Combined threats of climate change and land use to boreal protected areas with red-listed forest species in Finland

Maattanen, Aino-Maija

2023-01

ELSEVIER

Combined threats of climate change and land use to boreal protected areas with red-listed forest species in Finland

Aino-Maija Määttänen [a,*], Raimo Virkkala [a], Niko Leikola [a], Juha Aalto [b,c], Risto K. Heikkinen [a]

[a] *Biodiversity Centre, Finnish Environment Institute, Latokartanonkaari 11, FI-00790 Helsinki, Finland*
[b] *Finnish Meteorological Institute, Weather and Climate Change Impact Research, Helsinki, Finland*
[c] *Department of Geosciences and Geography, University of Helsinki, P.O. Box 64, Gustaf Hällströmin katu 2a, 00014 Helsinki, Finland*

ABSTRACT

Protected areas (PAs) offer safe havens for threatened species, but their effectiveness is jeopardised due to climate change and habitat fragmentation in their surroundings. Species are forced into the unhospitable matrix in search of more favourable areas as climate conditions change, leading to negative effects on biodiversity. For red-listed forest species, the accelerating climate change can strengthen the negative effects of logging around PAs. In this work, we examine climate-change and land-use threats to biologically valuable PAs with red-listed species occurrences in Finland. Where the highest combined threats occur, do they coincide with accumulations of red-listed species, and how much do they vary between different boreal zones? This provides important knowledge for conservation planning in a managed matrix amid climate change. We use three spatial scales (100 m, 1 km, 10 km) to explore where the effects of clear-cutting have been the most intense during this millennium: right outside the PA border, exposing PAs to local-scale edge effects, or at landscape scales disrupting species movements due to degraded connectivity and increased fragmentation. For each PA, we also quantify how the January mean temperature (T_{Jan}), growing degree days (GDD5) and water balance (WAB) conditions are predicted to change by the end of the century under the RCP4.5 scenario. Additionally, for these variables, we estimate the velocity of the changes within valuable PAs. The proportion of forests which underwent clear-cutting was the highest in the more productive southern boreal zone and at the landscape scale of 10 km around the PAs. The combined threats of land use and climate change were evident, as there were positive correlations between logging levels around PAs with red-listed species and both the velocity values of GDD5 and T_{Jan} in the PAs. T_{Jan} is changing particularly fast in the northern boreal zone, where the coldest current climate conditions are projected to disappear by the end of the century. GDD5 in turn is changing fastest in the topographically flat southern boreal zone. GDD5 and T_{Jan} had generally a positive relationship with the magnitude of clear-cuts in a 10 km buffer zone. However, the direction of this relationship varied between the boreal zones. In climate-wise conservation planning for red-listed boreal forest species, multiple elements are needed. First and foremost, valuable sites for the red-listed species in the PA network should be identified and the climate change and land use-based threats to them measured. This information provides an elementary basis for additional threat analyses focusing on species habitat requirements and dispersal ecology. Together, this information can be used to assess the potential of different conservation measures to mitigate the

---

* Corresponding author.
E-mail address: aino-maija.maattanen@syke.fi (A.-M. Määttänen).

combined climate-change and land-use risks, and ultimately to improve the conservation status of red-listed forest species.

1. Introduction

Pressures on biodiversity have increased during the past decades (Butchart et al., 2010; Díaz et al., 2019) and are predicted to continue during this century (Pereira et al., 2010). Land use and climate change are the main drivers of biodiversity change (Sala et al., 2000; Segan et al., 2016) via the loss of natural ecosystems and changes in the climatic suitability for species (Mantyka-Pringle et al., 2012; Oliver and Morecroft, 2014; Travis, 2003). Moreover, anthropogenic land use causes degradation and fragmentation of habitats (Aycrigg et al., 2022; Haddad et al., 2015). Due to the fragmentation, the remaining habitat occurs in smaller, often disconnected patches in the human-modified landscape (Hanski, 2005, 2011; Svensson et al., 2019).

Climate warming has been linked to observed changes in species distributions, and it is expected to cause accelerating poleward shifts in the ranges of species (Chen et al., 2011; Garcia et al., 2014; Lenoir and Svenning, 2015; Virkkala et al., 2013; Virkkala and Lehikoinen, 2014). Climate change is projected to be the most pronounced in the high latitude environments because of the greater temperature increase in the north (Baettig et al., 2007; Elmhagen et al., 2015; Jetz et al., 2007). However, although the observed overall warming in high-latitudes has been nearly four-fold compared to the global average (Rantanen et al., 2022), temperature and precipitation trends may show substantial regional and local scale variation (Aalto et al., 2016; Walsh et al., 2011). Consequently, the magnitude of climate change impacts on biodiversity may significantly vary between different areas.

It is increasingly considered that the impacts of harmful land use and climate change may pose combined negative impacts on biodiversity (Travis, 2003; Oliver and Morecroft, 2014; Shrestha et al., 2021). Thus, identifying the areas where high rates of climate change and detrimental land use co-occur and produce major threats to biodiversity has become a key task in climate-wise conservation planning (i.e., planning to support the adaptation of biodiversity to climate change) (Ordonez et al., 2014; Nadeau et al., 2015; Aycrigg et al., 2022). Moreover, the usefulness of the combined assessments of climate-change and land-use threats for conservation planning can be further increased by linking these threats to spatial patterns of red-listed species and their accumulations (Heikkinen et al., 2021; Shrestha et al., 2021).

Land use and climate change may influence species distributions and populations both outside and within protected areas (PAs) (Araújo et al., 2004, 2011; Hansen and DeFries, 2007; Vincent et al., 2019). For forest habitats and species, local-scale clear-cuts occurring close to PA edges cause edge effects which can influence the humidity conditions within PAs (Hylander et al., 2004; Moen and Jonsson, 2003; Murcia, 1995). At greater landscape and regional scales, forest management with clear-cuts often results in mature forest habitat loss and fragmentation, which has two-fold impacts on forest biota. First, increased habitat fragmentation can disturb forest species metapopulation dynamics, i.e., the ability to maintain local populations in their current range areas through between-patch dispersal (Hanski and Simberloff, 1997; Hansen and DeFries, 2007). Second, in the longer term, forest fragmentation decreases the ecological connectivity between the forested PAs (Mikusiński et al., 2021; Ward et al., 2020) and may obstruct species to disperse to new climatically suitable areas and PAs (Travis, 2003; Hamilton et al., 2013; Murray et al., 2017).

Forestry is a central driver affecting boreal species in northern Europe (Abrego et al., 2017b; Curtis et al., 2018, 2006). In Finland, almost all forest land outside protected areas is subject to systematic silvicultural practices, which include the thinning of young and middle-aged stands, clear-cutting of mature stands and replanting. Thus, forest management has produced a truncated age-class distribution with a reduced area of old-growth forest (Kuuluvainen and Aakala, 2011; Kuuluvainen and Gauthier, 2018; Kuuluvainen et al., 2012) and caused many forest species to become threatened (Hyvärinen et al., 2019). Temporary loss of forest cover in managed boreal forests does not, strictly speaking, correspond to the complete loss of forest areas as it does in tropical biomes (Curtis et al., 2018; Davis et al., 2020). However, boreal forests subjected to a management cycle with short, 60–80-year-long rotations and cyclical clear-cuts represent permanently ecologically degraded ecosystems for red-listed species of mature and old-growth forests (Abrego et al., 2017a; Moen and Jonsson, 2003; Roberge et al., 2018; Tikkanen et al., 2006). For monitoring the degradation of mature and old-growth forests into younger managed boreal forests, remote sensing products, such as Global Forest Change (A Landsat-based change detection spatial data layer, see Hansen et al., 2013), provide useful tools for covering large areas systematically (Ceccherini et al., 2020, 2021; Määttänen et al., 2022).

Forest-use history differs between different parts of Finland. In southern Finland, forests have been used for centuries, previously slash-and-burn-cultivation affected large forest areas; and in central Finland, tar production was common (Virkkala and Toivonen, 1999). Large-scale industrial forestry with logging increased in the 20th century, and clear-cuts started also in northern Finland. According to the national forest inventories, in the northern half of Finland, over 50 % of forests were over 120 years in the early 1920 s (1921–1924), while the proportion of these forests in 2014–2018 was only 17 % (Korhonen et al., 2021). In the southern half of Finland, the proportion of forests over 80 years was lowest in the early 20th century due to slash-burn cultivation carried out in earlier centuries but increased in the mid-20th century (Korhonen et al., 2021). The logging volume has increased in Finland during the past decades, i.e., during the time period of our GFC-based analysis (see, e.g., Virkkala et al., 2020), decreasing clearly the proportion of forests over 80 years in southern Finland and forests over 120 years in northern Finland.

A key aim of the PA network is to ensure the maintenance of populations, species and communities (Gaston et al., 2008), also in the face of climate change (Hiley et al., 2013). In Finland, bird populations in PAs have been observed to shift northwards by a rate of 1.8 km/year (Virkkala et al., 2018), and these range changes have been supported by the PAs network (Virkkala et al., 2014). However, in human-dominated landscapes, there are apparent carryover impacts from the matrix into the boreal PAs causing negative impacts on

biodiversity. Thus, PAs have not been able to maintain their species composition and abundances in severely degraded forest land-scapes (Häkkilä et al., 2017), and increased logging has caused a decline in many resident forest bird species especially in the PAs located in southern Finland (Virkkala et al., 2020). Consequently, a PA network may be susceptible to intensification of land use outside protected areas, particularly when the PAs are small, and their network is sparse. This suggests that the connectivity of the PA network may largely define the ability of the PAs to support the northward shifts of sensitive species, such as old-growth forest biota.

In our previous paper, we examined the harmful impacts stemming from forest logging around PAs with red-listed mature and old-growth forest species at three buffers, i.e., 100 m, 1 km and 10 km, corresponding to local, landscape and regional scales (Määttänen et al., 2022). Using Global Forest Change data (Hansen et al., 2013), we showed that there was high logging pressure, measured from clear-cuts, in Finland in 2001–2019 around PAs with valuable species. Here, we complement our previous study on the land use around the PAs with an assessment of climate change-based threats. We restrict our analysis to PAs where red-listed species have been observed, i.e., PAs which harbour documented important biodiversity values. We analyse the climatic threats to PAs by assessing how severely exposed they are to climate-change impacts in two ways: first, based on the change in climatic variables between present-day and future climates in the PAs; and second, based on average climate velocity calculated for each PA. Here, climate velocity metrics are measured based on the distance between climatically analogous present-day and future locations. These metrics illustrate the speed of how rapidly species should move to remain under similar climatic conditions; typically, velocities receive the highest values in vast flatland areas (Brito-Morales et al., 2018; Heikkinen et al., 2020). The importance of integrating climate-change exposure to con-servation planning in our case is highlighted by the fact that climate velocities in boreal areas are among the highest, and the climate residence time (i.e., the amount of time needed for a climate isoline to emerge from a given PA) of the high latitude PAs, including boreal PAs, are globally among the lowest (Loarie et al., 2009; Brito-Morales et al., 2018).

Our examination of the spatial variation in land-use and climate-change threats, combined with the known occurrences of red-listed forest species and their accumulations, will produce essential information for the planning and targeting of new conservation and management actions to support the protection of forest biodiversity under climate change. Our main study questions are: (1) How do climate change and climate velocity in PAs and land use around PAs with red-listed forest species differ in the south-north gradient across the boreal zones in Finland? (2) Are the high rates of climate change and harmful land-use risks coinciding in certain areas and PAs? (3) Are some of the PAs with the most valuable accumulations of red-listed species facing high climate-change and land-use threats, calling for increased management planning?
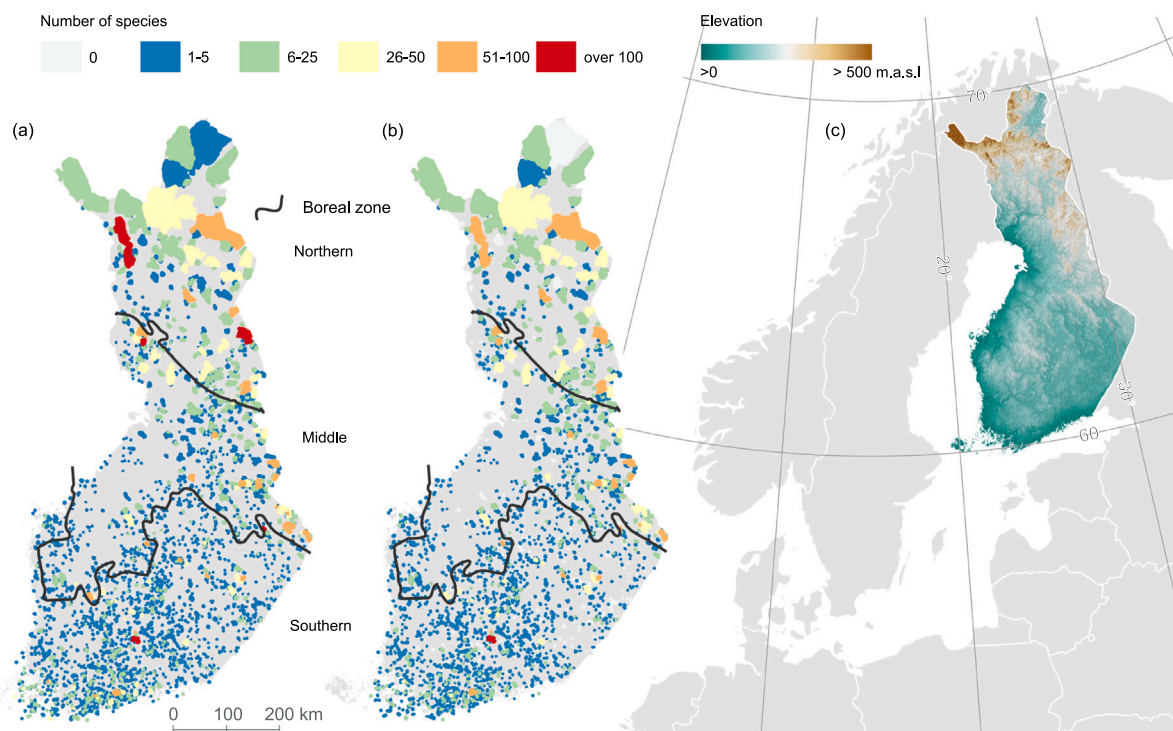

Fig. 1. (a) Number of red-listed forest species in a protected area (PA). (b) number of red-listed species in a PA, whose primary habitat is old-growth forest. (c) The location and topography of Finland. Finland is located in Northern Europe and extends between latitudes 60º and 70º and exhibits different zones of the boreal forest vegetation: southern, middle and northern, representing the underlying abiotic properties of the environment (Hyvärinen et al., 2019). In southern Finland, and along the shore, the terrain is mostly flat, whereas northern parts of the country exhibit higher variation in elevation and topography. The protected area network that harbours red-listed forest species in Finland is centred in the northern boreal zone with vast areas under conservation, whereas the PAs in southern Finland are often small and embedded in a matrix of intensive land use. Sizes of PAs have been exaggerated for visibility.

2. Material and methods

2.1. Protected areas

We extracted the spatial data on the PAs of Finland according to the situation in July of 2021 from the geographic information system ULJAS (SATJ), maintained by Metsähallitus Parks and Wildlife Finland. Eighteen types of PAs (Supplementary material, Table S1) were considered, the main body of the data consisting of PAs on government-owned and privately owned areas (e.g., strict nature reserves, national parks and PAs established for the protection of old-growth forests, peatlands and herb-rich forests, and areas that are designated to be future PAs by Metsähallitus Parks and Wildlife Finland.

The spatial polygons for the different types of PAs were in many cases overlapping. Thus, following Määttänen et al. (2022), we dissolved all the overlapping and adjacent PA polygons in the raw data together. Next, in contrast to Määttänen et al. (ibid.), here we excluded PA polygons smaller than 1 hectare in size, as well as PAs situated on small-sized islands in the Baltic Sea and PAs with no forest cover. The higher cut-off size level ensured that the calculation of climate change metrics was based on more than just one climate data pixel in all PAs (see Section 2.3). The resulting dataset consisted of 14,965 PA polygons, ranging from 1 to 355,708 ha in size. Basic descriptive statistics of PAs in different boreal zones are provided in Table S2.

A clear majority of the polygons had no red-listed forest species observations (see Section 2.2) and were excluded from our main analysis. The final set of PAs with red-listed forest species included 3507 areas whose size varied similarly as in the full PA data set. Following Määttänen et al. (2022), these 3507 PAs were assigned to and analysed separately for the three different forest vegetation zones: the southern boreal, the middle boreal and the northern boreal zone, because they represent different biotic and abiotic conditions (Hyvärinen et al., 2019), which need to be considered in conservation planning (see Fig. 1).

2.2. Species data

From the 6683 species regarded as red-listed (29.8 % of all evaluated 22,418 species) in the most recent assessment of the Red List species in Finland (Hyvärinen et al., 2019), we studied 886 forest-dwelling, red-listed species (IUCN categories CR - Critically Endangered, EN – Endangered, VU – Vulnerable and NT - Near Threatened). Following Määttänen et al. (2020), we focused on species that primarily inhabit mature forests (forests that have reached maturity but are not yet old-growth (Martikainen et al., 2000)) or old-growth forests and excluded species that can thrive equally well in forests with a semi-open canopy and shrubby habitats. This selection enabled us to base our analyses on forest species for which clear-cutting causes a loss of suitable habitat (Tikkanen et al., 2006), a land use trend that was measured for the surroundings of each PA (see Section 2.4). The primary habitat of the included species was determined based on online species databases and literature on species' ecological requirements. Red-listed bird species were excluded from our study, because their observations were generally not of a sufficient spatial accuracy.

Observations of 886 red-listed forest species were acquired from two sources: the Finnish Biodiversity Information Facility (FinBIF) and Parks and Wildlife Finland's geographic information system, ULJAS (LajiGIS). From the 886 species, 391 were species which are strictly confined to old-growth forests. Two criteria were employed when selecting observations for our study: (i) observations with a spatial accuracy of less than 100 m were excluded; (ii) observations made earlier than the year 1990 were not considered.

The selected observations from the FinBIF and LajiGIS databases were combined, observations with an accuracy of > 1 m were averaged to their centre locations, and based on this location, each observation was assigned to one of the 100-m square included in a 100×100-m lattice system covering the whole country. This was done using the FCS biological records tool (version 3.3.0) in QGIS. Next, duplicate records for a given species were excluded from each of the 100-m square. After these steps in data management, the species occurrence data contained 99,180 100-m records from the 886 red-listed species. Of these, 45,175 observations (45.5 %) were recorded within the protected areas or intersecting with the border of the PAs. This set of 45,175 species observations occurring in the PAs included 765 species and constituted the final set of red-listed species used in the subsequent analysis (for the full list of species, see Supplementary material, Table S3).

In the final step of the species data processing, we developed two metrics ('importance indices') to assess the conservation importance of the PAs harbouring occurrences of the 765 red-listed species. The calculation of our first importance index (hereafter 'rarity weighted index') included several steps. First, for each of the 765 species, a percentage of occurrences across all the 100-m squares the species inhabits was calculated. Thus, if a given species was recorded in fifty 100-m squares, each occupied cell was assigned a value of 0.02 for that species. Next, for a given species, these percentage-based values were summed across all the 100-m squares in each PA, and the corresponding percentage-based values were summed across all red-listed species observed in that PA. The same process was repeated for all PAs with red-listed species records.

The second importance index (hereafter the 'red-list weighted index') was calculated to reflect the differences between PAs in terms of how many occurrences of red-listed species they harbour. Here, we weighted our study species following Forsius et al. (2021) to reflect their IUCN Red List status as follows: DD (data deficient) - 0, NT - 1, VU - 5, EN - 10 and CR - 20. Next, the occurrences of the 765 red-listed species in each 100-m square were replaced by these Red List status values. In the final step, the rescaled occurrence values were summed across all species and across all 100-m squares within a PA, and this process was repeated for each of the studied protected areas. All calculations were conducted using R (R Core Team, 2014) and the GIS procedures were executed using QGIS (version 3.16.4).

2.3. Climate data

Climate change-based threats to the studied PAs were measured based on data developed by Heikkinen et al. (2020), which were employed also by Heikkinen et al. (2021) to assess the joint climate-change and land-use threats to EU Habitats Directive species. Thus, a more in-depth description of the climate data construction process is provided in these two papers.

In short, using weather data from 313 stations located in Finland, northern Sweden and Norway (European Climate Assessment and Dataset [ECA&D]) (Klok and Tank, 2009) generalised additive models, the geographical location (latitude and longitude, included as an anisotropic interaction), local topography (elevation, potential incoming solar radiation, relative elevation) and water cover (sea and lake proximity) variables, we developed measures of the monthly average temperatures for 1981–2010 ('baseline climate') at a resolution of 50 × 50 m (see Aalto et al., 2017).

Monthly precipitation data for 1981–2010 were developed for the same 50-m resolution grid using global kriging interpolation, implemented in R package gstat version 1.1-0. Kriging was carried out based on data from 343 rain gauges obtained from the ECA&D dataset, geographical location, topography (elevation and eastness index) and proximity to the sea.

The 50-m resolution topoclimatic monthly air temperature and precipitation data were employed to construct the measures of three bioclimatic variables to describe the baseline 1981–2010 climate conditions: (1) the annual temperature sum indicating the accumulated warmth (growing degree days, GDD5, °C days); the mean January air temperature (T_{Jan}, °C); and the climatic water balance (WAB, mm). These three variables were selected so that they together provide complementary measures of the winter- and summertime temperature and moisture conditions that are the key drivers of northern ecosystems and species (Howard et al., 2015; Huntley et al., 2008; Luoto et al., 2006; Sykes et al., 1996). The climatic water balance indicates the difference between the total annual precipitation sum and the potential evapotranspiration (PET). The PET value was estimated from the monthly air temperatures following Skov and Svenning (2004):

$$PET = 58.93 \times T_{above0°C}/12$$

For the future climate surfaces, we used ensemble data, which is a combination of 23 individual global climate models (Taylor et al., 2012), as available from the Coupled Model Intercomparison Project (CMIP5) archives. To explore the patterns of climate change and climate change velocity across PAs, we used GCM ensemble data averaged for the years 2070–2099 and the Representative Concentration Pathway RCP4.5. Since our aim was to explore the spatial variation of climate-change risks on PAs, we only used one climate scenario and assumed that using lower or higher concentration scenarios would yield similar responses, varying in intensity (Heikkinen et al., 2020; Mair et al., 2018; McGuire et al., 2016) The extracted GCM ensemble climate surfaces included monthly air temperature and precipitation data, which we bilinearly interpolated to match the 50 × 50 m grid. These interpolated climate surfaces were added to the baseline 1981–2010 climate data to develop the 50-m monthly climate data for 2070–2099. After this, the values for the three bioclimatic variables (GDD5, T_{Jan}, WAB) were recalculated for the 50-m resolution grid across the whole study area (see Heikkinen et al., 2020).

The three 50-m topoclimate data surfaces, i.e., GDD5, T_{Jan}, and WAB, developed for the baseline time slice and the RCP4.5 future slice of 2070–2099 were used to construct two types of climate exposure measures for the 50 × 50-m lattice system covering all of Finland. The first exposure measure was the absolute difference between the two time slices, i.e., a substitution of the baseline climate surface from the future climate surface, conducted for each of the 50-m cells and all three variables. These three measures are referred to as the absolute difference in GDD5 (GDD5 Diff), in T_{Jan}, (T_{Jan} Diff) and in WAB (WAB Diff).

Our second exposure measures were the climate change velocity metrics developed for each of the 50-m cell and all three variables. Climate velocities were calculated using the climate-analogue velocity method (Brito-Morales et al., 2018; Hamann et al., 2015) following Heikkinen et al. (2020). In the climate-analogue method, velocities are calculated as the distance between climatically similar grid cells in present and future climates divided by the number of years between the two time periods.

In the baseline and in the future climate surfaces, the continuous climate values in each of the 50-m grid cells were converted into categorical values before actual velocity calculations. The following class ranges were used in the conversion: GDD, within-class range 50 °C; T_{Jan}, within-class range 0.5 °C; WAB, within-class range 50 mm (for details, see Heikkinen et al., 2020). Based on the categorised climate surfaces, a search of the minimum distances between grid cells with similar present-day and future GDD5 / T_{Jan} / WAB climates was executed using the ArcGIS software (Desktop 10.5.1) and the Euclidean distance function, as well as the climate velocity values generated for each bioclimatic variable and each 50-m grid cell to describe the level of different climate exposure risks a given site is projected to face.

2.4. Land-use data

Following Määttänen et al. (2022), we estimated the amount of negative land use concerning the red-listed forest species around the PAs using three buffers of 100 m, 1 km and 10 km in size. In our study area, changes in forest cover largely consist of clear-cuttings, which typically lead to detrimental impacts and habitat loss for old-growth forest species (Svensson et al., 2019; Tingstad et al., 2018).

To assess the changes in forest cover, we first determined the forest extent prior to the year 2000 based on the Corine Land Cover (hereafter CLC2000) data with a spatial resolution of 25 m. For this, a forest distribution raster was developed based on combined data on occurrences of CLC2000 classes of broad-leaved forest, coniferous forest, mixed forest and transitional woodland where the canopy cover was > 10 %. The change in the forest cover was assessed as a cumulative measure over the years 2000–2020 based on the Global Forest Change (hereafter GFC) dataset Forest Loss layer (version 1.8) (Hansen et al., 2013). Using the GFC data, we identified CLC2000

Table 1

Values and significance in the velocity (km/year, mean±S.E., range in parentheses) of growing degree days (GDD5), January mean temperature (T_{Jan}) and water balance (WAB) between 1981 and 2010 and 2070–2099 in the PAs where red-listed forest species were observed in the three forest vegetation zones. The statistical significance is based on the Kruskall-Wallis one-way analysis of variance (K=3) with a posteriori tests. Velocity is measured as the distance between the nearest climatically similar locations in 1981–2010 and 2070–2099, divided by the time difference.

Climate velocity variable	Forest vegetation zone			Test statistic		Southern boreal vs. middle boreal		Southern boreal vs. northern boreal		Middle boreal vs. northern boreal	
	Southern boreal (km/year) (n = 2343)	Middle boreal (km/year) (n = 899)	Northern boreal (km/year) (n = 265)	z	P	z	P	z	P	z	P
GDD5	3.86 ± 0.02 (1.21–5.75)	2.81 ± 0.03 (1.00–5.32)	1.28 ± 0.04 (0.16–2.57)	1184.18	<0.001	927.40	<0.001	1892.63	<0.001	965.23	<0.001
T_{Jan}	3.93 ± 0.02 (1.37–6.29	4.03 ± 0.03 (1.75–5.91)	5.90 ± 0.12 (1.78–8.99)	272.51	<0.001	14.39	0.717	1063.67	<0.001	1078.06	<0.001
WAB	0.08 ± 0.00 (0–2.82)	0.06 ± 0.00 (0–1.14)	0.01 ± 0.00 (0–0.19)	206.63	<0.001	358.33	<0.001	820.13	<0.001	461.80	<0.001

forest areas that have been transformed in our study area predominantly due to clear-cuttings and marginally due to forest fires or storms (see Määttänen et al., 2022). After this, the forest cover change was calculated by subtracting the pixels appointed as losses according to the GFC from the starting point CLC2000 forest distribution raster. This provided relative measures of forest loss (range 0 – 100 %) for the 100 m, 1 km and 10 km buffers in each study PA.

2.5. Data analysis

All intersecting pixels were considered when calculating the mean climate changes and climate velocities for PAs and the land use intensity in the surrounding buffers. The results are shown as a set of scatterplots and maps of the individual threat variables and selected joint combinations of the variables (forest change vs. T_{Jan} velocity, forest change vs. GDD5 velocity, forest change vs. WAB velocity). These analyses were done for each of the three vegetation zones. Correlation (Spearman rank, r_S) and significance were calculated between the variables in the analyses. To compare the significance of the changes in the velocity of climate variables between forest vegetation zones, as well as the significance in the values of species indices (rarity weighted index and red-list weighted index) between PAs of the different zones, we adopted a non-parametric Kruskall-Wallis analysis of variance with pairwise a posteriori tests. Finally, a separate examination of the relationships between the highest 10 % fraction of the PAs based on the rarity weighted index and red-list weighted index and the climate-change velocity and land-use threats were carried out.

3. Results

3.1. Patterns in bioclimate

January temperatures in the PAs are predicted to warm on average by 4.5 ℃ degrees (values varying between 3.6 and 5.4 ℃ degrees) by the end of the century. The projected warming will be most pronounced, just over 5 ℃ degrees on average, in the northern boreal PAs, 4.9℃ degrees in the middle boreal and 4.4 in southern boreal PAs. The change in growing degree days sum (GDD5 Diff) across all PAs is on average 454 ℃ days (range between 292 and 507 ℃ degree days). This change is strongest in southern boreal PAs
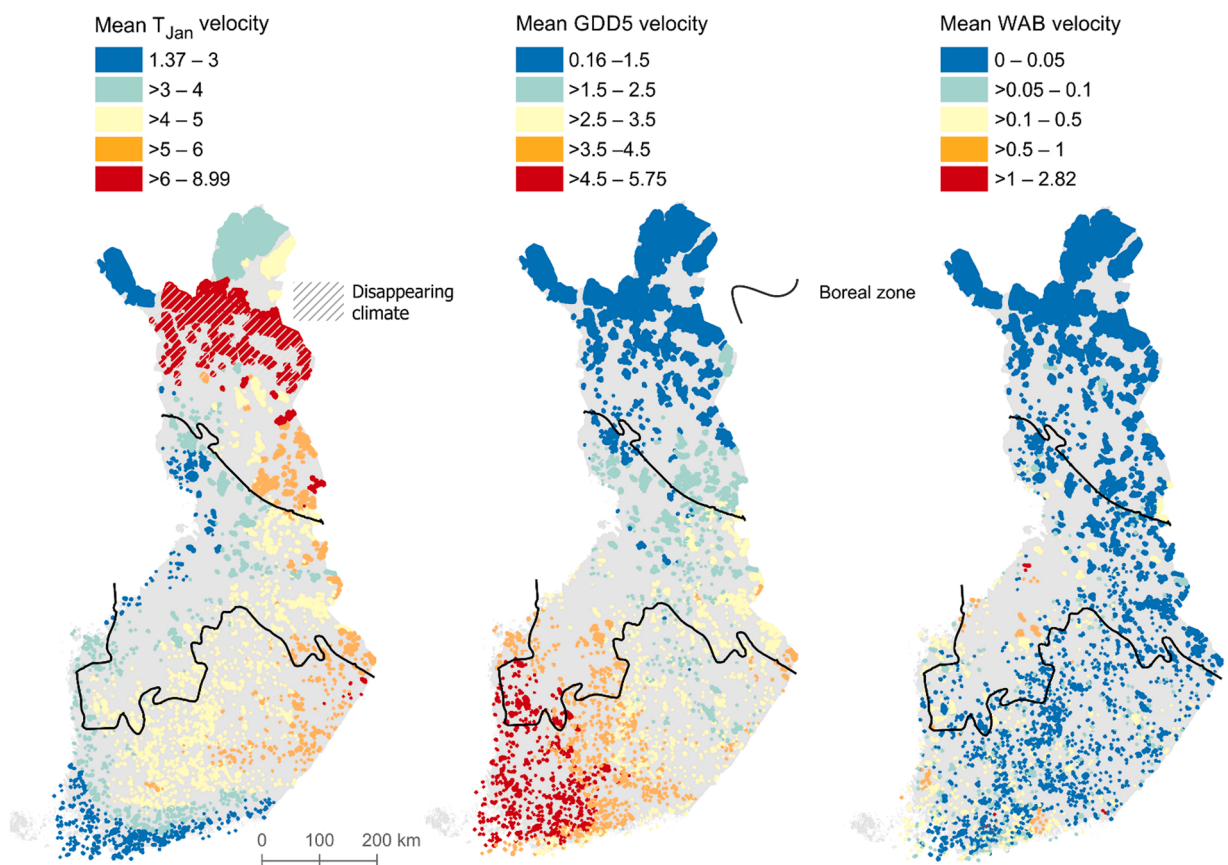

Fig. 2. Mean velocities of January mean temperature (T_{Jan}), growing degree days (GDD5) and water balance (WAB) within PAs with red-listed forest species. Velocities show the rate (km/year) of spatial changes in analogous climatic conditions between present-day (1981 – 2020) and future (RCP 4.5 based predictions for 2070–2099) climates. Sizes of PAs have been exaggerated for visibility.

(with a mean of 473 °C days) and declines towards middle and northern boreal PAs being on average 422 °C days and 395 °C days, respectively. Water balance is predicted to stay positive in the studied PA network, but the surplus of water decreases slightly, on average 36 mm with an average of − 40 mm, − 30 mm and − 22 mm in southern, middle and northern boreal PAs, respectively. However, the overall patterns of WAB Diff are sporadic, and the average values across PAs range between 105 mm less water in a PA to 50 mm more water in a PA.

The velocities of the three climate variables in the PAs are significantly different between the three biogeographic zones (Table 1). Additionally, all pairwise comparisons of vegetation zones for the velocities of the three climate variables are significant except for the T_{Jan} velocities between southern and middle boreal forest vegetation zones. The GDD5 velocity declines from south to north, whereas the velocity for the T_{Jan} shows contrasting patterns (Fig. 2). The WAB velocities in the PAs are low with a mean of 10–80 m/year in the different zones compared to the GDD5 velocity (mean 1.3–3.9 km/year in the different zones) or that of T_{Jan} (mean 3.9–5.9 km/year).

Similar trends emerge when the relationship between T_{Jan} Diff, GDD5 Diff and WAB Diff, and their respective velocities in the PAs, are examined in the three biogeographic zones (Fig. 3). There is a fairly linear relationship between the T_{Jan} Diff and T_{Jan} velocities as well as a clear south-to-north gradient with increasing values. In some of the northern boreal PAs with high T_{Jan} velocities, current harsh winter climate conditions are projected to disappear by the end of the century. The relationship between the GDD5 Diff and GDD5 velocities is also linear but contrasts with the T_{Jan} variables; it increases towards the south. The correlation between the T_{Jan} Diff and T_{Jan} velocities is highly positive ($r_S = 0.421$, $p < 0.001$, N = 3507) as well as between the GDD5 Diff and GDD5 velocities ($r_S = 0.617$, $p < 0.001$). The WAB Diff is negatively correlated with the WAB velocity ($r_S = −0.572$, $p < 0.001$) but values for these variables are low and their relationships do not show overall clear trends (Fig. 3).

3.2. Combined land-use – climate-change threats

Scatterplots of relative forest cover in the year 2000 within the three buffers around PAs (100 m, 1 km, 10 km) and mean PA velocities of T_{Jan}, GDD5 and WAB (Fig. S1) show that the PAs with a low proportion of forests around them are not at a higher risk in terms of climate velocity. There are no clear relationships with the projected climate velocity in the buffers of 100 m or 1 km in T_{Jan}, GDD5 and WAB velocities. The same lack of a clear relationship is also evident in the 10 km buffer in the middle and northern boreal zones and in the 10 km zone in GDD5 and WAB in the southern boreal zone. However, in the southern boreal zone, in the 10 km buffer, the forest cover increased as T_{Jan} increased.

The highest proportion of clear-cuts occurs in the 10 km buffer around the studied PAs being, on average, 23.8 %, 19.3 % and 10.3 % in the southern, middle and northern boreal PAs, respectively, followed closely by the 1 km buffer, where corresponding values were 21.4 %, 19.3 % and 11.5 %. In comparison, clear-cuts in the 100 m buffer were lower, on average 16.7 %, 16.7 %, and 9.6 %, in the studied southern, middle and northern PAs, respectively (Fig. S2). The covariation of mean climate velocities in PAs and the 10 km buffer forest change around them is visualised in Fig. 4 (see Supplementary material, Fig. S3 and Fig. S4, for scatterplots with forest change in the 1 km and 100 m buffers). The correlation between forest change in the 10 km buffer and GDD5 velocity is positive ($r_S=0.356$, $p < 0.001$) as is also the case between forest change and T_{Jan} velocity ($r_S = 0.167$, $p < 0.001$). In contrast, forest change and WAB velocity are not correlated ($r_S = 0.031$, $p = 0.064$).
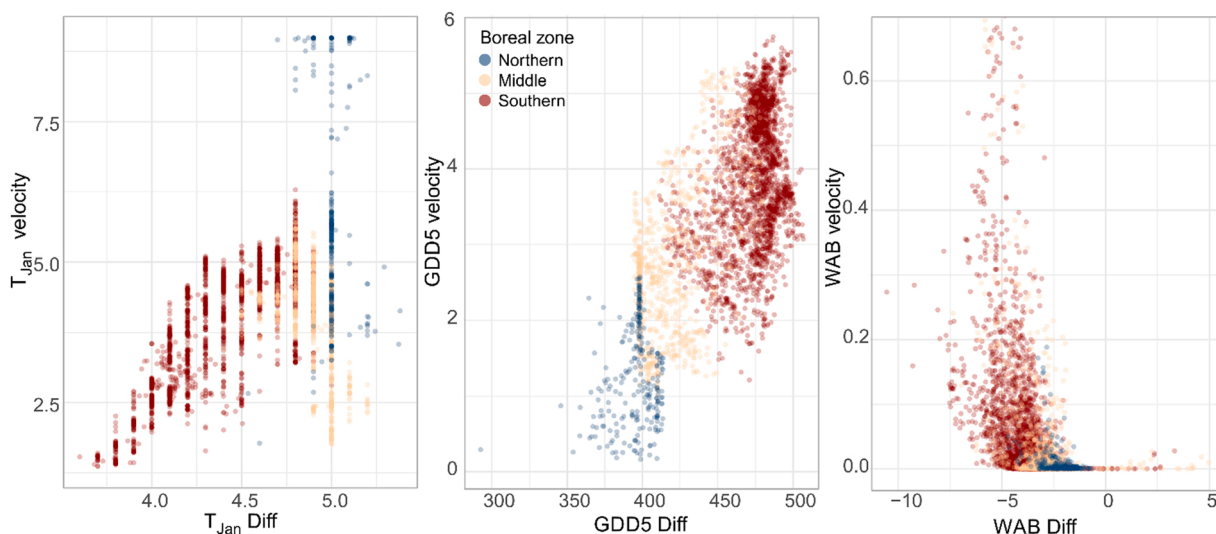

Fig. 3. Relationships between mean absolute change and the mean velocity of T_{Jan}, GDD5 and WAB in the PAs with red-listed forest species in the three boreal zones of Finland. Those northern PAs where January temperature velocities are coded to exceed 8 km per year are projected to experience disappearing winter climate conditions. For WAB results, only the lowest 99 % of the PA velocity values are plotted due to the highly skewed distribution of values around 0. The maximum WAB velocity value was 2.8 and there were 10 PAs with a WAB velocity value greater than 1.
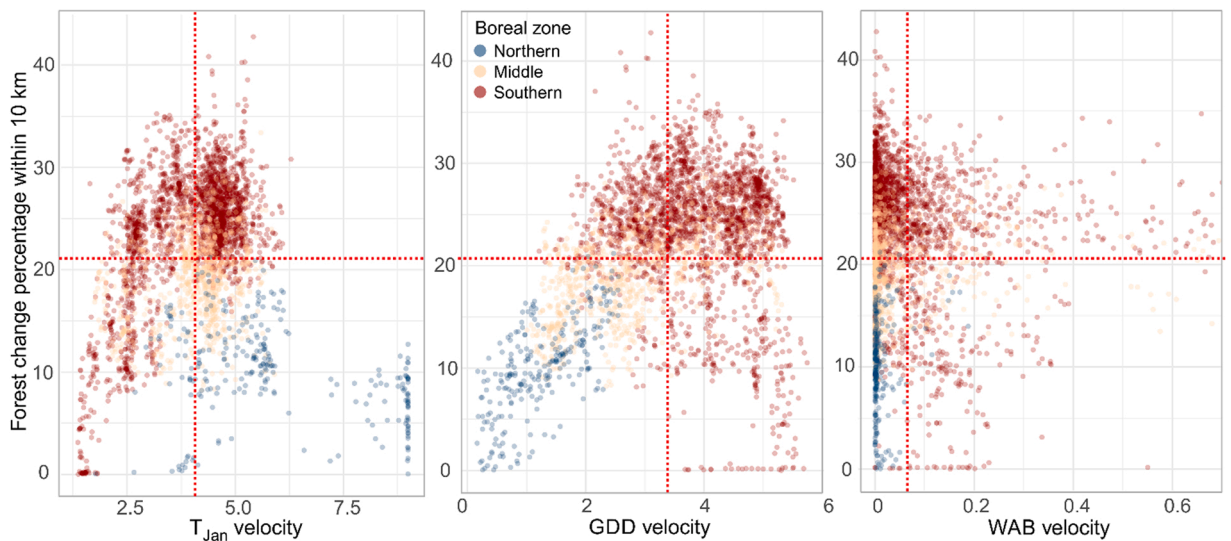
Fig. 4. Combined threats of climate change velocities within PAs and the proportion of clear-cuts around 10 km from the PAs during the last 20 years. On average, the forests within 10 km from the PAs with red-listed species have been clear-cut at the rate of 21 %. Mean velocities for all PAs are 4.1 km/year, 3.4 km/year and 67 m/year for TJan, GDD5 and WAB, respectively. Top right in the figures are PAs with high combined risks, bottom left PAs with low risks, and top left and bottom right PAs with joined medium-level risks (sections separated with dashed lines representing the mean values of each variable). The PAs in the southern boreal zone that exhibit no change in the surrounding forest cover are protected islands in the Baltic Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Conservation importance indices

The two indices describing the biological importance of a PA were positively correlated ($r_S = 0.491$, $p < 0.001$, N = 3507), mirroring the relationship of species' red-list status and their observation density. PAs located in the northern boreal zone were biologically the most important, while southern boreal PAs scored higher than their middle boreal counterparts according to the occurrence rarity weighted index, but lower according to the red-list weighted index (Table S2 and Table S4). Values of both rarity weighted index and red-listed weighted index differed significantly between PAs of the three zones (Table S4). However, in a pairwise
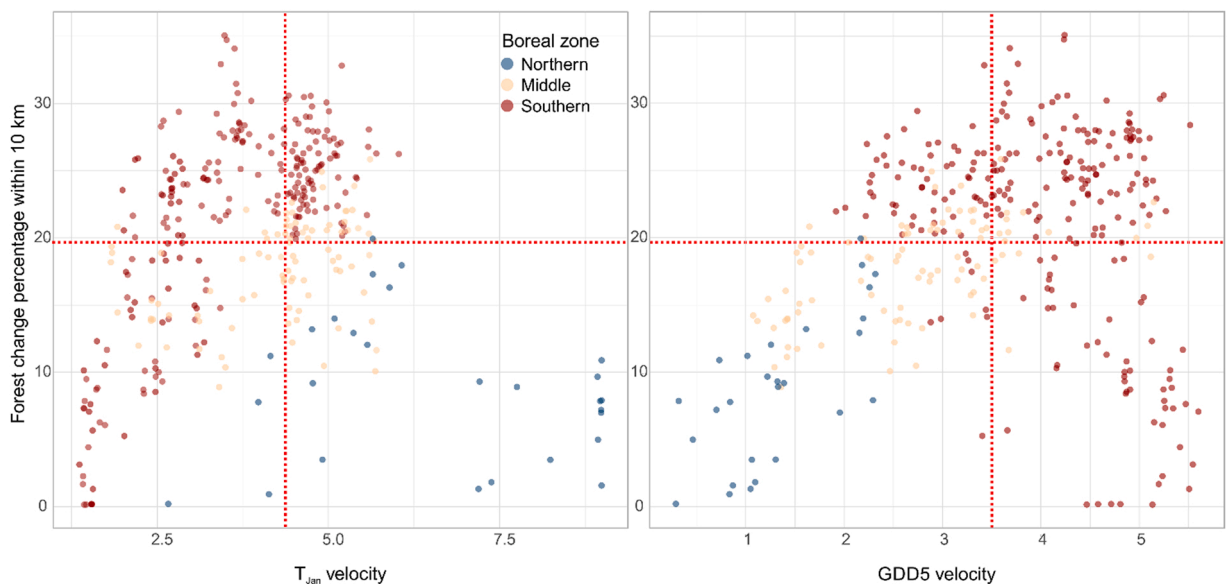

Fig. 5. The top 10 % of the PAs according to their red-list weighted species importance scores and their joined threats of land use (percentage of forest clear-cuts around 10 kilometres) and velocities of GDD5 and TJan. Top right in the figures are high combined-risk PAs, bottom left low-risk PAs, and top left and bottom right joined medium-level risks (sections separated with dashed lines representing the mean values of each variable). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

comparison, only northern boreal PAs differed in both indices from the middle boreal or southern boreal PAs, while index values between southern and middle boreal PAs did not differ in either of the indices (Table S4).

Both indices were moderately correlated with PA size (rarity weighted index and PA area $r_S = 0.33$ and red-list weighted index and PA area $r_S = 0.28$), but there was substantial variation in the relationships (Fig. S5). Since both indices are derived from species occurrence data, the spatial patterns of PAs with high index values (Fig. S6) are similar to the species richness represented in Fig. 1.

The top 10 % of PAs based on red-list weighted and rarity weighted species index scores were plotted to visualise their exposure to the combined threats of the clear-cuts in the 10 km buffers and the climate change velocities. The joint threats to the top 10 % of the red-list weighted index PAs show somewhat contrasting patterns in the three biogeographic zones and between T_{Jan} and GDD5 velocities (Fig. 5), and similar trends were also detected for the 10 % rarity weighted PAs (Fig. S7; for corresponding scatterplots for WAB and the top 10 % PAs, see Fig. S8).

The correlations between forest change in the 10 km buffer zone and the GDD5 velocity for the top 10 % of PAs (Fig. 5) were positive in the northern boreal zone (red-listed weighted index: $r_S = 0.672$, $p < 0.001$, N = 27) and in the middle boreal zone (red-listed weighted index: $r_S = 0.564$, $p < 0.001$, N = 90). In contrast, there was a negative correlation between the forest change in the 10 km buffer zone in the southern boreal zone and the GDD5 velocity for the top 10 % of the PAs (red-listed weighted index: $r_S = -0.201$, $p = 0.002 = 234$).

The T_{Jan} velocity had a moderate positive correlation in the southern boreal zone (red-list weighted index: $r_S = 0.600$, $p < 0.001$) and a weak positive correlation in the middle boreal zone (red-list weighted index: $r_S = 0.333$, $p < 0.001$,), with the amount of forest change in the 10 km buffer. This pattern was discovered both for the top 10 % red-list weighted PAs (Fig. 5) as well as the 10 % rarity weighted PAs (Fig. S7). However, these two variables did not covary in the top 10 % of the PAs in the northern boreal zone (red-list weighted index: $r_S = -0.122$, $p = 0.545$). The WAB velocity and forest change within the 10 km buffer did not correlate for the northern and middle boreal top 10 % PAs, but there was a weak negative correlation in the southern boreal PAs (Fig. S8).

4. Discussion

4.1. Combined climate-change and land-use impacts

In our study, we have shown that the harmful land use emerging from clear-cuttings and climate change may pose joined high risks to boreal PAs, which harbour populations of red-listed old-growth and mature forest species. These combined threats were evident as overall positive correlations between logging levels around PAs with red-listed species and their velocity values for GDD5 and T_{Jan}. We focused on areas where red-listed forest species occur with certainty. However, our climate and land-use threat surfaces can also be applied to the entire PA network in Finland, including areas where species of conservation concern have not yet been observed, or where new populations are discovered.

The effect of the South-to-North gradient and the proximity to the Baltic Sea was apparent in all the climate variables calculated for the PAs, especially for GDD5 and T_{Jan}. The GDD5 velocities in the PAs were particularly high in the southern boreal zone and slowest in the northern boreal zone. This pattern is due to more flat terrain with analogous future climate spaces found much farther away in the southern boreal zone compared to the hilly landscape in the middle boreal zone and the rugged relief in the northern boreal zone (see Heikkinen et al., 2020).

However, the relationship between the GDD5 velocity and the level of forest change around the PAs varied notably between the three boreal zones. In the middle and northern boreal zones, the GDD5 velocity values increased as the proportion of logged forests around the PAs increased. In contrast, in the southern boreal zone, the GDD5 velocities decreased as the proportion of clear-cuts around the PAs increased. This is probably because logging levels have been higher in SE Finland than in SW Finland (see Määttänen et al., 2022), whereas GDD5 velocity was, in contrast, higher in SW Finland than in SE Finland due to flat terrain in the south-west. Thus, although both GDD5 velocities in the PAs and logging levels around them were highest in the southern boreal zone, they did not correlate there. In the PAs in the middle and northern boreal zone, both logging levels outside the PAs (Määttänen et al., 2022) and the GDD5 velocity were lower than in the southern boreal zone, but they appeared to pose combined threats to the studied PAs.

Velocity and change of the January temperature both showed the highest values in the PAs situated in the northern boreal zone. Alarmingly, current winter temperatures are projected to disappear in vast areas in the northern boreal zone by the end of the century, even based on the moderate RCP4.5 scenario (Heikkinen et al., 2020). This can have dramatic effects on the northern boreal species that are adapted to the present winter conditions (ACIA, 2004; Callaghan et al., 2004; Lesica and Crone, 2017).

In contrast, changes in the WAB velocity were small and highly local and did not correlate with forest change around the studied PAs. However, the WAB velocities in the PAs were projected to show somewhat faster changes around the shore of the Baltic Sea in southwestern and southern Finland. Thus, changes in precipitation and potential evapotranspiration will probably, jointly with temperature changes, affect species via local-scale seasonal effects, such as changes in snow cover (Barnett et al., 2005; Slatyer et al., 2022).

The average velocity of the January temperature and GDD5 was about 4 km/year in the southern boreal PAs and 3–4 km in PAs in the middle boreal zone. Climate velocities as high as these would mean a shift of 150–200 km in 50 years. Furthermore, the T_{Jan} velocity was about 6 km/year (300 km in 50 years) in northern boreal PAs. These values are much higher than the observed northward density shifts of boreal birds in Finnish PAs in 1981–2017, which were measured to be ca. 1.8 km/year (Virkkala et al., 2018) or boreal birds in Finland in 1970–2012 (ca. 1.5 km/year; Lehikoinen and Virkkala, 2016). Moreover, birds probably have a fairly high dispersal ability compared to many red-listed forest species preferring old-growth forests (but see Komonen and Müller, 2018). Recent studies

have shown that the northward shift of species may lag behind climate warming, leading to the so-called climate debt of species (Devictor et al., 2012; Lehikoinen and Virkkala, 2016). The most detrimental effects of such lags will concern species which are highly dependent on the sparsely occurring old-growth forest habitats and have poor dispersal abilities, such as *Pytho kolwensis* (Siitonen and Saaristo, 2000).

When the landscape matrix deteriorates due to logging, climate change induced northward shifts of many red-listed forest species with specific habitat requirements are hampered. In the southern half of Finland, protected forests currently cover only about 3 % of all forests (National Resources Institute Finland, 2019), and logging levels are expected to increase even further (Maa- ja metsätalousministeriö, 2015) with added pressures due to bioeconomy and the energy crisis. In the wider landscape around the PAs, clear-cutting can also pose negative impacts on the persistence of species in individual PAs, as well as in the PA network. Particularly susceptible are specialist species with low numbers of occurrences and small population sizes (Heikkinen et al., 2021; Nordén et al., 2013; Pykälä, 2019), whose occurrences in the PAs are becoming more and more isolated. Already, a decrease has been seen in many resident forest bird species, also in PAs (Virkkala et al., 2020). Furthermore, even good dispersal ability may not be sufficient in the long term when climatic conditions start to become unsuitable for the local populations. This is because species restricted to high-quality old-growth forest habitats may have significant challenges in finding suitable habitats in the intensively managed forest landscape (Komonen and Müller, 2018).

In essence, our results show that the land-use and climate-change effects in our study are generally additive, as logging levels are highest in PAs where climate velocity is also highest, putting southern boreal PAs at the greatest risk. Yet, all the studied PAs are exposed to either climate change or land-use change, or both, at different magnitudes, reflecting the high spatial variation in the velocities of the three climate variables. Furthermore, we found that the joined threats of land use and climate change were similar between the biologically most valuable PAs according to our importance indices and all the studied PAs (Fig. S9). As a comparison, Ordonez et al. (2014) studied the projected effects of climate and land-use change in the United States from 2001 to 2050 and observed high variability in the combined speed of climate and land-use change. The authors identified certain areas which were severely exposed to high climate velocities, contrasting rates of change between climate and land-use change, but also areas which are most vulnerable due to combined pressures. Moreover, similarly to our results, Ordonez et al. (ibid.) found that climate velocities can show substantial variation between different climate variables.

The red-listed species included in our data are likely to face accelerating negative climate-change impacts. Moreover, even the southerly distributed species, with edge populations in the studied PAs, potentially benefitting from future warming, such as certain herb-rich forest plant species, may have difficulties in shifting their populations northwards in an intensively managed landscape. Since a large proportion of known occurrences of the study species are situated in the PAs (see Table S3; for the EU Habitats Directive species, see Heikkinen et al., 2021), the combined effects of intensive land use and increased climate change and velocity may increase the extinction probability of red-listed species populations (see Oliver and Morecroft, 2014).

4.2. Implications for conservation planning of boreal forests

As harmful impacts of climate change and land use escalate, it is increasingly important to identify priority areas for conservation planning and management, where valuable elements of biodiversity are most vulnerable (Aycrigg et al., 2022; Barber et al., 2016; Mawdsley, 2011; Shrestha et al., 2021). High-latitude boreal environments are projected to experience substantial changes in their climatic conditions (ACIA, 2004; Elsen et al., 2020, 2022), including also PAs (Heikkinen et al., 2020; Kharouba and Kerr, 2010; Parks et al., 2022), potentially leading to losses of habitat and life zones (Elsen et al., 2022). Although the boreal biome includes some large, relatively intact areas, the boreal forests in Fennoscandia have faced intensive management with clear-cuttings, resulting in the replacement of old-growth forests and naturally regenerated forests by young managed production forests, causing fragmentation and loss of natural forest habitats (Koivula and Vanha-Majamaa, 2020; Mikusiński et al., 2021; Svensson et al., 2019; Ward et al., 2020). A key challenge for forest biodiversity conservation is that when the clear-cuttings are targeted at old-growth forests and managed but older-than-average forests (>120 years), they will be permanently converted into structurally homogenous forests with shortened rotational periods (ca. 50–70 years). This can significantly reduce the amount of potential habitat for species favouring old-growth forest conditions (Roberge et al., 2018; Tikkanen et al., 2006; Tremblay et al., 2018).

Mawdsley et al. (2009) reviewed the potentiality of seven strategies for land and water protection and management applicable in the matrix or in the PAs themselves. As a starting point for improving the ability of species populations to persist in the PAs, there are two valid strategies for red-listed forest species in the network of boreal PAs: (i) facilitating resilience by improving the management and restoration of PAs and (ii) increasing the extent of PAs. In Finland, restoration measures have indeed played a key role in improving the ecological conditions of forested PAs. This is because some PAs, particularly in southern Finland, include previously commercially managed forests, which provide a limited amount of crucial characteristics to support red-listed species populations, such as large old trees, diverse vertical stand structure and dead wood (Junninen and Komonen, 2011; Koivula and Vanha-Majamaa, 2020; Siitonen, 2001).

However, in the era of climate change, forest restoration needs to increasingly consider 'prestoration' (restoration including anticipation of climate change) in addition to the earlier focus on ecological and habitat restoration, which concentrate more on recovering species assemblages and conditions of degraded environments (Mansourian, 2018). At the same time, decision makers are facing challenges concerning Fennoscandian boreal forests, as there are concurrent pressures to increase both biodiversity values and wood extraction (Eggers et al., 2022). To tackle these discrepancies, prioritisation based on the best available knowledge and (spatial) data is vital (Synes et al., 2015). Even though it is widely recognised that species would benefit from improving the matrix surrounding boreal PAs, making it more permeable for species as climate conditions change (Synes et al., 2015), projecting landcover changes at

landscape scales will, however, be hampered by forest ownership patterns (Duflot et al., 2022; Eggers et al., 2022).

Ultimately, the drastic long-term projected changes in the high-latitude climatic conditions (Elsen et al., 2022; Heikkinen et al., 2020) will produce high pressures on boreal forest species to shift their ranges northwards. Particularly in areas with a sparse PA network, this will drive species to disperse across human-impacted landscapes, where suitable habitat patches for red-listed forest species are in short supply and will very likely further decrease (Mikusiński et al., 2021; Määttänen et al., 2022; Svensson et al., 2019). Species that depend on shady forests with a humid microclimate and abundant coarse woody debris, including certain moss and hepatics species, specialised wood-inhabiting fungi and many epiphytic lichen species (Abrego et al., 2017b; Koivula and Vanha-Majamaa, 2020; Moen and Jonsson, 2003) are among the species most at risk due to excessive warming following clear-cutting (Greiser et al., 2018).

Thus, promoting the movements of red-listed forest species requiring shady humid interior forest conditions across the matrix areas is clearly one priority in the climate-wise conservation planning for boreal forests. Such movements can be supported by the two strategies, i.e., by protecting corridors or stepping stones with microrefugia or otherwise designing new conservation and restoration sites. However, the foremost priority is protecting the remaining valuable mature and old-growth forests. A recent review by Komonen and Müller (2018) concluded that successful movements of many deadwood species, including red-listed forest species, to new areas may depend more on the availability of high-quality habitats appearing as suitable landing patches in the matrix, enabling colonisation and establishment of a new population than conservation planning focusing only on improving structural connectivity.

5. Conclusions

In Finland, boreal forest species that require old-growth and mature forest features in their habitat, are increasingly threatened by intensive forestry practices and climate change. We developed two red-listed species-observation-based indices to describe the conservation value of a PA. Around these valuable PAs, the magnitude of clear-cuts was highest in the largest 10 km and 1 km buffers and lowest in the near vicinity, 100 m buffer. Furthermore, the intensity of forestry practices was highest in the southern boreal vegetation zone. Under the RCP4.5 scenario, T_{Jan}, GDD5 and WAB conditions and velocities are generally correlated with land-use intensity, strengthening its negative effects on PAs, making southern boreal PAs the most exposed to combined threats. However, the strength and direction of these relationships varied between the different vegetation zones and topoclimatic variables.

When designing effective climate-wise planning for red-listed boreal forest species, multiple elements need to be considered. However, the foremost critical starting point is the identification of the most valuable sites for these species in the PA network (and where necessary, also in the unprotected matrix) and the climate change and land use-based threats to them, as accomplished in this study. Important further steps in the process can then be built upon this baseline knowledge, particularly by linking the information with species habitat requirements and dispersal ecology, as well as analysing the potential of different conservation measures to mitigate the combined climate change and land use risks for the valuable agglomerations of red-listed species. Outputs from such a multistep process may then be used to improve the conservation status of many of the declining, red-listed boreal forest species.

Author contributions

A.M.M, R.V., N.L. and **R.K.H.** developed the research questions and designed the study; **A.M.M., N.L.** and **J.A.** compiled the data; **A.M.M.**, and **N.L.** analysed the data; and **A.M.M., R.V.** and **R.K.H.** wrote the paper. All authors commented on the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02348.

References

Aalto, J., Pirinen, P., Jylhä, K., 2016. New gridded daily climatology of Finland: permutation-based uncertainty estimates and temporal trends in climate. J. Geophys. Res. Atmos. 121, 3807–3823.

Aalto, J., Riihimäki, H., Meineri, E., Hylander, K., Luoto, M., 2017. Revealing topoclimatic heterogeneity using meteorological station data. Int. J. Climatol. 37, 544–556. https://doi.org/10.1002/joc.5020.

Abrego, N., Christensen, M., Bässler, C., Ainsworth, A.M., Heilmann-Clausen, J., 2017b. Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models. Fungal Ecol. 27, 168–174. https://doi.org/10.1016/j.funeco.2016.07.006.

Abrego, N., Dunson, D., Halme, P., Salcedo, I., Ovaskainen, O., 2017a. Wood-inhabiting fungi with tight associations with other species have declined as a response to forest management. Oikos 126. https://doi.org/10.1111/oik.03674.

ACIA, 2004. Impacts of a Warming Arctic; Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Araújo, M.B., Alagador, D., Cabeza, M., Nogues-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecol. Lett. 14, 484–492. https://doi.org/10.1111/j.1461-0248.2011.01610.x.

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Glob. Change Biol. 10, 1618–1626. https://doi.org/10.1111/j.1365-2486.2004.00828.x.

Aycrigg, J.L., Mccarley, T.R., Belote, R.T., Martinuzzi, S., 2022. Wilderness areas in a changing landscape: changes in land use, land cover, and climate. Ecol. Appl. 32, e02471 https://doi.org/10.1002/eap.2471.

Baettig, M.B., Wild, M., Imboden, D.M., 2007. A climate change index: where climate change may be most prominent in the 21st century. Geophys. Res. Lett. 34 https://doi.org/10.1029/2006GL028159.

Barber, Q.E., Nielsen, S.E., Hamann, A., 2016. Assessing the vulnerability of rare plants using climate change velocity, habitat connectivity, and dispersal ability: a case study in Alberta, Canada. Reg. Environ. Change 16, 1433–1441. https://doi.org/10.1007/s10113-015-0870-6.

Barnett, T.P., Adam, J.C., Lettenmaier, D.P., 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438, 303–309. https://doi.org/10.1038/nature04141.

Brito-Morales, I., García Molinos, J., Schoeman, D.S., Burrows, M.T., Poloczanska, E.S., Brown, C.J., Ferrier, S., Harwood, T.D., Klein, C.J., McDonald-Madden, E., Moore, P.J., Pandolfi, J.M., Watson, J.E.M., Wenger, A.S., Richardson, A.J., 2018. Climate velocity can inform conservation in a warming world. Trends Ecol. Evol. 33, 441–457. https://doi.org/10.1016/j.tree.2018.03.009.

Butchart, S.H.M., Walpole, M., Collen, B., Strien, Av, Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G. M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168. https://doi.org/10.1126/science.1187512.

Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E., Zockler, C., 2004. Biodiversity, distributions and adaptations of arctic species in the context of environmental change. Ambio 33, 404–417. https://doi.org/10.1579/0044-7447-33.7.404.

Ceccherini, G., Duveiller, G., Grassi, G., Lemoine, G., Avitabile, V., Pilli, R., Cescatti, A., 2020. Abrupt increase in harvested forest area over Europe after 2015. Nature 583, 72–77. https://doi.org/10.1038/s41586-020-2438-y.

Ceccherini, G., Duveiller, G., Grassi, G., Lemoine, G., Avitabile, V., Pilli, R., Cescatti, A., 2021. Reply to Wernick, I. K. et al.; Palahí, M. et al. Nature 592, E18–E23. https://doi.org/10.1038/s41586-021-03294-9.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026. https://doi.org/10.1126/science.1206432.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361, 1108–1111. https://doi.org/10.1126/science.aau3445.

Davis, K.F., Koo, H.I., Dell'Angelo, J., D'Odorico, P., Estes, L., Kehoe, L.J., Kharratzadeh, M., Kuemmerle, T., Machava, D., Pais, Ad.J.R., Ribeiro, N., Rulli, M.C., Tatlhego, M., 2020. Tropical forest loss enhanced by large-scale land acquisitions. Nat. Geosci. 13, 482–488. https://doi.org/10.1038/s41561-020-0592-3.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliola, J., Herrando, S., Julliard, R., Kuussaari, M., Lindstrom, A., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I., Jiguet, F., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nat. Clim. Change 2, 121–124. https://doi.org/10.1038/nclimate1347.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366, eaax3100. https://doi.org/10.1126/science.aax3100.

Duflot, R., Fahrig, L., Mönkkönen, M., 2022. Management diversity begets biodiversity in production forest landscapes. Biol. Conserv. 268, 109514 https://doi.org/10.1016/j.biocon.2022.109514.

Eggers, J., Lundström, J., Snäll, T., Öhman, K., 2022. Balancing wood production and biodiversity in intensively managed boreal forest. Scand. J. For. Res. 1–13. https://doi.org/10.1080/02827581.2022.2066170.

Elmhagen, B., Kindberg, J., Hellström, P., Angerbjörn, A., 2015. A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. Ambio 44, 39–50. https://doi.org/10.1007/s13280-014-0606-8.

Elsen, P.R., Monahan, W.B., Dougherty, E.R., Merenlender, A.M., 2020. Keeping pace with climate change in global terrestrial protected areas. Sci. Adv. 6, eaay0814 https://doi.org/10.1126/sciadv.aay0814.

Elsen, P.R., Saxon, E.C., Simmons, B.A., Ward, M., Williams, B.A., Grantham, H.S., Kark, S., Levin, N., Perez-Hammerle, K.-V., Reside, A.E., Watson, J.E.M., 2022. Accelerated shifts in terrestrial life zones under rapid climate change. Glob. Change Biol. 28, 918–935. https://doi.org/10.1111/gcb.15962.

Forsius, M., Kujala, H., Minunno, F., Holmberg, M., Leikola, N., Mikkonen, N., Autio, I., Paunu, V.-V., Tanhuanpää, T., Hurskainen, P., Mäyrä, J., Kivinen, S., Keski-Saari, S., Kosenius, A.-K., Kuusela, S., Virkkala, R., Viinikka, A., Vihervaara, P., Akujärvi, A., Bäck, J., Karvosenoja, N., Kumpula, T., Kuzmin, A., Mäkelä, A., Moilanen, A., Ollikainen, M., Pekkonen, M., Peltoniemi, M., Poikolainen, L., Rankinen, K., Rasilo, T., Tuominen, S., Valkama, J., Vanhala, P., Heikkinen, R.K., 2021. Developing a spatially explicit modelling and evaluation framework for integrated carbon sequestration and biodiversity conservation: application in southern Finland. Science of the Total Environment 775, 145847. https://doi.org/10.1016/j.scitotenv.2021.145847.

Garcia, R.A., Cabeza, M., Rahbek, C., Araújo, M.B., 2014. Multiple dimensions of climate change and their implications for biodiversity. Science 344, 1247579. https://doi.org/10.1126/science.1247579.

Gaston, K.J., Jackson, S.F., Cantú-Salazar, L., Cruz-Piñón, G., 2008. The ecological performance of protected areas. Annu. Rev. Ecol. Evol. Syst. 39, 93–113.

Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., Hylander, K., 2018. Monthly microclimate models in a managed boreal forest landscape. Agric. For. Meteorol. 250–251, 147–158. https://doi.org/10.1016/j.agrformet.2017.12.252.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052 https://doi.org/10.1126/sciadv.1500052.

Häkkilä, M., Le Tortorec, E., Brotons, L., Rajasärkkä, A., Tornberg, R., Mönkkönen, M., 2017. Degradation in landscape matrix has diverse impacts on diversity in protected areas. PLoS One 12, e0184792. https://doi.org/10.1371/journal.pone.0184792.

Hamann, A., Roberts, D.R., Barber, Q.E., Carroll, C., Nielsen, S.E., 2015. Velocity of climate change algorithms for guiding conservation and management. Glob. Change Biol. 21, 997–1004. https://doi.org/10.1111/gcb.12736.

Hamilton, C.M., Martinuzzi, S., Plantinga, A.J., Radeloff, V.C., Lewis, D.J., Thogmartin, W.E., Heglund, P.J., Pidgeon, A.M., 2013. Current and future land use around a nationwide protected area network. Plos One 8, e55737-e55737. https://doi.org/10.1371/journal.pone.0055737.

Hansen, A.J., DeFries, R., 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecol. Appl. 17, 974–988. https://doi.org/10.1890/05-1098.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853. https://doi.org/10.1126/science.1244693.

Hanski, I., 2005. The Shrinking World: Ecological Consequences of Habitat Loss. International Ecology Institute, 21385 Oldendorf/Luhe, Germany.

Hanski, I., 2011. Habitat Loss, the Dynamics of biodiversity, and a perspective on conservation. Ambio 40, 248–255. https://doi.org/10.1641/0006-3568(2006)56[355:HLFTPO]2.0.CO;2.

Hanski, I., Simberloff, D., 1997. The metapopulation approach, its history, conseptual domain, and application to conservation. In: Hanski, I., Gilpin, M. (Eds.), Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, San Diego, California, USA, pp. 5–26.

Heikkinen, R.K., Leikola, N., Aalto, J., Aapala, K., Kuusela, S., Luoto, M., Virkkala, R., 2020. Fine-grained climate velocities reveal vulnerability of protected areas to climate change. Sci. Rep. 10 https://doi.org/10.1016/j.gecco.2021.e01664.

Heikkinen, R.K., Kartano, L., Leikola, N., Aalto, J., Aapala, K., Kuusela, S., Virkkala, R., 2021. High-latitude EU Habitats Directive species at risk due to climate change and land use. Glob. Ecol. Conserv. 28, e01664.

Hiley, J.R., Bradbury, R.B., Holling, M., Thomas, C.D., 2013. Protected areas act as establishment centres for species colonizing the UK. Proc. R. Soc. B Biol. Sci. 280, 20122310. https://doi.org/10.1098/rspb.2012.2310.

Howard, C., Stephens, P.A., Pearce-Higgins, J.W., Gregory, R.D., Willis, S.G., 2015. The drivers of avian abundance: patterns in the relative importance of climate and land use. Glob. Ecol. Biogeogr. 24, 1249–1260. https://doi.org/10.1111/geb.12377.

Huntley, B., Collingham, Y.C., Willis, S.G., Green, R.E., 2008. Potential impacts of climatic change on European breeding birds. PLos One 3. https://doi.org/10.1371/journal.pone.0001439.

Hylander, K., Nilsson, C., Göthner, T., 2004. Effects of buffer-strip retention and clearcutting on land snails in Boreal Riparian Forests. Conserv. Biol. 18, 1052–1062. https://doi.org/10.1111/j.1523-1739.2004.00199.x.

Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., Liukko, U.-M. (Eds.), 2019. The 2019 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.

Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. PLoS Biol. 5, e157 https://doi.org/10.1371/journal.pbio.0050157.

Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: a review. Biol. Conserv. 144, 11–20. https://doi.org/10.1016/j.biocon.2010.07.010.

Kharouba, H.M., Kerr, J.T., 2010. Just passing through: Global change and the conservation of biodiversity in protected areas. Biol. Conserv. 143, 1094–1101. https://doi.org/10.1016/j.biocon.2010.02.002.

Klok, E.J., Klein Tank, A.M.G., 2009. Updated and extended European dataset of daily climate observations. Int. J. Climatol. 29, 1182–1191. https://doi.org/10.1002/joc.1779.

Koivula, M., Vanha-Majamaa, I., 2020. Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. Ecol. Process. 9, 11. https://doi.org/10.1186/s13717-019-0209-1.

Komonen, A., Müller, J., 2018. Dispersal ecology of deadwood organisms and connectivity conservation. Conserv. Biol. 32, 535–545. https://doi.org/10.1111/cobi.13087.https:///.

Korhonen, K.T., Ahola, A., Heikkinen, J., Henttonen, H.M., Hotanen, J.-P., Ihalainen, A., Melin, M., Pitkänen, J., Räty, M., Sirviö, M., Strandström, M., 2021. Forests of Finland 2014–2018 and their development 1921–2018. Silva Fenn. 55 (5), 10662. https://doi.org/10.14214/sf.10662.

Kuuluvainen, T., Aakala, T., 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. Silva Fenn. 45, 823–841. https://doi.org/10.14214/sf.73.

Kuuluvainen, T., Gauthier, S., 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. For. Ecosyst. 5, 26. https://doi.org/10.1186/s40663-018-0142-2.

Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in Boreal Fennoscandia: a review. Ambio 41, 720–737. https://doi.org/10.1007/s13280-012-0289-y.

Lehikoinen, A., Virkkala, R., 2016. North by north-west: climate change and directions of density shifts in birds. Glob. Change Biol. 22, 1121–1129. https://doi.org/10.1111/gcb.13150.

Lenoir, J., Svenning, J.-C., 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography 38, 15–28. https://doi.org/10.1111/ecog.00967.

Lesica, P., Crone, E.E., 2017. Arctic and boreal plant species decline at their southern range limits in the Rocky Mountains. Ecol. Lett. 20, 166–174. https://doi.org/10.1111/ele.12718.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. Nature 462, 1052–1055. https://doi.org/10.1038/nature08649.

Luoto, M., Heikkinen, R.K., Pöyry, J., Saarinen, K., 2006. Determinants of biogeographical distribution of butterflies in boreal regions. J. Biogeogr. 33, 1764–1778. https://doi.org/10.1111/j.1365-2699.2005.01395.x.

Maa- ja metsätalousministeriö, 2015. Kansallinen metsästrategia 2025 – Valtioneuvoston periaatepäätös 12.2.2015 (National forest strategy 2025). Maa-ja metsätalousministeriön Julk. 6/2015, 54.

Määttänen, A.-M., Virkkala, R., Leikola, N., Heikkinen, R.K., 2022. Increasing loss of mature boreal forests around protected areas with red-listed forest species. Ecol. Process. 11, 17. https://doi.org/10.1186/s13717-022-00361-5.

Mair, L., Jönsson, M., Räty, M., Bärring, L., Strandberg, G., Lämås, T., Snäll, T., 2018. Land use changes could modify future negative effects of climate change on old-growth forest indicator species. Divers. Distrib. 24 (10), 1416–1425.

Mansourian, S., 2018. In the eye of the beholder: reconciling interpretations of forest landscape restoration. Land Degrad. Dev. 29, 2888–2898.

Mantyka-Pringle, C.S., Martin, T.G., Rhodes, J.R., 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Glob. Change Biol. 18, 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x.

Mawdsley, J., 2011. Design of conservation strategies for climate adaptation. Wiley Interdiscip. Rev. -Clim. Change 2, 498–515. https://doi.org/10.1002/wcc.127.

Mawdsley, J.R., O'Malley, R., Ojima, D.S., 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conserv. Biol. 23, 1080–1089. https://doi.org/10.1111/j.1523-1739.2009.01264.x.

McGuire, J.L., Lawler, J.J., McRae, B.H., Nuñez, T.A., Theobald, D.M., 2016. Achieving climate connectivity in a fragmented landscape. Proc. Natl. Acad. Sci. 113 (26), 7195–7200.

Mikusiński, G., Orlikowska, E.H., Bubnicki, J.W., Jonsson, B.G., Svensson, J., 2021. Strengthening the Network of High Conservation Value Forests in Boreal Landscapes. Front. Ecol. Evol. 8, 595730 https://doi.org/10.3389/fevo.2020.595730.

Moen, J., Jonsson, B.G., 2003. Edge effects on liverworts and lichens in forest patches in a mosaic of Boreal forest and wetland. Conserv. Biol. 17, 380–388. https://doi.org/10.1046/j.1523-1739.2003.00406.x.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10, 58–62. https://doi.org/10.1016/S0169-5347(00)88977-6.

Murray, D.L., Peers, M.J.L., Majchrzak, Y.N., Wehtje, M., Ferreira, C., Pickles, R.S.A., Row, J.R., Thornton, D.H., 2017. Continental divide: predicting climate-mediated fragmentation and biodiversity loss in the boreal forest. PLoS One 12, e0176706. https://doi.org/10.1371/journal.pone.0176706.

Nadeau, C.P., Fuller, A.K., Rosenblatt, D.L., 2015. Climate-smart management of biodiversity. Ecosphere 6, art91. https://doi.org/10.1890/ES15-00069.1.

National Resources Institute Finland , 2019: Forest protection. Forest Protection 1.1.2019. – 27.9.2019. ⟨https://stat.luke.fi/en/forest-protection-112019_en⟩.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J. Ecol. 101, 701–712. https://doi.org/10.1111/1365-2745.12085.

Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. Wiley Interdiscip. Rev. Clim. Change 5, 317–335. https://doi.org/10.1002/wcc.271.

Ordonez, A., Martinuzzi, S., Radeloff, V.C., Williams, J.W., 2014. Combined speeds of climate and land-use change of the conterminous US until 2050. Nat. Clim. Change 4, 811. https://doi.org/10.1038/nclimate2337.

Parks, S.A., Holsinger, L.M., Littlefield, C.E., Dobrowski, S.Z., Zeller, K.A., Abatzoglou, J.T., Besancon, C., Nordgren, B.L., Lawler, J.J., 2022. Efficacy of the global protected area network is threatened by disappearing climates and potential transboundary range shifts. Environ. Res. Lett. 17, 054016 https://doi.org/10.1088/1748-9326/ac6436.

Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guenette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U. R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. Science 330 (6010), 1496–1501. https://doi.org/10.1126/science.1196624.

Pykälä, J., 2019. Habitat loss and deterioration explain the disappearance of populations of threatened vascular plants, bryophytes and lichens in a hemiboreal landscape. Glob. Ecol. Conserv. 18, e00610 https://doi.org/10.1016/j.gecco.2019.e00610.

Rantanen, M., Karpechko, A.Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., Laaksonen, A., 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Commun. Earth Environ. 3, 168.

Roberge, J.-M., Öhman, K., Lämås, T., Felton, A., Ranius, T., Lundmark, T., Nordin, A., 2018. Modified forest rotation lengths: long-term effects on landscape-scale habitat availability for specialized species. J. Environ. Manag. 210, 1–9. https://doi.org/10.1016/j.jenvman.2017.12.022.

Sala, O.E., Chapin, F.S.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., 2000. Global biodiversity scenarios for the year 2100. Science 287 (5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770.

Segan, D.B., Murray, K.A., Watson, J.E.M., 2016. A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. Glob. Ecol. Conserv. 5, 12–21. https://doi.org/10.1016/j.gecco.2015.11.002.

Shrestha, N., Xu, X., Meng, J., Wang, Z., 2021. Vulnerabilities of protected lands in the face of climate and human footprint changes. Nat. Commun. 12, 1632. https://doi.org/10.1038/s41467-021-21914-w.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian Boreal forests as an example. Ecol. Bull. 11–41. https://doi.org/10.2307/20113262.

Siitonen, J., Saaristo, L., 2000. Habitat requirements and conservation of Pytho kolwensis, a beetle species of old-growth boreal forest. Biol. Conserv. 94, 211–220.

Skov, F., Svenning, J.-C., 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. Ecography 27, 366–380. https://doi.org/10.1111/j.0906-7590.2004.03823.x.

Slatyer, R.A., Umbers, K.D.L., Arnold, P.A., 2022. Ecological responses to variation in seasonal snow cover. Conserv. Biol. 36, e13727 https://doi.org/10.1111/cobi.13727.

Svensson, J., Andersson, J., Sandström, P., Mikusiński, G., Jonsson, B.G., 2019. Landscape trajectory of natural boreal forest loss as an impediment to green infrastructure. Conserv. Biol. 33, 152–163. https://doi.org/10.1111/cobi.13148.

Sykes, M.T., Prentice, I.C., Cramer, W., 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. J. Biogeogr. 23, 203–233.

Synes, N.W., Watts, K., Palmer, S.C.F., Bocedi, G., Barton, K.A., Osborne, P.E., Travis, J.M.J., 2015. A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape. Ecol. Inform. 30, 222–229. https://doi.org/10.1016/j.ecoinf.2015.06.004.

Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. Bull. Am. Meteorol. Soc. 93, 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1.

Tikkanen, O.P., Martikainen, P., Hyvarinen, E., Junninen, K., Kouki, J., 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Ann. Zool. Fenn. 43, 373–383. https://doi.org/10.1016/j.biocon.2007.08.020.

Tingstad, L., Grytnes, J.A., Felde, V.A., Juslén, A., Hyvärinen, E., Dahlberg, A., 2018. The potential to use documentation in national Red Lists to characterize red-listed forest species in Fennoscandia and to guide conservation. Glob. Ecol. Conserv. 15, e00410 https://doi.org/10.1016/j.gecco.2018.e00410.

Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc. R. Soc. Lond. Ser. B Biol. Sci. 270, 467–473. https://doi.org/10.1098/rspb.2002.2246.

Tremblay, J.A., Boulanger, Y., Cyr, D., Taylor, A.R., Price, D.T., St-Laurent, M.-H., 2018. Harvesting interacts with climate change to affect future habitat quality of a focal species in eastern Canada's boreal forest. PLoS One 13, e0191645. https://doi.org/10.1371/journal.pone.0191645.

Vincent, C., Fernandes, R.F., Cardoso, A.R., Broennimann, O., Di Cola, V., D'Amen, M., Ursenbacher, S., Schmidt, B.R., Pradervand, J.-N., Pellissier, L., Guisan, A., 2019. Climate and land-use changes reshuffle politically-weighted priority areas of mountain biodiversity. Glob. Ecol. Conserv. 17, e00589 https://doi.org/10.1016/j.gecco.2019.e00589.

Virkkala, R., Lehikoinen, A., 2014. Patterns of climate-induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. Glob. Change Biol. 20, 2995–3003. https://doi.org/10.1111/gcb.12573.

Virkkala, R., Heikkinen, R.K., Fronzek, S., Kujala, H., Leikola, N., 2013. Does the protected area network preserve bird species of conservation concern in a rapidly changing climate? Biodivers. Conserv. 22, 459–482. https://doi.org/10.1007/s10531-012-0423-y.

Virkkala, R., Lehikoinen, A., Rajasärkkä, A., 2020. Can protected areas buffer short-term population changes of resident bird species in a period of intensified forest harvesting? Biol. Conserv. 244, 108526 https://doi.org/10.1016/j.biocon.2020.108526.

Virkkala, R., Pöyry, J., Heikkinen, R.K., Lehikoinen, A., Valkama, J., 2014. Protected areas alleviate climate change effects on northern bird species of conservation concern. Ecol. Evol. 4, 2991–3003.

Virkkala, R., Rajasärkkä, A., Heikkinen, R.K., Kuusela, S., Leikola, N., Pöyry, J., 2018. Birds in boreal protected areas shift northwards in the warming climate but show different rates of population decline. Biol. Conserv. 226, 271–279. https://doi.org/10.1016/j.biocon.2018.08.015.

Virkkala, R., Toivonen, H., 1999. Maintaining biological diversity in Finnish forests. Finn. Environ. 278, 1–56.

Walsh, J.E., Overland, J.E., Groisman, P.Y., et al., 2011. Ongoing climate change in the Arctic. AMBIO 40 (Suppl 1), 6–16. https://doi.org/10.1007/s13280-011-0211-z.

Ward, M., Saura, S., Williams, B., Ramírez-Delgado, J.P., Arafeh-Dalmau, N., Allan, J.R., Venter, O., Dubois, G., Watson, J.E.M., 2020. Just ten percent of the global terrestrial protected area network is structurally connected via intact land. Nat. Commun. 11, 4563. https://doi.org/10.1038/s41467-020-18457-x.