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Negative effects of climate warming on red-listed boreal peatland plant species can be mitigated through restoration

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ABSTRACT

Peatlands are crucial ecosystems for biodiversity conservation and carbon storage but are largely degraded due to human impact. Climate change poses an additional threat to peatland biodiversity, affecting, for example, red-listed species. We investigate how the projected climate change and peatland restoration may jointly influence the habitat availability of red-listed peatland plant species in Finland. We use maximum entropy model to predict future changes in species distributions under different climate scenarios (representative concentration pathways [RCP] 2.6, 4.5, and 8.5) and potential restoration levels (0 %, 30 %, 50 %, and 100 % of drained peatlands) for 2040–2069 and 2070–2099. Our results show that the proportion of undrained peatland area, mean January temperature, and mean growing degree days are the main variables affecting habitat suitability for red-listed species. Furthermore, our results indicate that restoration can hypothetically expand potential suitable habitats, reduce habitat loss, moderate northward shifts, and preserve species richness. As climate warms, south and middle boreal species are projected to experience habitat expansion, while northern boreal species face more pronounced habitat loss, particularly under RCP8.5. Suitable habitat tends to shift northward for all species groups, with species richness being highest in the northern boreal zone. However, under RCP8.5 by 2070–2099, even extensive restoration cannot prevent habitat loss, northward movement, or species richness decline, particularly in the northern regions. Our findings highlight the need for immediate protection of current suitable habitats for red-listed peatland plant species and large-scale peatland restoration to ensure future suitable habitats for the red-listed species.

1. Introduction

Peatlands are critical carbon sinks and biodiversity hotspots, storing nearly one-third of global soil carbon (Harris et al., 2022) and providing habitat for specialized plant and animal species (Hyvärinen et al., 2019; Minayeva et al., 2017). However, extensive drainage for forestry, agriculture, and peat extraction during the 20th century has severely altered these ecosystems (Aakala et al., 2023). Drainage has lowered water tables (Luscombe et al., 2016; Young et al., 2017) and caused habitat degradation (Kontula and Raunio, 2019), severely threatening the survival of red-listed plant species by reducing both species diversity and population sizes (Maanavilja et al., 2014). Restoration efforts have increasingly focused on rewetting as a key strategy to reverse drainage effects (Emsens et al., 2020; Humpenöder et al., 2020), but climate change poses another threat when trying to reinstate suitable habitats.

Arctic and boreal regions are warming faster than the global average rate (Post et al., 2019; Rantanen et al., 2022). Over the past 50 years, annual precipitation in these areas has risen by >6 % (Box et al., 2019).

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Despite precipitation increases, higher temperatures are expected to intensify evapotranspiration, potentially leading to drying of northern peatlands (Helbig et al., 2020; Swindles et al., 2019). This drying process threatens moisture-dependent species and highlights the complexity of restoring peatlands under climate change (Heikkinen et al., 2023).

Consequently, climate change is driving significant shifts in plant species distributions (Campbell et al., 2021) and affecting their survival (Norby et al., 2019), particularly given that northern peatlands respond more rapidly and prominently to changes in moisture conditions compared to their southern counterparts (N. A. K. Kokkonen et al., 2019). As temperature rises, most species typically shift to higher latitudes and altitudes towards cooler regions (Deschênes et al., 2024; Mallen-Cooper et al., 2023). For instance, the suitable habitats for *Sphagnum* mosses may expand in boreal regions above 50°N, while contracting significantly at the southern edges of boreal peatlands (Ma et al., 2022).

Despite growing evidence of region-specific responses to climate change, there is limited knowledge of how climate change and peatland restoration efforts jointly affect the habitat suitability of red-listed species. We use species distribution models (SDM) to predict suitable habitats for 27 red-listed peatland species (vascular plants and bryophytes) in Finland under various restoration and climate change scenarios. We investigate how projected climate change and hypothetical peatland restoration may jointly impact red-listed peatland plant species. Specifically, we analyze: (1) the availability of suitable habitats, (2) shifts in species' latitudinal distribution patterns, and (3) changes in species richness.

2. Material and methods

2.1. Study area

Finland is located between 60 and 70° N in northern Europe (Fig. 1). The climate is predominantly continental, with some maritime influences, resulting in distinct seasonal variations. Annual mean temperatures range from −2 °C to +7 °C, with precipitation varying between 400 and 800 mm (Aalto and Pirinen, 2023).

The study area is divided into northern boreal (NB), middle boreal (MB) and southern boreal (SB; including hemiboreal) zones. The NB zone has the largest expanse of undrained peatlands, predominantly consisting of northern minerotrophic aapa mires. It exhibits cold temperatures, with mean annual temperature ranging from −2 to 2 °C and annual precipitation levels between 430 and 720 mm. The MB zone contains Finland's highest total peatland area, primarily composed of aapa mires, with corresponding temperatures between 0 and 5 °C and precipitation levels of 460–790 mm. In contrast, SB zone has the smallest total peatland area and the highest proportion of drained peatlands (Sallinen et al., 2019). It is dominated by ombrotrophic raised bogs and experiences a relatively milder climate, with mean annual air temperatures ranging from 2 to 7 °C and precipitation levels of 500–760 mm.

We divided Finland into 25-ha grid cells (500 m × 500 m). We excluded grid cells with <10 % peatland coverage (based on peatland drainage status raster of Finnish Environmental Institute (2009)), leaving 744,226 grid cells (186,056 km^2), approximately 55 % of Finland's total land area.

2.2. Plant species data

We utilized the national database to obtain presence-only records for red-listed peatland plant species (Hyvärinen et al., 2019). This database includes field records collected by both amateur and professional botanists, as well as data from scientific literature and herbaria. We then applied the following criteria to select species: (i) occurrence records of vascular plants and bryophytes in undrained peatlands; (ii) data from 2000 onwards; (iii) location accuracy ≤ 100 m; and (iv) ≥ 10 records. Based on these criteria, we included 27 species, which were classified into NB, MB, and SB groups according to their most frequent locations (Table S1).

2.3. Environmental variables

We calculated 16 environmental variables with moderate cross-correlations ($|\text{Spearman correlation}| < 0.7$) for each 25-ha grid cell to capture key biophysical gradients affecting plant physiology and habitat suitability. These included three climate variables, one topographical variable, and 12 local habitat features (Table 1). For continuous variables, we used the average of pixels within each grid cell to maintain proportional representation and avoid outlier effects, while we resampled categorical variables using the majority rule to preserve dominant class characteristics.

Climate variables were derived from the Finnish Meteorological Institute for 1981–2010 at a 50 × 50 m resolution (Aalto, 2023). These included:

1. Mean Growing Degree Days (GDD, °C days): The effective temperature sum above 5 °C (Carter et al., 1991). GDD reflects both the length and intensity of the growing season, helping to assess how thermal changes impact habitat suitability for red-listed peatland plant species under varying climate scenarios.
2. Mean Water Balance (WAB, mm): The difference between precipitation and potential evapotranspiration (Skov and Svenning, 2004), WAB indicates net water availability, essential for plant growth, photosynthesis, nutrient uptake, and overall health.
3. Mean January Temperature (TJan, °C): The average temperature in January, quantifying the severity of winter conditions that affect plant survival and distribution. This variable is commonly used in plant distribution modeling (Määttänen et al., 2023).

Using a peatland drainage status map with a 25 × 25 m resolution, we calculated the proportion of undrained (UNDRAINED) and drained (DRAINED) peatland area for each grid square. These variables reflect the extent of near-natural versus forestry-drained peatlands, which are crucial for species adapted to different moisture regimes.

We used the mean Topographical Wetness Index (TWI) to describe local moisture conditions (Beven and Kirkby, 1979), where higher values indicating wetter areas. TWI, a proxy for soil moisture, was derived from a 10 m resolution digital elevation model (DEM) provided by the National Land Survey of Finland and calculated using the formula by (Burrough et al., 2015):

$$TWI = ln(\alpha / tan\beta)$$

where α is the upslope contributing area per width, orthogonal to the flow direction, while β is the local slope in radians.

Given that many threatened plant species require calcareous substrates, we included the presence of calcareous rock (ROCK) as a binary variable (0/1), derived from digital maps of Quaternary deposits and pre-Quaternary rocks from The Geological Survey of Finland.

We obtained information on the percentage cover of main peatland site types and site fertility from the 2021 Multi-source National Forest Inventory (MS-NFI) (Natural Resources Institute Finland, 2021) at a 16 × 16 m resolution. Site types were categorized based on fertility: herb-rich site type (ST1) is the most fertile, with a field layer dominated by herbaceous plants and a tree layer primarily consisting of Norway spruce (*Picea abies*) and downy birch (*Betula pubescens*); *Vaccinium myrtillus* site type (ST2) is moderately fertile, with a field layer dominated by shrubs and some herbaceous vegetation, and a tree layer of Scots pine (*Pinus sylvestris*), Norway spruce, and downy birch; *Vaccinium vitis-idaea* site type (ST3) is less fertile, featuring a shrub-dominated field layer and a primarily pine-dominated tree layer; and *Cladina* site type (ST6), the least fertile, is characterized by a lichen-rich field layer and sparse tree cover, mainly consisting of Scots pine. We also calculated the proportion of open peatlands (OPEN) and the mean volumes (m^3/ha) of four tree

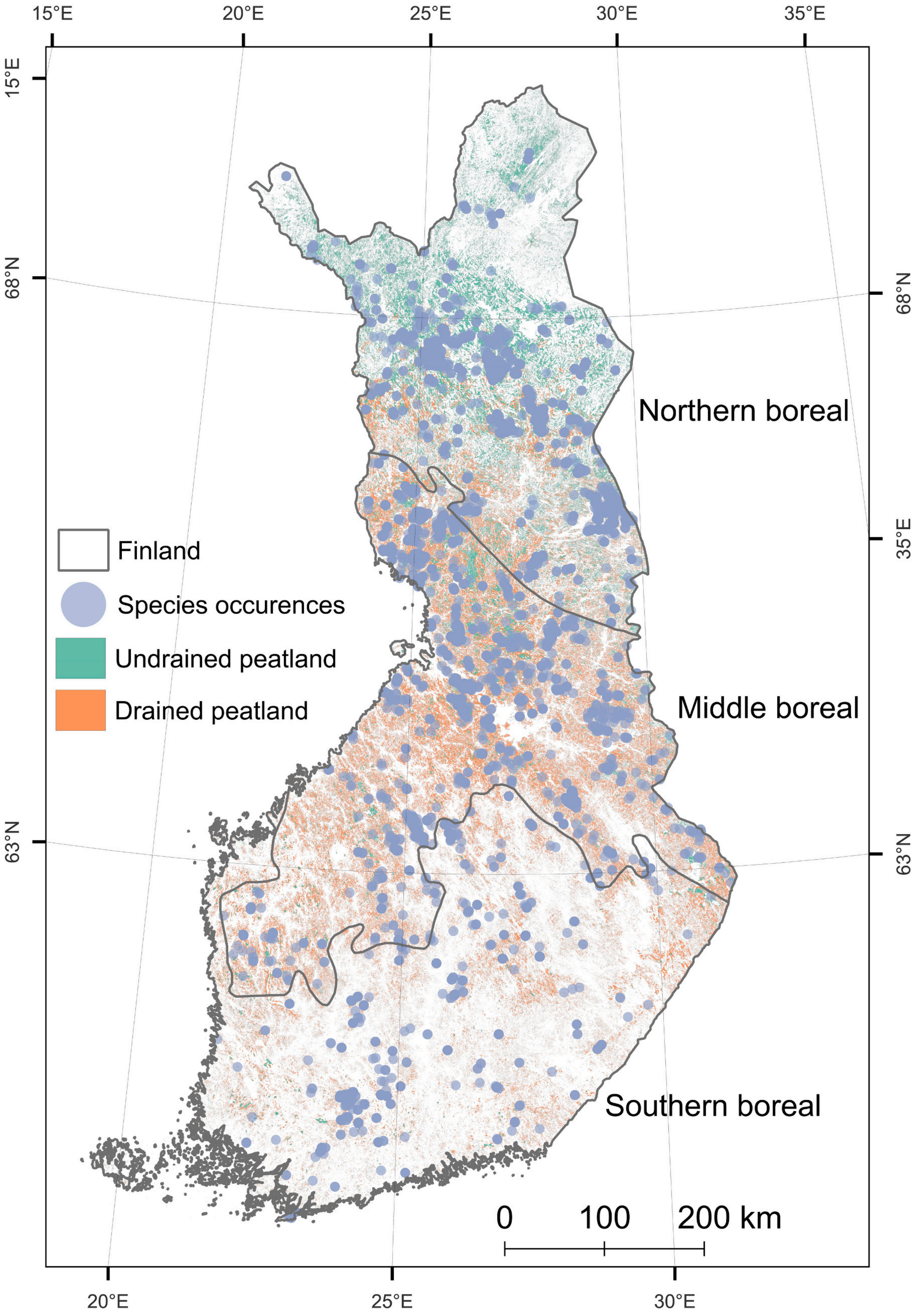

Fig. 1. Study area within three boreal zones (northern boreal (NB), middle boreal (MB), and southern boreal (SB)) in Finland. Species occurrence records are overlaid on peatland drainage status information.

Table 1
List of selected environmental variables used as explanatory variables in the modeling experiments.

Environmental variable	Abbreviation	Unit	Mean [min–max]	Spatial resolution (m)	Data source
Mean growing degree days (1981–2010)	GDD	°C days	972 [38–1471]	50	FMI; Heikkinen et al. (2020)
Mean annual water balance (1981–2010)	WAB	mm	252 [123–620]	50	FMI; Heikkinen et al. (2020)
Mean January temperature (1981–2010)	TJan	°C	-9 [−15 to −0.5]	50	FMI; Heikkinen et al. (2020)
Mean topographical wetness index	TWI	–	8 [3−23]	10	NLS, DEM
Proportion of undrained peatlands in grid square	UNDRAINED	%	17.9 [0–100]	25	Syke
Proportion of drained peatlands in grid square	DRAINED	%	24.1 [0–100]	25	Syke
Proportion of open peatlands in grid square	OPEN	%	0.6 [0–100]	16	Syke
Proportion of herb-rich site type (peatlands) in grid square	ST1	%	0.4 [0–55]	16	Luke, MS-NFI
Proportion of *Vaccinium myrtillus* site type (peatlands) in grid square	ST2	%	5.5 [0–100]	16	Luke, MS-NFI
Proportion of *Vaccinium vitis-idaea* site type (peatlands) in grid square	ST3	%	40.6 [0–100]	16	Luke, MS-NFI
Proportion of *Cladina* site type (peatlands) in grid square	ST6	%	1.6 [0–100]	16	Luke, MS-NFI
Presence of calcareous rock in grid square	ROCK	–	0/1	N/A	GTK
Mean volume, pine	PINE	m^3/ha	50 [0–314]	16	Luke, MS-NFI
Mean volume, spruce	SPRUCE	m^3/ha	21.4 [0–485]	16	Luke, MS-NFI
Mean volume, birch	BIRCH	m^3/ha	13.7 [0–232]	16	Luke, MS-NFI
Mean volume, other broad-leaved trees	OTHER	m^3/ha	2 [0−202]	16	Luke, MS-NFI

Data source abbreviations: FMI Finnish Meteorological Institute, NLS National Land Survey, DEM Digital Elevation Model, Syke Finnish Environment Institute, Luke Natural Resources Institute Finland, MS-NFI Multi-source National Forest Inventory, GTK Geological Survey of Finland.

species—pine (PINE), spruce (SPRUCE), birch (BIRCH), and other broad-leaved trees (OTHER)—from the MS-NFI data. These variables reflect habitat patterns and structural complexity within each grid cell.

2.4. *Restoration scenarios and climate projections*

We developed four theoretical restoration scenarios for all grid cells containing forestry-drained peatland, based on the work from Tolvanen et al. (2020). These scenarios simulated varying degrees of potential restoration by proportionally reducing drained and increasing undrained peatlands. The scenarios represent 0 %, 30 %, 50 %, and 100 % restoration of drained peatlands, labeled REST0, REST30, REST50, and REST100, respectively. It is important to note that our model assumes restored habitats mirror undrained habitats in terms of ecological characteristics and functionality, simplifying the complex restoration process.

For climate projections, we obtained future GDD, WAB, and TJan data from Heikkinen et al. (2020) at a 50-m resolution. These projections were based on an ensemble of 23 global climate models from the CMIP5 archives. The data project changes in mean temperature and precipitation for two future periods, 2040–2069 and 2070–2099, relative to the baseline period of 1981–2010. The projections cover three Representative Concentration Pathways (RCPs): RCP2.6 (stringent mitigation), RCP4.5 (intermediate), and RCP8.5 (high emissions), representing different future greenhouse gas concentration scenarios and potential climate outcomes.

2.5. *Habitat suitability modeling*

We used the Maxent algorithm (Phillips et al., 2006) in R version 4.2.2 (R Core Team, 2022) to predict habitat suitability for each red-listed plant species across the study area. Maxent is a presence-only modeling technique that estimates species presence probability based on environmental variables, producing a continuous output from 0 (least suitable) to 1 (most suitable). It is effective for species distribution modeling with limited presence data (Phillips and Dudík, 2008).

To account for sampling bias and control for false absences, we generated 10,000 randomly located background pseudo-absence points, a number shown to be sufficient for robust models (Barbet-Massin et al., 2012). Model parameters included a regularization multiplier of 1, auto-features, a maximum of 500 iterations, and a convergence threshold of 10^{-5}, all set to avoid overfitting (Valavi et al., 2022). We used the logistic output to compare prediction maps between species (Rana and Tolvanen, 2021; Saarimaa et al., 2019). We applied the same environmental variables and Maxent settings for all species to facilitate model comparison and aggregation. To reflect realistic species movement constraints, we incorporated a dispersal limitation of 20 km, a conservative estimate based on plant dispersal in fragmented landscapes (O'Connell et al., 2013).

To evaluate our model, we used 5-fold cross-validation and reported the average results across all iterations. We assessed model performance with three complementary metrics: the area under the receiver operating characteristic curve (AUC; Fielding and Bell, 1997), which measures the model's ability to discriminate between presence and absence; the continuous Boyce index (CBI), which assesses how model predictions differ from random expectation, with positive values indicating consistency with observed distributions and values close to zero suggesting random predictions (Boyce et al., 2002; Hirzel et al., 2006); the true skill statistic (TSS), calculated as the sum of sensitivity and specificity minus 1 (Allouche et al., 2006), providing a threshold-independent measure ranging from -1 to $+1$, where $+1$ indicates perfect agreement and values ≤ 0 suggest random performance. We considered models good if they achieved AUC > 0.8 (Swets, 1988), TSS > 0.5 (Liu et al., 2011), and CBI > 0.6.

To determine the relative importance of different environmental variables, we used the permutation importance which assesses each variable's contribution by randomly permuting its values among the training points and measuring the resulting decrease in model performance (Phillips et al., 2017). A greater drop in model gain indicates higher importance. Permutation importance offers a reliable measure of explanatory power as it is independent of the model's training path (Saarimaa et al., 2019).

2.6. *Analysis of habitat changes, latitudinal shifts, and species richness*

To create binary habitat suitability maps, we applied the maximum training sensitivity plus specificity threshold to the continuous Maxent predictions. This threshold optimizes the trade-off between sensitivity and specificity (Liu et al., 2013). Areas with suitability values above this threshold were classified as suitable habitat.

To quantify changes in suitable habitat between current and future conditions, we calculated habitat expansion (areas predicted to become suitable in the future but not currently suitable) and habitat loss (areas currently suitable but predicted to become unsuitable in the future). We also examined potential latitudinal shifts by comparing the centroids (geometric mean centers) of current and future suitable habitats. The latitudinal shift was calculated as the north-south displacement between centroids, with positive values indicating northward shifts.

To analyze changes in species richness of red-listed species (i.e., the number of species present in the study area), we stacked the binary maps for all species and summed them, showing the number of species with suitable habitat in each grid cell. We then calculated change maps reflecting the difference between current and future richness. For each vegetation zone, we calculated the percentage of grid cells with substantial changes in species richness, using a threshold of ±1 species to focus on meaningful ecological changes and minimize the effect of minor model variations.

3. Results

3.1. The SDM and main variables

We obtained well-performing models for 21 of the considered 27 species (Figure S1), with training AUC ≥ 0.83 (mean 0.94), evaluation AUC ≥ 0.84 (mean 0.93), CBI ≥ 0.64 (mean 0.84), and TSS ≥ 0.61 (mean 0.77). For the remaining six species which we excluded from further analyses, TSS was <0.5 and CBI < 0.6. Drainage and climate-related variables were on average the most influential ones (Figure S2), with UNDRAINED having the highest permutation importance (28.78 %), followed by TJan (15.57 %), and GDD (13.67 %).

3.2. Potential future changes in suitable habitats

Restoration efforts impacted habitat expansion across species groups. MB species showed the strongest response, with the largest increases in habitat expansion from REST0 to REST100 scenarios (Fig. 2). NB species benefited moderately, while SB species exhibited the smallest absolute changes.

RCP scenarios significantly influenced habitat expansion and loss. Under REST0, MB species had the highest expansion potential across all scenarios, accompanied by substantial habitat losses. NB species experienced moderate expansion, but severe habitat losses under higher RCP scenarios. SB species showed more conservative changes, with relatively modest and comparatively lower habitat losses. Notably, habitat loss intensified with higher RCP levels, particularly for NB and MB.

When combining restoration and climate change effects, the impact of restoration became evident. Under RCP2.6, all species groups showed consistent patterns, with increased restoration (REST100) leading to greater habitat expansion and slightly reduced habitat loss compared to REST0. Under the RCP8.5, restoration increased suitable habitat expansion and prevented habitat loss, but its effectiveness diminished over time, especially for NB and MB, where habitat expansion decreased significantly by 2070–2099 and habitat loss increased. SB species showed a different pattern, with increased habitat expansion under RCP8.5 in 2080–2099.

3.3. Potential latitudinal changes of the habitats

There was a clear south-to-north gradient in migration distances (Fig. 3), with SB species showing the largest northward shifts ($\leq$ 142 km) compared to NB species ($\leq$ 80 km). Without restoration, the severity of climate change strongly influenced latitudinal movements, with RCP4.5 and RCP8.5 consistently resulting in larger northward shifts than RCP2.6. Restoration generally decreased the shifts. For instance, under REST100 and RCP2.6, MB species shifted 77.5 km in 2040–2069, compared to 84.9 km under REST0. Under RCP8.5, there were notable reductions particularly for NB (from 79.5 km under REST0 to 70.7 km under REST100 in 2040–2069) and SB species (from 137.1 km under REST0 to 132.3 km under REST100 in 2070–2099).

3.4. Potential change in species richness distribution

In both 2040–2069 and 2070–2099, moderate increases in species richness were the most prominent in the MB and NB regions under RCP2.6 (Fig. 4). However, by 2070–2099, under RCP8.5, a significant shift occurred in the NB zone, with areas of red-listed species richness decline emerging. This negative trend in the north persisted even with increased restoration. In other cases, restoration efforts consistently increased red-listed species richness across all zones (Figure S3).

4. Discussion

Our results indicate that restoration hypothetically expands suitable habitats, reduces habitat loss, and slows down northward range shifts under RCP2.6 and RCP4.5. Red-listed species richness increases most notably in the NB zone where restoration has the greatest positive impact. However, under RCP8.5 scenario, habitat loss is more severe, particularly for NB and MB species, with significant northward shifts and reduced red-listed species richness. These findings align with global studies documenting climate-driven habitat contraction and northward migration across various taxa. Ma et al. (2022) observed similar northward shifts in *Sphagnum* mosses in response to climate warming, with suitable habitat expanding extensively in high-latitude boreal peatlands while decreasing in southern regions. Likewise, tree species across continents are predicted to migrate to higher altitudes and latitudes as temperatures rise, with suitable areas for certain species contracting

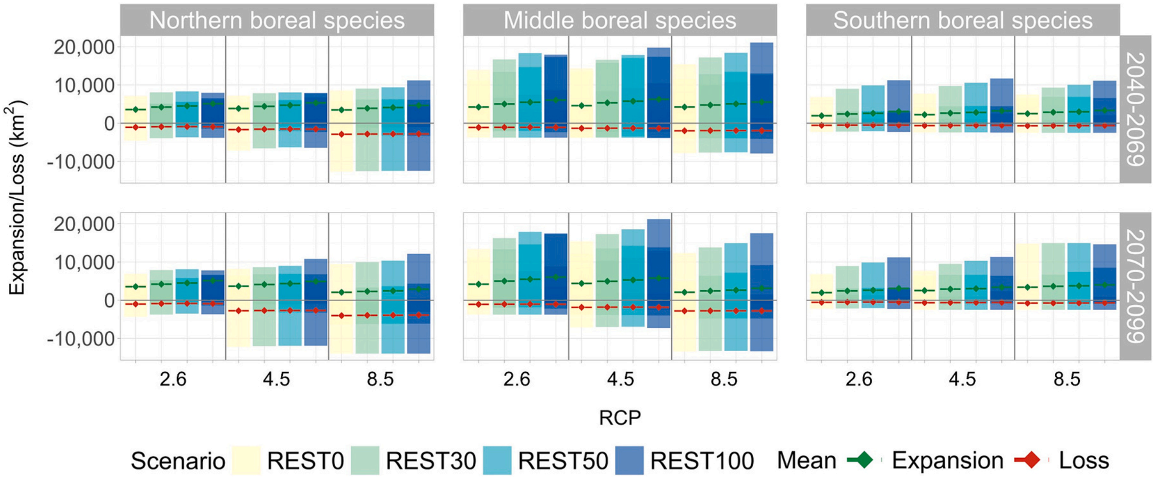

Fig. 2. Projected changes in suitable habitat area for northern, middle, and southern boreal species under different Representative Concentration Pathway (RCP) scenarios and restoration levels (REST0-REST100) for 2070–2099 compared to current distribution. Bars represent minimum and maximum value across individual species' responses, with positive values (above zero) indicating habitat expansion and negative values (below zero) indicating habitat loss. Dashed lines with diamond markers show mean values for all species for both expansion and loss.

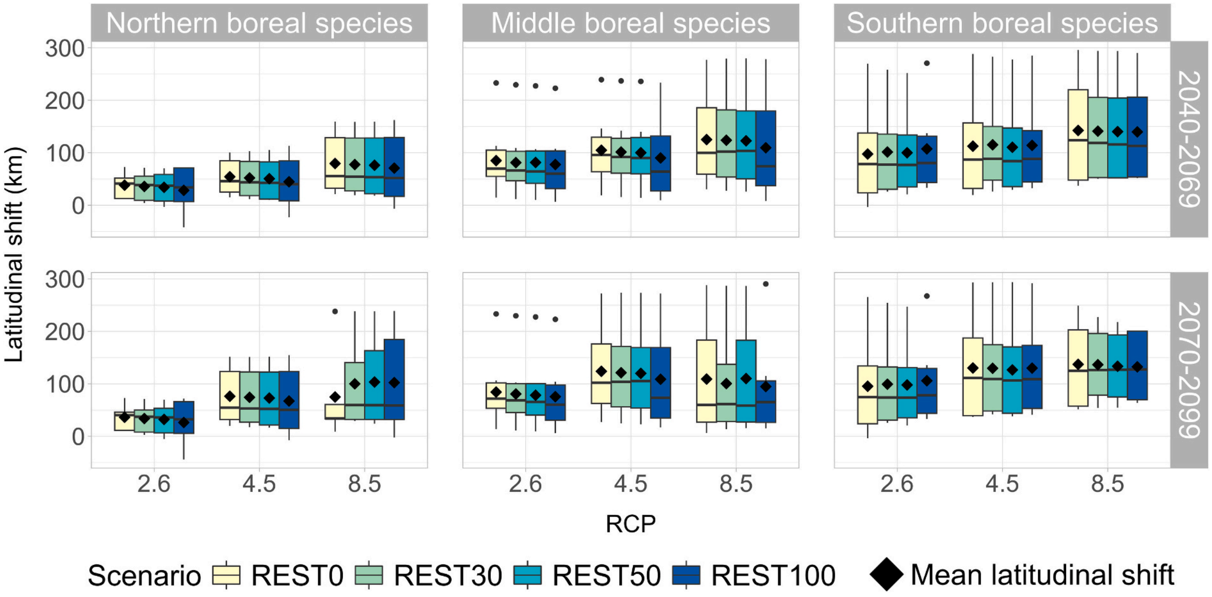

Fig. 3. Projected latitudinal shifts (km) for northern, middle, and southern boreal species under different Representative Concentration Pathway (RCP) scenarios and restoration levels (REST0-REST100) for 2040–2069 to 2070–2099 compared to current distribution. Positive values indicate northward movement while negative values indicate southward movement.

considerably—patterns observed in both Canada and China (Boisvert-Marsh and De Blois, 2021; Sun et al., 2020). In Europe, Thurm et al. (2018) quantified substantial northward shifts in tree species under warming scenarios, projecting that approximately 60 % of their potential distribution range could be lost. These earlier results support our finding that while restoration can mitigate habitat loss under moderate climate scenarios, more extreme warming may overwhelm these restoration efforts.

4.1. *Modeling performance and limitations*

Despite the good performance of our SDMs, the results should be interpreted with caution. In our hypothetical restoration scenarios, we assumed that the restored habitats would immediately and functionally mirror undrained habitats. This simplification overlooks the complex and time-dependent processes involved in ecological restoration. Drainage-induced water table drawdown exacerbates aerobic microbial decomposition in the topsoil, causing potentially irreversible changes to the physical properties of peat (Menberu et al., 2021; Morris et al., 2022) which impact ecohydrological processes. Hydrological recovery is a gradual process and can be challenging to achieve perfectly (Menberu et al., 2016, 2017). Furthermore, restored peatlands often remain incomplete in their vegetation recovery even after 10 or 30 years, with full recovery seldom achieved (Atkinson et al., 2022; Elo et al., 2024; Kreyling et al., 2021). Therefore, our predictions should be interpreted as best-case scenarios, with actual habitat availability potentially being lower or taking longer to achieve.

Another key consideration is the spatial resolution of our analysis. While species locations were recorded as points, we analyzed drainage conditions by aggregating the original 25 m resolution data to 500 m grid cells, calculating the proportions of drained and undrained areas within each cell. This means that even observations from predominantly undrained sites may be associated with grid cells containing some percentage of drained area, and vice versa. It is possible that most of the species' observations are located nearby drained areas as fully undrained areas are more difficult to find particularly in southern Finland and they are usually more difficult to reach (and thus inventory) than areas nearby drainage. Consequently, our models may underestimate habitat suitability in fully undrained or restored areas, instead reflecting their current observed presence mostly in partially drained grid cells. Spatial aggregation of other environmental variables introduces additional uncertainty. Seasonal water table fluctuations, local hydrology, and fine-scale habitat heterogeneity may not be fully captured at our scale of analysis. Temporal mismatches between species occurrence records and environmental data could further affect model accuracy, particularly in areas with recent land-use changes.

SDMs do not guarantee species presence or absence, as they do not account for biotic interactions, which also influence species distributions. Incorporating biological mechanisms (i.e., species interactions (Virtanen et al., 2010), physiology, evolutionary potential (Urban et al., 2016)) and fine-scale microclimatic data (Kolstela et al., 2024) would offer a more comprehensive understanding of species distributions in peatland ecosystems. Additionally, our study does not account for the differential responses of different peatland complexes or habitat types, which remains an important aspect for future research. Future climate projections also carry inherent uncertainty, especially under extreme scenarios, where novel conditions may challenge model assumptions.

Lastly, the assumption of a 20 km dispersal limitation may not accurately reflect the dispersal capabilities of all the studied species, which can vary significantly among species due to factors like seed size and dispersal mechanisms (Kyrkjeeide et al., 2016; Zanatta et al., 2020). Many peatland species, especially those adapted to stable conditions, may have more limited dispersal abilities. This could mean that our projections overestimate species' ability to colonize newly suitable habitats, particularly under restoration scenarios. Conducting species-specific dispersal studies or assessing migration rates could provide more accurate predictions in future studies. Additionally, this would be essential for identifying species that may require active introduction or translocation programs.

4.2. *Benefits of restoration*

Restoration at 30 %, 50 %, and 100 % effectively mitigates habitat loss and preserves habitat availability under both RCP2.6 and RCP4.5. By re-establishing natural hydrological conditions—primarily through rewetting—restoration recreates the waterlogged environments (Holden et al., 2017; Menberu et al., 2016) critical for peatland specialist species, which are highly sensitive to moisture fluctuations and warming

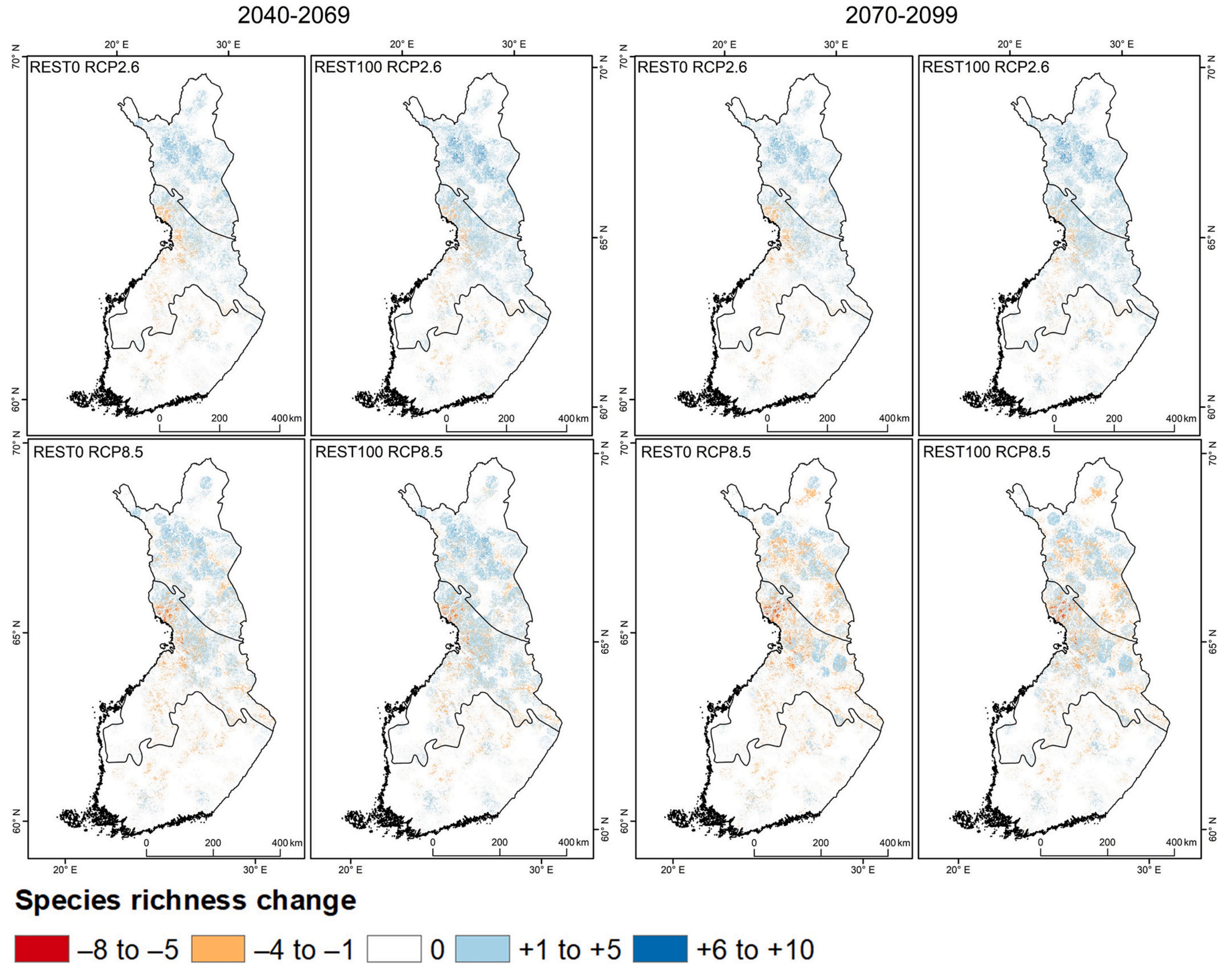

Fig. 4. Maps showing predicted changes in species richness distribution for the red-listed peatland plant species under different Representative Concentration Pathway (RCP) scenarios and restoration levels (REST0-REST100) for 2040–2069 to 2070–2099 compared to current distribution. Different colors (from red to blue) indicate different species richness change levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Campbell et al., 2021; Heikkinen et al., 2021). These conditions maintain cooler microhabitats and stabilize hydrological processes, buffering peatlands against the impacts of increased evapotranspiration and aerobic peat decomposition driven by warming.

The benefits of restoration were most pronounced for MB species, which exhibit the greatest habitat expansion. This response likely reflects the large extent of drained peatlands in the MB zone, providing more opportunities for habitat creation, and its intermediate climatic conditions compared to SB and NB zones. Restoration also mitigates species' projected northward range shifts, with the strongest mitigation observed for MB species, followed by NB species. These shifts are primarily driven by the northward progression of climatic conditions under warming scenarios, which relocate suitable habitats to higher latitudes (Ma et al., 2022; Mallen-Cooper et al., 2023). Extended growing seasons in northern regions provide favorable conditions for establishment and growth (Primeau and Garneau, 2021), particularly for SB species. This movement is further accelerated by water table drawdown in southern habitats (Gong et al., 2012; N. Kokkonen et al., 2024), which degrades habitat quality and forces species to relocate. However, our results indicated that restoration may reduce the severity of these shifts by maintaining habitat quality within their existing ranges.

Patterns of species richness provide further evidence of restoration's benefits. The NB zone exhibited the largest increase in species richness under moderate climate scenarios, likely due to the region's relatively high proportion of undrained peatlands and the influx of species from the MB zone. These findings suggest that restoration not only helps conserve existing plant communities but also facilitates gradual range adjustments essential for long-term adaptation to climate change. However, the variability of outcomes across zones and species underscores the need for tailored restoration strategies that consider local ecological and climatic contexts. For example, research evidence from Finnish aapa mires has shown that the fen-like vegetation is changing towards bog-like vegetation, which might be partly caused by drainage and partly by the changing climate (Granlund et al., 2022; Kolari et al., 2022; Kolari and Tahvanainen, 2023). Additionally, it has been discussed that changing climate might shift minerotrophic complexes towards ombrotrophic complexes (Parviainen and Luoto, 2007; Robitaille et al., 2021). Therefore, restoration in these areas could be targeted to catchment-scale restoration of water-flow routes and hydrological connectivity to buffer against climate-induced warming and drying (Isoaho et al., 2024; Sallinen et al., 2019). Further, restoration efforts in general could particularly focus on restoring nutrient-rich peatlands which harbor red-listed species and habitat types and in which the ecological restoration success is more probable than in nutrient-poor peatlands (Elo et al., 2024).

4.3. Climate change and limits of restoration

Under RCP8.5, particularly during 2070–2099, suitable habitat losses, hypothetically, became more pronounced for NB and MB species, with increased northward movement for all species groups and decreased species richness in the NB zone, even under maximum restoration efforts. The NB and MB species are likely to face habitat loss due to rapid warming, with no cooler and wetter areas available for migration. The extreme conditions projected under RCP8.5, including higher January temperatures, longer growing degree days, and increased evapotranspiration, are likely to disrupt water balance in peatlands (Antala et al., 2022; Swindles et al., 2019). Increased drought or excessive water loss under extreme climate scenarios could accelerate peat decomposition (Lunt et al., 2019; Sihi et al., 2018), degrade habitat quality (Page and Baird, 2016; Zhang et al., 2018) and make restoration less effective. The rapid climate change may also outpace the peatland plant species' ability to adapt or migrate (Jiménez-Alfaro et al., 2016). Red-listed peatland plant species often struggle to adapt due to their poor dispersal capabilities (Essl et al., 2011) and narrow climatic niches (Wróblewska and Mirski, 2018).

SB species exhibited increased habitat expansion under RCP8.5, probably benefiting from the northward extension of their climatic ranges into newly suitable areas. The modelled expansion of SB species consequently leads to the decline of NB and MB species, highlighting the uneven effects of extreme warming. The creation of potential novel habitats for SB species in northern area suggests that while some species may adapt and migrate, others, particularly those at northern latitudes, may face significant risks of local extinction. These findings emphasize the dual pressures of warming and hydrological instability under extreme climate scenarios. Although peatlands may display resilience to moderate climate change (Loisel and Gallego-Sala, 2022; Sim et al., 2021), there seems to be a threshold of temperature and precipitation beyond which this resilience is compromised (Moore and Waddington, 2015; Norby et al., 2019). Additionally, increased competition from species better adapted to warmer conditions (Le et al., 2022; Oke and Hager, 2020) could further reduce habitat suitability, particularly under extreme warming scenarios. Consequently, even with restoration, the capacity of peatlands to support specialized species is likely to decline under RCP8.5.

5. Conclusions

We studied the role of peatland restoration and climate conditions in shaping the location and area of suitable habitats for 21 red-listed peatland plant species in Finland during 2040–2069 and 2070–2099. Our modeling demonstrated that both hypothetical restoration scenarios and climate change will influence the habitats. Restoration can sustain or increase suitable habitats, mitigate habitat loss, moderate northward shifts in species distributions, and preserve species richness. However, beneficial impacts of restoration varied across boreal zones and climate scenarios, with the positive effects increasingly compromised under severe climate conditions, particularly by 2070–2099. The temporal pattern underscores the urgency of initiating restoration efforts promptly, before critical climate thresholds are crossed. This aligns with the EU Nature Restoration Law, which emphasizes that timely action is crucial to prevent further biodiversity loss. In addition, priority should be given to protecting existing suitable habitats of red-listed species and areas with the potential to act as future refugia. Furthermore, since restoration benefits are most pronounced when implemented at larger scales, large-scale restoration of degraded peatlands is essential.

CRediT authorship contribution statement

Priscillia Christiani: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Aleksi Isoaho:** Writing – review & editing, Methodology, Investigation. **Merja Elo:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Lassi Päkkilä:** Writing – review & editing. **Hannu Marttila:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Juha Aalto:** Writing – review & editing, Data curation. **Jan Hjort:** Writing – review & editing. **Anne Tolvanen:** Writing – review & editing, Supervision, Conceptualization. **Parvez Rana:** Writing – review & editing, Methodology, Investigation. **Aleksi Räsänen:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111126.

Data availability

Data will be made available on request.

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