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Heikkinen, Risto K.

2022-12

Heikkinen , R K , Aapala , K , Leikola , N & Aalto , J 2022 , ' Quantifying the climate exposure of priority habitat constrained to specific environmental conditions : Boreal aapa mires ' , Ecological Informatics , vol. 72 , 101828 . https://doi.org/10.1016/j.ecoinf.2022.101828

http://hdl.handle.net/10138/356228
https://doi.org/10.1016/j.ecoinf.2022.101828

Ecological Informatics 72 (2022) 101828

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

Quantifying the climate exposure of priority habitat constrained to specific environmental conditions: Boreal aapa mires

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ARTICLE INFO

Keywords:
Climate change velocity
Climate exposure
EU habitats directive
Aapa mire
Peatland conservation
Priority habitat

ABSTRACT

Climate velocity is an increasingly used metric to detect habitats, locations and regions which are exposed to high rates of climate change and displacement. In general, velocities are measured based on the assumption that future climatically similar locations can occur anywhere in the study landscape. However, this assumption can provide a biased basis for habitats which are constrained to specific environmental conditions. For such habitats, a set of selected suitable locations may provide ecologically more realistic velocity measures. Here, we focus on one environmentally constrained habitat, aapa mires, which are peat-accumulating EU Habitats Directive priority habitats, whose ecological conditions and biodiversity values may be jeopardised by climate change. We assess the climate exposure of aapa mires in Finland by developing velocity metrics separately for the whole ≥10 ha aapa mire complexes ('aapa mires') and their wettest flark-dominated parts ('flark fens'). Velocity metrics were developed for six bioclimatic variables (growing degree days (GDD5), mean January and July temperatures, annual precipitation, and May and July water balance, based on climate data for 1981–2010 and for 2040–2069 as derived from global climate models for two Representative Concentration Pathways (RCP4.5 and RCP8.5). For the six variables, velocities were calculated based on the distance between climatically similar present-day and nearest future mire, divided by the number of years between the two periods, and by excluding the unsuitable matrix. Both aapa mires and flark fens showed high exposure (>5 km/year) to changes in January temperature, and often also considerably high velocities for GDD5 and July temperatures. The flark fens showed significantly higher climate velocities than the aapa mires and had a smaller amount of corresponding habitat in their surroundings. Thus, many of the studied mires, particularly the flark fens, are likely to face increased risks of exposure due to changes in winter and summer temperatures. Moreover, considerable changes in precipitation-related conditions may occur at the southern margin of the aapa mire zone. Our results show that specifically tailored climate velocity metrics can provide a useful quantitative tool to inform conservation and management decisions to support the ecosystem sustainability of this EU Habitats Directive biotope and targeting restoration towards the most vulnerable aapa mires.

1. Introduction

Climate change velocity is an increasingly used metric to develop quantitative information for detecting regions, specific ecosystems, protected areas and species populations which can be highly exposed to the impacts of climate change (Brito-Morales et al., 2018; Hamann et al., 2015; Lai et al., 2022). At the core of calculating climate velocity metrics is the spatial comparison of locations which have similar conditions under contemporary climate and projected future climate, measured based on one or more individual climate variables or combined composites of multiple variables (Brito-Morales et al., 2018; Heikkinen et al., 2020; Loarie et al., 2009; Nadeau and Fuller, 2015; Ordonez and Williams, 2013). Using the geographic information data (GIS) surfaces for the focal climate variables developed for different time periods, the distance between present-day locations with a certain climate and their future analogues can be measured. Dividing the distance values by the number of years between the two points in time provides velocity metrics, which illustrate the rate at which organisms should move to maintain similar climate conditions (Haight and Hammill, 2020). Such metrics provide a useful tool for identifying potential climate change

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https://doi.org/10.1016/j.ecoinf.2022.101828
Received 15 March 2022; Received in revised form 18 August 2022; Accepted 20 September 2022
Available online 28 September 2022
1574-9541/

hotspots, i.e., ecosystems, protected areas or habitats of conservation concern, where climate is changing most rapidly and biodiversity is thereby most vulnerable (Fuentes-Castillo et al., 2020; Lai et al., 2022). Assessing climate velocity does not require in-depth ecological knowledge or distribution data on species, which makes it a generic measure of the exposure to climate change (Carroll et al., 2015; Batllori et al., 2017).

However, there are certain technical uncertainties and user-based decisions which can affect the usefulness of the velocity metrics for climate-smart conservation and management planning (i.e., planning informed by projected climate-change impacts). These include, for example, the selection of velocity algorithm and focal climate variables, spatial resolution of the climate data and the challenges in interpretation of multivariate climate-analogue velocity measurements (Brito-Morales et al., 2018; Carroll et al., 2017; Hamann et al., 2015; Heikkinen et al., 2020; Kosanic et al., 2019). One hitherto insufficiently studied question is how to measure velocities for habitats whose occurrences are constrained to specific environmentally suitable conditions. In such cases, a key issue is whether future climatically similar locations are considered to occur anywhere in the study landscape or if only selected environmentally suitable locations are included in the calculation of the velocities. Most studies have measured velocities using information from the whole landscape (Burrows et al., 2011, 2014; VanDerWal et al., 2013). However, focusing on a set of selected locations may provide more realistic velocities. Batllori et al. (2017) showed that the nearest future climatic analogues for current protected areas may occur in degraded land due to which the calculated velocity values can be, in ecological terms, too low. Moreover, certain ecosystems can evolve only under specific environmental conditions, such as in stream habitats (Troia et al., 2019) and different wetland ecosystems (Horsáková et al., 2018; Johnson et al., 2010; Keith et al., 2014). For such habitats, large areas can represent unsuitable terrain, whose inclusion in the velocity measurements may lead to biased metrics.

In this study, we provide a novel climate velocity assessment of one high-latitude ecosystem of high conservation concern in Europe, the aapa mire complexes and the wet flark fens embedded in them. For these habitats, large parts of the landscape can be excluded from the velocity measurements to increase their realism. Development of the aapa mires, as natural peatlands in general, depends on specific environmental conditions, available in limited locations in the landscape (Horsáková et al., 2018; Sperle and Bruelheide, 2021). Generally, the most suitable conditions for peatland ecosystem development occur in the northern landscapes, where permanent water logging supports the accumulation and growth of peat (Charman, 2002; Pedrotti et al., 2014; Wieder and Vitt, 2006). In Northern Europe, boreal peatlands consist of minerotrophic groundwater-influenced fens and ombrotrophic bogs, where water and nutrients come from precipitation and atmospheric deposition (Parviainen and Luoto, 2007; Pedrotti et al., 2014; Tahvanainen, 2011). The south-north distribution of the peatland complex types in Fennoscandia – raised bogs, aapa mires and palsa mires – correlate with climatic gradients of precipitation and temperature (Parviainen and Luoto, 2007).

The importance of aapa mires for conservation is widely recognised. They are included among the priority habitat types in Annex I of the EU Habitats Directive, a legislative conservation instrument of the European Union (https://eunis.eea.europa.eu/habitats/10154). In addition to their value as unique habitat complexes, aapa mires provide suitable environments for many mosses, vascular plants and breeding wader bird species of conservation concern (Fraixedas et al., 2017; Saarimaa et al., 2019; Tolvanen et al., 2020). Peatlands, including aapa mires, are sensitive to increasing temperatures and decreasing water balance and precipitation (Essl et al., 2012; Horsáková et al., 2018; Keith et al., 2014; Sperle and Bruelheide, 2021; Swindles et al., 2019). In addition, aapa mires depend on the surface water flows from the surroundings. Altogether, this makes aapa mires particularly sensitive to hydrological alterations caused by land use (Sallinen et al., 2019) as well as climate warming (Gong et al., 2012). Globally, the largest changes in the climate are projected to occur in high-latitude environments (AMAP, 2017), suggesting increased exposure for aapa mires and their biodiversity (Kolari et al., 2021; Väliranta et al., 2017). Particularly critical is the rate of change in the key climatic variables for aapa mires, such as annual and summer temperatures, growing season conditions and evapotranspiration (Parviainen and Luoto, 2007).

To date, only a few studies have examined the risks that rapid climatic changes may cause to the priority habitats of the EU Habitats Directive (Bittner et al., 2011) or the European Natura 2000 network supporting the conservation of priority habitats (Heikkinen et al., 2020; Lai et al., 2022; Nila and Hossain, 2019; Stagl et al., 2015). Here, we increase this understanding by developing a climate exposure assessment across the whole aapa mire zone of Finland. Although in Finland the main current threat for aapa mires is land use, especially artificial drainage, we focus here solely on the climate-change-based exposure of aapa mires, which is a poorly examined topic. Specifically, we investigate the following questions: (1) Are there differences in the level of exposure of aapa mires to different climatic parameters and their velocities? (2) Are certain areas in the aapa mire zone projected to face higher climate change velocities than others? (3) Are climate change velocities higher for the wettest habitats, flark fens (i.e., sparsely vegetated fens with hummocky strings and open water-filled shallow pools, 'flarks'), than for aapa mires in general?

2. Material and methods

2.1. Aapa mires as a study system

In this section, we explain the typology, physiognomic and ecological characteristics of our study system, aapa mire complexes. The aapa mire concept employed in our study follows the typification and classification of Ruuhijärvi (1960, 1983, 1988). More recent introductions to the aapa mires of Finland can be found in Laitinen et al. (2007), Granlund et al. (2021) and particularly Sallinen et al. (2019), and the key characteristics of aapa mires have also been treated in some seminal peatland ecology books (e.g., Charman, 2002; Wieder and Vitt, 2006). The core feature of aapa mire complexes is the minerotrophic fen vegetation with string-flark patterning in their central parts (https://eunis.eea.europa.eu/habitats/10154) (Fig. 1). However, it should be noted that aapa mire complexes include several hydrotopographical and ecologically diverse components, ranging from mud-bottom fens and flark-fens to unraised *Sphagnum fuscum*-bogs and pine mires and spruce swamps in the margins of the complex, all of them showing gradual variation in the extent and clarity of their patterns caused by the geographic variation in the wetness and climatic conditions (see Laitinen et al., 2007; Sallinen et al., 2019). More generally, the typology of mires varies from country-to-country and study-to-study. Thus, the aapa mire zone has been referred to as a northern fen region and the aapa mires as string-flark fens and mixed mires in some European studies (Tanneberger et al., 2021), whereas as in North America, structurally and hydrologically similar mires to our aapa mires are often referred to as patterned fens (e.g., Foster et al., 1988; Vitt et al., 2022).

Aapa mires occur in continental regions characterised by long winters, spring floods from melting snow and a positive summer-time water balance, allowing water surfaces to persist (Parviainen and Luoto, 2007). The climate envelope of aapa mires varies for annual precipitation between 420 and 2350 mm and for mean annual air temperature from −3.8 to 4.3 °C, this space partly overlapping with raised bogs in the south and palsa mires (mires with peat mounds, characterised by permanently frozen core) in the north (Parviainen and Luoto, 2007). Concerning the annual temperature sum above the base temperature of 5 °C (growing degree days, GDD5), the southern border of the aapa mire zone mainly coincides with the 1100 °C isocline for GDD5 (Tahvanainen, 2011; Fig. 2b).

There are differences in the abundance and physiognomy of mires

Fig. 1. Aapa mire complex situated in a middle boreal (aapa mire) zone, showing typical patterned structure on the right side with drier strings spread across the waterlogged flark fens, and more evenly vegetated fens and bogs at the margins of the complex (at left in the figure). Kitkasuo, Lieksa, Finland. © Maarit Similä.

located in different parts of the aapa mire zone. In general, the wetness of mires increases northwards following decreasing summer temperatures and increasing humidity (Sallinen et al., 2019; Seppä, 2002). Consequently, aapa mires with flarks are most common in the northern boreal zone, whereas at the southern border of the aapa mire zone, the mires are drier (Seppä, 2002). In addition, local topography contributes to the development of aapa mires. Optimal conditions for large aapa mires occur in wide flatlands with favourable hydrology, coinciding with cool summers and spring floods, enhancing the wetness and inhibiting the development of ombrotrophic bogs (Ruuhijärvi, 1960; Sallinen et al., 2019; Tahvanainen, 2011). Such conditions prevail especially in the western part of the aapa mire zone in Finland (Fig. 2). Most characteristically, aapa mires constitute several square-kilometres-wide, morphologically variable mire complexes dominated by treeless string-flark fens in the central parts, surrounded by narrow forested bog margins (Laitinen et al., 2007; Ruuhijärvi, 1960; Sallinen et al., 2019). A distinctive physiognomic feature is the patterned surface structure, where elongated, drier strings are spread across the minerotrophic waterlogged fen surfaces and sparsely vegetated or open-water flarks (Fig. 1) (Sallinen et al., 2019).

A central prerequisite for the favourable ecological and conservation status of aapa mires is the continuous supply of water from the surrounding catchment and sufficient summer-time humidity (Tahvanainen, 2011). The dependence of aapa mires on the surface water flows makes them sensitive not only to the impacts of land use, i.e., artificial drainage for forestry, agriculture or the peat industry (Sallinen et al., 2019), but also to the effects of hydrological alterations caused by climate change (Gong et al., 2012). Critical changes in hydrological cycles may be caused by increased summer evaporation, diminished average spring floods and their earlier timing (Lotsari et al., 2010). Such changes can catalyse the replacement of groundwater-fed fen surfaces by ombrotrophic bog vegetation (Kolari et al., 2021; Pedrotti et al., 2014; Tahvanainen, 2011; Väliranta et al., 2017).

At present, a large local variation in water- and nutrient-based environmental conditions in different peatland ecosystems supports the persistence of over 400 red-listed species, which either primarily occupy peatland habitats or inhabit peatlands as one of their habitats (Hyvärinen et al., 2019; Saarimaa et al., 2019). In aapa mires, the potential impacts of a warming climate and resulting ombrotrophication may critically affect those species which are confined to the wettest parts of aapa mires. These microhabitats include various vascular plants, bryophytes and insect species, the latter of which are an important resource to many bird species (Arvidsson et al., 1992).

2.2. Aapa mire distribution data

We included both aapa mire and palsa mire zones (Fig. 2) as delimited in earlier works (Ruuhijärvi, 1960, 1988). We also considered palsa mires, because they share several features in common with aapa mires (except the actual permafrost core). Thus, they may provide suitable habitats for aapa mire species in future climates, especially as warming is predicted to melt the palsa mounds and increase the cover of thermokarst ponds (Aalto et al., 2017a).

The more southernly distributed raised bogs are also open mires and thus physionomically similar to aapa mires, yet ecologically different environments. This is primarily due to their *Sphagnum*-bog-dominated and rainwater-fed ombrotrophic nature, which does not provide suitable habitats for aapa mire dwelling species (Rydin and Jeglum, 2006). Raised bogs occur sporadically in topoclimatically suitable locations in the aapa mire zone (Ruuhijärvi, 1988). We determined such extrazonal occurrences based on information from the SAKTI database of Metsähallitus Parks and Wildlife Finland, and fine-resolution (25 m) information on the occurrences of mire habitats developed based on visual interpretations of aerial images from the Finnish Environment Institute (see Sallinen et al., 2019).

Occurrences of aapa mires were determined based on the CORINE CLC2018 land cover data (Härmä et al., 2019). We used the 20-m resolution CORINE CLC2018 data available for Finland, particularly the CORINE category 4121 (‘Peatbogs’) which includes various open mires occurring in raised bog, aapa mire and palsa mire zones. From these data, we first excluded the peatbog occurrences in the raised bogs zone using the ArcGIS (Desktop 10.5.1.). Next, from the remaining peatbogs located in the aapa and palsa mire zones, we identified the extrazonal raised bog occurrences and excluded them. All remaining peatbog 20-m pixels in the aapa and palsa mire zones, which were located adjacent to each other, were merged and converted into large contiguous peatland

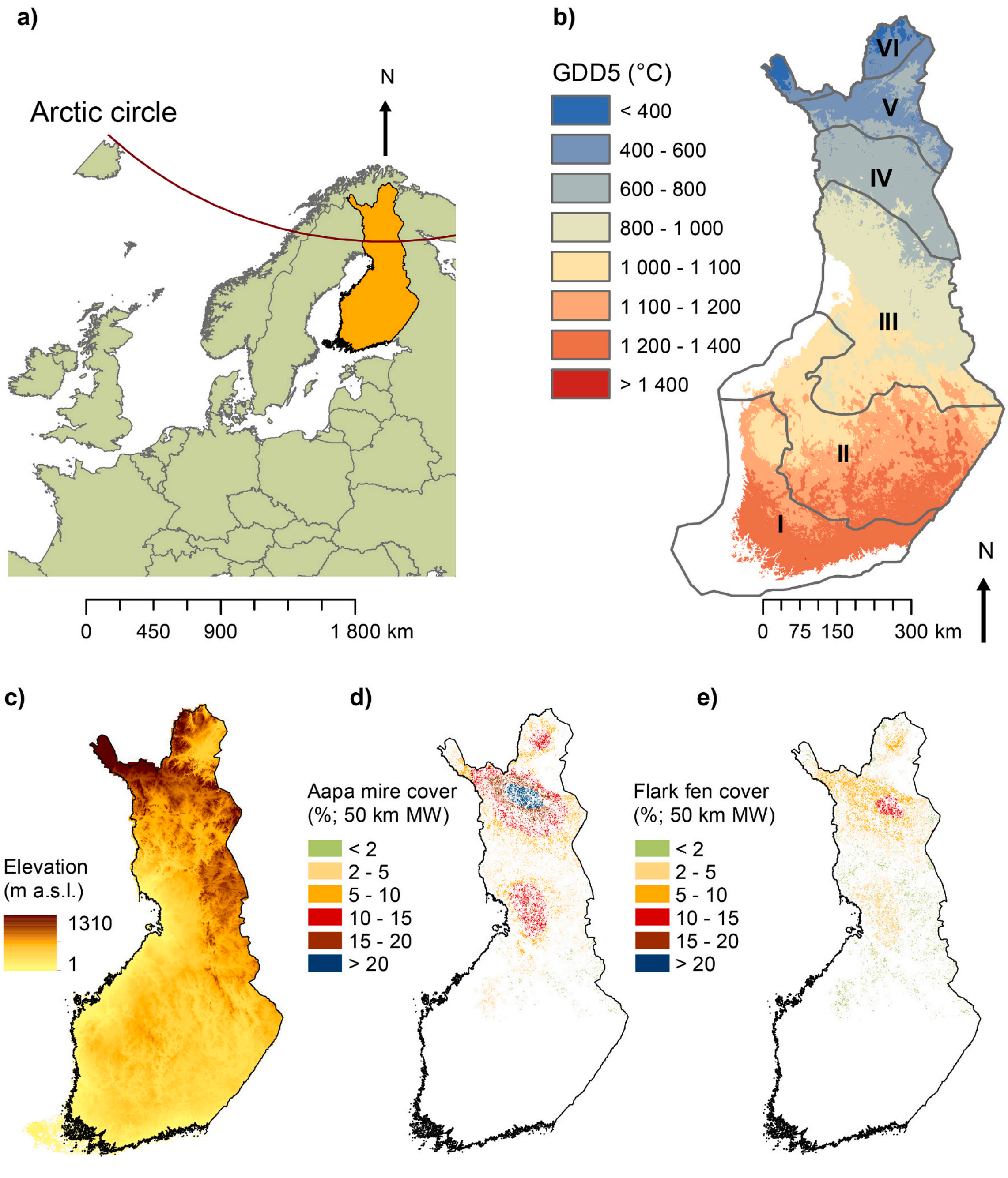

Fig. 2. The study area (Finland) and geographic variation of four environmental variables: a) the location of the study area in northern Europe; b) the growing degree days (base temperature 5 °C; GDD5), and the six main mire zones in Finland (I = plateau and concentric raised bogs, II = eccentric raised bogs, III = middle boreal aapa mires, IV = northern boreal aapa mires, southern subzone, V = northern boreal aapa mires, northern subzone, VI = palsa mires and oroarctic mires; source: Ruuhijärvi, 1988); c) elevation (m a.s.l.); d-e) relative cover (%) of the studied mires ≥10 ha in size calculated for the 50 × 50 m grid system, using a circular Moving Window (MW) with a 50 km radius, measured separately for (d) all the studied aapa mire complexes and only for (e) the flark fens. In (b), conditions for GDD5 are modelled and calculated at a resolution of 50 × 50 m and averaged over 1981–2010.

polygons. Merged polygons smaller than 10 ha in size were excluded from our data, as they generally do not contain typical physiognomic and ecological features of aapa mires. The number of aapa mires in this data was 17,781.

Two mire layers were developed from the set of ≥10 ha peatland polygons. First, to construct a layer for aapa mire complexes (i.e., the whole aapa mire complex containing all mire habitats within it, hereafter referred to as 'aapa mires'), all the selected mire polygons ≥10 ha were converted into 10-m resolution raster data. This raster data was aligned with 50-m resolution climate data (see 2.3) developed in a previous study (Heikkinen et al., 2020). Next, all 50-m climate data pixels which included at least one 10-m aapa mire pixel were selected to construct 50-m resolution climate raster data, including the studied ≥10 ha aapa mires.

Second, a layer including only the wettest parts of the aapa mire complexes characterised by patterned fens with strings and flarks, i.e., open water shallow pools, (hereafter 'flark fens'; see Fig. 1) were developed using the 50-m resolution aapa mire-climate raster data as a starting point. Here, we used the topographic database developed by the National Land Survey of Finland (NLS), and the land cover class

'Swamps classified as difficult, dangerous and impossible to cross' to dissect the wettest parts, i.e., flark fens, from the other parts in the aapa mire complexes. The derived set of 11,905 flark fens were used as a specific focal habitat in our velocity assessments. In other words, these highly wet mire habitats provide important microhabitats for specialist species that require open water or permanently wet environments. Flark fens occur more sparsely in the landscape, which may cause their climatic exposure to be greater than that of the entirety of the aapa mire complexes.

2.3. Climate data

The climate velocity metrics were measured for aapa mires using data on the 17,781 mire complexes and for flark fens based on the data from the 11,905 mires, correspondingly. However, the comparison of the climate exposure risks between these two types of mires was done in a paired manner, i.e., by focusing on the 11,905 aapa mire complexes which all have one or more flark fens as a nested habitat. The overall spatial distribution of the two mire types is asymmetrical; the flark fens are typically a part of a larger aapa mire complex, but not all aapa mire complexes contain flark fens (see Fig. A.1 and A.2).

The development of the 50-m resolution climate data and climate velocity metrics are described in Aalto et al. (2017b) and Heikkinen et al. (2020, 2021), thus only a short overview is provided here. First, gridded monthly average air temperature data for 1981–2010 for Finland were developed at the 50-m spatial resolution. For this, weather station temperature data sourced from 313 stations in Finland, northern Sweden and Norway (European Climate Assessment and Dataset [ECA&D] were modelled with generalised additive modelling, using variables of geographical location (latitude and longitude, included as an anisotropic interaction), topography (elevation, potential incoming solar radiation, relative elevation) and water cover (sea and lake proximity). Monthly precipitation data were developed for the same 50-m resolution grid using kriging interpolation and data from 343 rain gauges obtained from the ECA&D dataset, geographical location, topography and proximity to the sea (for more information for the derivation of both temperature and precipitation variables, see Aalto et al., 2017b).

Monthly air temperature and precipitation data were employed to construct six bioclimatic variables which provide ecologically different measures of the winter- and summer-time temperature and moisture availability, and which are critical drivers of the aapa mire ecosystems (Parviainen and Luoto, 2007; Ruuhijärvi, 1988; Rydin and Jeglum, 2006): (1) the annual temperature sum indicating the accumulated warmth measured as the air temperature sum above the base temperature of 5 °C (growing degree days, GDD5, °C), (2) mean January temperature (T_{Jan}, °C), (3) mean July temperature (T_{Jul}, °C), (4) monthly climatic water balance (mm) calculated for May (WAB_{May}) to reflect late spring air humidity, and (5) for July (WAB_{Jul}) to reflect midsummer air humidity, and finally, (6) the annual precipitation sum. The monthly climatic WAB was calculated as the difference between the May or July total precipitation sum and the potential evapotranspiration (PET) in the corresponding month, using the following measure for PET by Skov and Svenning (2004):

$PET_{May} = 58.93 \times T_{above}\ 0\ ^{\circ}C/\text{May}$, and $PET_{Jul} = 58.93 \times T_{above}\ 0\ ^{\circ}C/\text{July}$.

Next, we extracted future climate surfaces from the data based on an ensemble of 23 global climate models (Taylor et al., 2012). This GCM ensemble was derived from the Coupled Model Intercomparison Project (CMIP5) archives, averaged for the years 2040–2069 and the two Representative Concentration Pathways (RCP4.5 and RCP8.5). The derived climate surfaces, including monthly air temperature and precipitation data, were bilinearly interpolated to match the 50 × 50 m grid, and the change predicted by the GCMs was added to the monthly baseline 1981–2010 climate data. After these additions, the values for the six bioclimatic variables (GDD5, T_{Jan}, T_{Jul}, WAB_{May}, WAB_{Jul} and annual precipitation sum) were recalculated for the 50-m resolution grid across the whole of Finland. Next, these data layers, including values of the six bioclimatic variables for the years 2040–2069 and the two RCPs, were intersected by the two aapa mire datasets.

In the final step, we calculated climate velocities for the six climate variables using the climate-analogue velocity method (Brito-Morales et al., 2018; Hamann et al., 2015). In this method, velocity metrics are calculated by measuring the distance between climatically similar grid cells in present and future climates, divided by the number of years between the two periods. As a key difference to our earlier works (Heikkinen et al., 2020, 2021), and to most all velocity studies, here we measured the distance between the similar baseline and future climate 50-m grid cells included only in the dataset of (i) aapa mires or (ii) flark fens. Thus, in both cases, matrix areas were excluded, and only the distance from the present-day mire cell to the nearest corresponding mire cell with similar future climatic conditions was considered.

For the calculation of velocities with climate-analogue method, we converted the present-day and corresponding future climate data from scenarios RCP4.5 and RCP8.5, from continuous values into categorical climate surfaces following Hamann et al. (2015). These conversion processes were based on our earlier category setting tests (Heikkinen et al., 2020, 2021), other climate-analogue studies conducted in corresponding environments (e.g., Barber et al., 2016; Dobrowski and Parks, 2016) and the recommendation by Hamann et al. (2015) to determine the within-class range to be as small as possible, while avoiding excessive precision and unrealistic velocity patterns.

The following within-class ranges were used: (1) GDD5, within-class range 50 °C, (2) T_{Jan}, within-class range 0.5 °C, (3) T_{Jul}, within-class range 0.5 °C, (4) WAB_{May}, within-class range 2.5 mm, (5) WAB_{Jul}, within-class range 2.5 mm, and (6) PRECP, within-class range 25 mm. The present-day and future climate surfaces were reclassified by assigning the continuous climate values in each of the 50-m grid cells to one of the 29 GDD5, 27 T_{Jan}, 22 T_{Jul}, 21 WAB_{May}, 22 WAB_{Jul}, and 19 PRECP categories. Using these categorical climate surfaces and the Euclidean distance function in ArcGIS, we determined the minimum distances between mire grid cells with similar present-day and future climates for our six variables, and then divided the distances by the number of years between the two points in time (Brito-Morales et al., 2018; Heikkinen et al., 2020).

The velocity values measured for bioclimatic variables provided six individual estimates of climate exposure for our study mires, i.e., the magnitude of climate displacement that the mire species populations and ecosystems are projected to experience (Barber et al., 2016; Brito-Morales et al., 2018; Hamann et al., 2015). Following Dobrowski et al. (2013) and VanDerWal et al. (2013), we opted for using velocities measured for individual variables instead of integrating multiple variables into multivariate climate gradients, constructed using a principal components analysis, because this better allowed for the comparison of spatial variation of areas and mires facing high climate exposure to different separate key drivers. For each contiguous aapa mire, we calculated the mean velocity value for the climate variables as the average of the 50-m grid cells included in it. This was done separately for aapa mires and the subset of flark fens. The potential differences in the velocities between the two types of mires were assessed using paired *t*-tests, where only the 11,905 mires with both types of mires were included. For some of the six climate variables and some mire areas, the present-day climate conditions were projected to completely disappear from both aapa and palsa mire zones. For such mires, the disappearing climate space was recorded as the maximum velocity value for corresponding variables recorded in the data. This was done to enable the derivation of velocity values for all the studied mires and their comparisons. For this study, we defined climate velocity values ≥5.0 km/year as those that present particularly increased risks of exposure for the species and species communities of the aapa mires to cope with (cf. Barber et al., 2016; Heikkinen et al., 2021; Nadeau et al., 2015).

2.4. Additional analyses

To broadly assess the possibilities of a species to disperse and find suitable habitat in the aapa mire network, we measured the relative cover of mires in a 50 km buffer area around each individual aapa mire. First, for each 50-m resolution climate-data-cell, the cover of aapa mires with a circular 50-km Moving Window (MW) was recorded. Next, for each contiguous mire, the mean 50-km buffer cover of mire habitat was calculated as the average value of the 50-m cells included in that mire. These calculations were conducted separately for aapa mires (Fig. 2d) and flark fens (Fig. 2e).

The statistical comparison of the 50-km buffer cover of the two aapa mire types was conducted using the same 11,905 mires as in the velocity comparisons. This allowed us to examine the relationships between climatic exposure and the landscape-scale habitat cover both for our two mire types. Moreover, this enabled us to detect mires with particularly

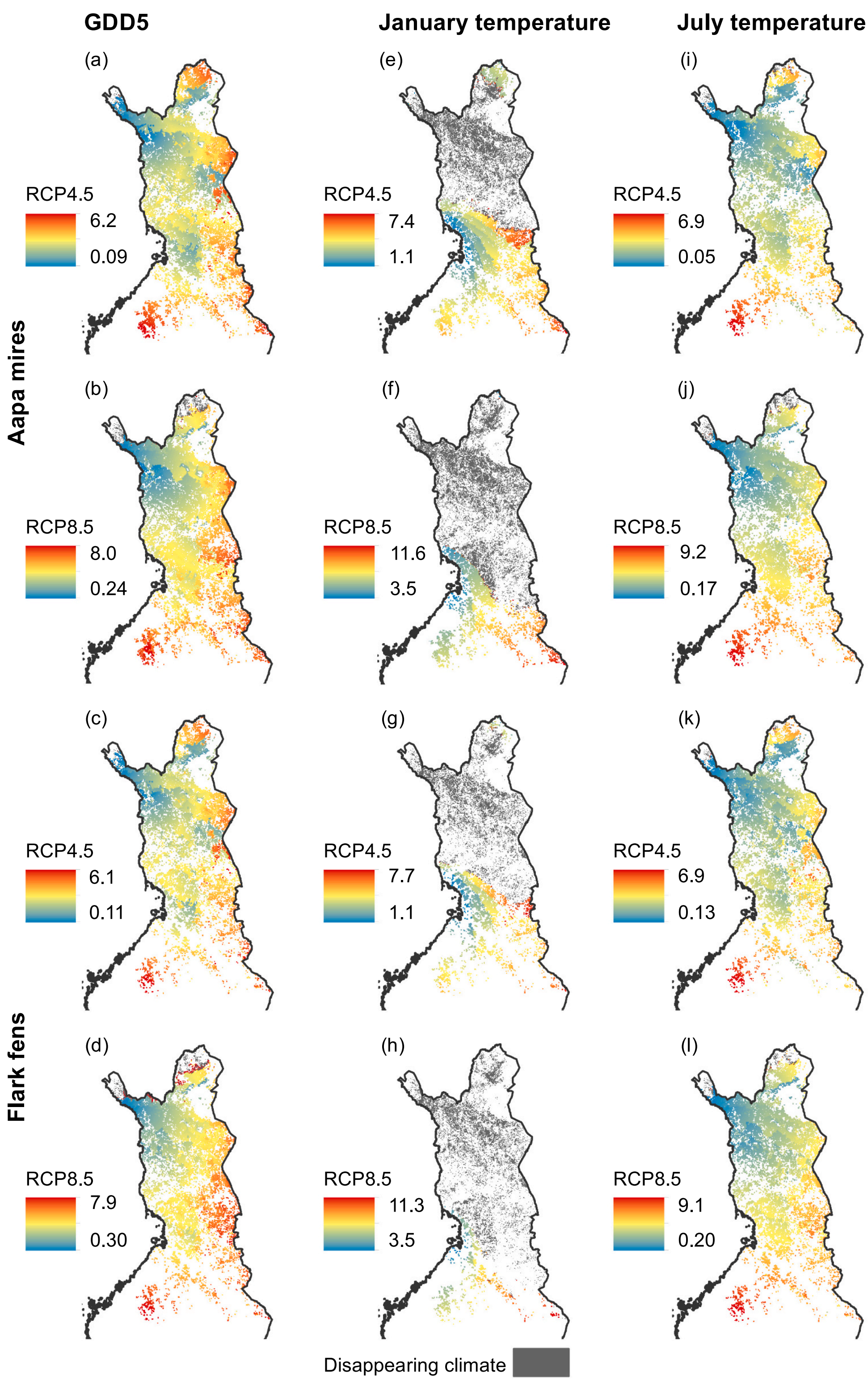

Fig. 3. Climate-analogue velocities (units = km/year in all maps) of three temperature-related climate variables calculated following Heikkinen et al. (2020): a-d) growing degree days (GDD5); e-h) mean January temperature; i-l) mean July temperature. The velocities are measured as the minimum Euclidean distance between the closest climatically similar mire locations under current and future climates divided by the time separating the two periods, 1981–2010 and 2040–2069. Mapped velocities are calculated separately for the two climate scenarios, RCP4.5 (a, c, e, g, i, k) and RCP8.5 (b, d, f, h, j, l), and the two differently delimited mire systems, aapa mire complexes (a, b, e, f, i, j) and flark fens (c, d, g, h, k, l) (for definitions of these two mire systems, see Section 2 and Fig. A.1). For clarity, the velocities in the maps are shown as Moving Window values calculated using 2 × 2 km squares. Climate conditions predicted to disappear from Finland are shown with grey colour.

notable joined risks of high velocity (driving species to move to new areas to follow suitable conditions) and low habitat cover (obstructing species dispersal).

3. Results

The geographic patterns of the six climate variables' velocities recorded for our study mires are, as expected, systematically higher for RCP8.5 future climates than RCP4.5 conditions (Figs. 3 and 4), with the highest values measured for January and July mean temperature velocities. The highest velocities for January temperatures exceed 10 km per year, and even more extremely, for many of the mires studied, the present-day January climate conditions are projected to disappear (Fig. 3e-h). Another systematic pattern is that for most of the six climate variables, high velocities occur in the SW corner of the aapa mire zone. However, for the other parts of the study area, there is notable variation

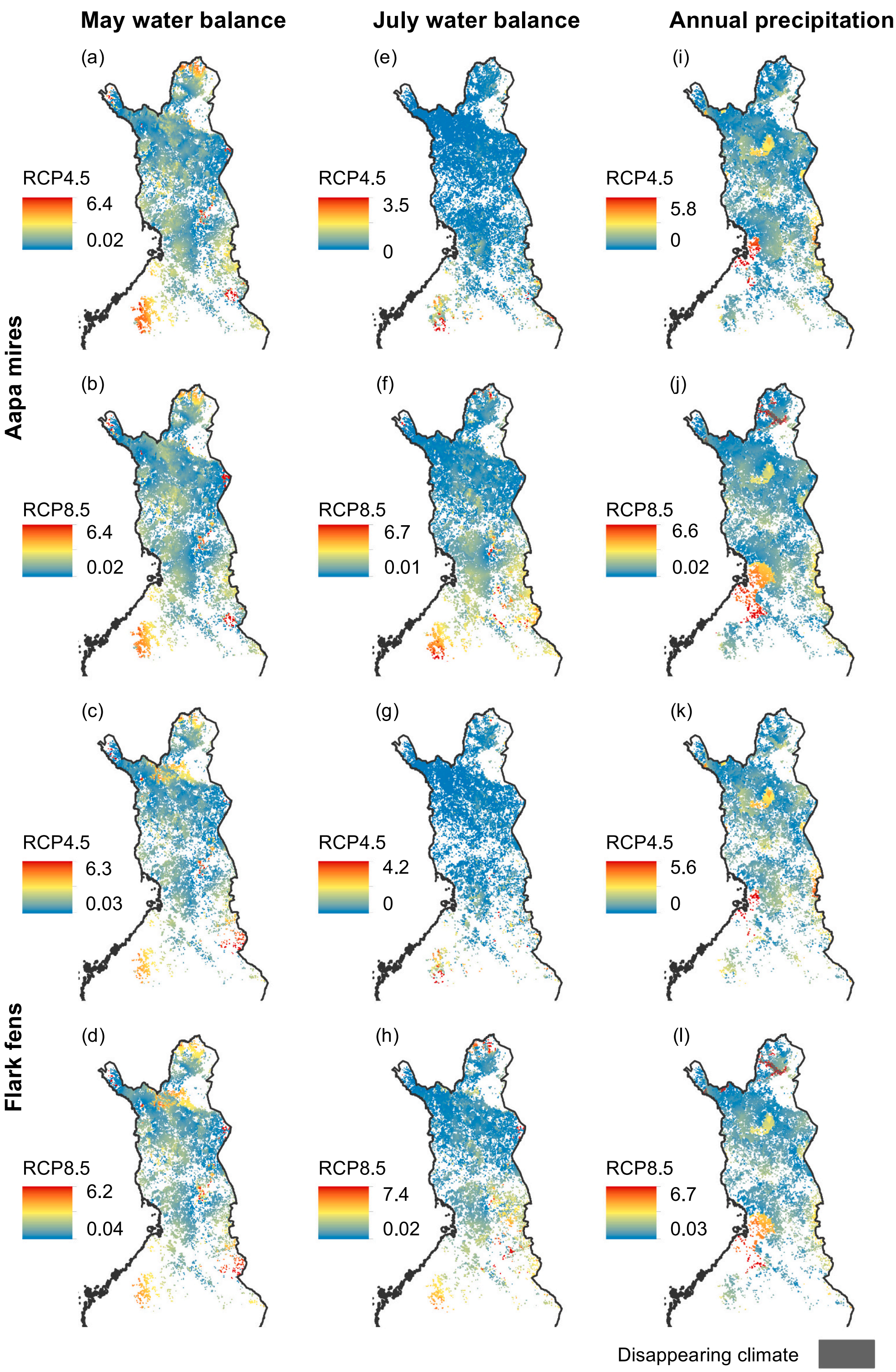

Fig. 4. Climate-analogue velocities (km/year) of three precipitation-related climate variables, calculated following Heikkinen et al. (2020): a-d) May water balance (WAB_{May}); e-h) July water balance (WAB_{Jul}); i-l) mean annual precipitation. Velocities are measured as the minimum Euclidean distance between the closest climatically similar mire locations under current and future climates, divided by the time separating the two periods, 1981–2010 and 2040–2069. Mapped velocities are calculated separately for the two climate scenarios, RCP4.5 (a, c, e, g, i, k) and RCP8.5 (b, d, f, h, j, l), and the two types of mires, aapa mire complexes (a, b, e, f, i, j) and flark fens (c, d, g, h, k, l). For clarity, velocities are shown as Moving Window values, calculated using 2 × 2 km squares. Climate conditions predicted to disappear from Finland occur in j and k.

in the locations of the highest velocities, suggesting that different mire areas will often face different exposure risks.

Spatial velocity patterns for the two water balance variables and annual precipitation include sporadic spots of high velocity, which are embedded in wide areas with low or moderate velocities (Fig. 4). For the three temperature-related variables, the areas with increased exposure risks are more common and widely spread (Fig. 3), exceeding the velocity level of 5 km/year particularly under RCP8.5 climate in 22.6% - 99.4% of the 11,905 flark fens (Table A.1). The portion of mires among these where two or more climate variables show coinciding high velocities varies from 2.3% to 31.3% depending on the RCP scenario and the mire type (Table A.2).

Differences in the range of velocity values between the aapa mire complexes and the flark fens are small for the six climate variables, with aapa mires showing marginally higher maximal velocities than flark fens for certain variables and RCP conditions, and vice versa in others (Figs. 3 and 4). However, the comparison of the mean velocity values for five of the studied climate variables (January temperature excluded due to the high number of mires with a disappearing climate) in the studied mires reveals that flark fens, in general, show higher velocities than aapa mires (Fig. 5). Although these differences are often not large in absolute terms, they are statistically significant for all five climate variables and the two RCPs, except for GDD5 velocities under the RCP4.5 climate (Table 1). In addition, for certain variables, such as the May water balance, the velocities for flark fens are markedly higher than for aapa mires (Table 1, Fig. 5).

Plotting the cover of aapa mires in the 50 km Moving Window (MW) buffer against the cover of flark fens (Fig. A.1) shows that there is, on average, two times more corresponding habitat in the landscape for the whole aapa mire complex than flark fens. Plotting the 50 km MW mire cover values against the velocity values of GDD5, the July water balance and annual precipitation under RCP8.5 (Fig. 6) and RCP4.5 (Fig. A.3) climate show that high climate exposure coincides with low cover of corresponding habitat in the surrounding landscape, more commonly for flark fens than aapa mires, particularly so for annual precipitation velocities. Mires featured both by high velocity values and low habitat cover are more common for July temperatures than for the May water balance (Fig. A.4) and July water balance (Fig. 6, Fig. A.3). The landscape-scale cover of both aapa mires and flark fens is lowest in southern range margin areas (Fig. 2), suggesting increased exposure to joint threats for those areas.

4. Discussion

Climate velocity assessments are increasingly used to develop understanding of the climate exposure that different protected and unprotected matrix areas, ecosystems and species populations are projected to experience (Barber et al., 2016; Brito-Morales et al., 2018). Earlier studies have reported wide-ranging velocities for different parts of the globe, including the northern hemisphere. Loarie et al. (2009) estimated that the mean annual temperature velocity in boreal biomes and other high-latitude environments is <0.5 km/year. In contrast, other studies based on continent-wide (Batllori et al., 2017; Carroll et al., 2015) or regional (Dobrowski et al., 2013; Haight and Hammill, 2020) climate data for the northern hemisphere have shown higher climate velocities for temperature variables, typically varying between 1.0 and 6.0 km/year and occasionally exceeding 10 km/year, particularly on mountaintops.

The velocities in our study fall roughly in the latter category, with the July mean temperature velocity showing a mean of 3.9 km/year for the flark fens under the RCP8.5 scenario. The highest mean velocities are associated with the January mean temperature changes under the RCP8.5 future climate, exceeding 10 km/year. Importantly, these high values are largely due to the wide areas with disappearing climate. In our study, to allow velocity calculations for the study mires, the velocities of cells without an equivalent climate in the future were recorded as the maximum velocity value for corresponding variables in the data. This practice has also been used in earlier studies for visualisation purposes (e.g., Loarie et al., 2009), but it should be noted that, in certain areas, it truncates and biases our mean velocity metrics for January temperatures towards lower values. In contrast, for our precipitation-related variables, no or extremely little disappearing climate space was discovered, and the mean velocities are <1 km/year, except for mean annual precipitation velocities under RCP8.5 conditions, where they marginally exceed 1 km/year.

Climate velocities exceeding 5.0 km/year can pose critical obstacles for many species to keep up with future climatic changes (Barber et al., 2016; Heikkinen et al., 2021; Nadeau et al., 2015). Indeed, multispecies studies and meta-analysis on the recent species range shifts have typically revealed shifts slower than 20 km per decade (Chen et al., 2011; Hickling et al., 2006; Pöyry et al., 2009), and even in mobile species groups, such as birds, the mean rates of range shifts have remained below 5.0 km/year (Lehikoinen and Virkkala, 2016). In comparison, simulation studies on species migration potential have sometimes used migration rate estimates derived from paleoecological studies, which vary from 1 to 10 km per year, but typically a minority of the species has been considered to have migration rates larger that 5 km/year (e.g., Morin et al., 2008). Thus, a common assumption is that the predicted rate of climate warming will initiate responses that can be substantially faster than the species' historical distribution shifts, and even relatively rapid changes in current range limits will be insufficient to keep pace with predicted future climatic change (Ash et al., 2017; Iverson et al., 2004).

For our 11,905 study mires, the 5.0 km/year velocity level was often exceeded under the RCP8.5 scenario and for the temperature-related variables, particularly for the January temperature in 11,747 (98.7%) aapa mires and 11,832 (99.4%) flark fens (Table A.1). In contrast, the three precipitation-related variables rarely showed velocities higher than 5.0 km/year. For example, for the annual precipitation, such velocities occurred only in 321 (2.7%) aapa mires and 323 (2.7%) flark fens. This suggests that threats from climate exposure to boreal aapa mires are much higher for thermal than water balance or precipitation variables. This is also reflected in mires where two or more climate variables simultaneously show velocities >5.0 km/year. Namely, the maximal level (31.3%) of mires with joint high exposure risks is reached for RCP8.5 and flark fens, but this mainly concerns high GDD5 and the two temperature variable velocities coinciding in the same mires (Table A.2).

The differences between exposure for temperature and precipitation-related variables revealed here highlight the importance of examining velocities across several climatic factors to develop a deeper understanding of climate change-based pressures on biodiversity (Dobrowski et al., 2013; Heikkinen et al., 2020; Ordonez and Williams, 2013). Most velocity studies have focused only on temperature due to its crucial role for biodiversity patterns. However, the inclusion of other climate variables is important when there are clear functional relationships between them and the studied biodiversity units (Brito-Morales et al., 2018), as is the case with aapa mires. Moreover, changes in seasonal climate conditions can be equally important as mean annual changes, supporting the careful scrutinisation of exposure to annual vs. seasonal variables (Ordonez and Williams, 2013).

In our results, in addition to the mean velocity differences between thermal and precipitation-related variables, there are spatial differences in the high velocity areas both between the three temperature and the three precipitation-related variables. While the majority of aapa mires face very high risks of exposure concerning winter temperatures, the velocity trends in GDD5 are somewhat stronger than the July temperature, and these two variables show some spatial discrepancies embedded within overall similar patterns (Fig. 3). The highest velocity areas for the two water balance variables differ from those revealed for the annual precipitation, although for both, the climatically most exposed areas are situated in the southernmost region of the aapa mire

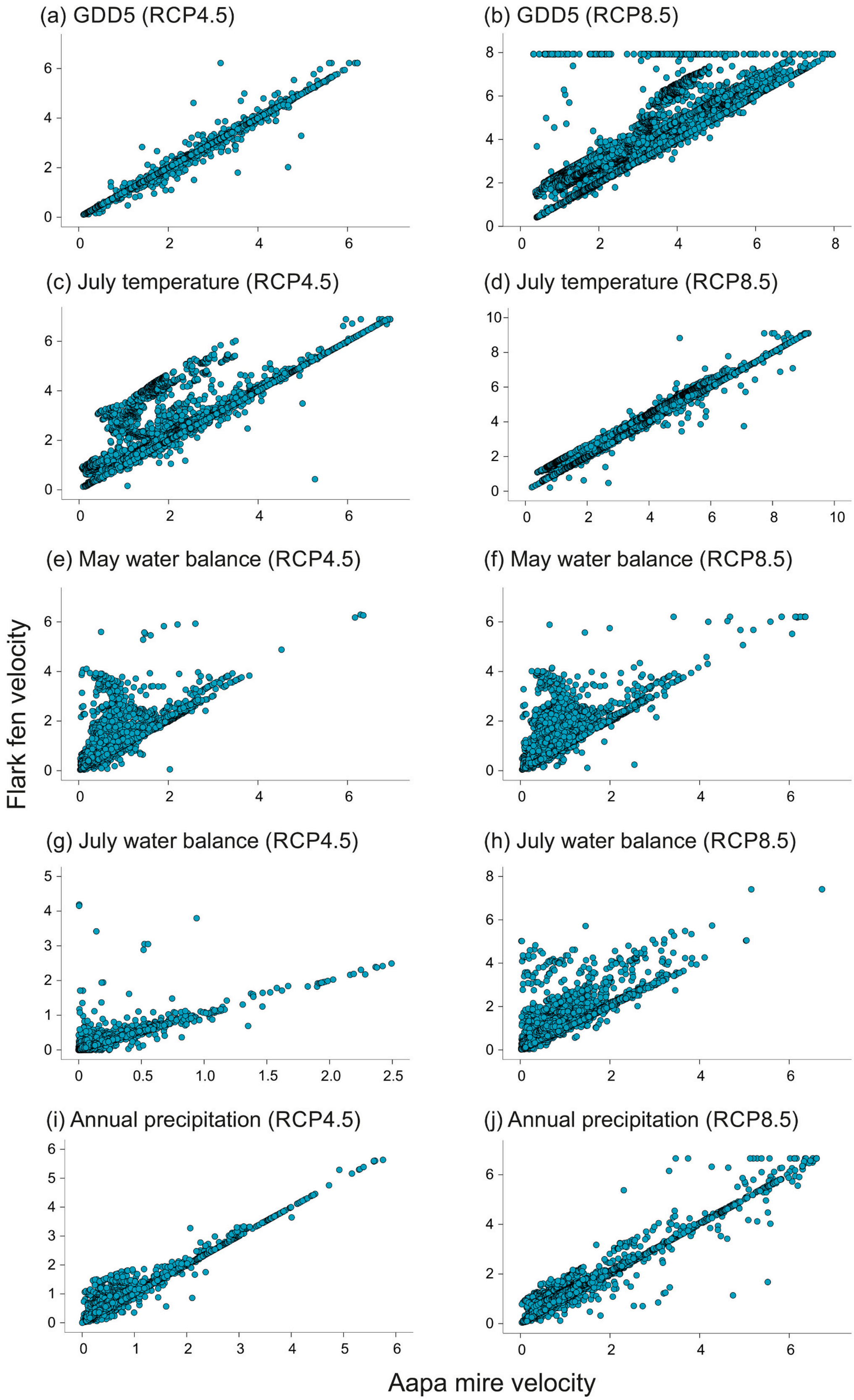

Fig. 5. The average climate velocity values (km/year) for the aapa mire complexes plotted against the average climate velocity values for the flark fens occurring paired within the same 11,905 study mires. Climate-analogue velocities are provided for five climate variables: a, b) GDD5; c, d) mean July temperature; e, f) May water balance (WAB_{May}); g, h) July water balance (WAB_{Jul}); i, j) annual precipitation, and separately for the two climate scenarios, RCP4.5 (a, c, e, g, i) and RCP8.5 (b, d, f, h, j). Velocity values are calculated as the distance between the closest climatically similar aapa mire locations (x axis) or flark fen locations (y axis) in the current (1981–2010) and future climate (2040–2069), divided by the time.

Table 1
Comparisons of velocity values of five climate variables measured for the 11,905 paired aapa mires and flark fens. For all five climate variables, velocity values (km/year) are measured with respect to the future climates under RCP4.5 and RCP8.5 conditions, averaged across the years 2040–2069. Degrees of freedom (Df) = 11,904 in all paired *t*-test comparisons.

Compared velocity pairs (A vs. B)	Mean velocity values (and SD) of compared pairs: Pair A	Pair B	Paired differences: Mean	Standard deviation (SD)	Std. error Mean	95% confidence interval of the difference: Lower	Upper	t	df	Sig. (2-tailed)
(A) Aapa mire vs. (B) flark fen; GDD5 velocity, RCP4.5	2.390 (1.140)	2.389 (1.143)	0.001	0.0720	0.001	−0.0001	0.003	1.844	11,904	0.065
(A) Aapa mire vs. (B) flark fen; GDD5 velocity, RCP8.5	3.645 (1.646)	4.122 (1.670)	−0.477	0.815	0.007	−0.492	−0.463	−63.923	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; July temperature velocity, RCP4.5	2.187 (1.260)	2.406 (1.267)	−0.220	0.539	0.005	−0.229	−0.210	−44.488	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; July temperature velocity, RCP8.5	3.700 (1.844)	3.851 (1.815)	−0.151	0.228	0.002	−0.155	−0.147	−72.070	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; May water balance velocity, RCP4.5	0.572 (0.456)	0.702 (0.614)	−0.131	0.369	0.003	−0.137	−0.124	−38.696	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; May water balance velocity, RCP8.5	0.660 (0.527)	0.823 (0.683)	−0.163	0.408	0.004	−0.170	−0.156	−43.563	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; July water balance velocity, RCP4.5	0.078 (0.148)	0.098 (0.188)	−0.021	0.102	0.001	−0.023	−0.019	−22.261	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; July water balance velocity, RCP8.5	0.513 (0.520)	0.663 (0.703)	−0.149	0.378	0.003	−0.156	−0.143	−43.067	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; annual precipitation velocity, RCP4.5	0.601 (0.553)	0.650 (0.563)	−0.040	0.112	0.001	−0.043	−0.038	−39.432	11,904	<0.001
(A) Aapa mire vs. (B) flark fen; annual precipitation velocity, RCP8.5	1.057 (1.145)	1.100 (1.159)	−0.043	0.166	0.002	−0.046	−0.041	−28.570	11,904	<0.001

zone (Fig. 4). This suggests that although aapa mires in general are projected to experience low or moderate exposure to the alterations in water balance and precipitation, on the southern edge of the aapa mire zone the impacts of these changes can be significant.

Velocity studies have so far paid insufficient attention to excluding unsuitable areas from their measurements. For example, when assessing climate exposure across protected area networks, velocities are commonly measured for the whole landscape. However, it is possible to determine how often the nearest climatically similar future conditions are found in protected areas vs. an unprotected matrix. Haight and Hammill (2020) showed that mean velocities in the protected areas of the Southern Rockies in North America are lower than in the region as a whole, largely due to the extensive elevational gradients existing in protected areas. However, in a study of the protected areas network across North America, Batllori et al. (2017) showed more than half of the nearest future climatic analogues are located in the matrix, sometimes in degraded land or a different habitat than the starting point. Our study differs from these two studies, and possibly from all earlier studies, in that we measured climate velocities considering only the locations with the study habitat. In our case, this is important, because aapa mires evolve only on flatlands in large depressions with substantial water accumulation and optimal thermal conditions. Thus, an extensive elevation range does not provide support for this habitat, and large dryish upland areas are unsuitable and may be rationally excluded from exposure measurements.

However, even though climate exposure assessments can be improved by considering only suitable sites for environmentally constrained habitats, velocity metrics may provide limited reflections of the spatial variation of habitat cover. In our case, there are notable differences in the cover of aapa mire complexes and that of the flark fens around the studied 11,905 mires. While the velocities measured for most of the climate variables are statistically significantly higher (in paired *t*-tests) for the less abundant flark fens, in absolute terms, these differences are often quite small. This suggests that velocity metrics provide limited information on the focal habitat cover between present-day and future climatic analogues. This is of concern because climate change and habitat fragmentation can amplify their threats to biodiversity by reducing the dispersal possibilities for species across degraded landscapes (Nadeau et al., 2015; Oliver and Morecroft, 2014). Thus, we echo the recommendations of considering habitat availability jointly with climate exposure (Hülber et al., 2020) to detect areas where high joint threats should be addressed in conservation planning (Heikkinen et al., 2021; Nadeau et al., 2015). Here, this particularly concerns those flark fens where low landscape-scale cover of habitat and high GDD5 or January/July temperature velocities coincide.

Peatlands in Europe have witnessed extensive drying in recent centuries (Swindles et al., 2019). Considering aapa mires, their dependency on the surface water flows can make them susceptible to the effects of hydrological alterations caused by climate change (Gong et al., 2012). An ecological outcome of such alterations are lower water levels and the replacement of groundwater-fed fen surfaces by ombrotrophic bog vegetation, suggesting particularly increased threats for flark fens (Kolari et al., 2021; Pedrotti et al., 2014; Tahvanainen, 2011; Väliranta et al., 2017). Critical changes in hydrological cycles may be caused by increased summer evaporation, diminished average spring floods and their earlier timing (Lotsari et al., 2010). Alarmingly for the future, climate models suggest alterations in the melting of snow and peaking of spring floods, potentially causing reduced summer-time water capacity in wet ecosystems (Barnett et al., 2005). Recent studies have already detected signs of ongoing transitions of fen vegetation into bog vegetation in the aapa mires of Finland (Kolari et al., 2021), which may pose accumulating threats to the specialised species of fen communities due to the diminishing habitat area (Granlund et al., 2021).

Our results suggest that boreal aapa mires are likely to increasingly face the expanding fen-bog transition threats due to projected climate change. Particularly high exposure metrics for summer thermal variables (GDD5 and July temperature) and water balance variables are projected to coincide for mires situated in the SW corner of the aapa mire zone, indicating elevated pressures for ecological sustainability of aapa mires and their biodiversity in that area. An alarming outcome can be the complete loss of suitable climate space for aapa mires in the southern parts of their current network (cf. Parviainen and Luoto, 2007).

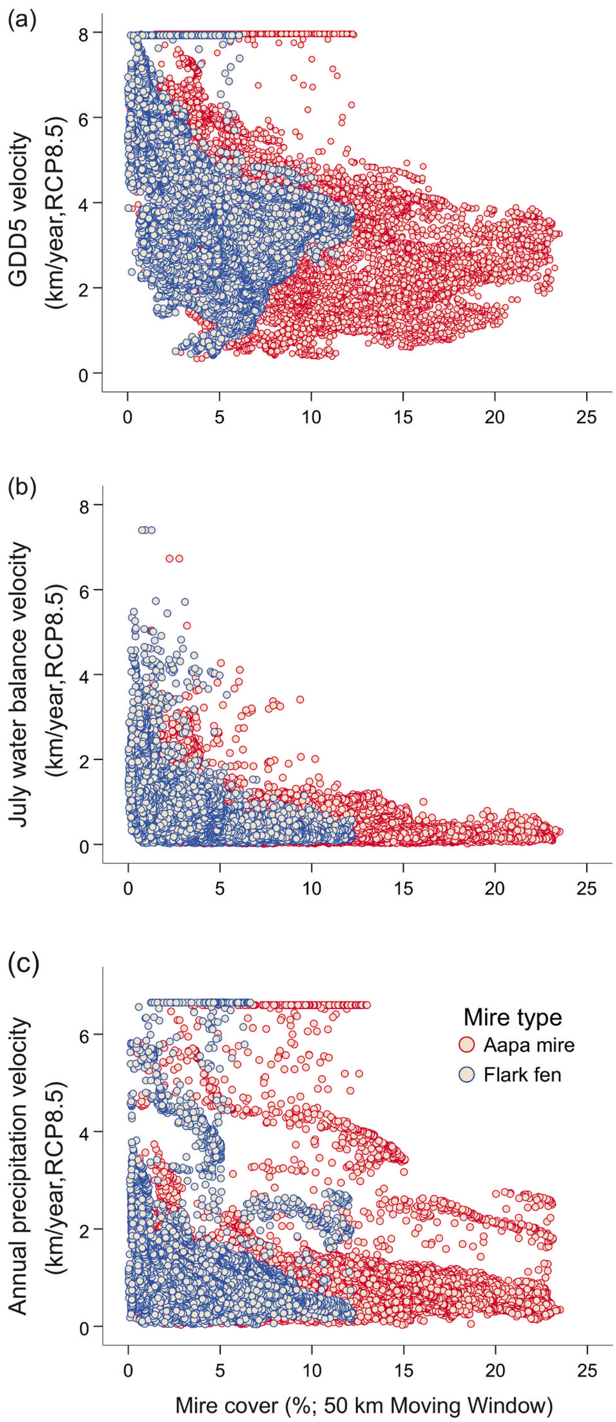

Fig. 6. The climate velocity of (a) GDD5, (b) July water balance and (c) annual precipitation in the 11,905 paired aapa mires and flark fens plotted against the landscape-scale cover of these two mire types. Each aapa mire includes one or more flark fens nested within it, but these two mire types have different amounts of corresponding habitat in their surrounding landscape. The velocities indicate the minimum Euclidean distance between the closest climatically similar mire location in the current climate and in the RCP8.5-based future climate divided by time, 1981–2010 and 2040–2069. The landscape-cover of the two mire types is measured using a Moving Window with a 50 km circle (see Fig. A.1 for details).

This may lead to a decrease of the geographic range and area covered by aapa mires if the habitat loss in the south cannot be compensated for by the development of new aapa mires in the north (where the Arctic Sea constitutes the ultimate barrier).

Under a changing climate, achieving and maintaining favourable conservation status of the EU's Habitat Directive priority habitats requires careful examination of the exposure of protected areas and occurrences of priority habitats to the projected climate change (Stagl et al., 2015). Many of the Habitat Directive's biotopes are projected to lose a large part of their suitable climate space by 2050 (Bittner et al., 2011); and the Natura 2000 network, a key conservation instrument for the Habitats Directive, may experience a major change of climate conditions (Heikkinen et al., 2020; Nila and Hossain, 2019). For aapa mires, our results suggest that these EU priority habitats are projected to face wide-ranging climatic exposure threats, considering both winter and summer temperatures, and in the southernmost areas of the aapa mire zone, also considerable exposure to the changes in water balance and annual precipitation. These findings highlight the importance of developing conservation planning which takes the projected impacts of climate change into account to support achieving and maintaining the favourable conservation status of this habitat type.

5. Conclusions

We have shown here that our study system, aapa mires and particularly the wettest parts of them, flark fens, are likely to experience major climate change exposure threats. These threats will especially concern the impacts of changing winter and summer temperatures, but it is important to note that the most highly exposed areas for these two variables are only partly occurring in the same areas. It is also important to note that the exposure threats caused by high climate velocities are accompanied by another critical ecological threat posed to the aapa mire species and communities, namely the projected loss of suitable conditions in the southern range margin of the aapa mire zone. This is shown in our results by the considerable projected changes in summer temperatures and also partly in water balance and annual precipitation. These future changes can lead to the decrease of the range and overall area of aapa mires, particularly if there are limited potential locations for the development of aapa mires in the northernmost area bordered by the Arctic Sea.

Our results also show that tailored climate velocity metrics, where an unsuitable matrix is excluded, provide useful information to support the conservation of EU Habitats Directive priority habitat and other corresponding environmentally constrained habitats of conservation concern. Such information may play a crucial role in developing climate-smart conservation and management actions to support reaching favourable conservation status and ecosystem sustainability for different priority habitats. In the case of aapa mires, one of the most important management actions would be targeting restoration towards the most vulnerable areas in aapa mire zone to counteract the potential losses of aapa mires with the changing climate.

Data availability statement

All relevant data supporting the results will be available after an embargo period in the Zenodo database (https://zenodo.org/record/5813267).

Author contributions

RKH, KA and NL designed the research; RKH, JA and NL performed the analysis and.

visualisation: RKH, KA and JA wrote the original draft; and all authors contributed to the interpretation of the results and the subsequent revisions of the paper.

Acknowledgements/funding

This work was supported by the Finnish Ministry of the Environment (SUMI project; grant number VN/33334/2021) and the Academy of Finland (grant number 307761).

Declaration of Competing Interest

None.

Appendix A

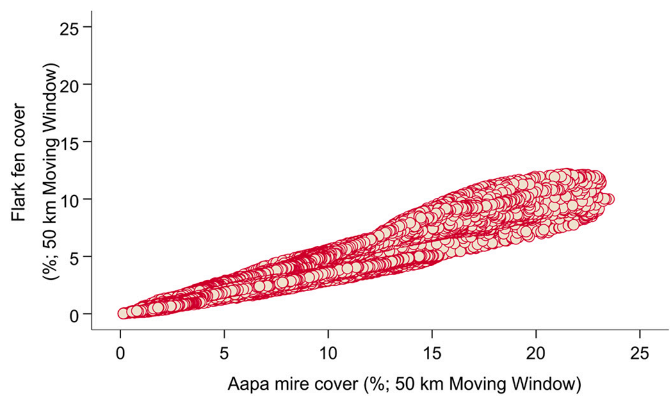

Fig. A.1. The landscape-scale cover of aapa mires (a mire complex system containing a variety of mire habitats) plotted against the landscape-scale cover of flark fens (the wettest parts in aapa mire complexes, characterised by sparsely vegetated and open-water shallow pools), measured for both the proportion (%) of the corresponding peatland surface in the surrounding 50 km Moving Window (MW) circle buffer area. The scatter plot is based on 11,905 contiguous aapa mire complexes which all have one or more flark fens occurring as a nested habitat embedded within the larger mire complex.

The landscape-scale 50 km MW measure was developed for each of the 11,905 aapa mires by first measuring the 50 km MW value for all the 50 × 50 m resolution grid cells occurring within the studied aapa mires, and then calculating the mean value of these 50-m grid cell MW values for each aapa mire. The derived mean values show the average MW proportion of aapa mires in the surrounding 50 km buffer area. The flark fen landscape-scale cover was measured in a similar manner, but by including only the more sparsely occurring flark fen occurrences in the surrounding 50 km buffer in the calculations. The relatively higher scarcity of flark fens (y axis) in relation to aapa mires (x axis) produces the landscape-level cover difference visible in the comparison of the paired 11,905 mires in the figure.

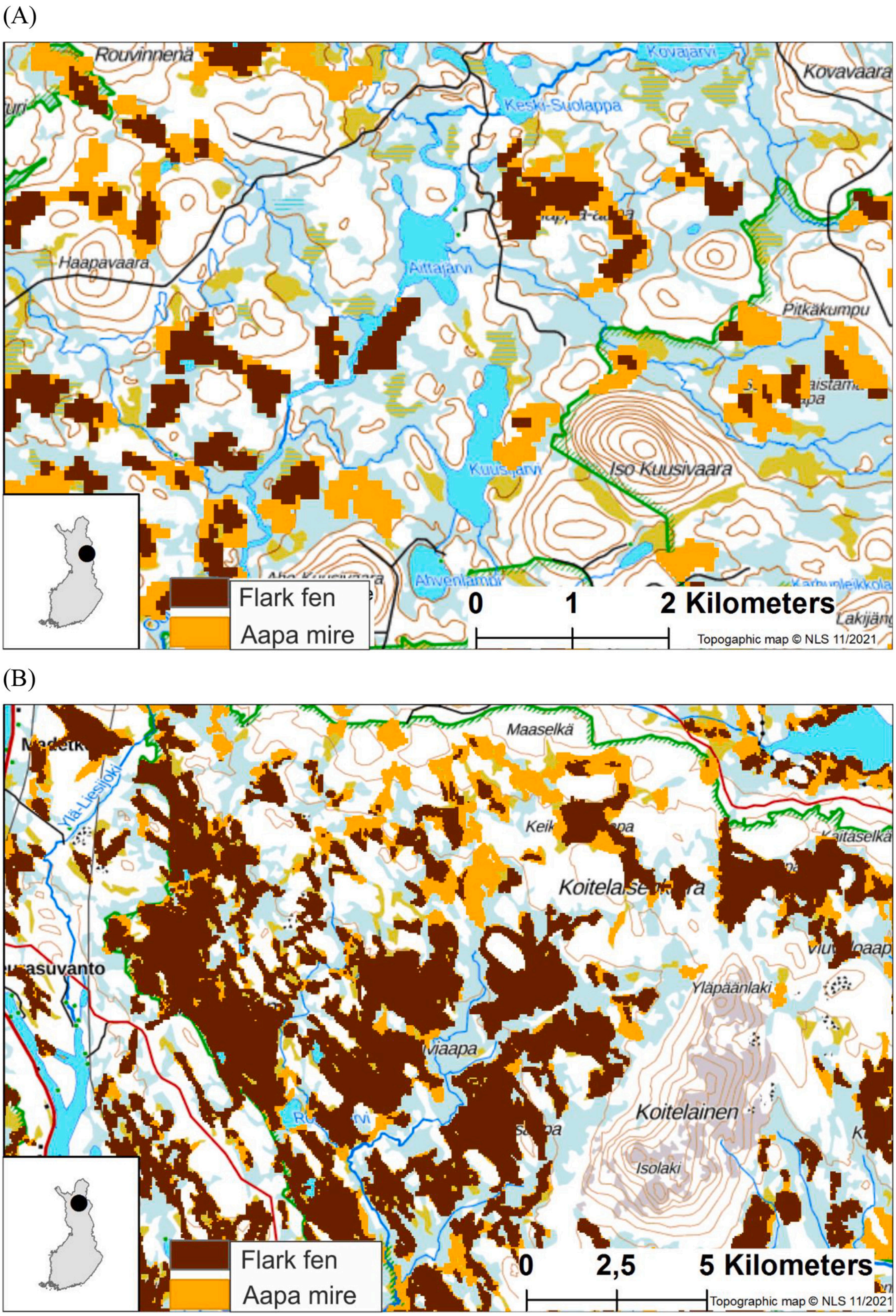

Fig. A.2. Examples of distribution patterns of aapa mires (whole mire complexes) and flark fens. (A) An example area across a wider region on the western border of Finland. (B) A landscape-scale snapshot zooming into one example area situated in the northern part of Finland, including a number of extensive aapa mires.

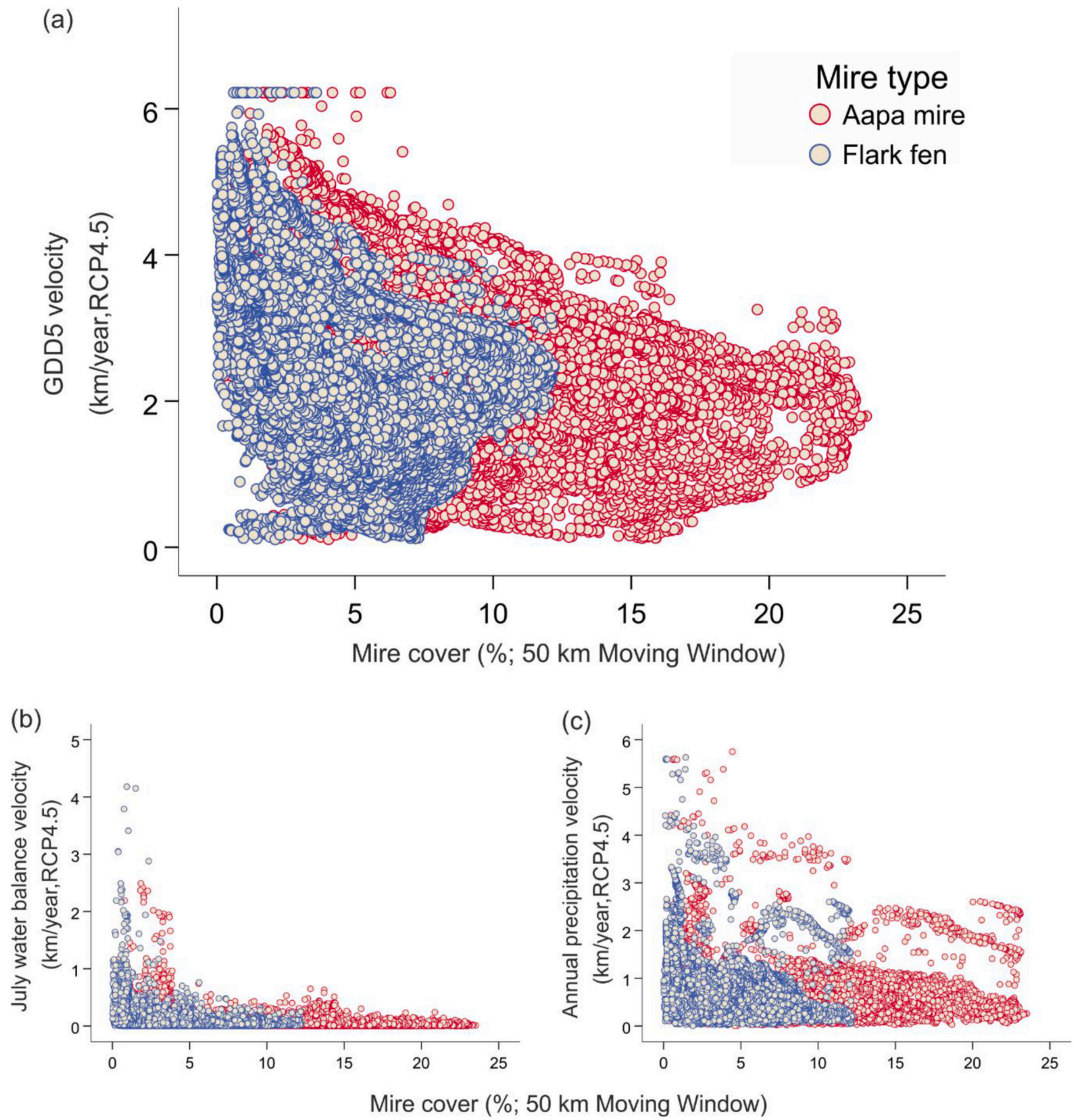

Fig. A.3. The climate velocity of (a) GDD5, (b) the July water balance, and (c) the annual precipitation of the 11,905 paired aapa mires and flark fens plotted against the landscape-scale level cover of these two mire types. Each aapa mire includes one or more flark fens nested within it, but these two mire types have different amounts of corresponding habitat in their surrounding landscape. The velocities indicate the minimum Euclidean distance between the closest climatically similar mire location in the current climate and in the RCP4.5-based future climate, divided by time, 1981–2010 and 2040–2069. The landscape-cover of the two mire types is measured using a Moving Window with a 50 km circle (see Fig. A.1 for details).

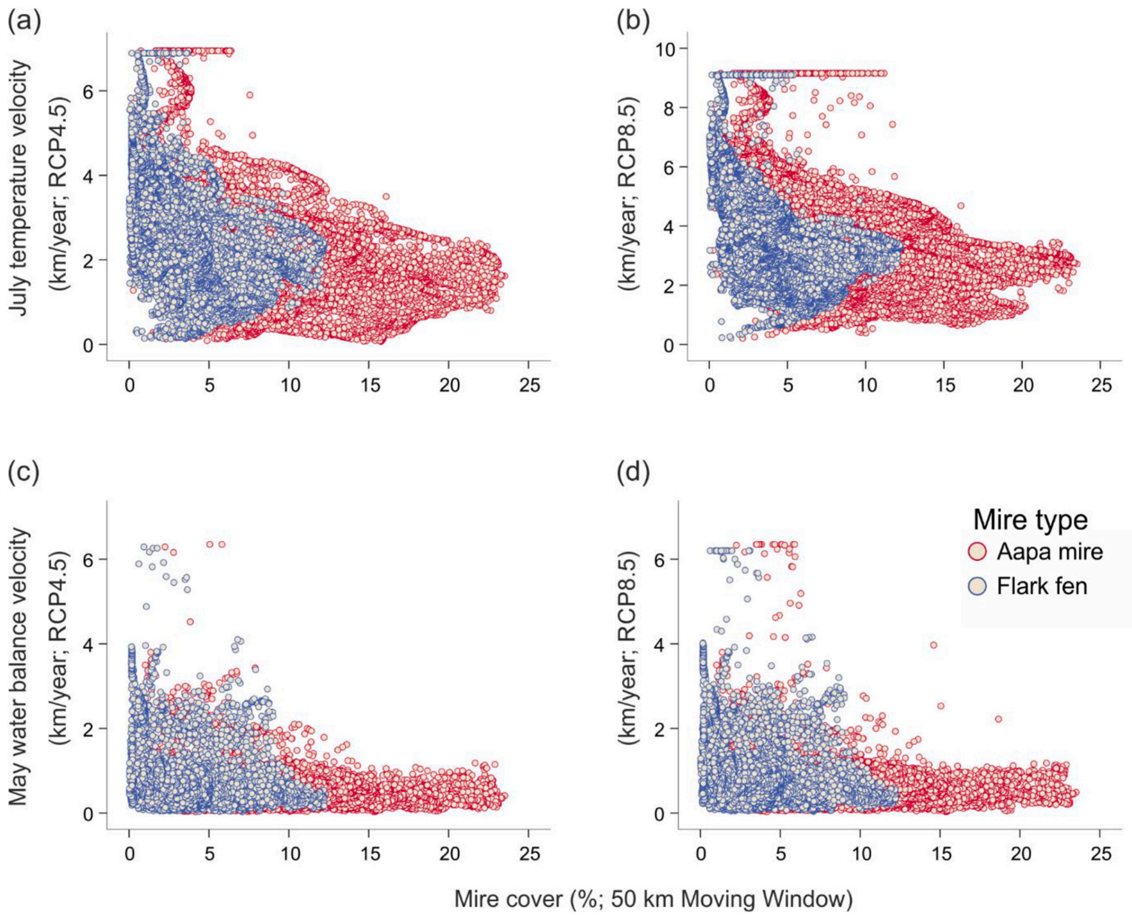

Fig. A.4. The climate velocity of (a, b) the mean July temperature and (c, d) the May water balance for the 11,905 paired aapa mires and flark fens, plotted against the landscape-scale cover of these two mire types. The velocities show the minimum Euclidean distance between the closest climatically similar mire location in the current climate and in (a, c) the RCP4.5-based future climate and (b, d) the RCP8.5-based future climate, divided by time, 1981–2010 and 2040–2069. The landscape-cover of the two mire types is measured using a Moving Window with a 50 km circle (see Fig. A.1 for details).

Table A.1
The number of aapa mires and flark fens (percentage in parenthesis) among the 11,905 study mires, where the measured climate velocity for GDD5, the mean January temperature (TJan), mean July temperature (TJul), May water balance (WAB_{May}), July water balance (WAB_{Jul}) and the mean annual precipitation (PRECP) is ≥5.0 km/year. These mires represent the aapa mires and flark fens where high climate velocity can pose particularly critical challenges for biodiversity to adjust to future climatic changes. The statistics are shown separately for the two mire types and the two climate scenarios.

Mire type	Climate scenario	GDD5	TJan	TJul	WAB_{May}	WAB_{Jul}	PRECP
Aapa mires	RCP4.5	215 (1.8%)	9168 (77.0%)	367 (3.1%)	4 (0.03%)	0	9 (0.1%)
	RCP8.5	2091 (17.6%)	10,062 (84.5%)	430 (3.6%)	12 (0.1%)	0	10 (0.1%)
Flark fens	RCP4.5	219 (1.8%)	11,747 (98.7%)	2377 (20.0%)	25 (0.2%)	5 (0.04%)	321 (2.7%)
	RCP8.5	3211 (27.0%)	11,832 (99.4%)	2695 (22.6%)	34 (0.3%)	15 (0.1%)	323 (2.7%)

Table A.2
(a) The number and (b) percentage of the aapa mires and flark fens among the 11,905 study mires, where velocity values for two or more climate variables are ≥5.0 km/year, indicating increased joint risks of climate exposure. (c)The highest number of climate variables with velocities ≥5.0 km/year coinciding in the same study mire. Statistics are shown separately for the two mire types and the two climate scenarios.

		Mires with multiple climate variables ≥ 5.0 km/year		(c) Maximum of variables with velocities ≥ 5.0 km/year
Mire type	Scenario	(a) Number	(b) Percentage	
Aapa mires	RCP4.5	272	2.3%	4
	RCP8.5	2951	24.8%	5
Flark fens	RCP4.5	350	2.9%	4
	RCP8.5	3730	31.3%	5

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