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High-latitude EU Habitats Directive species at risk due to climate change and land use

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ABSTRACT

The Habitats Directive of the European Union is a key legislative instrument in Europe, supporting the conservation of rare, threatened or endemic species. It aims at ensuring that the species listed in the Annexes of the Habitats Directive show a favourable conservation status, i.e., that they are able to maintain viable populations and that their natural range is sufficient and not decreasing currently, nor will in the future. However, climate change may hamper Habitats Directive species in achieving (or maintaining) a favourable conservation status, particularly when these impacts are amplified by adverse land use. Here, we studied Habitats Directive species in Finland for which $\geq 70\%$ of the occurrences were recorded with the resolution of ≤ 100 m. The number of occurrence sites for the 52 species studied ranged from one site to 13,653 sites, summing up to 19,367 sites. For all these sites and their surroundings, we assessed the vulnerabilities caused by climate change and land use. The climate exposure of occurrence sites was measured based on the rapidity of climatic changes (i.e. climate velocity) in three climate variables (growing degree days, mean January air temperature, water balance) at each site. Risks caused by land use were assessed using two negative and four positive variables that respectively described the quantity of land cover and habitats that is either harmful (e.g. clear-cut forest and drained peatlands) or supportive (protected areas and suitable habitats) to species occurrences. To complement climate and land-use variables, three additional variables describing protection status of the sites and the number of occurrences of the same species in the landscape were examined. Comparison of the mean vulnerability values for each species showed that some of the species inhabit, on average, areas with high climate exposure. Moreover, in certain species climate change-induced vulnerabilities consistently coincide with negative land use. However, in many of the 52 species there was large variation in the vulnerability levels between individual occurrence sites, concerning both climate exposure and land-use variables. Considering the vulnerabilities due to climate change separately, 40–60% of the species occurrence sites are expected to face high exposure caused by rapid changes in summer or winter temperatures, which presents challenges in maintaining a favourable conservation status. Our results also revealed numerous species occurrences where high climate velocity coincided with a large amount of negative land use and low amount of suitable habitat, for which climate-wise conservation planning could be targeted.

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1. Introduction

Anthropogenic land use and climate change are among the greatest threats to biodiversity, causing loss of natural ecosystems and changes in the climatic suitability for species occurrences within and outside protected areas (PAs) (Araujo et al., 2011; Hansen et al., 2014; Jetz et al., 2007; Pearce-Higgins et al., 2017; Vincent et al., 2019). In Europe, attempts to mitigate the loss of biodiversity include the development of several key conservation instruments, including the Natura 2000 (N2000) network, which aims to safeguard valuable natural and semi-natural environments (Nila and Hossain, 2019; Trochet and Schmeller, 2013), and implementation of the Habitats Directive and species Annexes via the adoption of Council Directive 92/43/EEC in 1992 (Cardoso, 2012; Lund, 2002). The Habitats Directive contains approximately 1300 species of Community interest, including endangered, vulnerable, rare and/or endemic species occurring in the European Union, listed primarily in Annexes II and IV (Cardoso, 2012).

The effectiveness of the N2000 network and Habitats and Birds Directives in protecting European biodiversity have been assessed by examining the completeness of the spatial and taxonomical cover of the Habitats Directive species under present-day conditions (Cardoso, 2012; Lund, 2002; Trochet and Schmeller, 2013). Results have been mixed, showing good spatial coverage for the N2000 network for the populations of threatened bird, mammal and reptile species, but also deficiencies in other species groups. However, the ecological effectiveness of the Habitats Directive also requires assessing the conservation status of species (McKenna et al., 2014; Normand et al., 2007). A given Habitats Directive species exhibits a favourable conservation status if its natural range is sufficient and currently not shrinking nor likely to shrink in the future, and if the species is able to maintain viable populations (Normand et al., 2007).

The ability of Habitats Directive species to achieve and retain a favourable conservation status can be challenging in an era of accelerating global changes. Modelling studies have suggested that many Habitats Directive species populations will be negatively affected by climate change (Araujo et al., 2011; Normand et al., 2007), and notable future alterations in climate conditions in N2000 areas may occur (Heikkinen et al., 2020; Nila and Hossain, 2019), introducing turnovers in species communities (Thuiller et al., 2014; Virkkala and Lehikoinen, 2017). Importantly, negative impacts of climate change may be boosted by interactions with adverse land use (Hülber et al., 2020; Jetz et al., 2007; Oliver and Morecroft, 2014; Segan et al., 2016). Such joint impacts may threaten Habitats Directive species populations particularly outside the PA network, but also within PAs due to improper management of N2000 sites (McKenna et al., 2014; van Swaay et al., 2012) or harmful environmental impacts carried over into the PAs from the immediate surroundings (Hamilton et al., 2013; Hansen and DeFries, 2007) or the wider landscape (Virkkala et al., 2020).

Substantial methodological developments have been made for assessing species vulnerability to climate change (Foden et al., 2019; Pacifici et al., 2015; Williams et al., 2008), some of which also consider vulnerabilities caused by land use (Barber et al., 2016; Heikkinen et al., 2010). These tools provide essential information on climate change vulnerabilities across different species and taxonomic groups (Case et al., 2015; Foden et al., 2013) and help target conservation and management to species facing the highest risks (Gardali et al., 2012; Williams et al., 2008). However, effective incorporation of climate change–land use adaptation strategies in the national-scale management of at-risk species, including Habitats Directive species, would benefit from further attention on three issues: (i) relevant spatial scale of vulnerability assessments, (ii) vulnerability differences between different local populations, and (iii) species-specific impacts of land use, including both negative and positive impacts. Most vulnerability studies have been conducted at a rather coarse scale and overlook local changes in the topoclimate (Heikkinen et al., 2020; Rapacciuolo et al., 2014). Ideally, scrutinizing fine-resolution climatic and land-use risks may help in detecting occurrences of the vulnerable species and directing conservation and management resources to sites providing maximal potential benefits (Crossman et al., 2012; Rannow et al., 2014; Suggitt et al., 2018), but experience on this is sparse. Moreover, the vulnerability assessments of local populations would benefit from using both negative (e.g., clear-cut areas and old-growth forest species) and positive (protected areas, suitable habitats) land-use measures tailored for the studied species based on their habitat preferences (Ewers and Didham, 2006).

We assessed climate change and land use-based vulnerabilities for 52 Habitats Directive Annex II and Annex IV species in Finland using fine-resolution (≤ 100 m) records of species occurrences. Assessments of their vulnerability to climate change may include metrics from three categories: species sensitivity, adaptive capacity and exposure to climate change (Foden et al., 2019). However, here we focused only on climatic exposure, i.e., the magnitude of projected climate change that species are expected to experience, because exposure provides rapid first-filter information systematically covering all the studied species and, importantly for the purposes of this study, an understanding of local-scale variation in vulnerability between individual species occurrences. When examined together with land use, this information enables sorting out the occurrences most at risk due to combined climate change–land use impacts. For species sensitivity and adaptability, comparable (occurrence-level) data rarely exist. Climate change vulnerability was assessed as the climatic exposure of local populations based on topoclimate velocity data (Heikkinen et al., 2020). Negative and positive land uses for local populations was measured as the cover of deteriorated habitats or unsuitable land use versus remaining suitable habitats or conservation areas in the vicinity of species occurrences (Hamilton et al., 2013; Hansen and DeFries, 2007) and wider landscape (Jules and Shahani, 2003; Segan et al., 2016). Specifically, we addressed the following questions: 1) Are there differences in climate change and land use-based risks between the 52 Habitats Directive species? 2) What are the differences in climate exposure and land use-based risks among the individual species occurrences? 3) Do climate change and land-use risks coincide in certain occurrence sites? 4) Can positive, more permeable land use mitigate climate-based risks in occurrence sites facing notable climatic risks? 5) Are there specific areas in the country with high joint risks?

2. Material and methods

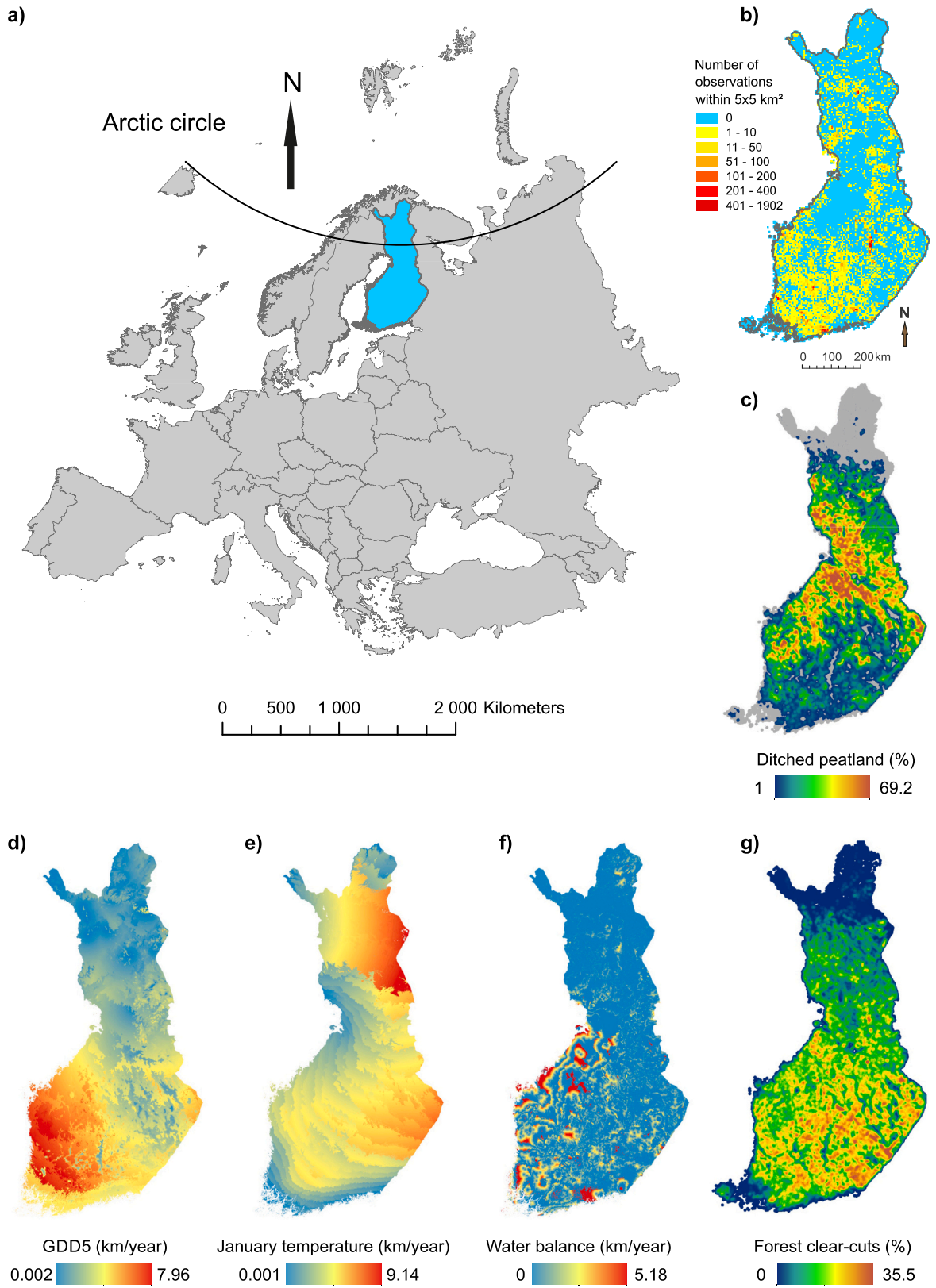
2.1. Species data

Of the 110 Habitats Directive Annex II or Annex IV species occurring in Finland (<https://www.eea.europa.eu/themes/biodiversity/state-of-nature-in-the-eu/article-17-national-summary-dashboards>), we focus on 52 species. This selection was based on the criteria that $\geq 70\%$ of the known localities of the species were recorded at a spatial resolution of 100×100 m or finer. The final species data included 14 bryophyte, 21 vascular plant, 1 Hemiptera, 5 Lepidoptera, 8 Coleoptera, 2 mollusc and 1 mammal species (Table 1). The georeferenced occurrence records for the 52 Habitats Directive species were extracted from the national database for endangered species maintained by the Finnish Environment Institute (HERTTA). For the purposes of this study, we considered only occurrences recorded from the year 1990 onwards and confirmed to exist still in the most recent survey. As the first step in data processing, all the selected Habitats Directive species occurrences were positioned at the centre point of the 100×100 m grid cell where they had been

Table 1

The 52 Habitats Directive species included in the study and their total number of fine-resolution (<100 m) occurrence records (individual grid cells or larger occurrence agglomerations including two or more adjacent grid cells) in Finland.

Species group	Species	Occurrences	
Bryophytes	<i>Buxbaumia viridis</i> (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl	69	
	<i>Cephalozia macounii</i> (Austin) Austin	12	
	<i>Cynodontium suecicum</i> (Arnell & C.E.O.Jensen) I.Hagen	44	
	<i>Dichelyma capillaceum</i> (L. ex Dicks.) Myrin	15	
	<i>Dicranum viride</i> (Sull. & Lesq.) Lindb.	7	
	<i>Encalypta mutica</i> I.Hagen	11	
	<i>Hamatocaulis lapponicus</i> (Norrl.) Hedenäs	33	
	<i>Hamatocaulis vernicosus</i> (Mitt.) Hedenäs	671	
	<i>Herzogiella turfacea</i> (Lindb.) Z.Iwats.	148	
	<i>Hygrohypnum montanum</i> (Lindb.) Broth.	1	
	<i>Meesia longiseta</i> Hedw.	95	
	<i>Orthothecium lapponicum</i> (Schimp.) C.Hartm.	4	
	<i>Plagiomnium drummondii</i> (Bruch & Schimp.) T.J.Kop.	38	
	<i>Scapania carinthiaca</i> J.B.Jack ex Lindb.	5	
	Vascular plants	<i>Agrimonia pilosa</i> Ledeb.	19
		<i>Arctagrostis latifolia</i> (R. Br.) Griseb.	7
		<i>Arctophila fulva</i> (Trin.) Rupr.	10
		<i>Arenaria pseudofrigida</i> (Ostenf. & O. C. Dahl) Juz. ex Schischk. & Knorring	29
		<i>Calypto bulbosa</i> (L.) Oakes	705
		<i>Carex holostoma</i> Drejer	54
<i>Cinna latifolia</i> (Trevir. ex Göpp.) Griseb.		161	
<i>Coptidium lapponicum</i> (L.) Gand. ex Rydb.		983	
<i>Crepis tectorum</i> subsp. <i>Nigritula</i> N. I. Fellm. ex Sennikov, ined.		3	
<i>Diplazium sibiricum</i> (Turcz. ex Kunze) Sa. Kurata		167	
<i>Draba cinerea</i> Adams		29	
<i>Dryopteris fragrans</i> (L.) Schott		27	
<i>Moehringia lateriflora</i> (L.) Fenzl		511	
<i>Persicaria foliosa</i> (H. Lindb.) Kitag.		168	
<i>Primula nutans</i> subsp. <i>Finmarchica</i> (Jacq.) Á. Löve & D. Löve		380	
<i>Puccinellia phryganodes</i> (Trin.) Scribn. & Merr.		8	
<i>Pulsatilla patens</i> (L.) Mill.		148	
<i>Saxifraga hirculus</i> L.		757	
<i>Silene involucrata</i> subsp. <i>Tenella</i> (Tolm.) Bocquet		1	
<i>Trisetum subalpestre</i> (Hartm.) Neuman		33	
<i>Viola rupestris</i> subsp. <i>Relicta</i> Jalas		9	
Hemiptera		<i>Aradus angularis</i> J. Sahlberg, 1886	3
		Lepidoptera	<i>Agriades aquilo</i> (Boisduval, 1832)
<i>Boloria improba</i> (Butler, 1877)			12
<i>Hesperia comma catena</i> (Staudinger, 1861)			3
<i>Lycæna helle</i> (Denis & Schiffermüller, 1775)			41
<i>Xestia borealis</i> (Nordström, 1933)			21
Coleoptera		<i>Agathidium pulchellum</i> Wankowicz, 1869	23
	<i>Boros schneideri</i> (Panzer, 1796)	54	
	<i>Cucujus cinnaberinus</i> (Scopoli, 1763)	6	
	<i>Oxyporus mannerheimii</i> Gyllenhal, 1827	12	
	<i>Pytho kolwensis</i> Sahlberg, 1833	57	
	<i>Stephanopachys linearis</i> (Kugelann, 1792)	36	
	<i>Stephanopachys substriatus</i> (Paykull, 1800)	26	
	<i>Xyletinus tremulicola</i> Y.Kangas, 1958	19	
Molluscs	<i>Vertigo genesii</i> (Gredler, 1856)	11	
	<i>Vertigo geyeri</i> Lindholm, 1925	16	
Mammals	<i>Pteromys volans</i> (Linnaeus, 1758)	13,654	



(caption on next page)

Fig. 1. Study area (Finland) and geographic variation in the number of study species occurrence sites and five environmental variables: a) location of the study area in northern Europe; b) number of occurrences of 52 Habitats Directive species in a 5×5 km grid system; c) proportion of ditched peatland calculated for the 25×25 m grid system using a moving window of 5×5 km in size; d-f) fine-grained, climate-analog velocities of three climate variables calculated following Heikkinen et al. (2020); d) growing degree days (GDD5); e) mean January temperature; f) climatic water balance; and g) proportion of forest clear-cuts extracted from the Global Forest Watch database (Hansen et al., 2013) for the years 2001–2017, shown similarly as in c). The velocities are calculated as the minimum Euclidean distance between the closest climatically similar location in the current climate and in the RCP4.5-based future climate divided by the time separating the two periods, 1981–2010 and 2040–2069.

recorded.

The next step included one data conversion operation that is central to all subsequent analysis: integration of the species records with the 50×50 m grid system including the fine-grained climate velocity data (see 2.2.). This was done by attaching the centre point of each species record to one of the 50-m cells in the 50×50 m grid and by ‘snapping’ the centre point to the nearest 50-m cell using ArcGIS procedure snapping. This 50-m cell constituted the (core) occurrence site, and the surrounding eight 50-m cells (‘ 150×150 m buffer zone’) were considered the immediate surroundings of the occurrence. However, the derived buffers overlapped in certain species, e.g. *Pteromys volans*, *Hamatocaulis lapponicus* and *H. vernicosus*. Such overlapping and adjacent records represent parts of a larger populations or metapopulations and were merged in ArcGIS as one larger agglomeration of occurrence cells. The single occurrences (one focal 50-m cell and its 150-m buffer) and the larger agglomerations of occurrences are collectively referred to as ‘occurrence sites’ in this study because the latter may consist of more than one species occurrence. Climate velocity and local-scale, land-use metrics were thus averaged either for the single occurrence sites (nine 50-m cells) or for the cells included in the larger agglomerations of cells (see 2.2. and 2.3.).

Table 1 provides the number of occurrence sites for each species, and Table S1 the primary habitat type of the Habitats Directive of a given species in Finland. The total number of occurrence sites entered into the analyses was 19,367, of which 13,653 (70.5%) belonged to the Siberian flying squirrel (*Pteromys volans*). Fig. 1b shows the number of species occurrences in a 5×5 km grid across the whole country, and Fig. S1 shows the distribution of occurrences as arranged into seven taxonomic groups. We acknowledge that while Table S1 shows the primary Habitats Directive habitat type for each species, many of the species may occur also in one or more other (directive) habitats.

2.2. Climate data

The approach used to produce fine-grained climate data and calculate the climate change velocity across Finland has been described by Aalto et al. (2017) and Heikkinen et al. (2020) and is only briefly summarized here. Using generalized additive modelling (GAM), variables indicating the geographical location of a site, topographical characteristics and water cover (sea and lake proximity), and weather data sourced from 313 meteorological stations covering Finland and large areas in northern Sweden and Norway (European Climate Assessment and Dataset [ECA&D]), we developed the monthly average air temperature data for the time slice of 1981–2010 over the study domain at a spatial resolution of 50×50 m. The fine-grained topoclimate data effectively incorporated the physiographic effects of solar radiation and cold-air pooling on monthly average air temperatures. Gridded precipitation data were developed for the same baseline time period using global kriging interpolation based on data from 343 rain gauges obtained from the ECA&D dataset, geographical location, topography and proximity to the sea. Based on the monthly air temperature and precipitation data, 50-m resolution measures of the annual air temperature sum above 5°C (growing degree days, GDD5, $^\circ\text{C}$), mean January temperature (T_{Jan} , $^\circ\text{C}$; or ‘TJan’ in certain figures) and annual water balance (WAB, the difference between annual precipitation and potential evapotranspiration; mm) were calculated for Finland and the adjacent areas.

Next, following Heikkinen et al. (2020) we extracted future climate surfaces from the data based on an ensemble of 23 global climate models from the Coupled Model Intercomparison Project (CMIP5) archives for the years 2040–2069 and the three Representative Concentration Pathways (RCP) (RCP2.6, RCP4.5 and RCP8.5) representing a range of greenhouse gas emission scenarios (Taylor et al., 2012). These climate surfaces were bilinearly interpolated to match the 50×50 m grid, the change predicted by the GCMs was then added to our fine-grained baseline climate data and the values for GDD5, T_{Jan} and WAB were recalculated over the grid system. For the purposes of this study, we used only the estimates calculated for the RCP4.5 and focused on mid-century future climates.

In the final step, we calculated the climate change velocities for GDD5, T_{Jan} and WAB (Fig. 1d–f) using the climate-analog velocity method (Brito-Morales et al., 2018; Hamann et al., 2015). With 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 baseline and future period. For these analyses, the present-day and future climate data for the climate scenario were converted from continuous values into categorical climate surfaces, including 51 different classes for GDD, 60 for T_{Jan} and 55 for WAB, respectively (see Heikkinen et al., 2020). Using these categorical climate surfaces, a search for minimum Euclidean distances between grid cells with similar present-day and future climates was conducted using ArcGIS (Desktop 10.5.1.).

The climate velocity values measured for GDD/ T_{Jan} /WAB provided estimates of climate exposure for the study species occurrence sites, i.e., the magnitude of climate change projected to be experienced by the populations (Barber et al., 2016; Case et al., 2015). Here, for each species occurrence site (single focal 50-m cell and its 150×150 m buffer, or the larger agglomerated cell combinations) we calculated the velocity value for the three climate variables as the average value of all 50-m grid cells included at a given occurrence site.

2.3. Land use and other environmental data

We assessed the cover of both negative, adverse land use and that of positive, supportive land-use variables (referred to also as 'suitable habitat') in the vicinity ('local-scale land use') and in the wider landscape ('landscape-scale land use') around the Habitats Directive species occurrence sites. The immediate surroundings of an occurrence site included the focal 50-m grid cell where the centre point of a given species record was assigned and the surrounding eight adjacent 50-m cells. In agglomerated populations, local-scale land use was measured based on the combined set of two or more focal cells with species records and their neighbouring grid cells by considering overlapping 50-m cells only once. Landscape-scale land use was measured from a 5×5 km square established using the Graphic Buffer tool in ArcGIS around the focal 50-m cell, or for the combined larger occurrence areas, from their centre point measured using the Feature to Point tool in ArcGIS.

Similar to the climate change vulnerability assessments (Gardali et al., 2012; Rannow et al., 2014), measurements of land use-based risks for species can be tailored to better reflect species-specific habitat requirements and vulnerabilities stemming from environmental conditions around species occurrences. We developed our assessments of the adverse or positive land use and environmental conditions based on the ecological habitat requirements of the 52 Habitats Directive species. All the species-specific negative and positive land uses are described in detail separately for each species in the [Supplementary information, Table S1](#).

For some species, multiple variables reflected either positive or negative land use, some of which were spatially overlapping. In our land-use calculations, such overlapping areas were considered only once, to derive the total measure for both suitable habitat and negative land use around species occurrence sites ranging from 0% to 100%.

2.3.1. Negative land use

The negative land-use variables were selected to indicate local-scale, species-specific adverse, direct and indirect effects and disturbances, such as changes in light and moisture conditions and human-induced disturbances, which carry over from nearby areas to the species occurrence site (Hansen and DeFries, 2007; Murcia, 1995). Primarily, the same species-specific variables were used to indicate the adverse landscape-level impacts causing habitat loss, degradation and fragmentation. At the landscape level, these impacts are manifested via such processes as increased isolation and lowered recolonization of local populations and increased obstructions inhibiting species from tracking geographic changes in climatically suitable areas (Heikkinen et al., 2010; Jules and Shahani, 2003; Oliver and Morecroft, 2014; Segan et al., 2016).

Some of the negative land-use variables were generic variables derived from the CORINE Land cover CLC2018 dataset (<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>), such as cover of urban areas and intensively managed agricultural areas, which rarely provide suitable habitats for wildlife (Grimm et al., 2008; Hansen et al., 2014). CORINE CLC2018 data are available for Finland in a 20×20 m grid, making it possible to calculate the relative cover of the CORINE land cover classes in the 150×150 m cells. For peatland species especially, the amount of degraded, drained peatland (extracted from a national database developed at the Finnish Environment Institute) was used as a land use-based risk measure (Fig. 1c) (Fraixedas et al., 2017; Haapalehto et al., 2017), while the negative land use for forest species was measured using data on forest clear-cuts from the Global Forest Watch database (Hansen et al., 2013), summed over the years 2001–2017 (Fig. 1g).

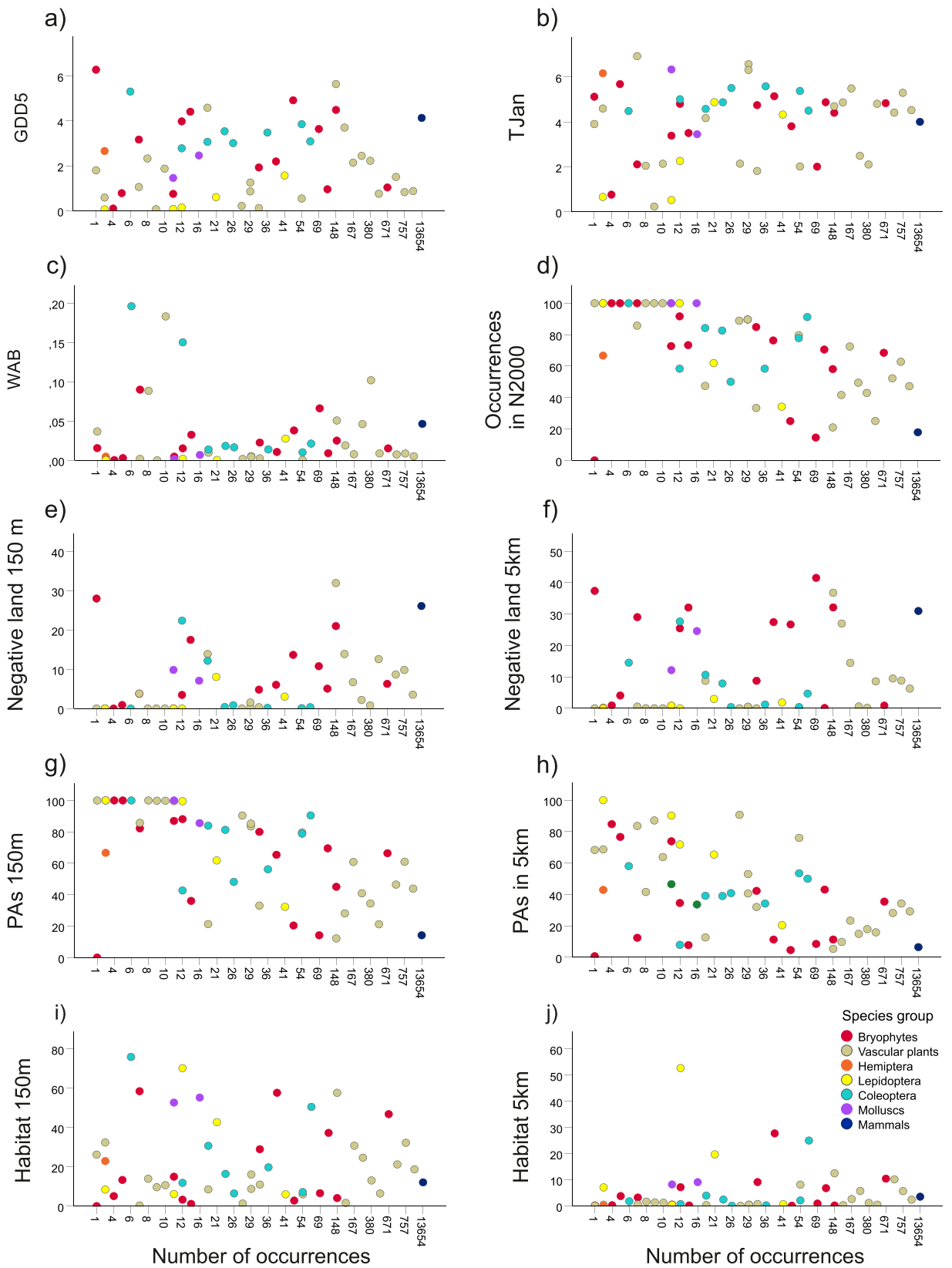
2.3.2. Positive land use

Positive land use around species occurrences was determined based on generic land-use variables but also by mapping the suitable habitats individually for each study species. As a generic measure, we used the number of PAs, which provides an overall measure of positive land use. Specifically, for shore habitat species and certain forest species the PA data were first intersected with CORINE data or forest soil data to better detect suitable protected habitats. Moreover, we used multiple data sources to map the habitats of forest species dependent on specific moisture conditions, occurrences of steep cliffs in forests, gravel-sand-based esker forests or other specific forest habitats. These sources included inventory data on forest site types compiled by Metsähallitus Parks and Wildlife Finland (SAKTI database), geological soil and bedrock databases constructed by the Geological Survey of Finland, mean forest stand age and volume data gathered in the multi-source national forest inventory (MSNI) by the Natural Resources Institute Finland (LUKE), topographic wetness index (TWI) data developed by LUKE, occurrences of key habitats protected by Finnish Forest Act 10 § and data on restoration areas with controlled (prescribed) burning extracted from Metsähallitus Parks and Wildlife. For mire species, the cover of undrained and unditched peatlands was used. Both the cover of PAs and suitable habitat for the species were calculated at a 150×150 m buffer (local-scale) and 5×5 km buffer (landscape-scale) level for each of the 19,367 occurrences.

As additional information, we recorded whether each species occurrence was situated in a PA, in an N2000 area or both. Moreover, for each occurrence we calculated the number of focal species other occurrences in the 5-km landscape-level buffer. This, together with the cover suitable habitats, provides a measure of the potential of the matrix to support species migration to new sites, metapopulation viability and recolonization possibilities of declined populations (Oliver and Morecroft, 2014; Verboom et al., 2010).

2.4. Numeric analysis

As a starting point, all the occurrence sites for each species were ranked by their climate change and land use-based threats, measured using 12 different variables: (1–3) the three climate velocity metrics (climate change exposure), (4–5) the two (local-scale and landscape-scale) negative land-use variables, (6–9) the four (local-scale and landscape-scale PAs and suitable habitat) positive land-use variables, (10–11) the location of the occurrence in a PA or in an N2000 area (or not), and (12) the number of other occurrences in the 5-km landscape-level buffer (see [Supplementary Table S2](#)). These variables were used in two ways, first by comparing



(caption on next page)

Fig. 2. Mean values of ten climate change and land-use vulnerability measures for the 52 Habitats Directive species, arranged according to the number of species occurrences in the study area. The number of occurrences is plotted against a) GDD5 velocity (km/year), b) mean January temperature velocity (km/year), c) water balance velocity (km/year), d) proportion of occurrences situated in Natura 2000 areas, e) cover of negative land use in the 150-m buffer and f) in the 5-km buffer, g) cover of protected areas (PAs) in the 150-m buffer and h) in the 5-km buffer, and i) cover of suitable habitat in the 150-m buffer and j) in the 5-km buffer. In e–j, the cover is calculated as percentage value.

mean risk values between species and then by examining the vulnerabilities of different occurrence sites within each species.

When comparing different species (Study Question 1 in Introduction: ‘What are the between-species differences in climate change and land use-based risks?’), we calculated the mean values (and range of minimum–maximum value) for the occurrence sites of a given species to produce data for the between-species comparisons of the 12 variables. For each of the 12 variables separately, we determined the top 10% of species (i.e., 5 species out of the 52 study species) showing the highest mean vulnerability values (e.g., highest velocity, largest cover of negative land use, lowest PA cover). For the four positive land use measures, we also identified the top 10% of species with the highest mean PA cover and suitable habitat cover in the two buffer zones. We also plotted the number of occurrences of a species against the vulnerability measures to visually examine potential trends between vulnerabilities and species commonness in different taxonomical groups. For a statistical assessment, the 52 species were divided into species having small (< 30) or large (30 or more) numbers of occurrences and then tested using Bonferroni-corrected Mann-Whitney *U*-tests to identify significant differences between vulnerability values in the two groups. This was done for all risk measures except the number of occurrences in PAs and the number of occurrences in the 5 km, landscape-level buffer zone.

At the individual occurrences level (Study Question 2: ‘What are the between-occurrences climate exposure and land use-based risks?’; Study Question 3: ‘Do climate change and land-use risks coincide in certain occurrence sites?’), we plotted the velocity of two climate variables showing larger variation (GDD5 and T_{Jan}) against the cover of negative land use to scrutinise the commonness of double jeopardy occurrences (the 13,653 occurrences of *Pteromys volans* were excluded here to enhance scatterplot clarity). The two climate velocity measures were also plotted against the PA cover and suitable habitat cover in the 5-km buffer (Study Question 4: ‘Is positive land use potentially mitigating climate-based risks in certain occurrence sites?’) to study whether occurrences with high velocities coincide with landscapes rich in PAs or suitable habitat (potentially mitigating the climate change-induced risks). As a rough guideline for interpreting the vulnerabilities for species occurrence sites in relation to these two climate variables, we divided the velocity values into three broad categories based on the range of derived values: high velocities (values of GDD5 > 4.0 km/year; values of T_{Jan} > 5.0 km/year), intermediate velocities (GDD5 2.0–4.0 / T_{Jan} 2.0–5.0 km/year) and low velocities (GDD5 < 2.0 / T_{Jan} < 2.0 km/year). These three broad categories are useful for detecting climatically more at risk occurrences, as the intermediate and especially high-velocity values reflect spatial changes in climatic conditions, which can be challenging to track for many species groups, even mobile ones (Chen et al., 2011; Pöyry et al., 2009; Virkkala et al., 2018).

In the final step, we determined a set of most vulnerable species occurrences based on all 19,367 occurrences. This was done based on nine focal variables: the three climate velocity measures and the two negative (local-scale and landscape-scale) and four positive (suitable habitat and PA cover at the local-scale and landscape-scale) land-use variables. The most vulnerable occurrences were identified separately for each species, following broadly Heikkinen et al. (2010), but also by accounting for differences in the number of species occurrence sites. More precisely, for (i) species with <30 occurrences, we selected the top 10% (or, at minimum, one) of highest risk occurrence(s); (ii) for species ranging from 30 to 100 occurrences, the top 5% (or, at minimum, 3) of occurrences; and (iii) for species with >100 occurrences, the top 1% (or, at minimum, 5) of occurrences. This selection process provided a gradually increasing number of selected occurrences ranging from one high-risk occurrence (e.g., *Hygrohypnum montanum* and *Cucujus cinnaberinus*) to 137 high-risk occurrences (*Pteromys volans*), resulting in a total set of 282 highest risk occurrence sites. Here, we first identified the topmost risk occurrences for a given species based on all nine variables separately, next calculated how many times each occurrence ranked among the highest risk occurrences for the nine variables, and then selected occurrences with greatest number of joint highest risks (a summed value ranging from 0 to 9). In the case of ties, the selection was done by comparing values of all nine risk measures in the candidate occurrences.

The distribution of the 282 occurrence sites with the highest vulnerabilities (Study Question 5: ‘Are there specific areas with high climate exposure and land use-based risks?’) were mapped in two ways: (i) the number of risk occurrences summed for each of the 10-km grid squares in a 10 × 10 km lattice system covering the whole country; (ii) the summed weighted-risk-index where each risk occurrence was first weighted (i.e., divided) by the total number of corresponding species risk occurrences (e.g., for a species with three high risk occurrences, one occurrence had a value of 1/3), and then the weighted values were summed for the 10 × 10 km grid squares with risk occurrences. Finally, as comparison, we also selected 282 highest risk occurrences from the 19,367 occurrences by ignoring the species identity, because in (i) and (ii) each species are forced to have at least one occurrence, and thus, some occurrence sites may show only moderate vulnerabilities.

3. Results

3.1. Between-species vulnerabilities (Study Question 1)

Plotting the mean values of the ten climate velocity and land-use variables against the number of species occurrences (Fig. 2) does not reveal particularly clear patterns, except for the scatterplots of the portion of occurrences situated in N2000 areas (Fig. 2d) and the relative cover of PAs in the 150-m buffer (Fig. 2g) and 5-km buffer (Fig. 2h). These scatterplots suggest that species with low numbers

of occurrences more often inhabit N2000 areas and their occurrence sites have more protected area than species with high numbers of occurrences. When species are arranged into species with low versus high numbers of occurrences (Table 2), these same three patterns prove statistically significant (Mann-Whitney *U*-test; *p*-values ≤ 0.001). Marginally significant is the relationship with negative land use in the 150-m buffer, showing that adverse land use slightly increases with more common species (Fig. 2e, Table 2). Overall, the patterns in the scatterplots are rather scattered, but there are certain species where the low number of occurrence sites coincides with high species mean vulnerability metrics, e.g., in the scatterplot for T_{Jan} (Fig. 2b).

Examination of the top 10% of highest risk species shows that variables with high mean vulnerability coincide in some of the 52 species (Supplementary Table S2). However, typically joint vulnerabilities include only one of the climate metrics and one or more of the land-use variables because the three climate velocity variables show contrasting areas of high exposure (Fig. 1). Only for one species, *Cucujus cinnaberinus*, do the two highest mean climate exposure risks coincide, i.e., for GDD5 and WAB. A striking example of high risks is *Hygrohypnum montanum*. This species has only one occurrence, situated outside the PA / N2000 area network, and it has a high amount of negative land use and high GDD5 velocity. Other species where greatest climate exposure and negative land use coincide include species with very few (*Aradus angularis*), moderate (*Cynodontium suecicum* and *Oxyporus mannerheimi*) or quite many (*Pulsatilla patens*) occurrence sites. For some species (e.g., *Cucujus cinnaberinus*), the top 10% of vulnerability values coincide with the highest values for PA cover or suitable habitat in the surroundings, potentially alleviating the impacts of high climatic exposure (Supplementary Table S2).

3.2. Vulnerabilities between individual occurrences (Study Questions 2–4)

Individual occurrence sites of species show an extensive amount of vulnerability variation (Study Question 2; Supplementary Table S2). Between-occurrence variation for GDD5 and T_{Jan} velocity is particularly large, including species associated with mean high (e.g., *Agrimonia pilosa*, *Draba cinerea* and *Vertigo genesii*), intermediate (e.g., *Calypso bulbosa*, *Pteromys volans* and *Vertigo geyeri*) and low velocities (e.g., *Buxbaumia viridis*, *Hamatocaulis lapponicus* and *Persicaria foliosa*). Extreme between-occurrence differences emerge among some species. For example, GDD5 velocities range from 0.48 to 7.95 km/year between the occurrence sites of *Pteromys volans*, between 0.35 and 6.09 km/year in *Hamatocaulis lapponicus* and between 0.06 and 6.71 km/year in *H. vernicosus*, respectively. T_{Jan} velocities vary maximally from 0.18 to 8.44 km/year between the occurrences of *Encalypta mutica*. Variation in the relative cover of negative land use around the occurrence sites is equally great, e.g., among occurrences of *Calypso bulbosa*, *Pteromys volans* and *Saxifraga hirculus*. Similarly, the relative cover of PAs and suitable habitat show high variability between occurrences, ranging in many species from 0% to 100% (Supplementary Table S2).

Plotting the GDD5 velocities for all species occurrences – except *Pteromys volans* – against negative land use in the 150-m and at 5-km buffers (Study Question 3) suggests that most occurrences show moderate or lower than average joint risks (Fig. 3). However, notable double jeopardy emerge in some of the bryophyte and vascular plant species occurrences, i.e., at dozens of occurrence sites where high GDD5 velocities (> 4 km/year) coincide with negative land use covering $>50\%$ of the surrounding area (Fig. 3a and b). The scatterplots of T_{Jan} versus negative land use show slightly different overall patterns, as the core mass of occurrence sites are characterized by intermediate T_{Jan} velocity values (2–4 km/year) and less than 40–50% negative land cover (Fig. 3c and d).

Comparing GDD5 velocities to PA cover and suitable habitat in the 5-km buffer (Study Question 4) revealed that some occurrence sites with intermediate or high climate exposure also have a rather modest amount ($<10\%$) of PAs or suitable habitat in their surroundings but contrasting cases do occur (Fig. 4a and b). The corresponding scatterplots for T_{Jan} also include a number of occurrences where high GDD5 velocities coincide with modest PA cover or suitable habitat (Fig. 4c and d). Plotting the PA cover against suitable habitat cover reveals an overall positive trend between the two. However, it also shows that high PA cover does not automatically

Table 2

Mean values of three climate change velocity measures and six land cover variables for the occurrences of the 52 Habitats Directive species, and the proportion of occurrences located in Natura 2000 areas. Species are divided into two categories based on the number of occurrences: species having a small (range 1–29, $n = 29$) or large number (range 33–13,654, $n = 23$) of occurrences. Mean values (\pm standard error) of climate velocity for growing degree days (GDD5), January mean temperature (T_{Jan}) and water balance (WAB) are measured as the smallest distance between climatically similar locations under 1981–2010 conditions and under projected CMIP5 RCP4.5 conditions in 2040–2060. Mean values (\pm S. E.) of species occurrences in Natura 2000 areas, and negative land use, protected area (PA) cover and suitable habitat (both in the 150-m and in the 5-km buffer) were calculated as percentages for each species in the two categories (see text for details). Statistical significance for differences between species with a small vs. large number of occurrences are based on Mann-Whitney *U*-test ($n_1 = 29$, $n_2 = 23$). *P*-values that remain statistically significant after Bonferroni correction are indicated with bolded letters.

Variable	Small number of occurrences, mean \pm S. E.	Large number of occurrences, mean \pm S. E.	<i>z</i>	<i>p</i>
GDD5, velocity (km/year)	2.04 \pm 0.32	2.44 \pm 0.32	1.115	0.265
T_{Jan} , velocity (km/year)	3.90 \pm 0.36	4.18 \pm 0.25	0.120	0.905
WAB, velocity (km/year)	0.03 \pm 0.01	0.02 \pm 0.01	1.852	0.064
Occurrences in Natura 2000 areas (%)	84.23 \pm 4.30	52.37 \pm 4.82	4.484	<0.001
Negative land use, 150 m buffer (%)	4.62 \pm 1.39	8.16 \pm 1.80	2.419	0.016
Negative land use, 5 km buffer (%)	8.35 \pm 2.19	12.57 \pm 2.89	1.650	0.099
PA cover, 150 m buffer (%)	80.29 \pm 4.94	47.59 \pm 4.96	4.310	<0.001
PA cover, 5 km buffer (%)	52.97 \pm 5.21	26.44 \pm 3.79	3.381	0.001
Habitat available, 150 m buffer (%)	21.53 \pm 4.06	21.89 \pm 3.74	0.378	0.706
Habitat available, 5 km buffer (%)	4.42 \pm 1.89	5.94 \pm 1.57	1.686	0.092

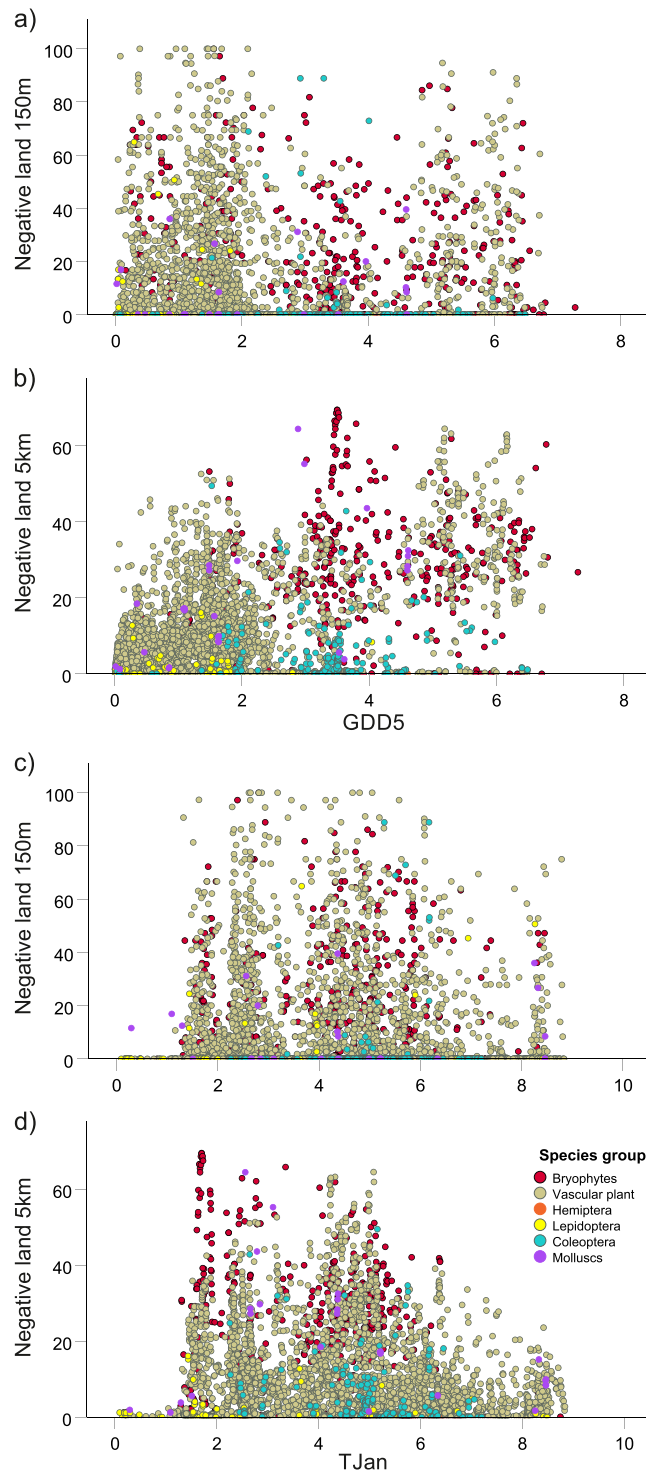


Fig. 3. The relationships between the two climate change velocity values and the two negative land-use measures (GDD5 a, b; mean January temperature c, d; negative land use in the 150 m buffer a, c; and in the 5-km buffer b, d), measured in the 5714 individual Habitats Directive species occurrences. For clarity, the 13,653 occurrences of *Pteromys volans* were excluded.

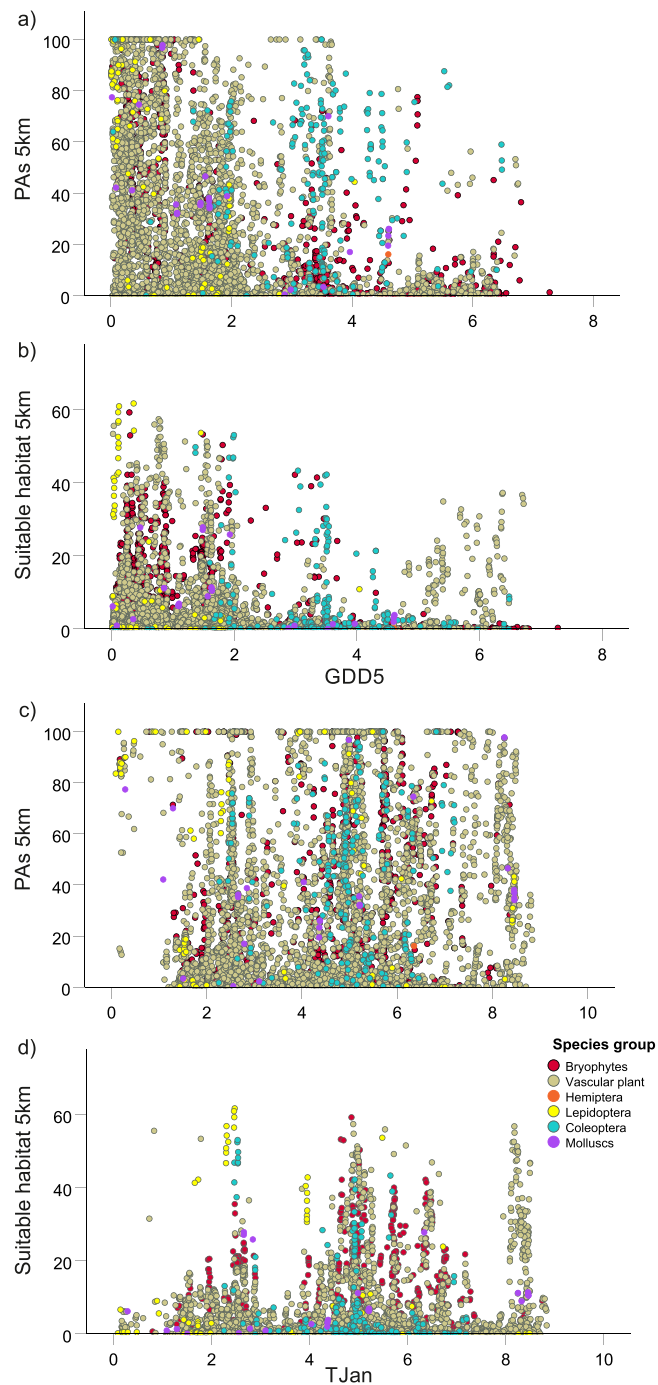


Fig. 4. The relationship between the two climate change velocity values and the two positive land-use measures (GDD5 a, b; mean January temperature c, d; PA cover in the 5-km buffer a, c; and suitable habitat cover in the 5-km buffer b, d), measured in the 5714 individual Habitats Directive species occurrences. For clarity, the 13,653 occurrences of *Pteromys volans* were excluded.

mean a high amount of suitable habitat (Supplementary Fig. S2).

3.3. Distribution of highest joint-risk occurrences

The distribution of the topmost at-risk occurrence sites selected from all 52 species (Study Question 5), weighted by the number of occurrences in each species and summed up to 10-km grid squares, shows sporadic geographic patterns (Fig. 5). The 10-km grid

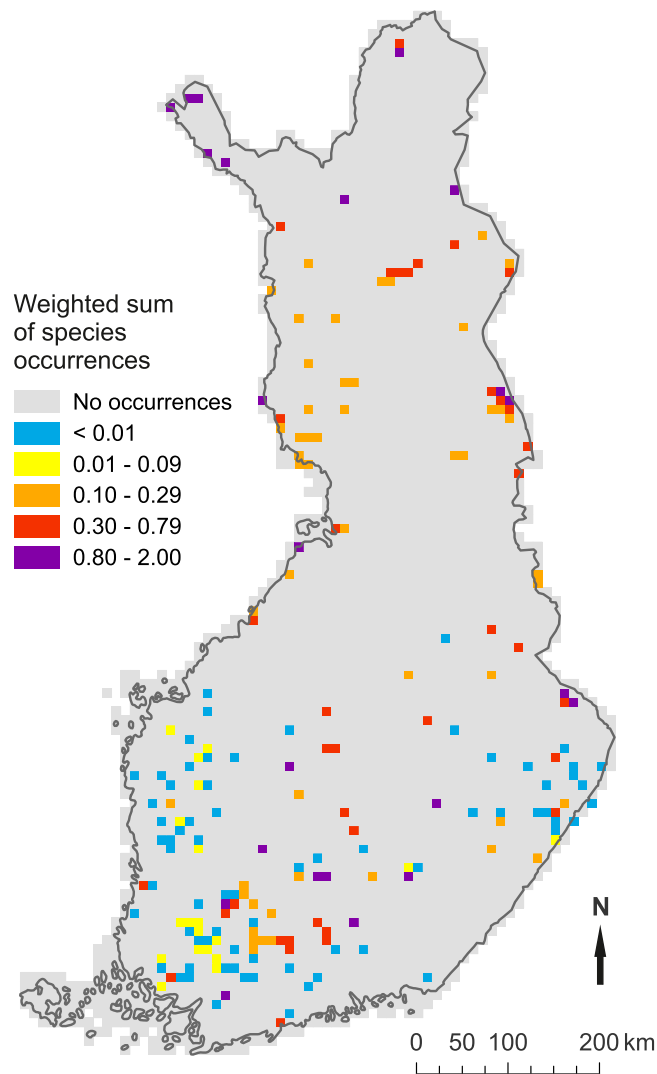


Fig. 5. The distribution of the 282 weighted, highest risk occurrences of the 52 Habitats Directive species. The map shows the summed weighted risk index for each of the 10×10 km grid square across Finland. When calculating the index, one or more occurrences (following species prevalence) showing overall highest climate velocity and land-use risks was selected from each of the 52 species, the occurrences were weighted (i.e., divided) by the total number of corresponding species risk occurrences and then the weighted values were summed for the 10×10 km grid squares.

squares with greatest summed risk values occur in a few subalpine and alpine regions in N Finland, certain locations in eastern border areas and sporadically in S-SW Finland. The corresponding map with the same occurrences but without weightings (Supplementary Fig. S3) shows that in absolute numbers, 10-km grid squares with a larger number of high-risk occurrences are mainly concentrated in heavily populated regions of SW-W Finland. Moreover, when occurrences of highest multiple risks are directly selected among all the 19,367 occurrences, the predominance of the SW-W region for risk population hot spots becomes even more apparent (Supplementary Fig. S4). However, in this selection *Pteromys volans* covers 259 (91.8%) of the 282 occurrences, accompanied by only six other species.

4. Discussion

4.1. Species vulnerability to climate change

There is a long tradition of conservation planning for threatened species and habitats (Hoffmann et al., 2008; Pressey et al., 2007; Sarkar et al., 2006). However, it is also crucial at present to pay attention to areas and species populations most vulnerable to climate change, develop an understanding of how climate change impacts alter spatial management and conservation priorities, and provide guidance on how to minimize biodiversity loss (Dawson et al., 2011; Heller et al., 2015; Heller and Zavaleta, 2009; Nadeau et al., 2015). Several approaches and decision frameworks have been constructed in recent decades, including criteria for determining what species are most at risk due to climate change (Case et al., 2015; Foden et al., 2019; Gardali et al., 2012; Pacifici et al., 2015; Reside

et al., 2016).

Metrics for assessing species vulnerability to climate change are often divided into three categories: species sensitivity (intrinsic traits determining, e.g., physiological tolerances), adaptive capacity (ability to adjust to changing conditions via, e.g., trait plasticity or moving to new suitable areas), and exposure (magnitude of climatic changes species are projected to face) (Dawson et al., 2011; Foden et al., 2019; Pacifici et al., 2015; Williams et al., 2008). Detailed information on traits and factors affecting the sensitivity and adaptive capacity of all the species included in a multi-taxa study is often laborious to compile and includes many unknowns (Brito-Morales et al., 2018; Gardali et al., 2012; Pacifici et al., 2015; but see Foden et al., 2019). Moreover, sensitivity and adaptability provide little information on the variation in vulnerabilities between individual species populations. In contrast, exposure to climate change is a more generic vulnerability measure. It provides reasonable first-filter estimates of climate-induced risk for between-species comparisons (Carroll et al., 2015; Maggini et al., 2014), and particularly for determining individual species occurrences most at risk due to climate change.

Given these benefits, we focussed here on climate change velocity to assess the exposure of species and their occurrence sites to climate change. Climate velocity is a metric that defines the speed and direction of climate shifts over a given area, making it possible to identify locations where climatic conditions are changing most rapidly (Barber et al., 2016; Brito-Morales et al., 2018; Heikkinen et al., 2020). Based on the findings of earlier studies (Dobrowski et al., 2013; Ordóñez and Williams, 2013), we assessed climatic exposure using multiple individual climate variables. This enabled us to map the spatial variation in the velocities of three key bioclimatic variables and assess the potentially divergent climate exposure threats to species occurrences in different locations.

Spatial patterns of the three climate variables differed in our results, and the species and their occurrence sites associated with the greatest GDD5 velocity changes were often different than those associated with the highest T_{Jan} or WAB velocities. Thus, species inhabiting different parts of the country may face very different climatic exposure challenges (Study Question 1). In addition, extensive variation exists between the climatic exposure of individual occurrences, ranging in GDD5 velocities maximally from 0.48 to 7.95 km/year and in T_{Jan} velocities from 0.18 to 8.44 km/year, respectively (Study Question 2). It is important to note that such an extensive variation in climate exposure can take place also in species with a rather low number of occurrences in, e.g., *Encalypta mutica* (11 occurrences) and *Hamatocaulis lapponicus* (33 occurrences). This large variation between species occurrences can effectively be concealed in species-level comparisons, which are based on mean values. Thus, developing vulnerability assessments by investigating finer species entities, such as individual populations, may significantly aid in targeting conservation priorities to locations facing minimal climate exposure or, when appropriate, enhanced management effort at sites with notable exposure risks (Rannow et al., 2014; Stagl et al., 2015).

Climate velocity measures used in our study were calculated at a much finer resolution than velocities in earlier studies (see Heikkinen et al., 2020, and the references therein). Yet, the mean velocities of GDD5 and T_{Jan} for our study species are roughly in the same magnitude as in other studies conducted in northern environments (Barber et al., 2016; Carroll et al., 2015; Hamann et al., 2015; Loarie et al., 2009). Here, higher velocities were derived for GDD5 and T_{Jan} than for WAB, suggesting that climate change risks related to changes in water balance will be less prominent in northern boreal landscapes than exposure risks related to thermal conditions. In comparison, water balance changes can be more severe in southern, moisture-limited environments, such as the Mediterranean biome (McCullough et al., 2016). The velocities of GDD5 and T_{Jan} in our results can be considered critically high as they exceed the rate of observed geographic changes in mobile species, such as boreal birds (Virkkala et al., 2018). Hence, future changes in winter and summer temperatures may significantly hamper many high-latitude Habitats Directive species from reaching and retaining a favourable conservation status (cf. Normand et al., 2007; Rannow et al., 2014).

4.2. Negative land use and joint risks with climate change

Intensive human-modified land use can have various negative impacts on the persistence of species populations (Hamilton et al., 2013; Hansen and DeFries, 2007). Adverse land use, particularly habitat loss and fragmentation resulting from it, can also operate synergistically with climate change to accelerate biodiversity decline (Oliver and Morecroft, 2014; Segan et al., 2016; Travis, 2003). Therefore, it is essential that the risks to biodiversity emerging from climate change and negative land use are jointly considered to identify locations that may face double jeopardy (Barber et al., 2016; Heikkinen et al., 2010; Tingley et al., 2014).

We selected negative land-use variables for each species individually based on the species' habitat preferences. Negative impacts of land use in the immediate surroundings include different carryover impacts from the unprotected area into PAs (Hamilton et al., 2013; Hansen and DeFries, 2007). In forested PAs, they include increased edge effects and disturbances and exposing natural biotopes to human impacts (Hansen and DeFries, 2007; Matlack, 1993; Murcia, 1995). In peatlands, ditching of the adjacent areas may cause disturbances in water table levels and water flows within the protected mires (Sallinen et al., 2019). Negative land use in a wider landscape has a variety of consequences, such as limited movements, altered source/sink dynamics and difficulties for species to track suitable areas. Decreasing habitat quality and quantity, which makes the matrix less permeable for species, is the main driver of such impacts (Hansen and DeFries, 2007; Jules and Shahani, 2003; Oliver and Morecroft, 2014; Sweaney et al., 2014). Together, the local and wider landscape land-use impacts can decrease the viability of species populations via, for example, decreased abundance, reduced gene flow and increased sensitivity to stochastic events (Jules and Shahani, 2003; Segan et al., 2016).

Our between-species comparisons show that high climate velocities coincide with a high amount of negative land use in some of the 52 species, such as *Hygrohypnum montanum* and *Pulsatilla patens* (supplementary Table S2). However, examining the between-occurrence vulnerabilities rather than just between-species mean vulnerability metrics again provides a much more in-depth understanding of the situation (Study Question 3). Indeed, high between-occurrence variability exists in joint risks. Investigation of these patterns reveals numerous occurrence sites where high climate exposure coincides with areas where adverse land use dominates the

landscape. Most of the species with occurrence sites featured by high GDD5 velocity and high negative land use are bryophytes, including *Buxbaumia viridis*, *Cynodontium suecicum*, *Hamatocaulis vernicosus*, *H. lapponicum* and *Herzogiella turfacea*, accompanied by two vascular plants, *Pulsatilla patens* and *Cinna latifolia*. Occurrences with joint high T_{Jan} velocity (> 5 km/year) and negative land cover ($> 50\%$) risks are less abundant, but they include a wider selection of species (13 species), with mire species (*Saxifraga hirculus* and the two *Hamatocaulis* species) and certain riverine habitat (*Moehringia lateriflora*) and forest species (*Diplazium sibiricum*, *Xyletinus tremulicola*) being most common.

4.3. Positive land cover and species habitat requirements

Large amounts of protected areas and suitable habitats for the species around their occurrence sites can help offset the impacts of climate change (Study Question 4), support processes important for species persistence and facilitate species range shifting (Jules and Shahani, 2003; Oliver and Morecroft, 2014; Sweaney et al., 2014). It is noteworthy that while PA cover provides a generic measure of positive land use, information on suitable habitat tailored for each species individually, as provided here, allows for a more detailed assessment of the essential parcels of land supporting persistence and movements of species. Moreover, our measurements of suitable habitat are closely related to one of the trait-based measures of species vulnerability, namely species habitat specialization (Case et al., 2015; Gardali et al., 2012), which defines highly specialized species as those most sensitive to climate change.

With our 52 Habitats Directive species, habitat specialization manifests in different ways and via different levels of specialization. For example, species inhabiting boreal forests are restricted to ecologically different habitats: *Cynodontium suecicum* depends on old coniferous Western Taiga forests situated adjacent to cliffs, *Dichelyma capillaceum* and *Scapania carinthiaca* favour wet locations in old boreal forests, including alluvial forests next to small rivers and brooks, *Calypso bulbosa* favours various forest biotopes situated in calcareous soil and *Pulsatilla patens* pine-dominated forests situated on gravelly-sandy glaciofluvial formations. More stringent ecological requirements result in few suitable habitats for *Cynodontium suecicum*, *Dichelyma capillaceum* and *Cinna latifolia*, whereas occurrence areas of *Pulsatilla patens* (which favours certain types of soil and semi-open, not particularly old, pine-dominated forests) may consist of large suitable patches of habitat disrupted by negative land use, i.e., clear-cut areas (Supplementary Table S2).

In 16 of the 52 study species, notable joint risks based on high GDD5 (>4 km/years) or T_{Jan} velocity (>5 km/years), substantial negative land use ($>50\%$) in either a 150-m or 5-km buffer, and low amounts of suitable habitat ($<10\%$) coincide. For the 16 species, the mean percentage of occurrences facing the three elevated risks is 8%, and it ranges from $< 1\%$ (*Coptidium lapponicum*, *Diplazium sibiricum* and *Hamatocaulis vernicosus*) up to 20% (*Pteromys volans*) and 33% (*Oxyporus mannerheimii*). A total of 2,799 of the 19,367 occurrence sites (14.5%) confront this type of triple jeopardy, potentially requiring increased attention in management planning.

Importantly, large numbers of PAs in the surrounding landscape do not necessarily indicate an equally large amount of suitable habitat for some ecologically specialized species. Thus, although there is a general positive tendency in the relationship between suitable habitat and PAs, 862 occurrence sites in our data have PA cover of $> 50\%$ in the 5-km buffer but, at the same time, suitable habitat cover of $<10\%$ (Supplementary Fig. S2). Corresponding species include those dependent on different specific habitat conditions, e.g. forest management by prescribed burning (*Aradus angularis*, *Stephanopachys substriatus*), Western Taiga forests with representative stands of *Populus tremula* (*Agathidium pulchellum*), old pine-dominated forests (*Boros schneideri*), certain types of coastal wetland habitats (*Arctophila fulva*) and calcareous rocky slopes with chasmophytic vegetation (*Draba cinerea*).

4.4. Implications for conservation planning of Habitats Directive species

The EU Habitats Directive and N2000 network are central instruments for the conservation of European biodiversity (Cardoso, 2012; Lund, 2002). Most research addressing the Habitats Directive has focused on taxonomic limitations in the Directive lists and spatial sufficiency of the protected Habitats Directive species occurrences under current conditions. In contrast, retaining favourable conservation status for Habitats Directive species has received insufficient attention (McKenna et al., 2014; Normand et al., 2007). This is a shortcoming because the ability of species to maintain long-term viable populations in their occurrence sites can be severely challenged by climate change (Rannow et al., 2014; Stagl et al., 2015). A study by Normand et al. (2007) showed that 69–99% of the 84 Habitats Directive plant species will be negatively affected in Denmark due to future climatic change, potentially causing notable turnovers in local species communities and highlighting the importance of adaptive climate-wise conservation. Our results also draw attention to the importance of changes in climatic conditions, as 37.5% of the 19,367 Habitats Directive species occurrences were at sites where projected GDD5 velocity exceeded 4.0 km/year and 59.2% at sites where T_{Jan} velocity exceeded 4.0 km/year, respectively. In comparison, few observed range shifts in any species groups have occurred at this rate (Chen et al., 2011; Pöyry et al., 2009; Virkkala et al., 2018).

However, as Tingley et al. (2014) emphasized, focusing only on climate change impacts can lead to limited vulnerability assessments for species, and other stressors such as negative land use need to be taken into account. Indeed, intensified land use around PAs has an acknowledged role in the increased vulnerability of biodiversity in PAs (Hamilton et al., 2013; Hansen and DeFries, 2007), and human-caused environmental changes have resulted in habitat loss and deterioration in the quality of the N2000 network, potentially increasing the vulnerability of Habitats Directive species populations (McKenna et al., 2014). Given the importance of multiple stressors, a number of studies have developed vulnerability assessment frameworks for climate-wise conservation planning that jointly consider climate change and land-use factors (e.g., Barber et al., 2016; Nadeau et al., 2015). This study combined three climate change velocity risk measures with several land use-based variables, including negative land use, protected areas and suitable habitats around the occurrence sites, to assess where Habitats Directive species populations are at risk due to multiple stressors. A key benefit of our approach is that once the necessary data for delimiting species-specific habitats and velocity maps for different climate variables have

been constructed, they facilitate vulnerability calculations across all the occurrence sites of the study species. Subsequently, identification of species occurrences at risk due to different drivers enables developing flexible management plans tailored to respond to the different challenges and various local conditions faced at individual sites (Rannow et al., 2014).

We acknowledge that the overall vulnerability of species to climate change can be more thoroughly assessed by examining the wide range of traits that affect species sensitivity or adaptability. However, such analyses are beyond the scope of this work because information on many of the traits, such as physiological tolerances, are known only for a limited set of species. Developing comparable data for a wide range of species may need extensive expert opinion assessments and determining precise vulnerability thresholds can be tricky (Gardali et al., 2012; Pacifici et al., 2015). Above all, trait information rarely reveals vulnerability differences between occurrences of the same species. Yet, where robust data on critical traits, such as dispersal ability or distribution range size (Gardali et al., 2012; Reside et al., 2016), are available, they can provide valuable further vulnerability notifications for species occurrences facing high climate change and land use risks. In our study, additional vulnerabilities may be of particular concern for the 12 species that have less than 10 occurrence sites in the country (i.e., limited geographic range) or species with known limited dispersal ability, such as *Pytho kolwensis* (Siitonen and Saaristo, 2000).

Mapping the species occurrence sites with high joint risks (Study Question 5) highlights certain areas in S-SW Finland and also some other more sporadically located areas. These areas can be used as tentative locations for targeting future management and conservation actions to decrease the impact of other stressors impacting the Habitats Directive species occurrences. It would be important to make these areas more permeable, expand current PAs and establish new stepping-stone PAs to increase the climatic variation of PA networks and support species migration (Ackerly et al., 2010; Normand et al., 2007; Oliver and Morecroft, 2014). Finally, flexibility in climate-wise conservation planning has a key role because drivers of species vulnerability may rapidly change in certain areas when, for instance, critical climatic or habitat decline thresholds are crossed. Positive changes in species occurrence data may also occur and realized through, e.g., adopting new field inventory techniques, which have recently helped in detecting new localities for some of the 52 species (e.g., *Buxbaumia viridis*). On the other hand, negative impacts stemming from increased forest clear-cuttings may rapidly escalate threats to forest species dependent on old forest stands. Thus, adaptive climate-wise approaches that allow flexible re-assessments of the spatial patterns of vulnerabilities are essential tools for the protection of biodiversity under dynamic global changes.

CRedit authorship contribution statement

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

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01664](https://doi.org/10.1016/j.gecco.2021.e01664).

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