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Disentangling the effects of management and climate change on habitat suitability for saproxylic species in boreal forests

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Abstract Forest degradation induced by intensive forest management and temperature increase by climate change are resulting in biodiversity decline in boreal forests. Intensive forest management and high-end climate emission scenarios can further reduce the amount and diversity of deadwood, the limiting factor for habitats for saproxylic species in European boreal forests. The magnitude of their combined effects and how changes in forest management can affect deadwood diversity under a range of climate change scenarios are poorly understood. We used forest growth simulations to evaluate how forest management and climate change will individually and jointly affect habitats of red-listed saproxylic species in Finland. We simulated seven forest management regimes and three climate scenarios (reference, RCP4.5 and RCP8.5) over 100 years. Management regimes included set aside, *continuous cover forestry*, *business-as-usual* (BAU) and four modifications of BAU. Habitat suitability was assessed using a species-specific habitat suitability index, including 21 fungal and invertebrate species groups. "Winner" and "loser" species were identified based on the modelled impacts of forest management and climate change on their habitat suitability. We found that forest management had a major impact on habitat suitability of saproxylic species compared to climate change. Habitat suitability index varied by over 250% among management regimes, while overall change in habitat suitability index caused by climate change was on average only 2%. More species groups were identified as winners than losers from impacts of climate change (52%–95% were winners, depending on the climate change scenario and management regime). The largest increase in habitat suitability index was achieved under *set aside* (254%) and the climate scenario RCP8.5 (> 2%), while *continuous cover forestry* was the most suitable regime to increase habitat suitability of saproxylic species (up to + 11%) across all climate change scenarios. Our results show that close-to-nature management regimes (e.g., *continuous cover forestry* and *set aside*) can increase the habitat suitability of many saproxylic boreal species more than the basic *business-as-usual* regime. This suggests that biodiversity loss of many saproxylic species

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in boreal forests can be mitigated through improved forest management practices, even as climate change progresses.

Introduction

Forests cover 30% of the global land area (FAO 2010), representing the most species-rich habitat types in the world (Lindenmayer 2009). Around one-third of the global forest area is covered by the boreal forest biome, located in the northern hemisphere between the tundra and the temperate forest biomes (van Lierop et al 2015). While tree species diversity is low, boreal forests still host diverse habitats for a wide range of species (Kellomäki 2017).

Boreal forests are under pressure to provide multiple ecosystem services while at the same time satisfy increased demands for raw materials (Blattert et al 2022; Mazziotta et al 2022) due to population growth, globalization, and climate mitigation policies (Jonsson 2013). This pressure leads to intensification of harvesting in managed forests or harvesting of previously unmanaged forests (Heinonen et al 2018). In the Fennoscandian boreal forests, the predominant management practice is rotation forestry, where trees are artificially regenerated by seeding or planting and almost all trees are harvested when they reach maturity (Burton et al 2003; Äijälä et al 2014; Svensson et al 2019; Peltola et al 2020). While intensive forest management increases the economic value of the forest, it might negatively impact biodiversity (Gossner et al 2013). For instance, the area of old-growth forests in Finland has diminished dramatically due to the intensification of timber harvesting over past decades (Henttonen et al 2019; Peltola et al 2020). Moreover, intensively managed forests are often represented by young tree monocultures with an even-aged profile, low deadwood volumes (Kuuluvainen et al 2019) and with a limited potential to provide habitat structures necessary to sustain biodiversity (Jonsson et al 2020).

Deadwood resources in specific microhabitats are critical for many species and support forest productivity by providing nutrients, moisture and organic matter, prevent soil erosion in climatic extreme events and mitigate climate change by storing carbon (Lassauce et al 2011). The volume of deadwood depends on the forest growth, mortality, and rate of decomposition (Stokland et al 2012). Deadwood characteristics, such as volume, tree species, diameter, and decay stage are often used as indicators of forest biodiversity (Lassauce et al 2011). In fact, high deadwood volume correlates with high species richness of wood-inhabiting organisms (Juutinen et al 2006; Yang et al 2021), with 20%−25% of forest species (saproxylic species involved in decomposition

processes and nutrient cycling), dependent on a variety of deadwood types (Siitonen 2001; Tikkanen et al 2006). The volume of deadwood in managed forests is substantially lower than in natural forests; managed forests lack well-decayed large logs and snags (Siitonen and Saaristo 2000; Siitonen 2001). From the latest Finnish National Forest Inventory (2014−2018), the volume of standing dead trees (snags) averaged 1.7 m^3 ha^{-1} and the volume of lying dead trees (logs) averaged 4.2 m^3 ha^{-1} (Peltola et al 2020). Estimates of the average volume of deadwood in natural forests in Finland ranges from 50 m^3 ha^{-1} in the north to 110 m^3 ha^{-1} in the south (Mönkkönen et al 2022). Red-listed saproxylic species, however, require at least (20–40) m^3 ha^{-1} of deadwood to survive (Siitonen and Saaristo 2000; Siitonen 2001; Penttilä et al 2004). Due to this substantial reduction in deadwood volume in managed forests, a large number of saproxylic species, such as fungi, lichens and invertebrates, have become threatened in Finnish forests (Tikkanen et al 2006; Rassi et al 2010).

Climate change impacts the future availability of deadwood in boreal forests. In Finland, the temperature is already over 2 °C warmer than in the middle of the nineteenth century (Mikkonen et al 2015) and may likely rise to more than 3 °C by the end of the century compared to 1981−2010 levels (Venäläinen et al 2020; IPCC 2021). In the boreal zone, the increase in atmospheric greenhouse gas concentrations will induce longer and warmer growing seasons, enhance biomass production, and the accumulation of carbon in trees and soil (Subramanian et al 2019). Consequently, increasing tree growth increases deadwood volume, which may potentially increase the availability of habitat for saproxylic species (Mazziotta et al 2014).

How forest management and climate change may jointly affect the future availability of deadwood resources in boreal forests is still unclear. Particularly, we do not know whether the combination of these two factors will increase suitable habitats for saproxylic species, qualifying the species as a "winner", or decrease it, qualifying the species as a "loser" (Foden et al 2013; Mazziotta et al 2016). As deadwood-associated species differ in their habitat requirements–volume and type of deadwood (snag/log), decay stage, tree species, microclimate–saproxylic species responses to management and climate change may differ.

In this study, we evaluated the impacts of management and climate change on saproxylic species using a simulation framework. We explored the development of deadwood resources under different management regimes and climate change scenarios and how they affect the habitat suitability of saproxylic species. We hypothesized that: (1) habitat suitability of saproxylic species will generally decrease under intensive management regimes, translating into more loser species; (2) habitat suitability of saproxylic species will generally increase under climate change due to

Fig. 1 Locations and names of the eight study landscapes within Finland. Names refer to the municipalities in which the study areas are located. Inset map shows the location of Finland within Europe
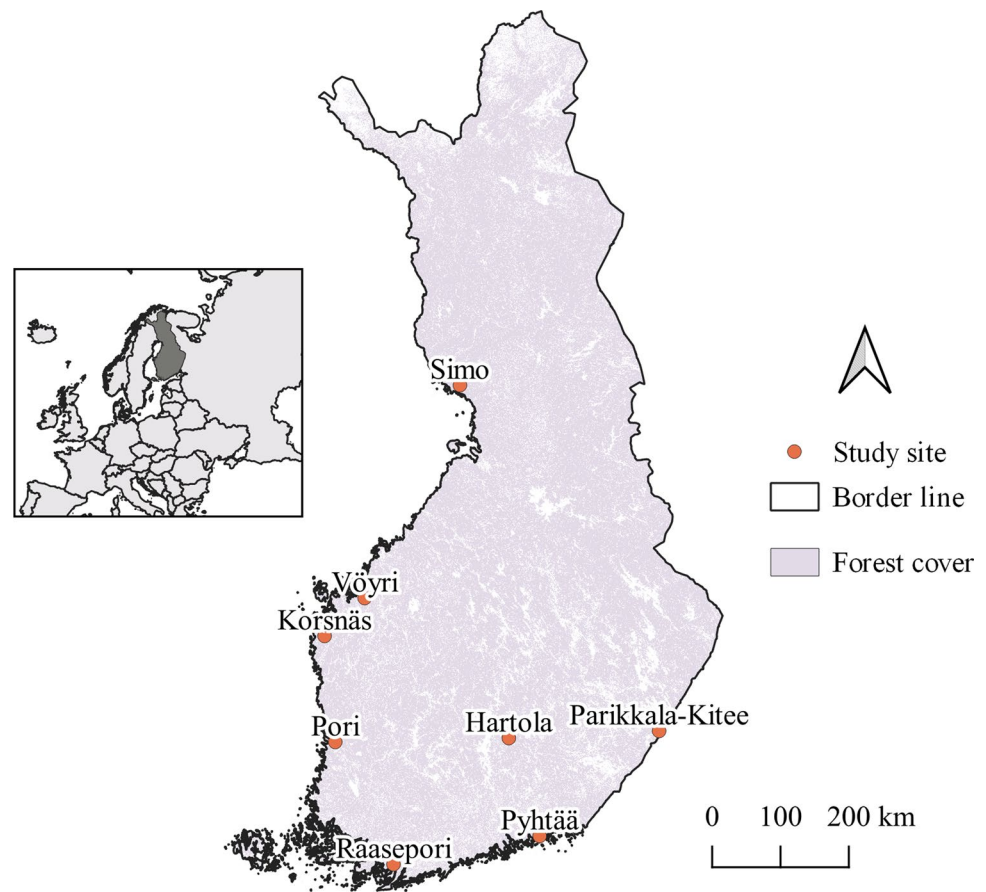
expected increases in boreal forest productivity and deadwood volume, translating into more winner species; and (3) the combination of the most intensive management regimes and the more extreme climate change scenario will have the strongest negative effects on the habitat suitability, as these conditions cause the loss and quick degradation of resources for deadwood biodiversity (Tuomi et al 2011).

Materials and methods

Study area and data

Eight forested landscapes were selected to explore the joint impacts of forest management and climate change on saproxylic species habitat suitability. These landscapes were located throughout Finland with an aim to cover a wide geographical gradient (Fig. 1). We used the openly available data provided by the Finnish Forest Centre (www.metsaan.fi; Finnish Forest Centre 2021). The data was aggregated into forest stands, forestry units with relatively homogenous forest structure and site conditions. The average area of the forest stands was 1.1 ha, with each forest stand having variations in soil type, age, tree species composition, mean

diameter at breast height, tree volume and basal area. The eight landscapes represented 1782 forest stands and, covered a total area of 19 km^2. Each landscape contained an average of 200 stands (range 120–315) with a mean stand age of 57 years (range 40–68 years). Scots pine (*Pinus sylvestris* L.) was the dominant tree species (47%), followed by Norway spruce (*Picea abies* (L.) H. Karst, 32%), and deciduous species (15%); 5% of the stands did not have a dominant tree species (Table 1).

Forest growth and management simulation

Forest development under alternative forest management regimes was projected using the SIMO framework (Rasinmäki et al 2009). SIMO is an open-source forest growth simulator and a tool for forest management planning. It consists of model chains that predict the growth of individual trees, and results are collected at a stand level (Rasinmäki et al 2009). The simulations were run for 20-time steps of five years in length for a total simulation length of 100 years. This long simulation horizon allows for a stand to complete a single rotation (planting, tending, thinning, and clear felling). A similar framework has been used to simulate forest

Table 1 Properties of the study areas

Municipality (South, Central or North Finland)	Area (km²)	Number of stands	Mean initial age of the stands (years)	Dominant fertility class	Dominant tree species
Hartola (Central)	1.8	154	53	OMT	*Picea abies*
Korsnäs (Central)	3.1	297	55	MT	*Pinus sylvestris*
Parikkala − Kitee (Central)	3.3	315	41	MT	*Pinus sylvestris*
Pori (Central)	2.1	207	57	MT	*Pinus sylvestris*
Pyhtää (South)	1.5	120	56	MT	*Pinus sylvestris/Picea abies*
Raasepori (South)	2.2	202	68	MT	*Pinus sylvestris*
Simo (North)	3.3	291	67	MT	*Pinus sylvestris*
Vöyri (Central)	1.7	190	61	VT	*Pinus sylvestris*

Fertility class definitions (according to Cajander (1949): OMT (*Oxalis − Myrtillus*) = grove-like heathland, fen or peatland, MT (*Myrtillus*) = fresh heathland or fen, blueberry peatlands, VT (*Vaccinium*) = dryish heathland and fen, lingonberry peatlands

development in the studies by Peura et al (2018) and Eyvindson et al (2021).

Using the initial starting conditions for the individual stands, their future development was simulated under seven management regimes (Table 2). These regimes varied by timing and intensity of timber harvesting and included: a traditional, even-aged rotation with thinning from below and final clear-cut (business-as-usual, BAU) which was modified with extended and shortened rotation lengths, excluded thinning, and increased number of unharvested trees after final harvesting. A management regime without final clear-cut (continuous cover forestry, CCF) was also simulated in which large-diameter trees were harvested individually (thinning from above) to achieve a diverse and continuous forest cover. Additionally, a 'set aside' regime was simulated where no harvesting occurred and the stands grew without intervention. The simulation of the forests included models for the natural mortality of trees, which decayed as deadwood after death.

Forest dynamics for each management regime was simulated under three future climate change scenarios: a reference climate scenario, which assumes that mean climatic conditions for 1996−2014 will be held constant over the 100-year simulation period, and two alternative greenhouse forcing scenarios, Representative Concentration Pathways (RCPs). RCP4.5 and RCP8.5 represent an intermediate scenario, with moderate greenhouse gas emission reduction, and a high warming scenario, with no greenhouse gas emission mitigation undertaken, respectively (van Vuuren et al 2011). In Finland, annual mean temperatures are projected to increase by 3.3 °C and 5.6 °C by the 2080s under the RCP4.5 and RCP8.5 scenarios, respectively, compared to 1996−2014 (Ruosteenoja et al 2016; Venäläinen et al 2020). Mean annual precipitation is expected to increase by 11% and 18% under these RCPs by the 2080s. Climate variables driving forest growth and soil dynamics were selected: the mean and variation of temperature, CO_2 concentration and precipitation. The impact of climate variables on forest growth dynamics

in SIMO was included and based on climate—sensitive statistical growth and yield models (Matala et al 2005, 2006). For the reference climate scenario, 5-year mean values were used for 1996−2014 (Lehtonen et al 2016), and for the two future climate change scenarios (RCP4.5 and RCP8.5), 5-year mean values from one General Circulation Model, the second—generation of the Canadian Earth system model CanESM (Von Salzen et al 2013) were used. A single GCM was selected, as the long-term trends between the climate models were similar, with only minor differences in the 5-year averages of precipitation and temperature.

The dynamics of deadwood formation through tree mortality and decay were simulated using the statistical models of Mäkinen et al (2006). These models were empirically derived for the primary tree species in Finland (Scots pine, *Pinus sylvestris*; Norway spruce, *Picea abies*; silver birch, *Betula pendula*), using data from long-term experiments in managed forests in southern and central Finland.

Habitat suitability index models

Habitat suitability indices (HSI) were used to measure habitat quality for saproxylic species groups sharing similar requirements (Table S1). These are models based on reported relationships between the deadwood resource / microclimatic variables and the richness of saproxylic species (Tikkanen et al 2006; Kouki and Tikkanen 2007). A species group consists of saproxylic species dependent on deadwood of the same tree species, type (snag/log), size and decay stage (from fresh, hard deadwood to well- decayed and soft). The groups also differ in their microclimatic requirements, and ranges from "Shady" to "Sunny" along with decreasing total stand basal area and the proportion of spruce. Species were classified as "Indifferent" if there were no specific microclimate requirements (Tikkanen et al 2007). Coarse woody debris (CWD) was used to describe

Table 2 Management regimes applied during the 100-year planning horizon in the study areas (1808 stands)

Management regime	Acronym	Description	Effect on forest structure important for biodiversity
Business-as-usual	BAU	Recommended management: rotation length 70−90 years; site preparation, planting or seeding trees, 1−3 thinning, final harvest with tree retention level 10 trees ha⁻¹	Reference scenario Stand dominated by single species with an even-aged forest structure. Low deadwood volume
Extended rotation	Extended	BAU with postponed final harvesting by 15 years	Postponing final harvest increases mortality (more deadwood) between the last thinning and final harvest, and allows development of older trees
No Thinning	NoThin	BAU without thinning; forest growth slower and final harvest delayed	Dense forest structure and self-thinning with more deadwood
Shortened rotation	Short-ened	BAU with shortened rotation by 20 years, no thinnings	Trees are cut at younger age and in smaller dimensions
Continuous cover forestry	CCF	Continuous cover forestry following Pukkala et al (2013). Thinnings from above, e.g., range of 16 − 22 BA depending on soil fertility (more fertile, higher BA) are harvested. Minimal return time between two consecutive thinning is 15 years	Continuous forest cover enhances structural diversity
Green trees retention	GTR	BAU with 30 live trees retained ha⁻¹ at final harvest	Enhanced structural diversity at final harvest; larger trees present
Set aside	SA	No management, natural regeneration, and mortality	Enhanced structural diversity, higher deadwood volume

Effect on biodiversity describes the most likely forest structural changes important to species habitats compared with the BAU regime

deadwood that was ≥ 10 cm in diameter and 1.5 m long and divided into snags, referring to standing deadwood, and logs i.e., lying deadwood (Harmon and Sexton 1996).

The HSI has a range between 0 and 1, where 0 represents unsuitable habitat and 1 a highly suitable habitat (Edenius and Mikusiński 2006). The HSI models were used for 21 of the 27 species groups from Kouki and Tikkanen (2007), which represented red-listed saproxylic species, including insects, fungi, and lichens included in the Finnish Red List of threatened species (Rassi et al 2010; https://punainenkirja.laji.fi/en). Six species groups were excluded from the final analysis as their HSI-values were 0 for all forest stands, simulation versions and time steps, possibly indicating that the habitats in the study areas did not meet their microclimate and resource requirements. The impacts of a changing climate will modify stand characteristics and deadwood decomposition rates—resulting in different habitat suitabilities for each forest management regime.

Analysis of the effects of management and climate change on habitat suitability index

To evaluate the individual and combined effects of management and climate change scenarios on HSI, the relative differences in HSI were identified among scenarios over the 100-year horizon by calculating HSI mean values for each time step, each management regime, each climate scenario, and each species group. To better understand the differences between management and climate, the relative differences

were assessed using three approaches. To explore the individual effect of management (without climate change), relative differences in HSI among regimes were calculated by including only HSI-values of reference climate scenario (Eq. 1). Therefore, differences in HSI across time were calculated respective to the initial HSI level in year 2016. To assess the effect of climate change, relative differences in HSI were calculated with respect to HSI-values achieved under the reference climate (cur) and no management (set aside, SA) (Eq. 2). To study the combined effects, we included all climate change scenarios and management regimes, evaluating the relative differences in HSI with respect to the reference climate scenario (Eq. 3),

$$d_{t,k,m,cur} = \sum_{h \in H_k} \left(\frac{HSI_{t,h,m,c} - HSI_{2016,h,m,c}}{HSI_{2016,h,m,c}} \right) / \#H_k, \forall t \in T,$$
$$k \in K, m \in M, c = cur \tag{1}$$

$$d_{t,k,SA,c} = \sum_{h \in H_k} \left(\frac{HSI_{t,h,m,c} - HSI_{t,h,m,cur}}{HSI_{t,k,m,cur}} \right) / \#H_k, \forall t \in T,$$
$$k \in K, m = SA, c \in C \tag{2}$$

$$d_{t,k,c,m} = \sum_{h \in H_k} \left(\frac{HSI_{t,h,m,c} - HSI_{t,h,m,cur}}{HSI_{t,h,m,cur}} \right) / \#H_k, \forall t \in T,$$
$$k \in K, c \in C, m \in M \tag{3}$$

Fig. 2 Differences in HSI under a current climate scenario relative to 2016 and grouped by microclimatic requirements; different colours represent individual management regimes. Calculated using Eq. (1). *BAU* Business-as-usual, *extended* Extended rotation, *noThin* No Thinning, *shortened* Shortened rotation, *CCF* Continuous cover forestry, *GTR* Green trees retention, *SA* Set aside
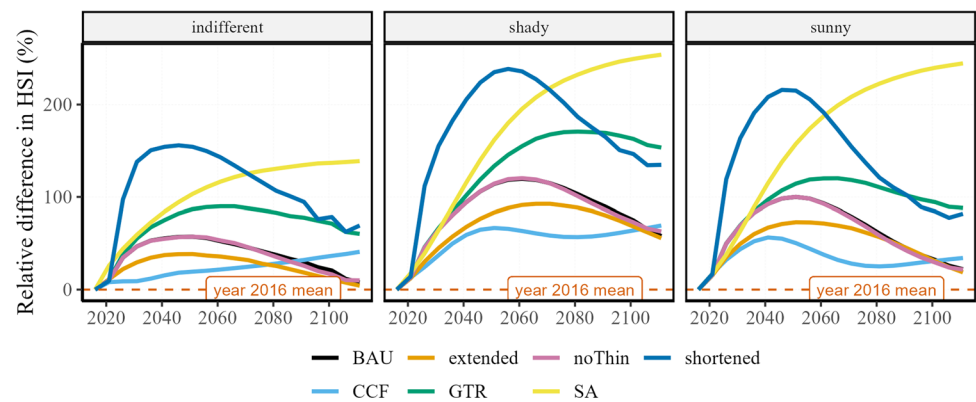
where *d* is the relative difference between the HSI and the reference HSI value, *T* the set of time periods under consideration, H_k the set of HSI values for the microclimatic preference group, with #H_k referring to the cardinality of the set (number of indices for the microclimate preference group), *M* the set of management options and *C* the set of RCP climate projections.

The HSI were determined for groups of species sharing the same microclimatic preference, and separately for each species group (Table S1). In addition, "winners" and "losers" group species were identified, depending on the changes in their HSI. Winners represented those groups whose habitat suitability improved; losers represented species groups whose habitat suitability declined by climate change under a specific type of forest management. The HSI for the groups that did not change under the climate change scenarios were categorized as "stable". The resource requirements for the winner and the loser species were determined to identify deadwood parameters most affected by climate change by analysing the tree species and decay classes (Table S1).

Results

Effects of forest management on habitat suitability indicies

The *set aside regime* showed a continuous increase in HSI through the entire simulation horizon (Fig. 2). Under *rotation forestry* (BAU and its modifications), HSI increased during the first few decades but decreased afterwards as the consequence of final harvesting, returning a level slightly higher than the initial level. BAU, *shortened rotation* and no thinning induced a sharp and large improvement in HSI during the first 40 years, and a sharp decrease after. Improvements in the HSI peaked later for the *extended rotation* and GTR and earlier for BAU regimes. In addition, HSI decrease was lower in BAU with the *green tree retention* (GTR) regime in the second half of the simulation horizon

compared to other BAU regimes. For *continuous cover forestry* (CCF), HSI did not deteriorate in the second half of the simulation period (2071 − 2111) as dramatically as for the BAU regimes (Fig. 2). However, in general, for CCF, the improvement in HSI was lower (max 65%) compared to the other management regimes over the simulation horizon (max 254% increase with *set aside*).

Shady and sunny species groups showed larger improvement in HSI (max 254%) compared to indifferent species groups (max 139%) under all management regimes. This is because the indifferent groups had generally lower HSI values than other microclimatic species groups (Table S2). The shady groups resulted in a higher increase in HSI under the GTR − regime compared to other groups (Fig. 2).

Effects of climate change on habitat suitability indices

When the effect by forest management was excluded (focusing on stands under the *set aside* regime), the effects of climate change on HSI of deadwood associated species were modest and increasing towards the end of the simulation period (Fig. 3). From the start to the finish of the 100-year planning horizon, the average HSI of saproxylic species increased by < 2% under RCP4.5 compared to the reference climate scenario, and slightly more than 2% under RCP8.5. Differences in HSI between microclimatic species groups were small (Fig. S1), and the increase in HSI approached similar levels by the end of the simulation period.

Combined effects of management and climate change on habitat suitability indices and deadwood dynamics

Climate change, by enhancing tree growth, resulted in higher timber volumes over the last 30 years of the simulation period (Table 3). Mean standing timber volumes increased by 14% (RCP4.5) and by 27% (RCP8.5) in managed stands, and by 7% (RCP4.5) and 11% (RCP8.5) in *set aside* stands. Average deadwood volumes increased with climate change but only by 5% under RCP4.5 and by 7% under RCP8.5 in
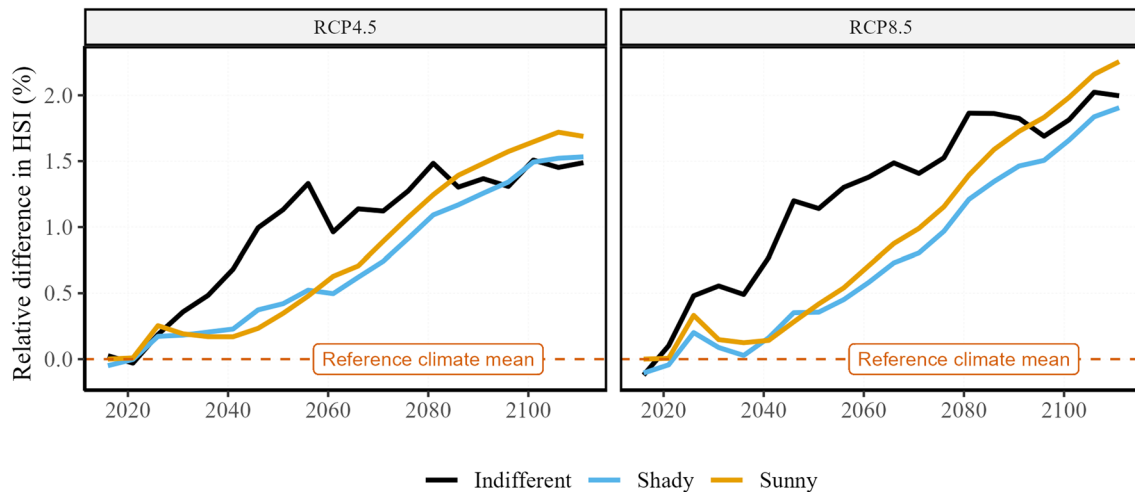
Fig. 3 Relative differences in HSI of microclimatic species groups (indifferent, shady, sunny) under two climate change scenarios (RCP4.5 and RCP8.5) relative to the reference climate for stands under the *set aside* management regime. Calculated using Eq. 2

Table 3 Deadwood and timber volumes over 2081−2111 (m³ ha⁻¹). Managed stands include other management regimes than set aside

Management	Climate change	Deadwood (Mean ± sd)	Deadwood range	Volume (mean ± sd)	Volume range
Managed	Reference	4.4 ± 4.3	0.1–30.5	169.9 ± 147.6	0–727.4
Set aside	Reference	24.6 ± 15.8	0–66.3	329.1 ± 142.3	0.6–769.5
Managed	RCP4.5	4.6 ± 4.3	0.2–29.4	194.3 ± 173.2	0–812.1
Set aside	RCP4.5	25.2 ± 15.8	0–61.5	351.9 ± 151.8	0.8–852.6
Managed	RCP8.5	4.7 ± 4.3	0.2–30.5	215.4 ± 190.6	0–996.9
Set aside	RCP8.5	25.5 ± 15.8	0–65.1	365 ± 159.4	1–979.6

the managed stands and by 2% under RCP4.5 and 4% under *set aside* stands. Deadwood and timber volumes varied greatly among stands which may be explained by their variability in site conditions and initial site characteristics.

Examining the combined effects on HSI, the relative difference in habitat suitability index was modest compared to management alone (Figs. 2 and 4). The first half of the simulation horizon (2016−2066) showed only minor differences in HSI due to climate change under different management regimes (−1% to 4%). In the second half of the simulation horizon (2071−2111), differences slightly increased and varied between management regimes (−2% to 11%).

For both RCP4.5 and RCP8.5 scenarios, the highest relative increase in HSI by the end of the simulation period was achieved with the CCF−regime for indifferent and shady species groups, while for the sunny group, it was achieved with the basic BAU−regime (Fig. 4). Habitat suitability indices increased for all management regimes under both climate change scenarios with respect to the reference climate scenario, except for *no thinning* and *shortened rotation*, which showed a reduction among shady and indifferent species groups during the second half of the simulation period (maximum of 2%) (Fig. 4).

Most of the 21 species groups were "winners", as their HSI increased by climate change (Figs. 5, S2). The number of winner species groups increased for the GTR, and the number of loser species groups decreased for BAU and GTR but increased for other management regimes (*extended rotation, no thinning, shortened rotation*) under the RCP8.5 scenario. From a tree species resource perspective, winner species groups were associated with deciduous trees 34%, pine 32%, spruce 20% and conifer trees in general 14% (Fig. 5, Table S1). Based on decay classes, 19% of the winner species groups were associated with fresh deadwood, 43% with fresh or medium decayed deadwood and 38% with medium or well-decayed deadwood.

Discussion

In this study, we analyzed the impacts of forest management regimes and climate change to explain changes in habitat suitability of red-listed saproxylic species. Forest management had a larger impact on habitat suitability than climate change. In the second half of the twenty-first century, forest
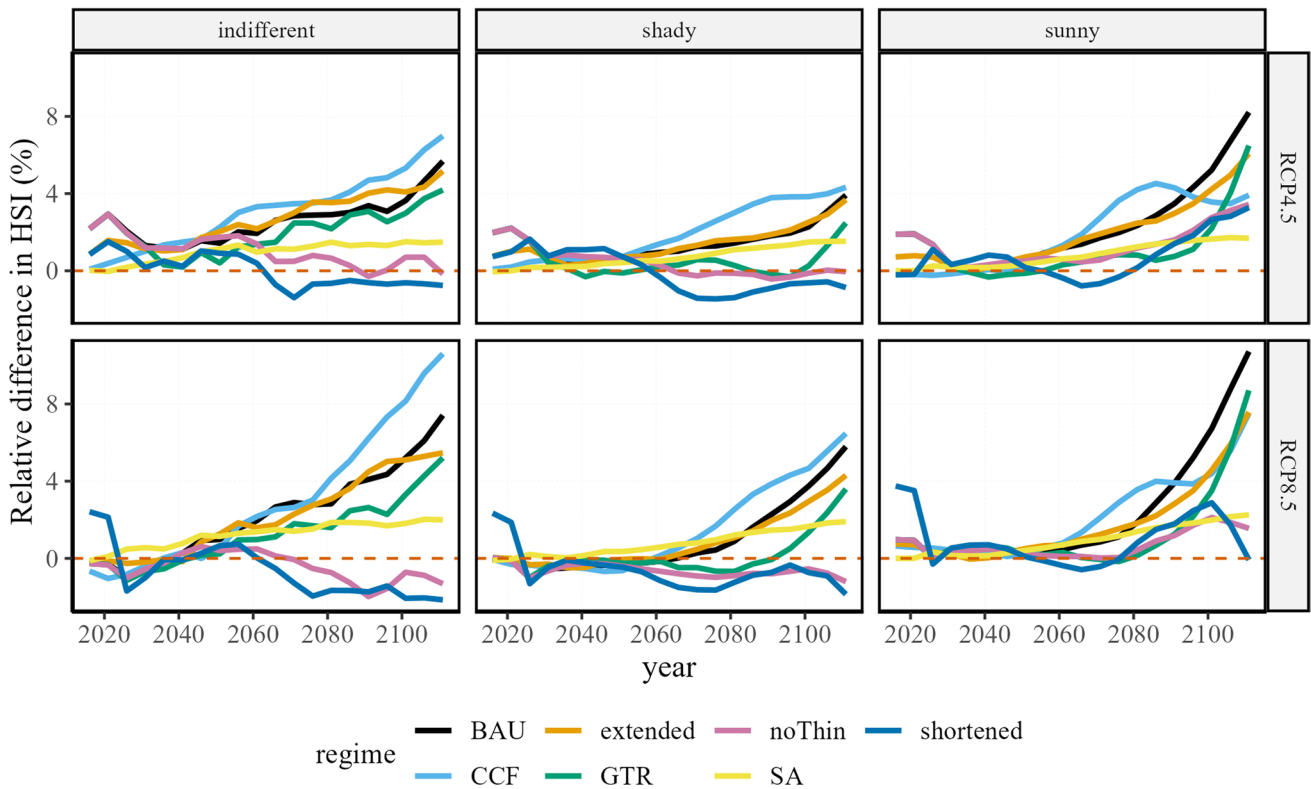
Fig. 4 HSI under alternative management regimes relative to the same management under a reference climate scenario for different microclimatic groups and climate change scenarios. The orange dotted line represents mean value for the management regime under the reference climate. Calculated using Eq. 3. *BAU* Business-as-usual, *extended* Extended rotation, *noThin* No Thinning, *shortened* Shortened rotation, *CCF* Continuous cover forestry, *GTR* Green trees retention, *SA* Set aside
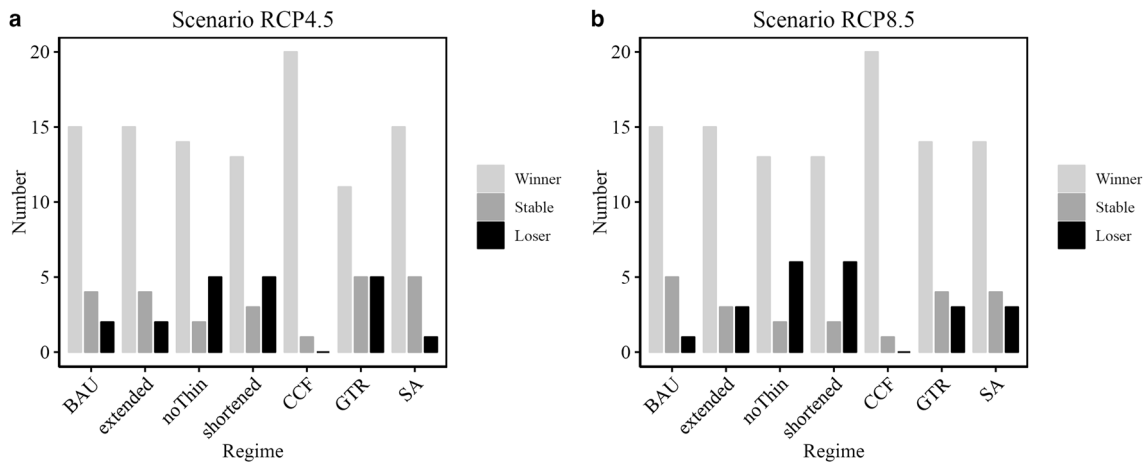
Fig. 5 Numbers of winner, stable and loser species groups under two climate change scenarios (*a* = RCP4.5 and *b* = RCP8.5), relative to the reference climate scenario. *BAU* Business-as-usual, *extended* Extended rotation, *shortened* Shortened rotation, *noThin* No Thinning, *GTR* Green trees retention, *CCF* Continuous cover forestry, *SA* Set aside

management increased in importance in altering the impact of climate change on habitat suitability.

Effects of forest management on habitat suitability indices

The *set aside* management regime had the highest HSI

values and the largest relative increase, while other management regimes were only 75% of the improvement in HSI under the *set aside* regime. This improvement in habitat suitability may be explained by higher deadwood volumes, tree species richness and forest structure under this management regime (Dyola et al 2022). Other simulations have shown that *set asides* retain more older trees and consequently more deadwood habitat for biodiversity than managed forests (Heinonen et al 2017). In fact, deadwood volumes in *set aside* stands of our study were on average 18% higher (24.6 m^3 ha^{-1}) than in managed stands (4.4 m^3 ha^{-1}) under the reference climate scenario. This *set aside* deadwood volume is enough to support some of the threatened saproxylic species, for which deadwood requirements start from 20−30 m^3 ha^{-1} (Siitonen 2001).

BAU regimes, including clear cuts as the primary harvesting method, followed similar HSI patterns with an initial increase and a peak after 30−65 years (the final harvest), and a decrease until the end of the simulation horizon, indicating the negative impacts of final harvesting on HSI. However, some species benefited from open stand structures created by the final harvest and remaining harvest residues for deadwood. Although high volumes of deadwood are created by final harvests, it is not all available as habitat for biodiversity because site preparation after clear-cut (e.g., harrowing) and movements of forest machinery destroys coarse woody debris left since the harvest (Hautala et al 2004). Most BAU - regimes (BAU, *shortened rotation*, *no thinning*) resulted in low HSI values at the end of the simulation period among microclimatic species groups. This may be explained by the fact that these regimes temporarily increased habitat suitability during a short window of time due to the creation of deadwood from harvest residues. However, this is not long-lasting due to its decomposition within a few decades.

Extended rotation and GTR maintained better habitat suitability after final harvesting for some species groups. Extending the rotation increased deadwood volume, as there is more time for deadwood to accumulate. Additionally, extending the rotation length may result in higher number of large trees and larger coarse woody debris (Felton et al 2017), with further habitats improvements, the more the rotation is prolonged. Previous studies have highlighted the positive effects of GTR on forest biodiversity (Siira-Pietikäinen and Haimi 2009; Work et al 2010; Hämäläinen et al 2014). GTR is associated with relatively constant amounts of deadwood volumes, including both medium- and well-decayed deadwood, which explains higher habitat suitability for saproxylic species.

Continuous cover forestry (CCF management regimes) did not increase habitat suitability as much as BAU - regimes, however it improved habitat suitability at the end of the simulation period better than some BAU - regimes.

This minimum improvement in habitat suitability may be partly explained by the selective harvesting of the largest trees, reducing their natural occurrence. CCF has numerous biodiversity benefits compared to BAU - regimes, and it was expected that it would have a larger, positive impact on HSI. In BAU clear-cutting, residues left on the ground contributed deadwood with small diameters and a limited variability in decay classes (Kuuluvainen et al 2012), while in the CCF, the selective removal of the largest logs reduced the fraction of large diameter deadwood. The amount of canopy remaining after timber extraction was larger in the CCF than in the BAU, and this affected the quantity and quality of deadwood. This is because gaps left following clearcutting in BAU management will lead to more sunlight striking the surface of the deadwood, leading to photodegradation and to warmer and drier conditions favouring or retarding decomposition (Harmon et al 2020). However, the long-term positive effects of *continuous cover forestry* on habitat suitability may be higher than BAU-regimes, and with a longer simulation horizon, we should have seen larger improvements in HSI. CCF management maintains a more diverse forest structure with trees of different ages and species. It also provides better habitat suitability for species dependent on mature forest structure and deciduous trees (Peura et al 2018).

Effects of climate change on habitat suitability indices

Climate change alone had a significantly lower effect on habitat suitability of deadwood compared to forest management alone, with overall positive effects among all microclimatic species groups. These findings agree with Mazziotta et al (2016) and Mair et al (2018), who showed that habitat suitability of many of the study saproxylic fungi and beetle species improved or remained stable under climate change conditions. This is possibly due to increasing temperatures enhancing tree growth and mortality, leading to higher deadwood volumes (Kellomäki et al 2008; Kellomäki 2022). In this study, timber volumes increased by an average of 7% (RCP4.5) or 11% (RCP8.5) by climate change in *set aside* stands. However, the increase of deadwood volume was modest, indicating that the increase in drought induced by climate change did not increase natural mortality to an extent that would have significantly increased the volume of deadwood (Mazziotta et al 2014).

Combined effects of forest management and climate change on habitat suitability indices and deadwood dynamics

During the second half of the twenty-first century, climate change and management had a larger impact on the habitat suitability of saproxylic species than in the first half and is likely explained by the fact that in the second half, the

impact of climate change is expected to intensify, leading to a higher temperatures and consequently earlier final harvests (Kellomäki et al 2008). This will result in higher amounts of timber residues, increasing temporarily the volume of deadwood.

The effects of increased climate change severity and forestry intensification on HSI were more positive than negative, as habitat suitability improved more than deteriorated by climate change under different management regimes, leading to higher number of winners than losers. This is likely because an increase in temperature will increase the availability of deadwood regardless of management applied. Only two regimes, *no thinning* and *shortened rotation*, reduced habitat suitability more among shady and indifferent species groups and with the RCP8.5 scenario than among sunny species groups and with the RCP4.5 scenario. It is possible that, in these two management regimes, earlier final harvests destroyed suitable habitats for some saproxylic species as younger trees were cut and the variation in different deadwood types was reduced. However, under high warming (RCP8.5 scenario), a deterioration of the quality of the forest for saproxylic species is expected, as highlighted by the smaller number of winner species groups and higher number of losers compared to the moderate climate change scenario (RCP4.5). This may be explained by the fact that, under high warming, increased decomposition rates will reduce the retention time of the deadwood, making the habitat of many saproxylic species more temporary (Tuomi et al 2011; Mazziotta et al 2016).

The results of this study indicate management regimes that may benefit saproxylic species under climate change. Of the 21 species groups examined, 10 were winners in both climate change scenarios regardless of the management regime. The remainder of the species groups were winners, stable or losers depending on the management regime. This difference highlights the importance of applying a diverse range of management practices in the forest landscape, as no single management maximizes habitat suitability for all saproxylic species, regardless of climate change. However, among the procedures applied, a close-to-nature regime like the CCF (where only single large trees were harvested) showed the largest gains in habitat suitability compared to BAU - regimes (based on clear-cutting). In fact, under CCF, the HSI increased the most for shady and indifferent species groups. In addition, CCF also featured the largest number of winner species groups, explained by the fact that CCF accumulated larger amounts of standing timber volumes under climate change compared to conventional rotation forestry (Jönsson et al 2015). Larger tree canopies in CCF also created more potential habitats for species preferring shady and moist conditions.

Microclimate and deadwood type played an important role in determining the impact of climate change and management on habitat suitability for saproxylic species. Sunny species groups had a generally higher HSI compared to shady and indifferent species groups under all management types and all climate scenarios. All species groups associated with sunny microclimates were dependent on fresh- or medium- decayed deadwood. In contrast, for the shady and indifferent species groups, there were more species associated with medium- or well-decayed deadwood. More than half of the winner species (62%) were associated with fresh or medium decayed deadwood. Increasing temperatures speed up the decomposition rate, reducing the deadwood stock (Tuomi et al 2011; Mazziotta et al 2014; Russell et al 2014), which may result in species depending on well-decayed deadwood having less available resources in the future. About 24% of the species groups were dependent only on fresh deadwood while the balance was dependent on medium or well- decayed deadwood. This may partly explain why HSI remained low in managed forest stands where the availability of medium- and well- decayed deadwood was scarce because of management operations.

Study limitations

This study did not consider the impact of abiotic and biotic events (e.g., windthrows, insect outbreaks, drought, and wildfires) on habitat suitability of saproxylic species. Such occurrences are becoming more frequent as the climate warms (Venäläinen et al 2020). Extreme events, such as windthrows, have a dramatic impact on the capacity of the forest to provide deadwood for saproxylic species (Jönsson et al 2015; Zubizarreta-Gerendiain et al 2019). Thus, there is a need to study further the complex relationships between forest management, biodiversity, and climate change. In addition, this study did not consider the dispersal capacities of the species, as this information was not available. Accounting for this might have further reduced the habitat suitability for red-listed saproxylic species, as many are poor dispersers and consequently, would have increased the number of losers under climate change (Jaeschke et al 2013; Della Rocca and Milanesi 2020).

Conclusions

Our main finding was that forest management has a major role in mitigating the negative impacts of climate change on habitat suitability of saproxylic species in Finland. Based on these results, it may be concluded that the best way to limit the negative impact of climate change on their habitat is to increase the number of closer-to-nature management regimes like *set aside*, *continuous cover forestry*, *extended rotation* and *green tree retention* which allow for

a sufficient and diverse volume of deadwood. Except for *set aside* (which currently has low economic importance), these closer-to-nature regimes simultaneously benefit deadwood-associated saproxylic species and wood production. Our findings agree with earlier studies showing that saproxylic species will benefit from diverse management practices (Mönkkönen et al 2014; Triviño et al 2017). The uncertainty associated with predicting the impacts of climate change on the availability of deadwood for saproxylic species is certainly higher than the uncertainty predicting the effects of management regimes. However, we found that the negative impacts of high timber extraction rates were much higher than the impacts of climate change. By implementing a wider range of management regimes, critical ecosystem resources can be increased to create and maintain valuable habitats for saproxylic species under climate change.

Declarations

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