarios. Deadwood volume ranged from 1.6 to 4.4 m³/ha, depending on the dominant tree species. Table 1 provides an overview of the forest stand input characteristics for our first simulation year.

Simulation of forest management regimes

We used SIMO (SIMulation and Optimization for forest management planning, https://www.simo-project.org/), an open-source forest growth simulator (Rasinmäki et al. 2009) to predict the development of the forest stands under various forest management regimes and climate change scenarios. SIMO is an empirical forest growth and yield model, allowing high versatility in developing forest management scenarios and comparing their outcomes using what-if scenarios (Kangas et al. 2008). SIMO is written in Python, C and XML languages. We used SIMO in a deterministic way to simulate tree growth, mortality, and regeneration for even-aged (Hynynen et al. 2002) and uneven-aged boreal forests (Pukkala et al. 2013). The deadwood volume was calculated based on (Mäkinen et al. 2006) models. The input dataset must contain information about the stand location,

Table 1 Initial forest stand characteristics (in 2013) used as an input for forest simulations for 2013–2113. Each stand originates from monospecific rotation forestry and therefore is dominated by a single tree species

Dominant tree species	Counts (%)	Height (m)	Age (years)	Volume (m³/ha)	Deadwood (m³/ha)
Scots pine (*Pinus sylvestris*)	19,001 [74.8]	16.2 ± 3.6	65.1 ± 17.4	135.5 ± 50.1	3.3 ± 2
Norway spruce (*Picea abies*)	2922 [11.5]	13.8 ± 3.6	37 ± 13.7	92.6 ± 40.7	1.6 ± 1.3
Other	3471 [13.7]	18.2 ± 4.5	56.9 ± 21.3	171 ± 74.3	4.4 ± 2.8

Dominant tree species are relevant for the wind damage probability model (Table S1). The values represent stand counts by dominant tree species, their share of total stands (%), and mean values over stands ± standard deviation for a total of 25,394 stands

and information about the tree layers of the specific forest stand. The model makes predictions on the single tree-level that are then summarized for stand-level outputs. The output datasets represent forest stand characteristics resulting from individual forest management actions (e.g., thinning, harvesting, planting) implemented within the respective management regime. Construction of specific management regimes depends on the specific rules placed on harvesting.

From earlier work (Eyvindson et al. 2018) we have selected a set of eight distinct regimes to allow their comparison across multiple climate scenarios (Table 2). The BAU scenario follows the national forest legislation and therefore represents the benchmark to evaluate the impact of alternative forest management regimes. The average current rotation length under BAU is 70–90 years (range of 60–120 years, Roberge et al. (2016, 2018), and varies across Finland, with relatively shorter rotation lengths in southern and longer rotation lengths in Northern Finland. Rotation length also differs with site-specific characteristics such as dominant tree species and soil fertility and type. The alternative management regimes seek to promote biodiversity as well as climate change mitigation, as they could increase the size of the trees or promote a more natural self-thinning mortality of trees, which results in higher accumulation of deadwood and of higher carbon sequestration in trees. For example, the regime excluding thinnings (no Thin) is expected to improve the habitat of

species dependent on deadwood and dense forests (Tikkanen et al. 2012), and increase the number of retained green trees after the final harvest (green tree retention, GTR, e.g., Vanha-Majamaa and Jalonen 2001), and continuous cover forestry (CCF) aims for uneven-aged and more diversely structured forests (Pukkala 2016). We used the percentage increase or decrease in rotation length (by 10% and 30%) to account for the stand-specific benchmark rotation length. The minimal harvest age was not allowed to be shorter than 60 years old (e.g., rotation length). The regeneration of the stands was either by planting (for BAU, the planting density is between 1600 and 2000 stems/ha, with spruce and pine being 2000 stems for fertile site types, lowering to 1600 stems/ha for less fertile sites), or relied on natural regeneration (CCF). The variation of the rotation length within the time period 2013–2113 was possible as the initial stand age varied on average from 37 to 57 years (Table 1) and a modification of the forest management schedule was implemented within this period.

For each stand and for each climate scenario, we simulated in total eight management regimes over 100 years (2013–2113) in twenty 5-years time steps (Table 2). The outputs of simulations for each time step, regime and climate change scenario were translated into estimates of wind damage risk, harvested timber volume, and biodiversity indicators (Table 3). The simulation length of 100 years allows representation of the full rotation length of standard,

Table 2 Management regimes applied during a 100-years simulation period in forest stands distributed across Finland ($n = 25,394$). Effect on biodiversity describes the most likely structural changes that are known to be important to forest biodiversity, compared with the BAU regime

Management regime	Acronym	Description	Effects on forest structure (biodiversity impact)
Business as usual	BAU	Recommended even-aged rotation forestry (Äijälä et al. 2014) management: rotation length 70–90 years; site preparation, planting or seeding trees, 1–3 thinnings, final harvest with green tree retention level 10 trees/ha, replanting after final harvest	Benchmark (0)
Extended rotation	ext_10 ext_30	BAU with final harvesting postponed by 10% and 30% of rotation length	Postponing final harvest increases tree mortality (more deadwood) between the last thinning and final harvest, and allows older trees (+)
Shortened rotation	short_10 short_30	BAU with rotation length shortened by 10% and 30%	Trees are cut at younger age and smaller dimension (−)
No Thinning	noThin	BAU without thinning; therefore, forests grow slower and final harvest is consequently delayed	Denser forest structures and self-thinning with more deadwood (+)
Green tree retention	GTR	BAU with 30 green trees retained/ha at final harvest; planting or seedling trees	Enhanced structural diversity at final harvest; larger trees are present (+)
Continuous cover forestry	CCF	Continuous cover forestry targeting non-even aged structure, following Pukkala et al. (2013). Thinnings from above, e.g., trees with BA range 16–22 depending on soil fertility (more fertile has higher BA). Minimal return time between two thinnings is 15 years. Natural regeneration of stand	Continuous forest cover, enhanced structural diversity (+)

All management regimes except CCF utilize clear-cut harvesting to extract timber resources. Adapted from Mönkkönen et al. (2014). Symbols represent positive (+), negative (−) or neutral (0) hypothesized effect on biodiversity compared to BAU. BA = basal area

Table 3 Indicators used to study the effect of changes in forest management on boreal forest ecosystems. All indicators were calculated as landscape-level averages across the 100-years simulation period, and changes are relative to a 'business as usual' benchmark (Äijälä et al. 2014)

Ecosystem service	Indicator	Unit/Range
Economic	Wind damage probability	%
	Net present value (NPV, sum)	€/ha
	Discounted productive value (PV)	€/ha
	Discounted Income	€/ha
	Harvested log timber (sum)	m^3/ha
	Harvested pulp timber (sum)	m^3/ha
Biodiversity	Deadwood volume	m^3/ha
	Combined Habitat Suitability Index (HSI)	0–1
	HSI Capercaillie (*Tetrao urogallus*)	0–1
	HSI Hazel grouse (*Tetrastes bonasia*)	0–1
	HSI Three-toed woodpecker (*Picoides tridactylus*)	0–1
	HSI Lesser-spotted woodpecker (*Dryobates minor*)	0–1
	HSI Long-tailed tit (*Aegithalos caudatus*)	0–1
	HSI Siberian flying squirrel (*Pteromys volans*)	0–1

BAU scenario, and rotation forestry dominant in Finland (Äijälä et al. 2014).

Climate scenarios

We used climate scenarios to modulate tree development under contrasted climatic conditions. Climatic variables such as temperature, precipitation, and CO_2 concentration drive soil development and subsequent tree growth, which affects the timing of the final harvest based on the target basal area for specific management regimes (Äijälä et al. 2014). The impacts of climate variables on forest growth dynamics were modeled in SIMO using climate-sensitive statistical growth and yield models that were developed by Matala et al. (2005, 2006). We conducted simulations for different forest management approaches under three distinct climate scenarios. The first scenario, referred to as the reference scenario, assumes that the mean climatic conditions for the period 1996–2014 will be held constant over the 100-years simulation period. The other two scenarios are based on alternative greenhouse forcing scenarios, termed Representative Concentration Pathways (RCPs): RCP4.5 and RCP8.5. These represent moderate and high levels of warming, respectively. To incorporate the RCP scenarios into SIMO we used regionally downscaled estimations for temperature, precipitation, and CO_2 concentration.

For the reference scenario, we used 5-years mean values over the time frame 1996–2014 (Lehtonen et al. 2016). For the two future climate change scenarios (RCP4.5 and RCP8.5), we used 5-years mean values obtained from a General Circulation Model, specifically the Canadian Earth system model CanESM (Von Salzen et al. 2013). Further details are in Triviño et al. (2023). As climate affected all regimes, our BAU benchmark was climate-specific for each climate change scenario.

Analyzed indicators

We considered both economic and biodiversity indicators to capture the complex effects of changes in forest management and climate on forest ecosystems (Table 3). Economic indicators included the probability of wind damage, the net present value of the forest and the amount of harvested marketable log and pulp timber. For biodiversity indicators, we considered deadwood volume as a critical resource for red-listed species, as well as separate and combined habitat suitability indices (HSI) of six key vertebrate species in boreal forests (Table 4).

Wind damage probability

We used a statistical wind damage risk model (a binomial generalized linear model with logit-link function) to predict the wind damage probability [0–100%] for each stand and time step (see full list of variables in Supplementary material Table S2, according to Suvanto et al. (2019)). The wind damage probability model was developed using MS-NFI inventory data (Tomppo et al. 2011; Korhonen 2016), covering a broad spectrum of forest stand conditions found throughout Finland. However, the model predominantly reflects stands that are managed under rotation forestry, which is the prevailing forest management approach in Finland. Utilization of the wind damage risk model using SIMO framework was previously tested in Potterf et al. (2022).

We collected respective variables for forest stand (tree species, dominant tree height), forest management (time since thinning) and soil conditions (type, depth and fertility) from SIMO outputs. Wind speed (Venäläinen et al. 2017) and temperature datasets (Aalto et al. 2016) were derived from the open-access geospatial information. We extracted the predicted 10-years return levels of wind speed

Table 4 Species' habitat descriptions used to calculate species-specific habitat suitability indices (HSI) (0 = unsuitable, 1 = most suitable). Boreal forest species were chosen to represent a wide range of habitat types and social and economic values. These indices were merged to form a combined HSI (as defined by Eq. 1) based on individual species' requirements

Species	Predictors	Optimal condition description (equals to 1)
Capercaillie (*Tetrao urogallus*)	Pine, spruce volume, and tree density (stems/ha)	Capercaillie was formerly considered associated with old or mature forests but lately shown to inhabit rather young forests as well (Miettinen et al. 2009). HSI equals 1 when pine volume is high (>80 m^3/ha), spruce volume is at an intermediate level (10–20 m^3/ha), and stem density is intermediate (600–800 stems/ha). Lekking sites are characterized by spruce (*Picea abies*) and understory under pine (*Pinus sylvestris*) canopy
Hazel grouse (*Tetrastes bonasia*)	Forest age, share of deciduous trees and share of spruce (by volume)	Indicator of adequate level of deciduous trees in boreal landscapes. HSI equals 1 if the age of forest is between 20 and 60 years, proportion of deciduous trees of the total tree volume is intermediate (20–40%) and the proportion of spruce is high ($>25\%$)
Three-toed woodpecker (*Picoides tridactylus*)	Total volume of living trees, basal area of fresh deadwood	HSI equals 1 when the total volume of living trees is >200 m^3/ha and basal area (BA; m^2/ha) of fresh deadwood is >2.5 m^2/ha. The latter threshold translates into about 20 m^3/ha of total deadwood in a mature stand ($V_{total} > 200$ m^3/ha)
Lesser-spotted woodpecker (*Dryobates minor*)	Forest age, number of recently dead deciduous trees	HSI equals 1 when basal area (BA; m^2/ha) of fresh deciduous deadwood is >1.5 m^2/ha and stand age is >200 years
Long-tailed tit (*Aegithalos caudatus*)	Forest age, total basal area, and the proportion of deciduous trees (by volume)	Suitable habitat is dominated by middle-aged to old deciduous forest dominated by alder (*Alnus* spp.) and birch (*Betula* spp., Jansson and Angelstam 1999). HSI equals 1 when forest age is >60 years, proportion of deciduous trees (by volume) is $>60\%$, and total basal area is >15 m^2/ha. Basal area of 15 m^2/ha translates into total volume above 100 m^3/ha in forests that are older than 60 years
Siberian flying squirrel (*Pteromys volans*)	Spruce volume, volume of deciduous trees, proportion of spruce	HSI equals 1 when the spruce volume is >175 m^3/ha, the proportion of spruce (by volume) is $>60\%$, and the volume of deciduous trees is >15 m^3/ha

For full details about HSI formulas, refer to Mönkkönen et al. (2014), supplementary material

values [provided at a resolution of 20 m, mean 10.9 m/s, (Venäläinen et al. 2017)], which represents the level of maximum wind speed (m/s) expected to be reached on average once every 10 years (for full details, refer to Venäläinen et al. (2017)). From daily temperature data (at a resolution of 10 km) we calculated a sum of the mean daily temperatures for the first 100 days warmer than 5 °C from 1990 to 2020 (mean 1219.7). The wind speed and temperature datasets are based on spatially explicit observed daily values over past decades. Given the challenges of accurately predicting where and when strong winds will happen in the future, and considering the substantial temperature variations within a year, we chose to maintain these values constant in our wind risk model throughout the 100-year simulation period. The increase in wind damages in the future is linked to the increased timber growth and increasing temperatures, rather than changes in strong winds incidence (Venäläinen et al. 2020). Increased timber growth rates due to increased temperature and precipitation under climate change are implemented in SIMO following formulas of Matala et al. (2005). To streamline our simulation process and address the patchy landscape in Finland, we assumed that all stands had at least one open edge during the entire simulation period, as indicated by earlier research (Potterf et al. 2022). We used model estimates to predict wind damage probability risk for individual forest stands at every time step, management regime and climate scenario.

All calculations were performed using ArcGIS 10.6 (ESRI 2021), R 4.1.1 software (R Development Core Team 2021), and packages *sf* (Pebesma 2018), *raster* (Hijmans 2021), and *rgdal* (Pebesma et al. 2014). *dplyr* (Wickham et al. 2022) and *data.table* (Dowle and Srinivasan 2021).

Net present value

The overall economic value of each forest management alternative was evaluated as the net present value (NPV) of the forest. This indicator aggregates the overall income and costs of forest management actions throughout the planning horizon per each stand, and productive value (PV) of the remaining standing trees at the end of the simulation period, using formulas from Pukkala (2005). PV estimates the maximum yield value of a forest stand, factoring in tree species, dimensions, age, interest rates, timber prices and growth locations (i.e., fertility). The NPV represents the sum of the discounted value of all future incomes, costs, and PV. The discount rate indicated the preference for money. We applied a discount rate of 3%, which is often used in long-term forest planning studies in boreal forestry (Peura et al. 2016; Pohjanmies et al. 2017a; Heinonen et al. 2020).

Harvested timber volume

Harvested timber volume represents the timber harvested at final felling and during the intermediate silvicultural treatments. We recorded two timber qualities. Log timber represents large diameter trees (pine > 15 cm, spruce > 16 cm, birch > 18 cm), used predominantly in the building industry. The pulp timber represents lower diameter timber (> 6 cm for pine, spruce and birch), mainly used in pulp and paper industries or as a source of bioenergy. The overall mean harvested timber volume (m³/ha) represents a mean sum of total harvested timber volume per site over 100 years.

Biodiversity indicators

Combined habitat suitability index (HSI, Triviño et al. (2017) (Eq. 1) represents habitat availability for six key vertebrate species in boreal forests: capercaillie (*Tetrao urogallus)*, Siberian flying squirrel (*Pteromys volans)*, hazel grouse (*Tetrastes bonasia)*, long-tailed tit (*Aegithalos caudatus)*, lesser-spotted woodpecker (*Dryobates minor)* and three-toed woodpecker (*Picoides tridactylus,* 4, (GBIF Secretariat 2022), Table 4). These are considered umbrella species covering a wide range of habitat associations and providing social and recreational value for bird watchers and hunters. Our habitat suitability calculations originate from Mönkkönen et al. (2014) and are based on both literature and expert knowledge. The habitat suitability index (HSI) for a species varies between 0 (unsuitable habitat) and 1 (most suitable habitat) and relates to the probability of the presence of the species in a stand. Our combined HSI (Eq. 1) for six species therefore represents the probability that at least one of the species is present (e.g., 0 is unsuitable habitat for all species, 1 is suitable habitat for at least one of the six indicator species). To calculate the exact extent of the suitable areas for combined HSI and for each species, we considered suitable habitats at two thresholds: HSI > 0.0 and HSI > 0.7 (Duflot et al. 2021). The lower threshold (HSI > 0.0) indicates a wider range of suitable habitats, whereas a stricter threshold (HSI > 0.7) represents only the best quality stands for particular species across regimes adaptations and climate change scenarios. The forest area estimation was derived from the MS-NFI sampling design, accounting for increasing sampling size of MS-NFI grid from South to North (from 3 × 3 to 4 × 4 pixels of 16 m resolution, refer to 3.1 for full details).

Equation 1: A combined habitat suitability index (HSI) based on individual species requirements, where 0 represents unsuitable habitat and 1 represents habitat benefiting at least one of the species.

$$\text{Combined Habitat Suitability Index} = 1 - \prod_{i=1}^{6}(1 - \text{HSI}_i)$$

$$(1)$$

We calculated the deadwood volume and the combined HSI for each forest stand at every time step and for each management regime and climate change scenario and summarized them as mean values across the 100-years period. We used average time scale for transparency and allowing for a holistic study of management and climate impacts on wind damage risk, economy and biodiversity. To determine if our combined HSI values were driven by one or more individual species in a given management and climate scenario, we also investigated the HSI for each species individually.

Results

Economic indicators

Probability of wind damage

Under the BAU regime, the mean probability of wind damage occurring in a stand at least once during the 100-year time window was 2% (sd = 0.2). This risk was considerably affected by altering the forest management regime. On average, CCF produced the largest increase in mean wind damage risk (+ 150%) compared to BAU regime, whereas shortening of rotation length and exclusion of thinning reduced mean wind damage probability by 28% and 17%, respectively (Table S2, Fig. 2). These changes in wind damage risk were present regardless of which climate change scenario was used. Extension of the rotation length by 10 or 30% and GTR had little or no effect on wind damage risk (Fig. 2).

Financial revenues

The average NPV in a stand under BAU is approximately 5200 €/ha (Table S2). The CCF and shortening of rotation length (both alternatives) increased the NPV by 60% and 10%, respectively, while both extensions of rotation length reduced the NPV by 10% and 30% (ext_30 and ext_10, respectively, Fig. 2). NoThin and GTR remain in NPV similar to BAU. Relatively low reduction of the NPV for noThin compared to BAU links to an increased PV of the standing trees at the end of the simulation period for noThin (Figs. 2 and S4, S5). Average discounted income for BAU was 4800 €/ha per stand over 100 years, whereas values were higher for short_30 and CCF, but lowest for ext_30.

Harvested timber volume

The average harvested timber volume under the BAU regime was 394 m^3/ha across a 100-years time window, of which 207 (52%) m^3/ha was log wood and 187 (48%) m^3/ha was pulp wood (Fig. S6). Adaptation of forest management strongly affected the harvested timber volume of both log and pulp wood (Fig. 2, Table S2). Irrespective of the climate change scenario, CCF increased the harvested volume of log timber compared to BAU by more than 50%, while reducing pulp wood production by one third. Pulp wood production increased under both types of shortened rotation length but decreased under CCF, extension of rotation length, and noThin.

Biodiversity

Deadwood volume and the combined habitat suitability index

The BAU scenario resulted in an average deadwood volume of ca 13 m^3/ha across our 100-years study period, with mean deadwood volume increasing considerably through time (Fig. S1). The highest increase in deadwood volume compared to BAU was recorded with the ext_30 regime (Table S2), followed by CCF, GTR, and ext_10 strategies (Table S2, Fig. 3). Both versions of rotation shortening reduced deadwood volume. Refraining from thinning (noThin) had relatively low effects on deadwood volume creation relative to BAU.

Combined HSI for the BAU scenario was 0.3, indicating that only 20% (1 800 ha) of the forest area was suitable for at least one forest species (HSI > 0.7, Fig. S2). CCF, noThin and ext_30 adaptations resulted in the highest increases in the combined HSI and doubled the extent of suitable areas relative to BAU. Shortening the rotation length by 30% reduced combined HSI the most (Figs. 3, S2).

Species-specific habitat suitability indices

Increases in the combined HSI were driven by the most abundant species; not all species contributed equally to the combined HSI across scenarios. Species-specific HSIs differed largely between management adaptations, both in the direction and the magnitude of the responses (Fig. 4) and remained relatively consistent across climate change scenarios (Fig. S7). Therefore, we present here only results under the reference climate change scenario (Fig. 4).

There is no management strategy that would result both in consistently higher habitat suitability for all species and in reduced wind risk damage. Extended rotations (ext_10 and ext_30) had consistently positive effects on species habitat suitability (Figs. 4, S2) but resulted in small increases
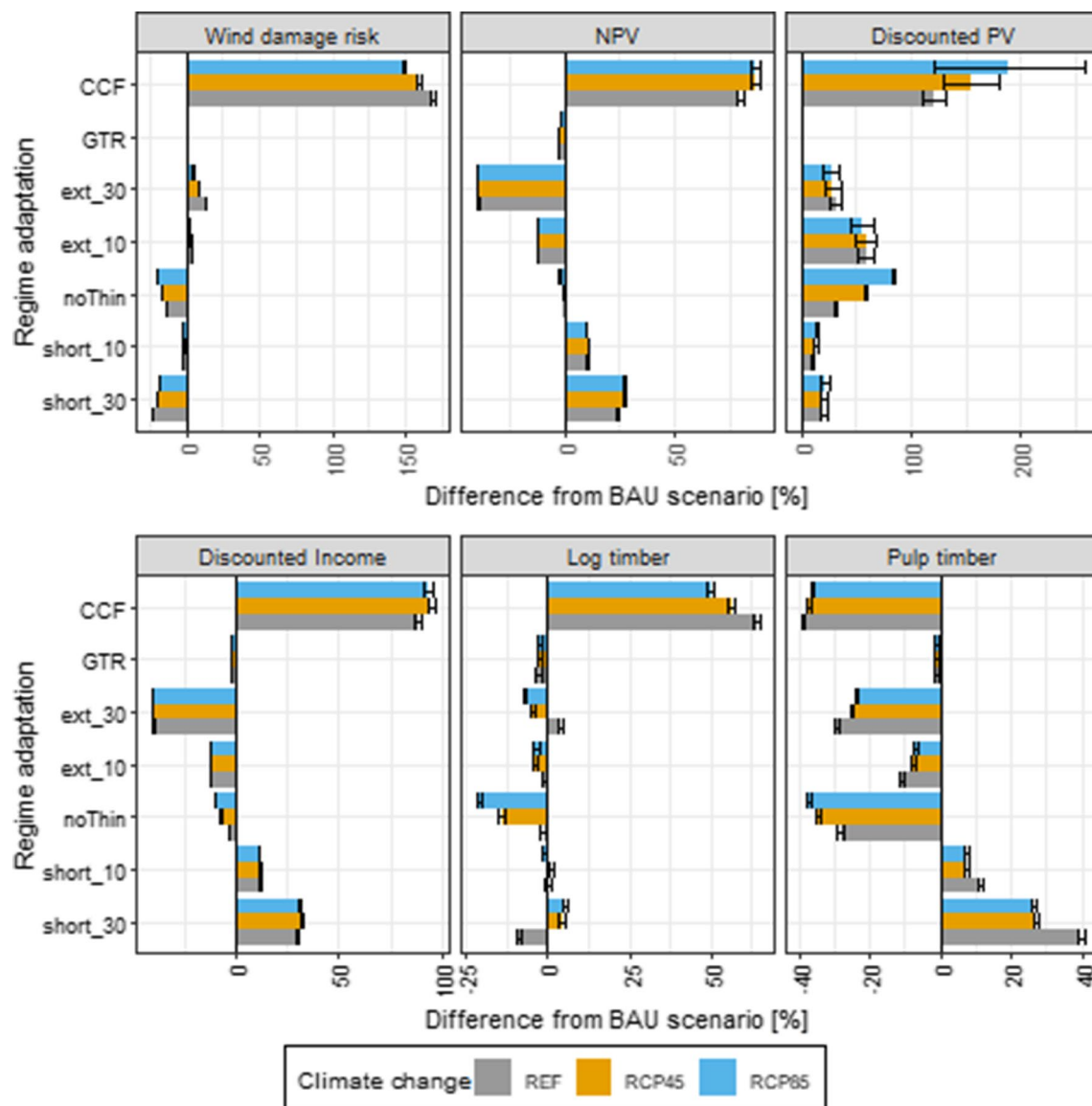
Fig. 2 Effects of forest management adaptation on stand wind damage risk [%], mean net present value (NPV), discounted productive value (PV), discounted income, and the mean volume (m³/ha) of harvested log and pulp timber over a 100-years simulation period and across climate change scenarios. Values are expressed as a percentage difference (x-axis) relative to the baseline rotation forestry (business as usual, BAU) for each climate change scenario (defined by color bars). Individual forest management adaptations are on y-axis. The whiskers represent 95% confidence intervals. GTR did not show differences compared to BAU reference scenario. REF – reference climate, RCP – Representative Concentration Pathway, CCF—Continuous Cover Forestry, GTR—Green Tree Retention, ext_30 and ext_10 extension of rotation length by 30 or 10 years, respectively, noThin—no thinning, short_10 and short_30 shortening of rotation length by 10 and 30 years, respectively. For full regime descriptions, refer to Table 2

in wind risk. The opposite was true of shortened rotation regimes. Refraining from thinning reduced wind damage risk but had inconsistent effects across six focal species. CCF also had inconsistent biodiversity effects among species but large increases in wind damage risk. Finally, green tree retention had negligible impacts on species habitat suitability and on wind risk.

Although the relative increase in species-specific HSIs is large under different management adaptations, the average predicted HSI values remained overall relatively low (maximum of 0.5) for all species under all climate scenarios (Online Table S2). In terms of suitable areas per species, three-toed woodpecker and lesser-spotted woodpecker benefited from CCF and noThin (Fig. S3), with their respective habitats extending up to 30% of all forest stands (HSI > 0.7, Fig. S8). The least prevalent species remained capercaillie and Siberian flying squirrel, both benefiting considerably from ext_30 (Fig. S3) compared
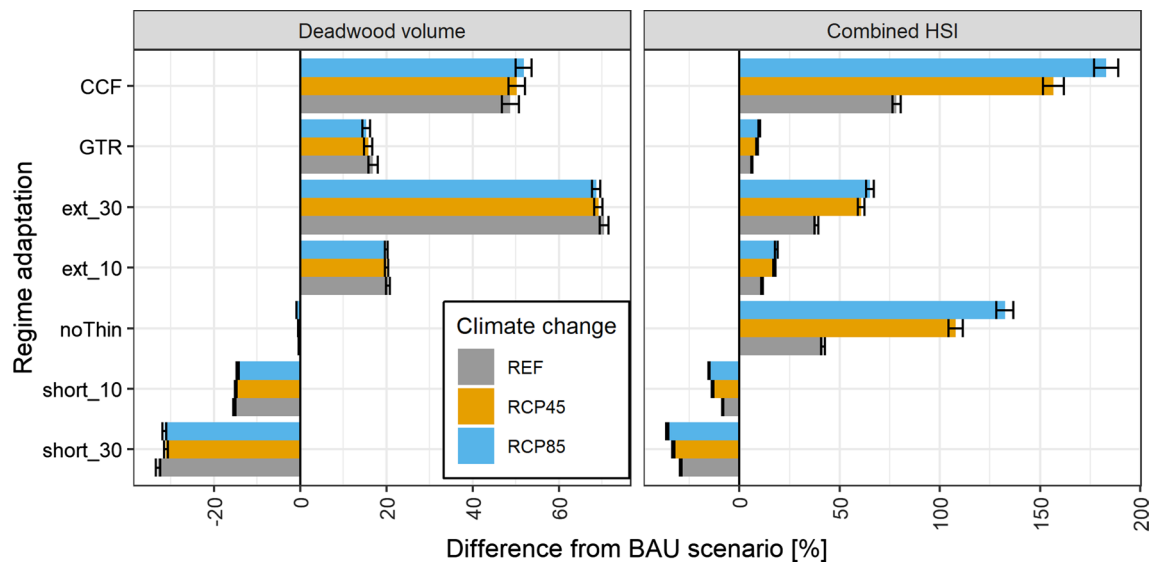
Fig. 3 Effects of alternate forest management adaptations on deadwood volume (m³/ha) and a combined habitat suitability index (HSI) over 100-year simulations, expressed as percentage difference relative to the default rotation forestry (business as usual, BAU) for each climate change scenario. Columns show differences between averaged values under BAU and the alternative regime. The whiskers represent a 95% confidence interval. BAU values are specific to each climate change scenario. REF – reference climate, RCP – Representative Concentration Pathway. CCF—Continuous Cover Forestry, GTR—Green Tree Retention, ext_30 and ext_10 extension of rotation length by 30 or 10 years, respectively, noThin—no thinning, short_10 and short_30 shortening of rotation length by 10 and 30 years, respectively. For full regime descriptions, refer to Table 2

to BAU. Yet, even under these beneficial scenarios suitable habitat for these least common species increased only from 1 to 3% of total forest cover, implying that these species would remain rare (and likely at risk) under any plausible scenario.

Effects of climate change

The effects of climate change were smaller than the effects of forest management on forest economics and biodiversity indicators. In general, climate change amplified both negative (e.g., from shortening rotations) and positive (e.g., from CCF and no-thinning) effects of individual forest management adaptations on economic and biodiversity indicators (Figs. 2 and 3). Climate change also reduced the effectiveness of shortening of rotation length to lower wind damage risk (Fig. 2) and increased overall timber productivity of each stand, specifically increasing NPV and harvested log timber (Table S1).

In terms of biodiversity indicators, climate change severity slightly affected deadwood volume, but had a strong effect on combined HSI (Fig. 3). Severe climate change combined with CCF, noThin and ext_30 benefited species habitat availability the most, while shortening rotation together with severe climate change strongly reduced species habitat availability.

Discussion

Changing climate increases the risk of natural disturbances (Senf et al. 2018; Seidl et al. 2020) and intensifying management in boreal forest threatens habitats loss for endangered species (Siitonen 2001; Roberge et al. 2018; Määttänen et al. 2022). Our findings support the scientific value of adapting forest management actions to improve the balance between ecological and economical objectives in commercial forests. Here, we examined the impacts of several potential adaptations of forest management on the probability of wind damage, timber revenues, and forest biodiversity under different climate scenarios. We quantified the trade-offs between economic and biodiversity objectives. We also identified the adaptation regimes providing opportunities to simultaneously reduce risks of forest damage and maintain high timber revenues while promoting diverse habitats for forest dwelling species. However, we also show how specific forest adaptations under more severe climate change can amplify conflicts between forest economics and biodiversity.

Effects of shortening the rotation length

We found that shortening of rotation length by 30% reduced the probability of future forest disturbance (by
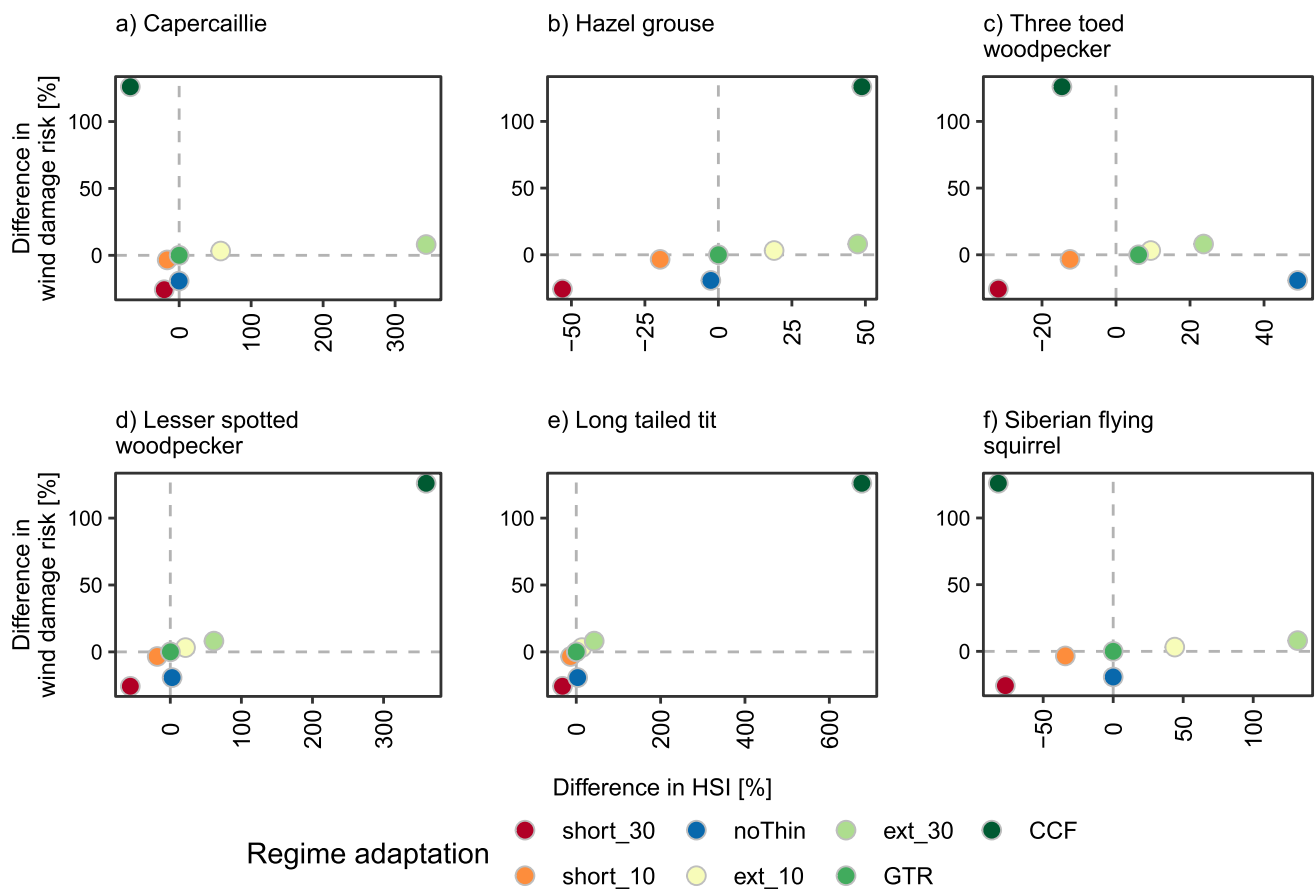
Fig. 4 Effects of forest management adaptations on habitat suitability indices (HSI) for individual vertebrate species under the reference climate change scenario Each dot represents the difference relative to the default business as usual (BAU) management adaptation for wind damage probability and species-specific HSI. Dashed grey lines represent no difference from BAU. Note different ranges of x-axes. REF – reference climate, RCP – Representative Concentration Pathway. CCF—Continuous Cover Forestry, GTR—Green Tree Retention, ext_30 and ext_10 extension of rotation length by 30 or 10 years, respectively, noThin—no thinning, short_10 and short_30 shortening of rotation length by 10 and 30 years, respectively. For full regimes description, refer to Table 2

28%), increased the overall harvested timber volume (by 20%), and the raised mean net present value (by 25%) comparing to BAU (Figs. 2, S4 and S5). Our results correspond to previous findings that shortening of rotation lengths can be one of the main adaptations to rising temperatures and increased tree growth under climate change in boreal forests (Kellomäki et al. 2008; Kellomäki 2017), a strategy that has also been shown to improve carbon sequestration (Liski et al. 2001; Triviño et al. 2015). Therefore, its application can be attractive to forest owners aiming to maximize their timber yields, minimize their losses from wind damage, and mitigate climate change. However, our results showed that the widespread use of shortened rotation length over the landscape reduces habitats of diverse forest dwelling species (Figs. 2 and 3, S2). Shortening the rotation length can also be detrimental for deadwood dependent species (Ranius and Roberge 2011), many of which are red-listed and likely at risk of extinction. It also

alters age structure towards younger trees (Henttonen et al. 2019), and reduces tree height (Henttonen et al. 2020; Potterf et al. 2022). Therefore, shortening the rotation length could be used as a tool to adapt forests to climate change (Kellomäki 2017). However, careful planning of its landscape level application as a complementary management tool would be beneficial along a diverse set of management regimes targeting balance between timber, non-timber forest ecosystem services, and species habitats (Eyvindson et al. 2021; Pohjanmies et al. 2021). This technique of forest management intensification could be compensated for using extensive and protective management approaches to balance its negative effects on biodiversity and old-growth forest structures over the landscape, which might further distribute the risk of the wind damage over the landscape. Specifically, the spatial segregation of these regimes could reduce the risk in areas where forest management is intensified, characterized by shorter rotation lengths and other

practices. Conversely, it may heighten the risk in forests with uneven age structure. This distinction would subsequently influence the approach to mitigating wind damage: prompt removal of affected timber in highly managed areas, while fostering biodiversity-enhancing deadwood in stands that prioritize biodiversity conservation.

Effects of forest management adaptations to promote biodiversity

Continuous cover forestry, green tree retention, extensions of rotation length, and refraining from thinning consistently increased deadwood volume and habitats of forest vertebrate species (Fig. 3). Among these, only continuous cover forestry simultaneously increased the probability of incidence of wind damage (Fig. 2), whereas other biodiversity-promoting adaptations had little effect or even reduced the wind damage probability compared to BAU (e.g., no thinning, Fig. 2). The increasing wind damage probability in continuous cover forestry likely stems from on average higher tree height and higher thinning frequency compared to BAU (Potterf et al. 2022). We emphasize that the wind damage probability represents the likelihood of damage rather than its severity (Suvanto et al. 2019). However, due to uneven and less-dense forest structure of stands under continuous cover forestry compared to BAU, fewer trees are actually exposed to wind damage, lowering the expected volume of damaged timber (Pukkala et al. 2016; Hahn et al. 2021; Potterf et al. 2022). The estimation of the damaged timber volume is highly dependent on the occurrence and spatial pattern of the strong winds in the future, which remain highly uncertain (Nikulin et al. 2011). Therefore, refraining from forest management techniques that increase wind damage risk [e.g., creating forest edges, forest fragmentation Zeng 2006; Zeng et al. 2009)] and promoting uneven-aged forestry to reduce exposed timber volume compared to rotation forestry provide viable ways to reduce overall effects of wind damage (Pukkala et al. 2016). The wind damage risk could be reduced by applying alternative CCF practices, for example by reducing the basal area threshold at which trees are harvested, as this would result in fewer number of large trees.

Our simulations indicated, that adaptations of the forest management regimes targeting biodiversity slightly reduced the harvested log timber volume (0 to -10%, Fig. 2) while substantially reducing harvested pulp timber volume compared to BAU (from −10 to −40%, Fig. 2). These reductions of harvested timber volume partly reduced overall income, compensated by the higher present values of trees remaining on the stand at the end of simulation period (Discounted PV, Fig. 2). We suggest that study period of 100 years, as done here, allowed only single rotation period for extended rotation length, leading to the reduction of the harvested log

timber. (Fig. 2). Comparing to BAU, CCF lower competitions in the less densely populated stands in combination with more frequent thinnings lead to development of the larger trees, and consequently to higher log timber (Fig. 2).

Refraining from thinnings and increasing green tree retention are considered to be cost effective strategies to increase old-growth forest structures and deadwood volume in commercial forests (Mielikäinen and Hynynen 2003; Felton et al. 2020; Gustafsson et al. 2020). Refraining from thinnings promotes 'self-thinning', e.g., mortality among young and densely growing coniferous tree species (Tikkanen et al. 2012) while green tree retention retains mature trees to increase structural diversity of the stands. Both approaches are expected to reduce the NPV by 20% (Tikkanen et al. 2012). Accounting for the value of the standing trees at the end of simulation period (as done here, Discounted PV, Fig. 2) further indicated that the refraining of thinnings is a cost efficient strategy to improve biodiversity (in terms of deadwood) in managed forests (Tikkanen et al. 2012) (Figs. 2, S5).

For green tree retention, our simulation results do not, however, benefit in the same way economic value, overall biodiversity or selected vertebrate species (Figs. 2 and 3). This finding corresponds well with recent critiques of green tree retention, that currently applied retention volumes and diversity of retained trees are often not sufficient to assure suitable habitats for diverse threatened species in Finland (Vanha-Majamaa and Jalonen 2001; Kuuluvainen et al. 2019). Our adaptation of green tree retention doubled the number of retained trees [30 retained trees/ha, Table 2, compared to currently retained 15 trees/ha, Niinistö et al. (2021)], but was still outperformed by CCF and extension of rotation length (by 30%) in terms of deadwood volume and diverse species habitats (Fig. 3). Therefore, to safeguard specific threatened species, retention levels would need to be increased to meet species-specific habitat requirements (Kuuluvainen et al. 2019).

As different adaptations benefited distinct species, and are known to create deadwood of different quality, a diversification of regimes would be beneficial to meet a wide range of habitat requirements in commercial stands. We highlight the potential of continuous cover forestry, refraining from thinnings, and extension of rotation length to benefit several vertebrate species at once (Fig. 4) and at increased forest revenues (Fig. 2) compared to BAU. The relatively low current levels of diverse forest habitats in Finnish boreal forests (Table S2) indicate that relatively small changes in management can largely improve the habitats for particular species. We found that economically low performing regimes such as extended rotation length greatly benefited the threatened species such as capercaillie and Siberian flying squirrel, with suitable habitats currently covering only 1 to 3%, respectively [Fig. S3, Duflot et al. 2021)]. Therefore, extending

the rotation length is particularly important to secure the continuation of endangered species habitats (i.e., Siberian flying squirrel).

Effects of climate change

Agreeing with previous studies, climate change had weaker effects than forest management on timber production and biodiversity (Mazziotta et al. 2015; Morán-Ordóñez et al. 2020). On the other hand, adaptation methods aiming to cope with increasing timber growth by shortening of rotation length showed severe trade-offs with biodiversity (Ranius and Roberge 2011; Roberge et al. 2016), and had a limited effect on reducing wind damage probability under more severe changing climate (e.g., in central Europe, Zimová et al. 2020; Dobor et al. 2020a). Therefore, while considering the wide-scale application of the shortening of the rotation length to reduce future risks, one could account for its uncertain effectiveness under changing climate. Our simulation results indicate that more severe climate change reduced expected log (e.g., for CCF, Fig. 2) or pulp timber volume (e.g., short_30, Fig. 2) relative to the rotation forestry (Table S2, Fig. 2). Yet, climate change is expected to increase the absolute net present value and the total volume of harvested timber (Table S2, Fig. 2), while allowing currently unproductive forests in the north to become more productive. Because climate change is expected to increase the potential to harvest timber in boreal forests (Kellomäki 2017; Brecka et al. 2018), forest management could rather focus on improving biodiversity (Mazziotta et al. 2015) and securing ecosystem functioning.

Study limitations and future perspectives

Our results are derived from simulation studies, offering a comprehensive examination of how different management strategies and changing climates might affect wind damage risk, economic factors, and biodiversity indicators. We focus on the likelihood of wind damage occurrence rather than its extent. Thus, we did not dynamically simulated wind disturbances and excluded wind-damaged trees, which would affect future timber availability and related ecological benefits. To quantify wind damage, one could use existing process-based models like iLand (Seidl et al. 2014) or mechanistic models like HWIND (Peltola et al. 1999) under varying wind patterns and extreme events. However, this would require consideration of several changing processes that are interlinked, such as increasing timber growth, especially in Northern Finland and shortening of the frozen soil periods in Southern Finland, which both lead to increased wind disturbance. Additionally, the higher likelihood of the cascading disturbances warrant consideration, such as

bark beetle outbreak triggered by windthrow or drought (Venäläinen et al. 2020).

Another limitation is our reliance on predictive models based on dominant rotation forestry in Finland. However, models for uneven-age continuous cover forestry are continuously improving, reflecting a growing focus on this management approach due to its ecosystem benefits (Pukkala 2016) and landscape multifunctionality (Peura et al. 2018; Eyvindson et al. 2021).

Additionally, our economic evaluation of timber values is sensitive to market fluctuations. We utilize average timber prices based on volume and tree attributes while overlooking specific characteristics like branching and nodes, which affect timber qualities and as such the final timber prices. Finally, individual owner preferences, such as the choice to harvest earlier or later than the optimal age, can substantially affect estimated economic and ecological benefits.

Implications for forest practice

Forest management offers many opportunities to foster forest diversity while providing reliable timber revenues under changing climate. We found that refraining from thinning provides a beneficial solution lowering wind damage probability, maintaining high harvest yields and net present value, and improving individual species habitats compared to currently applied rotation forestry [Figs. 2, 4, (Tikkanen et al. 2012)]. Yet, our results highlight the conflicting outcomes between forest economic and forest diversity within individual adaptations, amplified by more severe climate change.

We found that different management adaptations benefited different species (Fig. 4). Therefore, the diversification of the management regimes across the landscape is key in promoting landscape multifunctionality (Eyvindson et al. 2021), diversity of species habitats (Duflot et al. 2021), and restoration of natural forest structures in commercial forests (Savilaakso et al. 2021). Recent evidence from Finland indicated that fulfilling societal demands for multiple conflicting objectives—economic benefits, non-economic forest goods, and safeguarding biodiversity– would benefit from a shift from currently dominating rotation forestry to a higher prevalence of continuous cover forestry, complemented with set asides as well as areas for more intensive forest management (Eyvindson et al. 2021; Blattert et al. 2022). However, to improve climate resilience of forests, additional adaptations measures would be needed, including promoting mixed and more diverse stands (Dobor et al. 2020b), reducing the dominance of Norway spruce, the most vulnerable species to wind storms and bark beetles (Venäläinen et al. 2020), using artificial regeneration (Ikonen et al. 2020), and using climate change adapted tree species in stand regeneration (Torssonen et al. 2015). To promote a diversity of habitats, it may also be beneficial to increase the share of adaptations

like extension of rotations length, which although economically costly was the most effective at promoting habitat for endangered species dependent on mature forest structures such as capercaillie and Siberian flying squirrel.

Conclusions

Adaptations of forest management strategies affect timber revenues, risk of wind disturbance, and biodiversity under various future climate scenarios. Overall, climate change increased timber revenues but had relatively less impact on selected forest and biodiversity indicators than did management adaptations. Shortening of the rotation lengths provides high economic revenues and reduces wind damage probability, but also reduces deadwood volume and the habitats of a diverse group of forest vertebrate species in commercial boreal forests. Therefore, the execution of shorter rotation periods within the landscape could be carefully planned, compensating for potential negative effects on biodiversity by diversification of forest management benefiting heterogeneous and old-growth forest structures, such as refraining from thinnings, extension of rotation length, and implementing continuous cover forestry. Refraining from thinning represents a solution that could simultaneously reduce wind damage risk, keep high timber revenues and improve biodiversity under a changing climate.

Data availability Study is based on open-access datasets, stated in the Methodology section.

Code availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors have no conflict of interest to declare that are relevant to the content of this article. The authors have no relevant financial or non-financial interests to disclose.

Ethics approval Not applicable—no living material included.

Consent to participate Not applicable—no living material included.

Consent for publication Not applicable—no living material included.

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