



Research article

Contrasting forest management strategies: Impacts on biodiversity and ecosystem services under changing climate and disturbance regimes

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ABSTRACT

Natural disturbances may compromise the past and ongoing efforts to increase carbon sequestration and halt biodiversity loss in boreal forests. Measures to minimize the effects of forest disturbances i.e., adaptive management, offer solutions to secure future timber yields. However, the consequences of adaptive management on biodiversity, the climate change mitigation potential of forests, and other ecosystem services are not well understood. In addition, the impact of climate change and disturbances on future forest-based mitigation potential is not well known. We compared the effects of forest management options emphasizing climate change mitigation or adaptation on boreal forests in changing climate and disturbance regimes in southern Finland. We used the process-based forest landscape and disturbance model iLand to dynamically model interactions between climate change and disturbances together with forest management and protection options, and examined the consequent effects on forest carbon storage, berry yields, recreation, and structural attributes important for biodiversity. Mitigation managements resulted in up to one-fifth higher carbon stocks, even after accounting for disturbances by wind and bark beetles, but halved annual harvests over the 80-year simulation period. Adaptive managements reduced bark beetle disturbances, but in some cases the disturbed volumes were even higher than under business-as-usual management due to increased wind damage. The effects of proactive risk management depended on the time horizon considered, the adaptive management option chosen and the climate change scenario. In general, the mitigation managements had positive effects on the biodiversity indicators studied, while the effects of adaptive management were mixed. Our results highlight the complex interactions between disturbance risk prevention, biodiversity, carbon sequestration and storage, and other ecosystem services. The results guide forest managers and policymakers to plan mitigation and adaptation strategies optimizing multiple benefits, and strengthening forest resilience in a changing climate.

1. Introduction

Natural disturbances may compromise the past and ongoing efforts to promote forest-based climate change mitigation and halt biodiversity loss. Forest disturbances have increased in Europe in the recent decades due to changing forest demographics and climate change (Patacca et al., 2023; Seidl et al., 2011). Climate change is likely to increase the frequency and severity of forest disturbances (Seidl et al., 2017; Venäläinen et al., 2020). The boreal region is warming faster than any other forested region in the world (Gauthier et al., 2015), and here forest disturbances

have been found to be particularly sensitive to climate (Seidl et al., 2020). Hence, understanding the dynamics of boreal forest ecosystems, and predicting their responses to management, changing climate and disturbance regimes is essential to foster resilience of these forests.

Boreal forests, with their ability to sequester and store carbon, are critical to achieving ambitious climate goals. The boreal biome covers approximately one third of the remaining global forest area and stores one third of the terrestrial carbon stock (Bradshaw and Warkentin, 2015). Together with temperate forests, boreal forests are currently the main contributors to the global carbon sink (Yang et al., 2023). The

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stewardship of boreal forests has a large potential for climate change mitigation, but the potential is associated with high uncertainty (Griscom et al., 2017). To harness this potential, changes in forest management practices and setting aside forest land for conservation are means to enhance carbon sequestration and preserve C stocks (Griscom et al., 2017; Verkerk et al., 2022). Increasing rotation lengths and varying the timing and the intensity of thinnings offer effective measures to manage forest carbon budgets (Cooper, 1983; Kaipainen et al., 2004; Pukkala et al., 2011; Repo et al., 2015). Together with forest protection these measures have been identified as the ones having the largest net total carbon effects when comparing the potential of forestry measures to increase the sink capacity of European forest ecosystems (Schelhaas et al., 2007). Well-designed management changes can also help to halt biodiversity loss (Eyvindson et al., 2018; Felton et al., 2024; Koivula and Vanha-Majamaa, 2020; Kuuluvainen et al., 2012; Nunez et al., 2020; Roberge et al., 2018), and the targeted protection of old, carbon-rich stands may be beneficial both to carbon storage and forest biodiversity (DellaSala et al., 2022; Mikoláš et al., 2021). The importance of forest-based mitigation, and the means to enhance carbon sequestration in forests have been widely recognized (Nabuurs et al., 2018; Roe et al., 2021). Nevertheless, many previous estimates of forest-based mitigation potential have not considered the effects of natural disturbances in the assessments nor the permanence of forest-based solutions (Frank et al., 2021; Griscom et al., 2017; Roe et al., 2021). Roebroek et al. (2023) show that accounting for prevailing environmental conditions and natural disturbance regimes reduces the additional carbon storage potential of forests significantly. In addition, Lecina-Diaz et al. (2024) find that more than one tenth of ecosystem service supply is at risk from current disturbances in Europe. Nevertheless, the impact of climate change on future disturbance regimes in the boreal region remains insufficiently understood as well as the consequent effects on biodiversity and the provision of forest ecosystem services (Felton et al., 2024).

Adaptive forest management offers solutions to adapt to a changing climate and to secure timber yields and carbon sequestration potential in forests. Adaptive management is proactive management to minimize the effects of disturbances by e.g. increasing the proportion of mixed-species forests, shortening rotation periods, and planning land-use allocation (e.g. Honkaniemi et al., 2020; Huuskonen et al., 2021; Zimová et al., 2020). Different adaptive measures target different disturbance agents. While admixing broadleaves to conifer-dominated forests primarily aims to reduce the risks of European spruce bark beetle (*Ips typographus* L.) attacks (Faccoli and Bernardinelli, 2014; Griess et al., 2012), reducing rotation lengths mainly addresses the risk of windthrows by reducing the average tree height. Shorter rotations also reduce the time exposed to wind risk, lowering the likelihood for a catastrophic wind event to occur during a rotation period. Different disturbance agents also have either direct or indirect interactions with each other (Buma, 2015; Burton et al., 2020). As wind disturbances are an important trigger to bark beetle outbreaks, shorter rotation periods also indirectly reduce bark beetle damages (Jactel et al., 2009; Zimová et al., 2020). However, while strong shifts in tree species composition may reduce the losses from current disturbance agents, they may also catalyze a change in the disturbance regime (Seidl and Turner, 2022).

While adaptive management can reduce the effects of natural disturbances, it may have trade-offs with biodiversity conservation and the provisioning of ecosystem services (Albrich et al., 2018; Felton et al., 2024). Introduction of trees for adaptation purposes that become invasive, single species plantations, or forest management that affects habitat features and key ecosystems processes, such as deadwood formation, may counteract the past and ongoing biodiversity conservation efforts (Felton et al., 2016, 2017b; Roberge et al., 2018). For example, shorter rotations can lead to a reduction in deadwood, broadleaved trees and large diameter trees (Felton et al., 2017b; Zimová et al., 2020), which may be detrimental for species depending on these forest structures. Adaptive management may also alter forest structures in a way that affects aesthetic and recreational values (Gundersen and Frivold,

2008; Peura et al., 2016), microclimates (De Frenne et al., 2021), and lead to a lower carbon storage in forests, and hence work against the efforts to mitigate climate change (e.g. Stenzel et al., 2023, Walsh and Hudiburg 2021). While the connections between carbon storage and biodiversity and ecosystem services have been studied (Eyvindson et al., 2018; Mäkelä et al., 2023; Triviño et al., 2023) the effects of adaptive forest management on biodiversity, carbon sequestration and other ecosystem services in boreal forests have received less attention.

In this study, we compare the effects forest management options that emphasize climate change adaptation or mitigation on forest carbon stocks, berry yields, recreation and forest structural attributes important for biodiversity under changing climate and disturbance regimes. Using a boreal forest landscape in southern Finland as a case study, we address the following questions: 1) How will timber harvests, forest carbon stocks, and disturbed volumes evolve under different forest management and land use options that emphasize either climate change adaptation or mitigation under different climate scenarios? 2) What are the synergies and trade-offs between ecosystem services and biodiversity in adaptation and mitigation options under changing climate?

2. Materials and methods

2.1. Modelling the effects of forest management and disturbances under climate change

To investigate the effects of climate change, natural disturbances, and forest management, we used the individual-based forest landscape and disturbance model iLand (Seidl et al., 2012a; Rammer et al., 2024). iLand was chosen for its ability to i) directly integrate climate change impacts on forest dynamics, ii) model dynamic and spatially explicit disturbance risks, and iii) simulate detailed forest management. In iLand, primary production is modelled following a resource use efficiency approach (Landsberg and Waring, 1997), and is directly influenced by environmental drivers, particularly climate (temperature, precipitation, radiation, and vapor pressure deficit, on a daily resolution), annual atmospheric CO₂ concentration, and soil variables which are constant over time (sand, silt and clay fractions, effective soil depth and plant-available nitrogen). The carbon allocation and subsequent growth of each tree is then determined by its competitive status according to available light. The regeneration of trees is simulated spatially explicitly as tree species cohorts, which transition into individual trees once they have reached a height of 4 m. Regeneration processes include seed availability and dispersal, seedling establishment, survival, and growth of saplings, moderated by environmental conditions (Seidl et al., 2012). Mortality can occur through intrinsic (related to maximum age and size) and stress-related (based on the carbon balance of a tree) mortality as well as through disturbances. iLand includes a dynamic carbon cycle (Seidl et al., 2012b) tracking the main above- and belowground carbon pools (stem, branches, foliage, snags, coarse woody debris, coarse roots, fine roots, and soil carbon). The model has been tested and used for multiple landscapes in Europe, North America, and Asia (Kobayashi et al., 2023; Seidl et al., 2012; Thom et al., 2017).

We tested the general applicability of the model under boreal conditions against independent empirical data as this was the first application of the model in Finland (Supplementary material, Section 1.3). We used long-term experimental datasets from forest growth experiments in even- and uneven-aged forests from multiple sites in southern and central Finland (Mäkinen and Isomäki, 2004a, 2004b) to test forest growth and regeneration (Supplementary material, Fig. S7) focusing on the main tree species Norway spruce, (*Picea abies* L. Karst), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth). Only minor parameter changes were needed for these species relative to the original (Central European) parameter set (Thom et al., 2024), letting us assume that the original parameterization for rarer tree species is also reasonably applicable in Finland.

We focused on the effects of two disturbance agents: wind and European spruce bark beetle. Wind is represented in the model as the fastest wind event of the year (wind speed, wind direction and the day of the year to account for soil freezing and leaf status of deciduous trees). The impact of wind events is modified by forest structure (stand height, gaps and edges, sheltering effects) and composition (species-specific resistances to uprooting and breakage). The newly created edges are more vulnerable to wind. The age of the edges is also updated throughout the duration of each storm allowing for edge propagation during the event (Seidl et al., 2014). The bark beetle module represents the phenology of European spruce bark beetle and its dynamics with the host tree species Norway spruce (*Picea abies* L. Karst) (Seidl and Rammer, 2017). The bark beetle lifecycle (overwintering, dispersal, colonization, number of filial generations, mortality) is simulated accounting for host tree availability and climate effects on both beetle phenology and host tree defense. Bark beetles also respond to increased availability of breeding material from dead trees after windstorms, therefore directly modelling interactions between these two disturbance agents. We tested the simulated disturbances against observed data, namely the cutting notices submitted by forest managers planning salvage harvests. While there are uncertainties regarding the comparability as managers may list larger areas for harvest than just the exact disturbed area, and there is no information on disturbance severity, the simulated disturbance area was found to be in the general range of observed values (Supplementary material, Fig. S9).

Forest management was simulated through the Agent Based management engine ABE (Rammer and Seidl, 2015), which allows for detailed and spatially explicit forest management. For each stand a set of activities detailing the processes of regenerating, tending, thinning, and harvesting is prescribed along with target rotation lengths and species composition. Each activity is executed within a certain age range for the stand with the ABE scheduler balancing activities such that harvest volumes are relatively stable each year. ABE also includes salvage harvesting after disturbance, which allows for removing killed trees, resetting the stand rotation, and changing stand borders in case of partial destruction of a stand. This enables an appropriate management response for example after storms, when managers are obligated to remove dead trees, which may serve as breeding material for bark beetles.

2.2. Forest management and land-use options, climate scenarios and studied landscape

We simulated in total nine different forest management and land-use options, which were grouped under three overarching themes: business-as-usual (BAU), climate change mitigation (MIT) and climate change adaptation (ADA). The business-as-usual scenario followed the best practice forest management recommendations in Finland (Äijälä et al., 2019). The MIT and ADA scenarios were modified from that by adjusting rotation lengths, planted tree species selections, the allocation of set-aside areas, and the share of continuous cover forestry (CCF) (Table 1). In mitigation options rotation periods were prolonged to allow trees to grow larger and also produce more litter input to soil (Liski et al., 2001; Repo et al., 2015). In addition, in the MIT set-aside areas were chosen focusing on old and high-volume stands to increase carbon storage in the landscape (Pregitzer and Euskirchen, 2004; Repo et al., 2021). In ADA scenarios the rotation lengths were shortened to reduce the risk of loss of timber due to disturbances (Zimová et al., 2020), the set-aside areas were chosen as connected areas with a random starting point to minimize edge effects, and spruce was substituted with birch after clear-cuts to reduce the risk from bark beetle outbreaks by reducing the share of the primary host species (Honkaniemi et al., 2020).

All forest management options were simulated in three different climate scenarios: historical reference climate (randomly sampled with replacement from 1991 to 2020) and two future climate scenarios until 2100. The selected future climate scenarios were based on the EURO-

Table 1

Descriptions of forest management and land-use options. CCF refers to continuous cover forestry.

Regime	Rotation length	Set Aside	Broadleaf Share	CCF
BAU	min. 60–90 years	none	Not actively added	none
MIT1	+10%	15 % of area (old/high volume stands)	Not actively added	5 % of OMT sites
MIT2	+10%	30 % of area (old/high volume stands)	Not actively added	5 % of OMT sites
MIT3	+30%	15 % of area (old/high volume stands)	Not actively added	5 % of OMT sites
MIT4	+30%	30 % of area (old/high volume stands)	Not actively added	5 % of OMT sites
ADA1	−10%	15 % of area, connected area, randomly placed	50 % of spruce substituted	none
ADA2	−10%	15 % of area, connected area, randomly placed	100 % of spruce substituted	none
ADA3	−30%	15 % of area, connected area, randomly placed	50 % of spruce substituted	none
ADA4	−30%	15 % of area, connected area, randomly placed	100 % of spruce substituted	none

CORDEX model simulations (Jacob et al., 2020; Kotlarski et al., 2014). One simulation was selected to represent a high-end climate change scenario with substantial projected increases both in annual mean temperature and precipitation level, while another simulation was selected to represent a low-end climate change scenario with much more modest projected changes (see details in the Supplementary material). In the high-end scenario the annual mean temperature in Finland was projected to increase 5.9 °C from 1981 to 2010 to 2070–2099, on average, and in the low-end scenario 2.3 °C (Supplementary material, Fig. S1). The annual precipitation levels in the two scenarios were projected to increase at the same time by 40% and 9%, respectively. Thus, the temperature increase in the high-end scenario was very close to the multi-model mean in a large GCM ensemble both under the RCP8.5 and the more recent homologous Shared Socioeconomic Pathway (SSP) 5–8.5 (Ruosteenoja et al., 2016; Ruosteenoja and Jylhä, 2021). In the low-end scenario, the temperature increase was close to the projected multi-model change under the low-emission SSP1-2.6 pathway, remaining clearly smaller than projected by the large multi-model ensembles under the RCP4.5 and SSP2-4.5 pathways. The projected increase in the precipitation level, on the other hand, was in the high-end scenario clearly above the 95th percentile from the multi-model ensembles under the RCP8.5 and SSP5-8.5, and in the low-end scenario somewhat below the median estimates under the RCP4.5 and SSP2-4.5.

The climate variables needed for iLand are daily minimum and maximum temperature, precipitation, global radiation, wind speed, and vapor pressure deficit. The baseline climate was based on interpolated observational weather data from the Finnish Meteorological institute (Aalto et al., 2016), whereas the future climate scenarios were based on the bias-corrected EURO-CORDEX simulations. The bias correction of the model data was performed by applying a distributional-based quantile mapping technique, which is a routinely applied method in atmospheric sciences to correct model biases compared to observations (Maraun, 2013). As our observational data for bias correction, we used the gridded daily climatology over Finland at 10 km × 10 km resolution from the years 1971–2005 (Aalto et al., 2016), except for wind speed the observational data were derived from the ERA5 reanalysis (Hersbach

et al., 2020). For the iLand model simulations, the bias-corrected climate data was finally bilinearly interpolated onto a 1 km × 1 km grid. Due to the low topographical complexity in the case study area compared to previous iLand applications (Albrich et al., 2020; Thom et al., 2022), we used the directly available 1 km² resolution of the climate data. For wind data, we derived the strongest wind event (based on wind speed) for each year from the ERA5 reanalysis database (Hersbach et al., 2020, 2023). The development of wind under climate change is highly uncertain (Carvalho et al., 2017; Feser et al., 2015). When comparing the wind speeds from our climate model runs under historic and future climate, we did not find a clear signal on how the future wind would change. This is consistent with larger multi-model ensembles indicating little changes in projected mean and extreme wind speeds in Finland (Ruosteenoja et al., 2019; Ruosteenoja and Jylhä, 2021). Therefore, we reused the same wind events as in the historical scenario but randomly sampled them to different years for each replicate. However, wind disturbance is indirectly affected by climate change in iLand as higher winter temperatures reduce soil freezing and therefore root anchorage (Seidl et al., 2014).

To explore the relationship between forest management and protection options on biodiversity and ecosystem services we included a set of indicators in our study (Table 2). As structural indicators of biodiversity we used the number of large trees, the share of broadleaved trees and deadwood, because the link between these key forest structures and biodiversity is well established (Felton et al., 2017a; Gao et al., 2015; Hyvärinen et al., 2019; Johansson et al., 2013; Siitonen, 2001). As indicators for ecosystem services, we used total carbon storage (biomass and soil) harvested timber, bilberry yield (Miina et al., 2016), and the scenic beauty of forest (Pukkala et al., 1988). The scenic beauty index increases with the age and size of trees, with share of pines and deciduous trees, and with the openness of the stand. The coverage of bilberry increases with stand age and basal area until a certain limit. Clearcuts and soil preparation have a negative effect on cover, consequently bilberry yields are generally lower in young and dense stands (Miina et al., 2009). Since there are no bilberry models for broadleaf-dominated stands, models for pine stands were applied for birch-dominated stands (pers. communication J.Miina). To report the results, we calculated values for averages across the landscape in the short term (average over the first 30 years of the simulation period) and the long term (average over the last 30 years) and over full simulation period and compared the results under different climate scenarios.

We simulated the development of forests under various management options and climate change scenarios on a typical Norway spruce (*Picea abies* L. (Karst)) dominated landscape (Fig. 1, Table 3, Fig. S3). The studied landscape is in southwestern Finland (61.06, 23.44) and lies in

Table 2
Descriptions of indicators for ecosystem services and biodiversity in the study.

Indicator	Unit	Description
Total carbon	tC ha ⁻¹	Includes stems, branches, foliage, coarse roots, fine roots, regeneration, snags, downed wood, litter and soil
Harvested timber volume	m ³ ha ⁻¹ year ⁻¹	Includes both planned harvests and salvage harvests
Annual disturbed volume	m ³ ha ⁻¹ year ⁻¹	Volume killed by bark beetle and wind disturbance
Deadwood carbon	tC ha ⁻¹	Includes stems, branches and coarse roots of standing dead trees, and downed woody debris
Share of broadleaved trees	%	Basal area share of broadleaved trees
Large trees	N ha ⁻¹	Number of trees with a diameter at breast height larger than 30 cm
Bilberry yield	kg ha ⁻¹ year ⁻¹	Annual yield of bilberries, calculated according to Miina et al. (2016)
Scenic beauty	Index (0–10)	Index of perceived scenic beauty (higher is more beautiful), calculated according to Pukkala et al. (1988)

the phasing zone from agricultural Finland to forest dominated areas and thus the landscape is a mosaic of fields, lakes, and forest. The total area is 54,100 ha of which 30,850 ha are forested area. The average stand age weighted by area in 2020 was 51.5 years. Disturbance activity in the intensively managed Finnish forests has historically been rather low and driven mainly by wind and snow disturbances (Korhonen et al., 2021). Warming temperatures are likely to cause increasing disturbance impacts from biotic risks such as European spruce bark beetle (*Ips typographus* L.) in the southern parts of Finland (Venäläinen et al., 2020). Combined with the high multi-objective importance of these forests (i.e., economic, biodiversity, and recreational value), southern Finland presents a compelling case study to investigate the development of forest disturbances under climate change and their impact on forest ecosystem services. In addition to climate data, information on soil properties and the initial vegetation are needed to create a simulation landscape for iLand (Supplementary Material, Section 1.2) For soil data, we used a dataset of soil variables collected from 488 plots throughout Finland, which is a subset of National Forest Inventory permanent plots belonging to the ICP Level I network (Muukkonen et al., 2015) and stratified them according to forest site type. This data allowed us to derive the necessary information about soil texture fractions, effective soil depth, plant-available nitrogen and soil carbon. For the initial vegetation data (representing the year 2020), we utilized stand-level data from the Finnish Forest Center (Metsäkeskus, 2021) to create targets of forest composition (species shares) and structure (age, basal area) for a spin-up routine, which simulated the stands based on an approximation of historical management, iteratively adapting the management to reach the comparison values. The management was adapted dynamically over multiple rotations to get as close as possible to the conditions derived from the stand data. Through this process, the initial conditions reasonably approximate realistic forest conditions while also keeping the internal processes of the model (e.g. competition between trees, carbon cycles) consistent (Thom et al., 2018). This method of letting the model place trees on the landscape is preferable to generating tree lists from stand level variables as it ensures that trees are placed in consistent manner with the model logic and reduces the impact of potential idiosyncrasies of the initialization process on future simulations (Temperli et al., 2013). Details of the model initialization, data used, and testing is given in the Supplementary material and in Honkaniemi et al. (2024).

3. Results

Changing climate and forest management shaped the future development of forests in the studied landscape (Fig. 2). Generally, in mitigation options (MIT1-4) the total carbon stocks were larger than in adaptation or business-as-usual scenario (BAU) because of longer rotation times and forest protection. In adaptation options with shorter rotation times, connected set-aside areas and admixing with broadleaved species (ADA1-4), more harvesting took place to reduce the risk for disturbances (Fig. 2). In the long term, climate change alone increased total carbon stocks by an average of 9 tC ha⁻¹ (+5%) in low-end climate scenario and 19 tC ha⁻¹ (+11%) in the high-end climate scenario compared to business-as-usual management in the historical climate. Correspondingly, climate change and mitigation management combined increased carbon stocks 26–41 tC ha⁻¹ (15–23%) and 35–48 tC ha⁻¹ (20–28%), respectively, depending on the management scenario (Supplementary Material Fig. S10).

Annual disturbances increased over time (Fig. 2). The effect of disturbances started to show after 60 years in the low-end climate scenario and after 30 years in the high-end climate scenario. Climate change alone, with no changes in forest management, increased disturbed volumes on average in the long term from 0.05 to 0.17 m³ ha⁻¹ year⁻¹ in the low-end climate scenario and to 1.7 m³ ha⁻¹ year⁻¹ in the high-end climate scenario. The largest disturbed volumes were in the high-end climate change scenario and in mitigation options consisting of longer

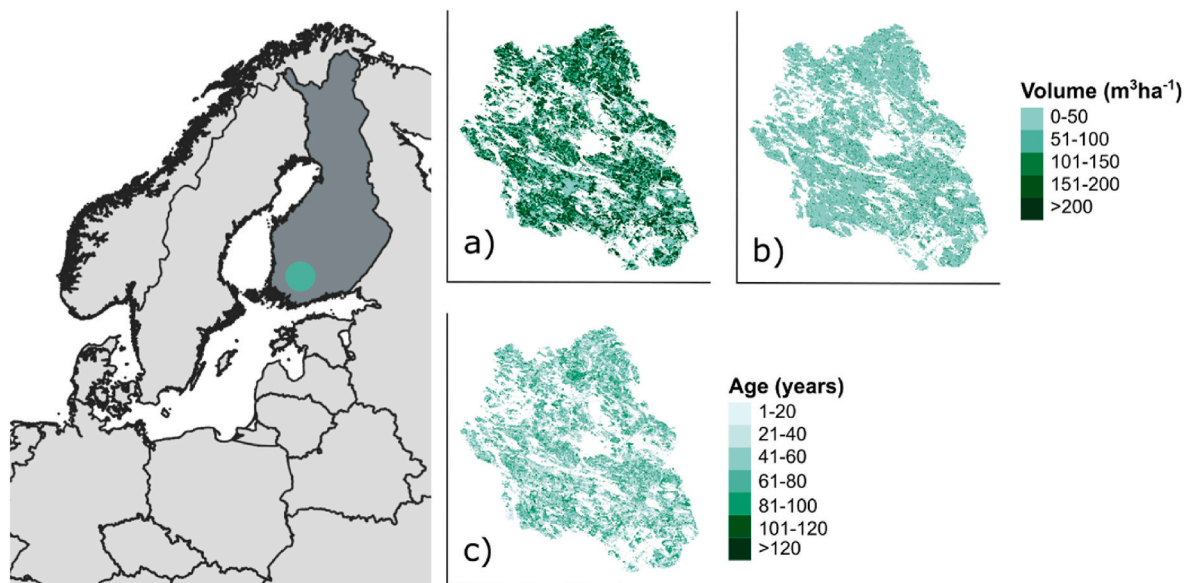


Fig. 1. Map of the study site location in Europe and the key characteristics of the landscape: conifer volume (a), broadleaf volume (b) and age (c). Volumes and age are derived from the Finnish Multi-Source NFI (year 2021).

Table 3

The characteristics of the studied landscape.

Site Types (% coverage)	
Herb-rich (OMT)	33
Mesic (MT)	56
Subxeric (VT)	7
Xeric (CT)	4
Tree Species (% share of volume)	
Norway Spruce	59
Pinus Sylvestris	24
Broadleaves	17
Climate	
Mean annual temperature (°C)	4
Mean annual precipitation (mm)	600

rotations and set aside areas focusing on old and high-volume stands (MIT 1–4) (Fig. 2). For example, in the long term in mitigation option with the longest rotation period and largest protected area (MIT4) the disturbed volumes were, on average, $0.75 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ in the low-end climate scenario and $3.9 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ in the high-end climate scenario. In the adaptation option with moderately shorter rotation period and 100% of spruce substitution (ADA2) disturbed volumes were larger than in business-as-usual after mid-century because of intensive substitution of spruce with broadleaves and the higher harvesting frequency. Despite the shorter rotation, the faster early height growth of birches (stand height being the primary driver of wind risk in iLand) combined with the more frequent creation of edges vulnerable to wind increased wind disturbances. In BAU and ADA, disturbances were mainly dominated by wind damages in all climate scenarios, whereas in MIT bark beetle damages were significant. For example, in MIT4 in the high-end climate scenario, bark beetle invasions accounted for over 60% of the total disturbed volumes in the long term (Fig. 3). The reasons explaining this were the increased availability of mature host trees in the managed stands under longer rotations and the setting aside of older spruce stands, which provide suitable conditions for bark beetles. The share of protected areas also affected total disturbance volumes on the landscape, in particular for MIT scenarios where disturbed areas disproportionately contributed to disturbed volume, but a higher share of protected area did not noticeably increase disturbances in surrounding managed areas (Supplementary material, Fig. S14). MIT allocated protection on productive, old stands on fertile sites (primarily spruce

stands), which therefore represented high volume at risk (Supplementary Material Fig. S14). An overall increase in growth under climate change also contributed to higher volume at risk and therefore higher disturbance volumes. Shorter periods of soil freezing also increased wind risk under climate change across management options due reduced root anchorage.

Disturbance risk prevention with adaptive management reduced the carbon storage potential of forests (Fig. 4). In mitigation managements the average total carbon stocks over the full simulation period were larger than adaptive managements or in BAU even when losses from disturbances were accounted for (Fig. 4, Supplementary material Fig. S8.). However, the variation in the disturbed volumes in mitigation options was almost two times larger than in adaptive managements. Generally, the adaptive management reduced carbon storage potential of forests by $13\text{--}38 \text{ tC ha}^{-1}$ (7–18%) over the full simulation period compared to mitigation options, and $2\text{--}14 \text{ tC ha}^{-1}$ (2–8%) compared to BAU. In the short term adaptive managements increased harvests $0.3\text{--}1.2 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ compared to BAU, while in the long-term or the effect was both increasing or decreasing harvests compared to BAU (Table S1) because of changes in species composition and the timing of the harvests. Over the full simulation period adaptive management resulted in larger harvests than in BAU in all climate scenarios except in ADA1 and ADA2 in the most intensive climate scenario (Figs. 2 and 4).

Adaptive management reduced the effects of disturbances compared to mitigation options but not necessarily compared to BAU (Figs. 2–4). The disturbance risk prevention achieved with adaptive management was dependent on time horizon, management option and climate scenario. In the short term adaptive management had no or small reducing effect on disturbed volumes corresponding to $0.01 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (10%) compared to BAU in the high-end climate scenario. In the long term, adaptive management increased disturbed volumes compared to BAU with the exception that adaptive management with the shortest rotation lengths (ADA3 and ADA4) reduced disturbed volumes $0.2\text{--}0.4 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (8–25%) compared BAU in the high-end climate scenario (Table S1). Across the full simulation period all adaptive management options increased disturbed carbon $0.01\text{--}0.07 \text{ tC ha}^{-1} \text{ year}^{-1}$ and mitigation management options $0.1\text{--}0.3 \text{ tC ha}^{-1} \text{ year}^{-1}$ compared to BAU (Fig. 4).

Climate change and management regimes modified forest structure causing changes in biodiversity and ecosystem service indicators (Fig. 5). In mitigation options the average stand age and basal area were

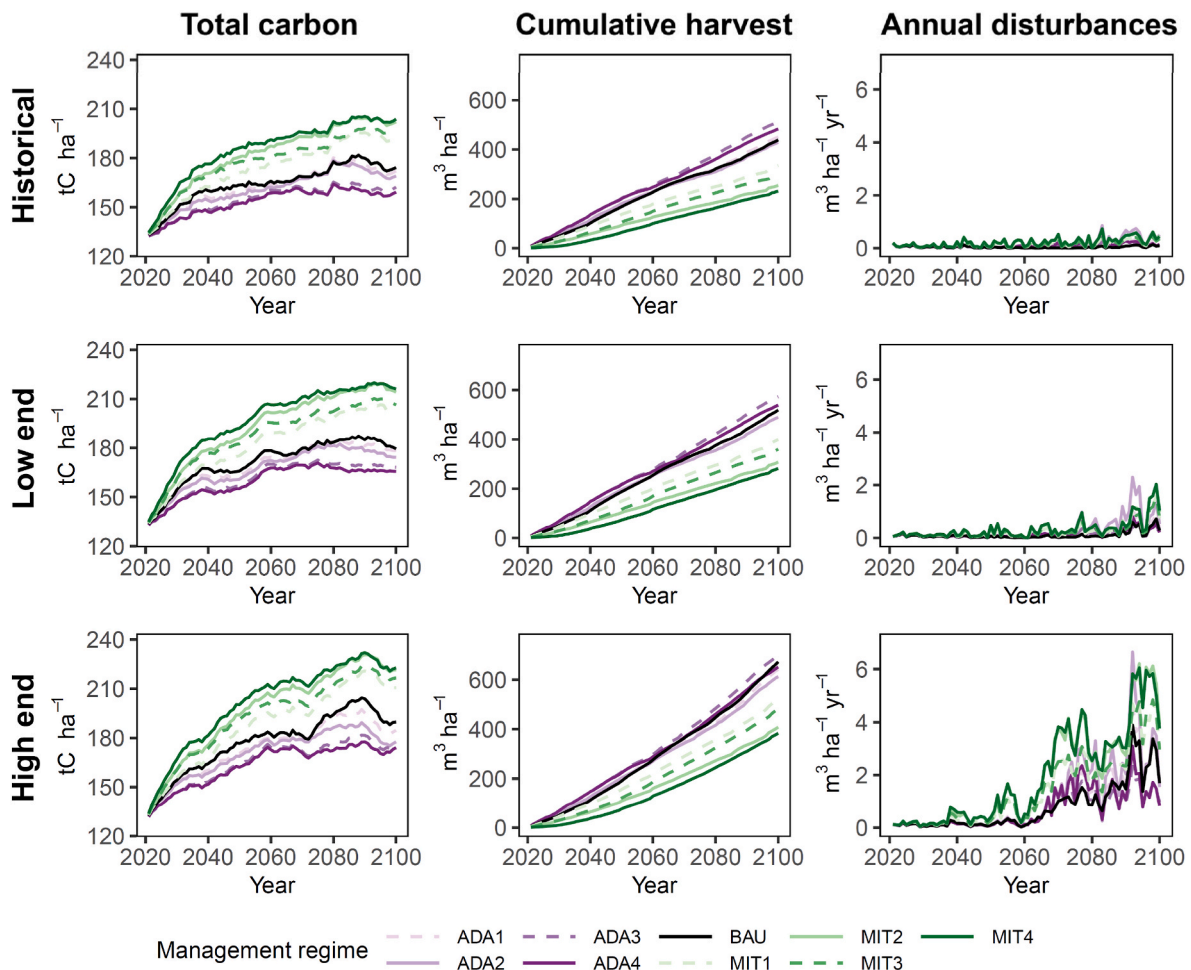


Fig. 2. The development of total carbon stocks, cumulative annual harvests, and annual disturbed volumes under historical and future climate conditions. [Table 1](#) presents the abbreviations of the management options. The values present averages over 10 simulation replicates.

larger and tree density smaller compared to business-as-usual in all studied climate scenarios (Supplementary material, Fig. S8). In adaptive managements the stand ages were generally lower than in business-as-usual management during the first years of the simulations because increased harvests, and more similar towards the end of the study period in all climate scenarios. The proportion of deciduous trees increased in adaptation options from 27 to 61% in the long term, whereas in the mitigation options the proportion of deciduous trees decreased a little compared to business-as-usual management (Supplementary material, Fig. S8.).

The combined effects of management and climate change on biodiversity indicators were mixed (Fig. 5). Generally, over the full simulation period, deadwood was increased in both mitigation (+3–21%) and adaptive managements (+4–7%) compared to business-as-usual with the largest increases in the most intensive mitigation regime and the high-end climate scenario (Fig. 4). The number of large trees increased 10–52% in mitigation options, but the severity of climate change reduced the positive trend. Adaptive managements increased the number of large trees by 3–6% or decreased it by –1 to –11% (Fig. 5). Scenic beauty index was impacted very little by climate change or management options. Bilberry benefitted from adaptive managements, and yields increased by 11–26% compared to BAU. Mitigation regimes had a small positive or negative impact on the bilberry yields. The absolute values for different indicators in the short and long term are given in the Supplementary material (Table S2). Generally, the magnitudes of the effects were more pronounced in the long term (Table S2).

4. Discussion

In this study we simulated the effects of two contrasting management strategies emphasizing either climate change adaptation or mitigation, on natural disturbances, biodiversity, and ecosystem services in boreal conditions under a changing climate. Adaptive management consisting of combinations of shorter rotations, admixing broadleaved species, and forest protection focusing on forest connectivity reduced especially bark beetle damages and under changing climate. Adaptive management reduced the amount of disturbances to some extent, but it also led to a reduction in the carbon storage potential of the forests. In some cases, adaptive management caused even higher disturbed volumes than business-as-usual management. The higher disturbed volumes resulted from more set-aside areas, more wind-exposed stand edges with frequent cuts compared to business as usual management, and the admixing of broadleaves. In this study, proactive management against bark beetle damages under a changing climate with admixing broadleaved species increased windthrows. Broadleaves have faster height growth and higher crown mass than coniferous species in young forests exposing them more strongly to wind damage, thus negating the effect of shortening rotations for wind risk. Therefore, this study suggests that there is a trade-off between adaptive management to reduce bark beetle damage and wind damage, and highlights the need for careful consideration of the risks most in need of attention and the impacts of proactive management to minimize these risks.

Mitigation management consisting of combinations of longer rotation periods and increasing forest protection focusing on old and high-

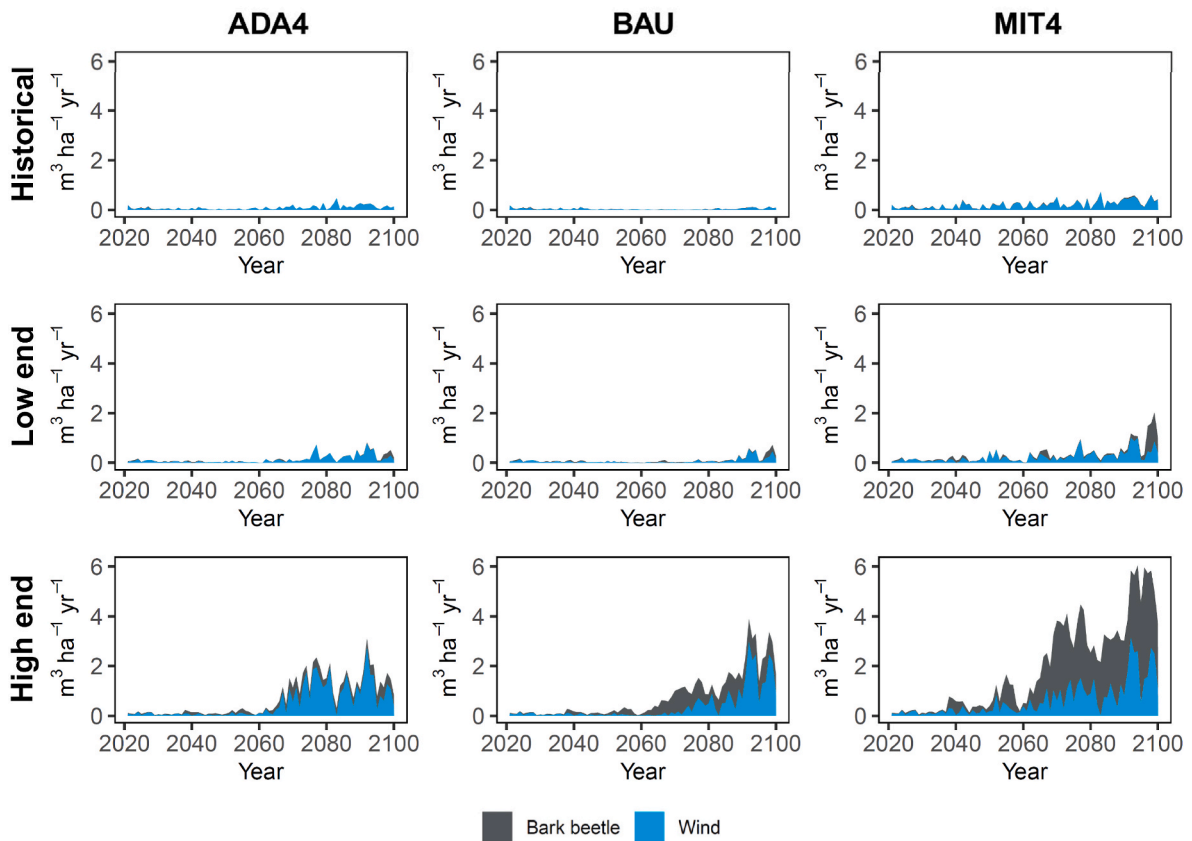


Fig. 3. Development of timber volumes affected by disturbances in the most intensive adaptation management (ADA4 left), business-as-usual scenario (BAU, middle) and most intensive mitigation option (MIT4, right) in different climate scenarios. The values present averages of 10 simulation replicates.

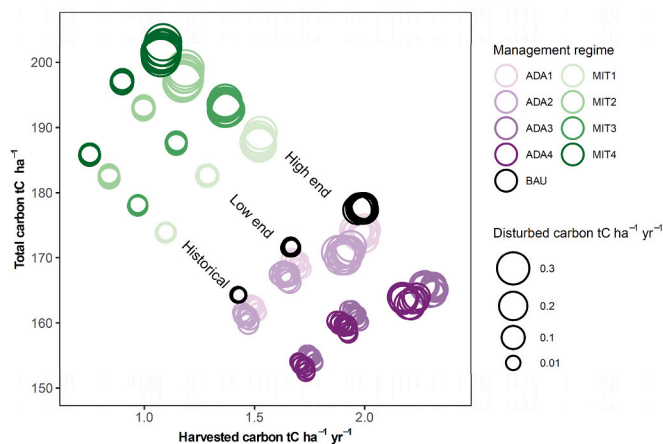


Fig. 4. Total carbon, harvested carbon, and carbon affected by disturbances (salvaged and not salvaged) in different management regimes and under different climate change scenarios. The values present averages across 80 years. The results of 10 simulation replicates are shown.

volume stands increased carbon stocks on average 6–15% in different climate scenarios across the full simulation period compared to business-as-usual management, and 7–18 % compared to adaptive management even when disturbance impacts were accounted for. The increases in carbon stocks were even larger when long-term effects of the last 30 years of the simulation period were compared. Consequently, this study does not support the view that carbon gains achieved with increasing protected areas or prolonging rotation lengths would be necessarily outweighed by increasing bark beetle outbreaks and wind

disturbances due to changing climate. We also found no evidence of protected areas increasing disturbance risks in surrounding managed forests. Such dynamics, particularly related to the spread of bark beetles, are a common concern but actual evidence is scarce and conflicting (Hlásny et al., 2021; Mezei et al., 2017; Valeria et al., 2016). In our simulations, disturbance volumes were particularly high in protected areas under mitigation management, but a higher share of protected area did not result in increasing disturbances in the managed parts of the landscape (Supplementary material, Fig. S14). While we did not analyze the spatial dynamics of bark beetle disturbances in detail, this is at least an indication that the protected areas did not act as substantial sources for bark beetle outbreaks in managed stands. It is also worth noting that our high-end climate scenario represents a very intensive warming and could be interpreted as a worst-case scenario (Riahi et al., 2011). In this study we focused on the changes in forest ecosystem and did not account for changes in harvested wood products. However, including harvested wood products in the analyses with the current product portfolio is unlikely to change the main findings. Previous studies have estimated that the substitution factor required to offset the carbon loss resulting from forest harvesting would need to be approximately four times higher than the current average estimated substitution factor (Hurmekoski et al., 2021; Köhl et al. 2021; Seppälä et al., 2019).

The cost of mitigation management was a significant decrease in timber harvests: even halving the annual harvests. Consequently, the social demands for timber also limit forest-based mitigation potential. In the end of the century the total carbon stocks were 30–37 t C ha⁻¹ higher and cumulative harvest 207–290 m³ ha⁻¹ smaller in the most intensive mitigation regime in different climate scenarios compared to business-as-usual. Assuming an average wood stumpage price of 30 € m³ (LUKE, 2023), the cost of forest-based mitigation would be 56–64 € t CO₂⁻¹. This rough estimate does not account for possible costs of

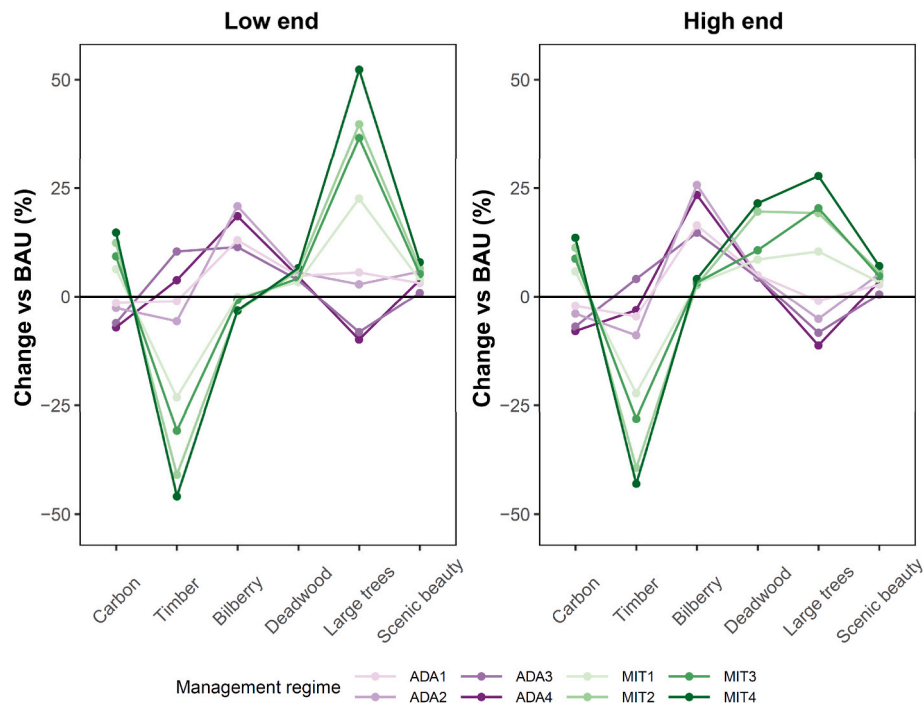


Fig. 5. The change in different ecosystem service and biodiversity indicators compared to business-as-usual management (BAU) in low-end (left) and high-end climate change scenario (right). The values present averages across 80 years and 10 simulation replicates.

changes in landownership due to forest protection, differences in stumpage prices for different wood assortments or the effects on national economy. However, it gives an indication of the cost of forest-based mitigation. For comparison, the average price for the EU emission allowances between January 2022 and October 2023 was 84 € t CO₂⁻¹ (Ember, 2023). The estimates for the use of carbon capture technologies range from 14 to 370 € t CO₂⁻¹ for bioenergy with carbon capture and storage, 30–930 € t CO₂⁻¹ for direct air capture and storage, and 2–220 € CO₂⁻¹ for afforestation and reforestation (Fuss et al., 2018).

We studied bundled actions of different forest management and land-use options that emphasize either adaptation or mitigation under different climate scenarios. This approach was chosen to cover multiple mitigation and adaptation actions, and to reflect forest management practices in a realistic way in a heterogenous landscape of different site types and initial conditions and management by various forest owners. The chosen approach makes it challenging to disentangle the effects of individual forest management actions or land-use allocations, such as changing only rotation period, on studied indicators, but it provides opportunities to unravel potential interaction effects between different actions. The approach highlights the complexity of the processes controlling development of ecosystem services biodiversity indicators, and disturbances by different agents in future climate. In central Europe, shortening rotation period reduced disturbance impacts of bark beetles but less so in changing climate. Shorter rotation dampened the impacts of wind disturbance more than those by bark beetles (Zimová et al., 2020). In our study, a combination of shorter rotation time, admixing broadleaved species and land-use allocations forming the adaptive management was more effective against bark beetle damages than against wind damages. These results highlight trade-offs between adaptive measures against different disturbance agents: hedging against bark beetle invasions by increasing share of deciduous trees increased volumes disturbed by wind due to the fast early height growth of birches, the main broadleaved species. Height growth being the major driver of wind risk in iLand, this caused stands to be exposed to wind risk at a younger age. Additionally, while shortening rotations can reduce wind risks through lower stand heights, it also causes more frequent harvests and therefore more exposed stand edges in the landscape

(another important driver of wind risk). Climate change makes wind-throw dynamics even more complex and increases risks particularly in the winter season, due to less ground frost to anchor the trees (Venäläinen et al., 2020). Covering more disturbance agents adds more complexity to the processes and creates new synergies and trade-offs. Therefore, when planning adaptive management it is good to bear in mind the objective of the proactive management, whether it is minimizing disturbed volumes or economic losses, or enhancing multifunctionality or forest resilience.

We focused only on disturbance agents affecting mature trees, and thus having the largest immediate impacts on carbon storage and timber volume (Patacca et al., 2023). Increasing the share of broadleaves may increase the impacts by ungulate browsing (i.e. moose, deer), but this is also highly dependent on their population densities. Browsing affects mostly sapling growth, timber quality, and tree species composition (Bernes et al., 2018; Heikkilä et al., 2003). These do not have immediate impacts on landscape-level carbon storage but could have more long-term impacts on forest structure and composition nudging forest landscapes to a whole new development trajectories (Seidl and Turner, 2022). While the simulations include a rudimentary representation of ungulate browsing, we do not represent potential shifts in population sizes and food preferences of browsers under changing climate and forest conditions, hence the simulated impact on forests are minor in this model implementation.

Mitigation management had generally a positive effect on the amount of deadwood and large trees. The increase in large trees was smaller in the high-end climate change scenarios than in other climate scenarios likely due an increase in wind risk. The positive relationship between these forest structures and studied mitigation measures has been show also in previous studies (Asbeck et al., 2021; Eyvindson et al., 2018; Felton et al., 2016; Triviño et al., 2023). The disturbed volumes were the highest in the mitigation options. However, natural disturbances generate and maintain structures important for biodiversity. Stands that have been regenerated through clear-cut harvesting hold less biological and structural diversity than those originating from natural disturbances (Gauthier et al., 2015).

In this study adaptive management combining shorter rotations,

admiring and forest protection also had a positive effect on deadwood compared to business-as-usual management. Generally, the effect of shorter rotation on deadwood is the opposite (Felton et al., 2017b). Two reasons explain our result: first, the increased protected areas in the adaptive management options and, second, iLand accounts in the deadwood pool in addition to stem wood also logging residues, hence shorter rotations lead to increased litter input from harvest residues (Repo et al., 2015) to the deadwood pool. For example, Felton et al. 2017, account only deadwood >10 cm. They also show that large diameter deadwood (>30 cm) originates mainly from retention trees in shorter rotations highlighting the relative importance of leaving retention trees in these management options. Felton et al. (2017) emphasize that increasing the number of retention trees may dampen but does not fully compensate the negative impact of shorter rotations to biodiversity. Increasing the share of broadleaved species and promoting species diversity generally results in more productive and stable systems compared to monocultures, and support higher level of ecosystem services and biodiversity (Felton et al., 2024; Huuskonen et al., 2021; Messier et al., 2022; Salemaa et al., 2023; Tilman et al., 2014). Mixed species forest provide resources and habitat for specialist species, more vertical and structural variability and microhabitats than monocultures (Felton et al., 2016; Huuskonen et al., 2021). However, many species groups relying on broadleaved tree species require certain kinds of host trees, such as old or large trees, or deadwood of certain decay class (Tikkanen et al., 2007), and planting birch or other broadleaves after clearcut may not be sufficient to fulfill their habitat requirements and halt the loss of habitats of endangered species (Hyvärinen et al., 2019). In addition, increasing the share of birches in spruce-dominated forests may have negative effects on some species groups such as bryophytes and lichens. An increase in stand density resulting from increasing broadleaved species may have a negative effect on understory vegetation richness (Huuskonen et al., 2021).

Adaptive management had a positive effect of bilberry yields, while mitigation management had small negative (in the low-end climate change scenario) or small positive effect (other climate scenarios) on bilberry. Generally, the coverage of bilberry increases with stand age and basal area until a certain limit for stand shading. Clearcuts and soil preparation have a negative effect on bilberry, hence bilberry yields are lower in young and dense stands (Miina et al., 2009). This could indicate that prolonging rotation lengths may increase bilberry yields as shown in a simulation study by Peura et al. (2016) where longer rotation length increased the average bilberry yield over 50 years but decreased cowberry and cep (*Boletus edulis*) yields. In this study shorter rotations combined with increasing the share of birch increased bilberry yields. These results should be interpreted with caution. The applied bilberry models are based on data from spruce and pine dominated forests (Miina et al., 2009). For mixed forests, models developed for pine were applied for birch considering the proportions of basal areas of different tree species. The same approach has been used with other Finnish forest simulators like MOTTI (pers. comm. J. Miina, J.-P. Hotanen). As bilberry is a semi-shade species, the bilberry yields are generally higher in pine-dominated than spruce dominated stands (Miina et al., 2009). While berry models for birch-dominated or mixed forests are not available, data on systematic sample plot network in Finland shows that an increase in the proportion of broadleaved share and stand density decreased bilberry cover in southern Finland, but increased the cover in the middle boreal zone. The reported opposite effects are likely result from differences in the tree species proportions, stand density and stand age, as in southern Finland spruce basal area, canopy cover and stem density were higher than in the middle boreal zone (Salemaa et al., 2023).

We evaluated the reliability of the results by comparing simulation outputs from different modeling steps to independent data. Due to the complexity of process-oriented, agent-based models such as iLand, their evaluation requires a pattern-based approach (Grimm et al., 2005), focusing on the model's ability to reproduce ecological patterns in a

realistic way. To evaluate the model implementation in Finland, we focused on multiple patterns, such as tree growth, forest composition and structure and disturbance impacts. While the model was able to reproduce patterns from independently observed data reasonably well, uncertainty remains due to limitations in data availability and comparability, e.g. growth data only being available for Norway spruce, Scots pine and silver birch, meaning we had to largely rely on the applicability of the Central European species parametrization for other species. Another factor of uncertainty relates to disturbances, both under present and changing conditions. While we do model the two most relevant disturbance agents causing mortality in adult trees, wind and bark beetle, and their interaction with each other and changing climate, we do not represent the full disturbance regime and all potential predisposing factors. For example, snow-loading, not yet implemented in iLand, amplifies the risk of wind disturbance, particularly for conifers (Päätaalo et al., 1999; Suvanto et al., 2020). Heterobasidion root rot, while being primarily an economic concern (Ahtikoski et al., 2024), may also predispose trees to damage from other agents, especially wind (Honkaniemi et al., 2017). Bark beetle has only recently become a notable disturbance agent in the Finnish context, and understanding of its dynamics in the Nordic region is still emerging (e.g. Tikkanen and Lehtonen, 2023). We therefore use the Central European parametrization of the iLand bark beetle module. As better process-understanding and data become available (e.g. Aalto et al., 2022), it may become possible and necessary to adapt the model structure and parametrization to nordic conditions. Similar restrictions in data availability and process-understanding apply to the modelling of other agents of potential future relevance (Melin et al., 2023), e.g. Black arches (*Lymantria monacha*, Melin et al., 2020). Further uncertainties and opportunities for model development relate to the representation of carbon and nitrogen cycling. The present model implementation assumes plant-available nitrogen to be static over time, therefore not taking into account potential feedbacks of changing climate and forest vegetation on the nitrogen cycle and site fertility. Similarly, while decomposition rates are climate-sensitive in iLand, the model does not explicitly include soil biotic communities, their responses to environmental changes and their biomass, which may constitute an additional carbon pool (e.g. Fan et al., 2021) and affect the stability of the soil carbon pool (Hao et al., 2024). Therefore, further research and model development is needed to fully capture the interacting effects of climate, forest disturbances and forest management on ecosystem services in boreal forests.

The seedlings of the today are the forest of the future. The consequences of forest management decisions are characterized by time lags and nonlinear dynamics. On the one hand, reducing harvest intensity by increasing the proportion of protected areas, reducing thinning to create denser forests, and extending rotation lengths are all means of increasing carbon stocks in the short term, providing climate change mitigation potential over the next years and decades. These rather fast nature-based climate solutions can significantly help to meet the climate goals and give time for the technological development for carbon capture and storage methods (Fuss et al., 2018; Griscom et al., 2019). On the other hand, the benefits of forest management decisions that prioritize adaptation to climate change in order to enhance resilience of forest landscapes to disturbances will come with delays. In Fennoscandia monocultures of conifers have been favored in the last decades, hence the future forests are likely to be dominated with conifers (Huuskonen et al., 2021). In this study, adaptive management changed the species composition so that by the end of the simulation period more than over half of the basal area was deciduous species in the most intensive adaptation options. Therefore, large changes in species shares, as in this study, would also affect the timber quality and volumes harvested and potentially the wood industry. In addition, the rapid changes in tree species composition would change landscapes and forest structure affecting biodiversity and potentially creating new disturbance regimes (Seidl and Turner, 2022; Turner and Seidl, 2023). Since the effects of

changing disturbance regimes started to have larger effects in second half of the century, and possible benefits of admixing broadleaved species occur with delays, decisions about future mitigation potential and resilience of forests happen today. Forest management to foster forest resilience under changing climate and disturbance regimes requires balancing multiple functions and services under uncertainty.

CRedit authorship contribution statement

Anna Repo: Writing – original draft, Supervision, Resources, Methodology, Investigation, Conceptualization. **Katharina Albrich:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Aapo Jantunen:** Writing – review & editing, Visualization, Data curation. **Juha Aalto:** Writing – review & editing, Resources, Investigation. **Ilari Lehtonen:** Writing – review & editing, Methodology, Investigation. **Juha Honkaniemi:** Writing – review & editing, Resources, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used DeepL Write in order to improve grammatics in part of the text. After using this tool the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Anna Repo reports financial support was provided by Research Council of Finland. Juha Aalto, Katharina Albrich, Ilari Lehtonen, Anna Repo, Juha Honkaniemi, Aapo Jantunen reports financial support was provided by Ministry of Agriculture and Forestry Finland. Juha Honkaniemi reports financial support was provided by Research Council of Finland. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary material for Repo et al. “Contrasting forest

management strategies: impacts on biodiversity and ecosystem services under changing climate and disturbance regimes” describes in detail the initialization and validation of modelling framework, the details of the climate scenarios and includes more results. The supplementary material to this article can be found online at <https://doi.org/10.1016/j.jenvman.2024.123124>

Data availability

The data and analysis code supporting the findings of this study can be retrieved from <https://doi.org/10.5281/zenodo.13929632>.

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