Ecological Indicators 138 (2022) 108829

Contents lists available at ScienceDirect

Ecological Indicators

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

Emerging spatial prioritization for biodiversity conservation indicated by climate change velocity

Qi Lai [a,*,1], Samuel Hoffmann [a,1], Anja Jaeschke [a,b,d], Carl Beierkuhnlein [a,b,c]

[a] Department of Biogeography, University of Bayreuth, Universitaetsstr. 30, 95447 Bayreuth, Germany
[b] Bayreuth Center of Ecology and Environmental Research, BayCEER, University of Bayreuth, Universitaetsstr. 30, 95447 Bayreuth, Germany
[c] Geographical Institute of the University of Bayreuth, GIB, Universitaetsstr. 30, 95447 Bayreuth, Germany
[d] Bayerisches Landesamt für Umwelt, Bürgermeister-Ulrich-Straße. 160, 86179 Augsburg, Germany

ARTICLE INFO

Keywords:
Climate change velocity
Europe
Natura 2000
Protected area management
Biogeographical regions
Biodiversity conservation
Spatial prioritization

ABSTRACT

Anthropogenic climate change is challenging biodiversity conservation worldwide. Climate change metrics derived from future climate predictions help to assess potential impacts of climate change on biodiversity. Here we calculated future climate change velocities across biogeographical regions of terrestrial Europe and the Natura 2000 protected area network, the largest protected area network on Earth. We applied climate projections for the year 2070, considering two emission scenarios, six global climate models and a fine spatial resolution. Areas with very high climate change velocity were identified as climate change hotspots, while areas with very low velocity were recognized as coldspots. We further revealed where and to what extent climate change hotspots and coldspots coincide with Natura 2000 sites. We found that climate change velocities are projected highest in the Continental and Boreal regions, and lowest in the Mediterranean and Anatolian regions. However, the Alpine region will likely contain largest areal proportions of climate change hotspots, while areal proportions of coldspots are projected largest in the Mediterranean region. High mountain regions such as the Alps show a high proportion of Natura 2000 sites that coincide with climate change hotspots. Both, hotspots and coldspots, are geographically associated with areas of topographic diversity. Low topographical diversity indicates high climate change exposure. The impact of hotspots increases with spatial isolation. Oceanic climate buffers climate change exposure in contrast to continental climate. However, continental regions of Europe tend to exhibit less spatial isolation. We recommend conservation action in climate change hotspots and coldspots to simultaneously protect the most climate-exposed biodiversity as well as climate change refugia. Climate change hotspots and coldspots overlapping with Natura 2000 sites should be considered priority conservation sites because new protected areas are hard to realize in densely populated landscapes of Europe. This study directs European conservation management and policy towards meeting international conservation goals in a climate-smart way.

1. Introduction

Anthropogenic climate change poses a key challenge to biodiversity conservation (Dawson et al., 2011). Predicting climate change impacts on biodiversity is required to guide climate-proof conservation. Responses of species to climate change are of central interest in the conservation context. Species may tolerate climate change, may adapt to novel climate by physiological alterations or behavioural modifications, migrate to track suitable climate, or go extinct (Williams and Jackson, 2007). Changes of species diversity result in alterations of other components of biodiversity such as genetic diversity, ecosystem functioning and services (Mascaro et al., 2012; Scheffers et al., 2016; Walther, 2010). The uncertainties of climate change projections, along with the broad spectrum of biotic responses, increase the difficulty of climate-smart conservation planning.

Conservation objectives must be prioritized because conservation resources such as time, workforce and funds are limited (Laurance et al., 2012). Protected areas are such priority conservation objectives. The geography of protected areas is mainly based on the occurrence of threatened biodiversity and human land use, but locating protected areas often ignores threats from climate change (Hoffmann, 2021a). Climate change can make habitats inside protected areas unsuitable for

* Corresponding author.
E-mail address: Qi.Lai@uni-bayreuth.de (Q. Lai).
[1] QL and SH have contributed equally to this work and wish to be considered as joint first authors.

https://doi.org/10.1016/j.ecolind.2022.108829
Received 24 June 2021; Received in revised form 30 March 2022; Accepted 30 March 2022
Available online 7 April 2022

species of conservation focus (Thomas and Gillingham, 2015). Whether species populations can adapt to these future conditions within the limits of protected areas is dependent on their life cycles, adaptive capacity, dispersal ability and biotic interactions (Williams et al., 2008). It is expected that protected areas may not retain the species diversity they were meant to protect (Holsinger et al., 2019; Velazco et al., 2019). Protected areas may lose species diversity (Araújo, Alagador et al., 2011; Fuentes-Castillo et al., 2019). Furthermore, protected areas are spatially fixed. Options for adding new protected sites or for relocating existing sites are limited in human-dominated landscapes. Consequently, developing climate-smart management for existing protected area networks should be a primary task of conservationists (Hole et al., 2011). Gaining insight into the climate change exposure of protected area networks is a vital first step to facilitate and prioritize climate-proof conservation management.

The European Union's (EU) Natura 2000 network is one of the most important protected area networks on Earth (Gaston et al., 2008). The Natura 2000 network is a transnational and spatially coherent protected area network which spans across all EU member states (EEA, 2019). It is based on the EU's Birds Directive 2009/147/EC (1979) and Habitats Directive 92/43/EEC (1992). The formation of the Natura 2000 network is to overcome political boundaries and aims at protecting the most characteristic, valuable, rare and threatened species and habitats across Europe. Natura 2000 sites are expected to safeguard species and habitats in the long term. However, the dynamic impacts of climate change were barely included in the planning of the Natura 2000 network (European Commission, 2013). Hence, the Natura 2000 network is prone to missing its conservation objectives due to climate change impacts (Araújo et al., 2011; Mazaris et al., 2013; Nila, Beierkuhnlein et al., 2019; van Teeffelen et al., 2015). To ensure the enduring effectiveness of this continental protected area network, conservation management must adapt to potential climate change impacts.

Here we inform about potential climate change impacts on terrestrial Europe and the Natura 2000 network. While there are several global studies on predicted climate change in protected areas (Elsen et al., 2020a; Hoffmann and Beierkuhnlein, 2020; Hoffmann et al., 2019; Loarie et al., 2009), only few analyses explicitly applied climate change metrics to terrestrial Europe and the Natura 2000 network (Araújo et al., 2011; Nila et al., 2019). Patterns of climate change velocities across Europe and its Natura 2000 network have not been addressed so far, although climate change velocity is an essential metric for conservation under global warming (Brito-Morales et al., 2018; Garcia et al., 2014).

We consequently map climate change hotspots and coldspots that are characterized by extremely high and low climate change velocity, repsectively. We hypothesize that climate change velocities will be low in coastal and mountainous regions and high in continental lowland regions of Europe. Global warming is expected to be faster over land than over sea due to the contrast in heat capacity (Sutton et al., 2007). The oceanic influence leads to a smaller magnitude of temperature increase. Coastal areas with oceanic climate can buffer temperature increase. Climate in oceanic regions is likely to change slower than climate in continental regions (Compo and Sardeshmukh, 2009). Furthermore, climate change velocity is expected to be low in mountain ranges where considerable elevational gradients, i.e., climatic gradients, occur within small spatial extent (Carroll et al., 2017; Dobrowski and Parks, 2016). Hence, geographical distances between current and future climate analogs are mostly short, leading to low climate change velocities. In contrast, we expect climate change velocity to be high in areas with less pronounced elevational gradients, i.e., in lowland regions. Since it is important to know how the current Natura 2000 sites will perform under climate change compared to non-protected areas, we also assessed whether predicted climate change velocities are higher inside or outside Natura 2000 sites. This assessment was done for every biogeographical region in Europe.

Moreover, we highlight climate change hotspots and coldspots within the Natura 2000 network. We suggest considering climate change hotspots and coldspots within Natura 2000 network as priority conservation sites. In climate change hotspots, species are assumed to be more climate-threatened because their time to adapt to changing climate conditions is shorter and the migration or dispersal distance to analog climates is longer. Climate change coldspots are considered climate change refugia with more time to respond to changing climate conditions. Such coldspots are providing more promising options for migration or dispersal because of higher similarity between current conditions and future climate analogs. This study is aiming to provide a spatial assessment of climate change velocity that can play a key role in guiding climate-smart biodiversity conservation at the continental scale of Europe.

2. Methods

2.1. Study region

Climate change velocity was calculated for terrestrial Europe including the Natura 2000 network. Natura 2000 is the largest protected area network worldwide (Orlikowska et al., 2016). This study focused on the Natura 2000 Special Protection Areas (SPA) and Special Areas of Conservation (SAC) designated under the Birds Directive 2009/147/EC (1979) and Habitats Directive 92/43/EEC (1992), respectively. The site data was obtained from the European Environment Agency (EEA, 2019) (Fig. 1a). It consists of 6045 SPAs and 20,027 SACs within 27 EU member states and the United Kingdom. The network covers approximately 1.3 million km^2, i.e., ca. 18% of the EU land area (Fig. 1a). Aichi Target 11 of the Convention of Biological Diversity aimed at a global terrestrial protected area coverage of 17% by 2020.

To present the geographic variation of climate change velocity, we sub-divided the study extent into biogeographical regions following the standard classification of European biogeographical regions (Cervellini et al., 2018). In contrast to individual countries, they help to abstract and summarize findings in an ecological way. An integrated review study on Natura 2000 by Orlikowska et al. (2016) suggested emphasizing biodiversity conservation actions inside individual biogeographical regions, which can address conservation efforts for similar biotas and help with implementing research results into more effective conservation practices. Accordingly, the climate change velocities both inside and outside the Natura 2000 network were compared among eleven terrestrial biogeographical regions across Europe in this study (Fig. 1b). We note that the names of biogeographical regions used in the classification can be misleading as they can be associated with climate zones (e.g. Atlantic), biomes (e.g. Boreal) and cultural regions (e.g. Anatolian). The term "Alpine" can refer to an elevational zone, the Alps specifically, or high mountain ranges in general. However, this biogeographical classification is an official product of the European Environmental Agency and thus well-known to European conservationists and policymakers.

2.2. Climate data

The workflow of our methodological approach can be seen in Fig. 2. We used current climate data for the years 1970–2000 from WorldClim version 2.0 (Fick and Hijmans, 2017) and projected climate data for the years 2061–2080 (i.e., for 2070 on average) from WorldClim version 1.4 (Hijmans et al., 2005). The climate data consisted of 19 bioclimatic variables at a 2.5 arc minutes resolution (approx. 5 km). We selected future climate data sets from a medium emission scenario (RCP 4.5) and a high emission scenario (RCP 8.5). Both RCPs span a range of likely future climate scenarios. The future climate data sets were taken from six global climate models (GCMs): CNRM-CM5, HadGEM2-AO, INMCM4, MIROC5, MPI-ESM-LR, IPSL-CM5A-LR. We used the combination of the current climate data set and one of the six future climate data sets to build a principal component analysis (PCA); i.e., six PCAs in total, one PCA for each GCM. We built the PCAs to reduce each set of 19

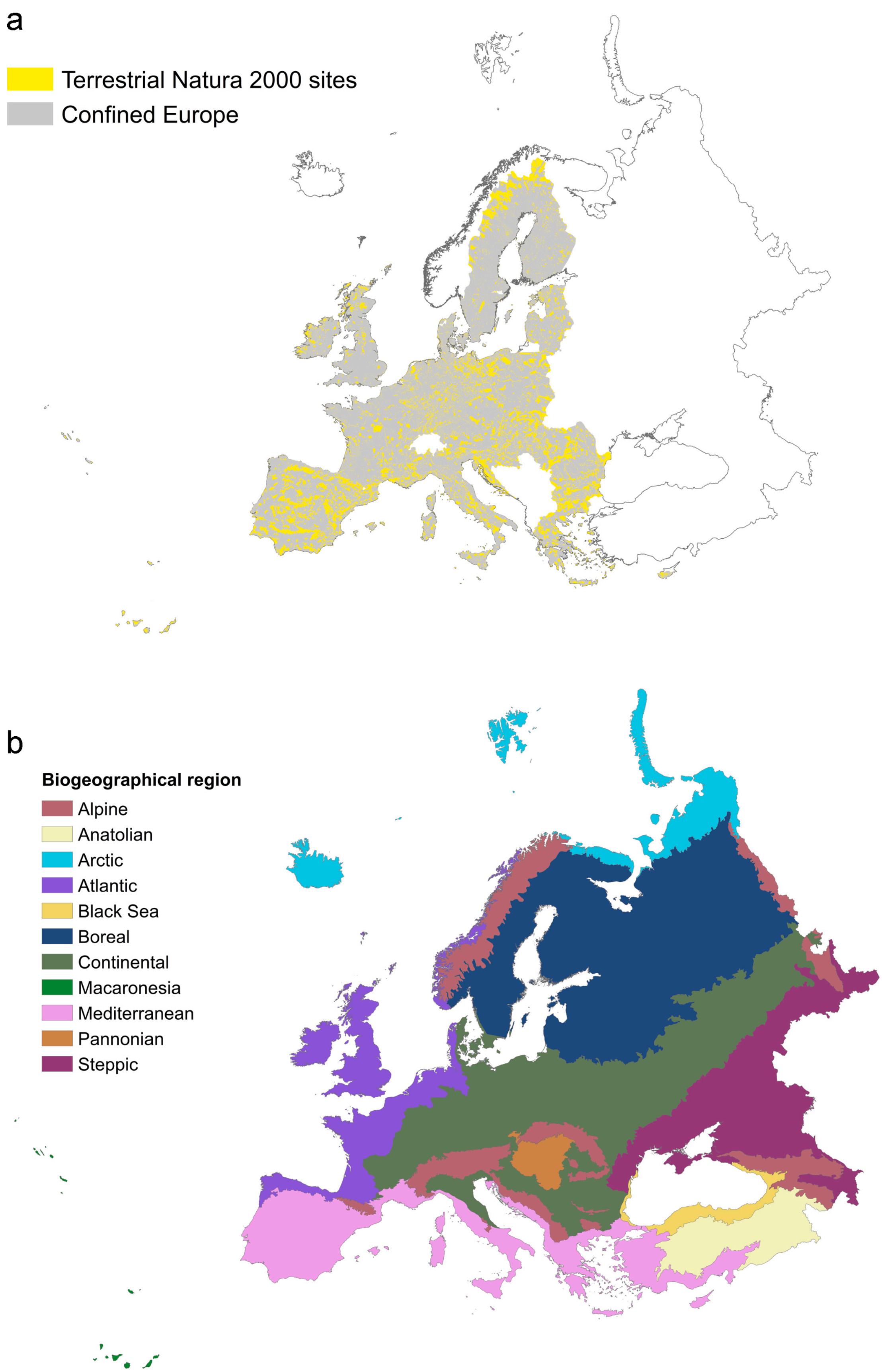

Fig. 1. Terrestrial Natura 2000 sites and biogeographical regions in Europe. a) Terrestrial Natura 2000 sites adapted from (EEA, 2019). Grey area represents confined Europe, i.e., countries including Natura 2000 sites. b) Map of biogeographical regions in Europe (Cervellini et al., 2018).

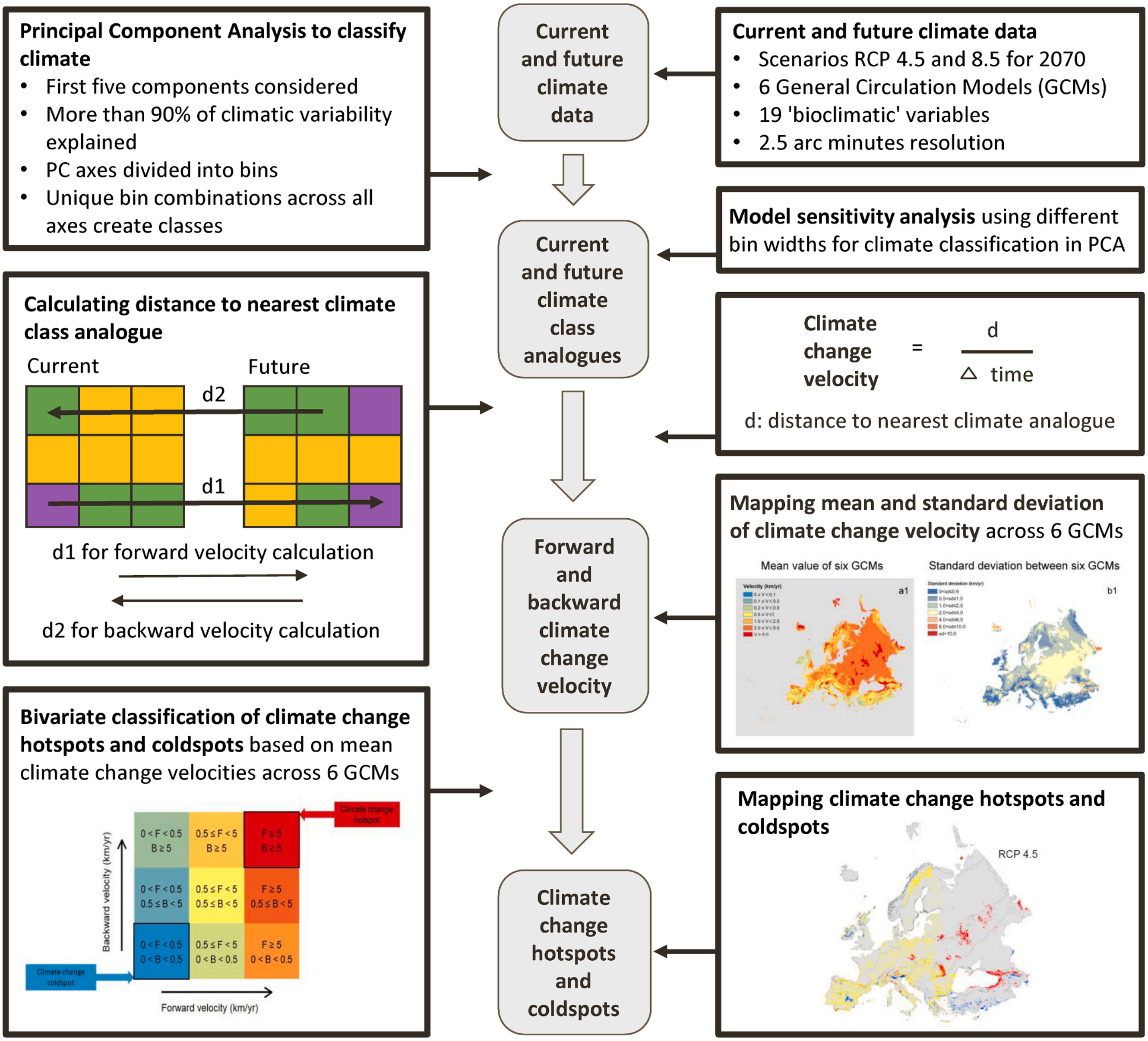

Fig. 2. Workflow of the methodological approach. We used current climate data and future climate prediction to calculate current and future climate analogs. Forward and backward climate change velocities were computed based on the displacement of current and future climate analogs. A bivariate classification of backward and forward climate change velocities was taken to define climate change hotspots and coldspots, which were later overlaid by Natura 2000 sites.

bioclimatic variables to five independent bioclimatic variables. The first five components of each PCA explained more than 90% of the climatic variability (Appendix I).

The future climate data could largely vary among different GCMs (Knutti et al., 2013) and continents (Bring et al., 2019). The selected GCMs focus on the European climate system. Also, the independence of the GCM was considered, to ensure that there was low similarity among the selected GCMs (Knutti et al., 2013). Multiple GCMs reflect a variety of projections, i.e., potential variation in predicted climate change. Individual results from each of the selected GCMs are given in the Appendix (Appendix II and III).

2.3. Forward and backward climate change velocity

Climate change velocity can be calculated in various ways (García Molinos et al., 2019). The climate velocity metric by Hamann et al. (2015) was especially developed for species conservation. It is used in this study because it allows calculating forward and backward climate change velocities, two complementary measures reflecting the velocity which species need to migrate or disperse to track their climate niche (Carroll et al., 2015, 2017; Hamann et al., 2015). The velocity metric is based on geographical distances between locations of current climate classes and their future analogs (Hamann et al., 2015).

The forward climate change velocity is calculated by the minimum distance between a grid cell's current climate class and the nearest cell with the same climate class under future conditions (Hamann et al., 2015). From an ecological perspective, forward climate change velocity refers to the minimum distance an organism must migrate or disperse to track constant climate conditions in future. The search for analogous or non-analog climates, respectively, is still a methodological challenge due to the complexity of climate traits (Li et al. 2018b). Accordingly, in this context, forward velocity assesses the conservation status of species and populations under climate change. The backward climate change velocity uses the future climate class of a grid cell as a baseline and reflects the minimum distance to the nearest cell with the same climate class under present conditions. In other words, backward velocity refers to the minimum distance that a climatically adapted organism would have to migrate or disperse to colonize the given location holding analogous climate in future. Backward velocity thus represents the difficulty of species in colonizing newly suitable habitat via migration or dispersal. Forward and backward velocity provide complementary information for climate-smart conservation planning. Forward velocity assesses the climate-induced extinction risk of local species and populations, while backward velocity estimates the risk of localities to receive fewer colonizing species in future, which potentially decreases biodiversity, ecosystem functioning and services. The velocity values are equal to the minimum distance divided by the time, which is 80 years in this study. The unit of the velocity metric is thereby km/yr.

The climate change velocity metrics are based on distances between grid cells with analogous climate classes under present and future climate conditions. Accordingly, a climate class was assigned to each grid cell in terrestrial Europe. The climate classes were defined by dividing the PCA climate space, which was built on 19 bioclimatic variables from all 5,379,939 grid cells of terrestrial Europe. Each PC axes was divided into bins. The unique combinations of bins along the five PCs constitute the climate classes. The value of climatic velocity is, however, sensitive to the delimitation of climate classes, i.e., the bin width to construct climate classes along the five PC axes in the PCA. Thus, a sensitivity analysis was carried out to decide on the PC bin width. The sensitivity is not affected by different GCMs or RCPs (Carroll et al., 2018). Accordingly, we conducted the sensitivity analysis for one GCM and one RCP (INMCM4 and RCP 8.5) to reduce computation time. To select a bin width that balances overestimation (i.e., too narrow climate classes) and underestimation of predicted climate change (i.e., too wide climate classes), we evaluated the sensitivity of the relationships between the number of bins along the first PC, which is equivalent to the bin width, and the number of resulting climate classes across Europe; between the number of bins along the first PC and the proportion of climate classes without future analogs; and, between the number of bins along the first PC and the median distance between current and future climate analogs (Appendix IV). Subsequently, we selected a moderate amount of climate classes (i.e., a moderate bin width) to calculate climate change velocity. We applied five bins on the first PCA axis which mean a bin width of 4.6 PCA units that result in 82 climate classes across Europe. We found this an appropriate bin width to optimize the information content of the resulting velocity maps by balancing loss of velocity information because of extremely broad bins versus exaggerated velocity information because of extremely narrow bins. The forward and backward climate change velocities were calculated using the R code from Carroll et al. (2015), adapted from Hamann et al. (2015).

2.4. Statistical analyses of differences between climate change velocity inside and outside the Natura 2000 network per biogeographical region

Since it is important to know how the current Natura 2000 sites will perform under climate change compared to other land use areas, we assessed whether predicted climate change velocities are higher inside or outside Natura 2000 sites per biogeographical region. We used Least Significant Difference (LSD) test with p values adjusted by the Bonferroni method to test for significant differences between climate change velocity values inside and outside the Natura 2000 network.

2.5. Climate change velocity-based hotspots, coldspots and priority conservation sites

A bivariate choropleth approach was applied to classify the degree of climate change exposure by a combination of forward and backward climate change velocity (Fig. 3). We used the highest and lowest degree of climate change exposure to identify grid cells of climate change hotspots and coldspots, respectively.

Forward climatic velocity and backward climatic velocity were each assigned to three classes. The maximum velocity value is about 50 km/yr. The grid cell size roughly equals 5 km × 5 km. According to the grid cell size, a climatic velocity value of 0.5 km/yr can be interpreted as a climate displacement of approx. 10 years, and a climatic velocity value of 5 km/yr can be interpreted as a climate displacement of approx. 1 year. 0.5 km/yr and 5 km/yr were used as the demarcations in classifying each climate change velocity distribution into three quantiles.

The red category that has the highest forward velocity and highest backward velocity marks climate change hotspots. Climate change hotspots correspond to grid cells with both a mean forward velocity value and a mean backward velocity value higher than 5 km/yr. In these grid cells, the climate displacement could be completed in less than 1 year, which means a species could lose its climatic habitat within a year. Climate change coldspots correspond to grid cells with both a mean forward velocity value and a mean backward velocity value lower than 0.5 km/yr. In these grid cells, the climate displacement could be completed in about 10 years, which means a species could lose its climatic habitat in 10 years.

We characterize areas with extremely high forward and backward climate change velocities (≥5 km/yr) as climate change hotspots, and areas with extremely low forward and backward climate change velocities (less than 0.5 km/yr) as climate change coldspots (Fig. 3). In climate change hotspots, species are assumed to be more climate-threatened because their time to adapt to changing climate conditions is shorter and the migration or dispersal distance to analog climates is

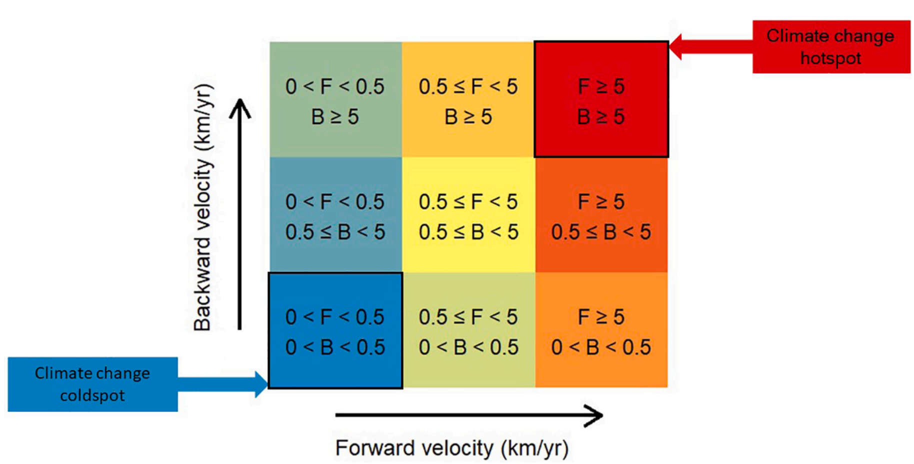

Fig. 3. Bivariate choropleth colour chart of forward and backward climate change velocity. F: forward velocity in km/yr, B: backward velocity in km/yr. The red category involves the highest forward velocity and highest backward velocity values and marks climate change hotspots. The blue category involves the lowest forward velocity and lowest backward velocity values and marks climate change coldspots.

longer. In climate change coldspots, current and future climate analogs are closer than in hotspots. Hence, species are assumed to be less threatened by climate change because there is more time for their populations to respond to changing climate conditions. Furthermore, the migration or dispersal distance to sites with analog climates are shorter. Accordingly, both, climate change hotspots and coldspots, can be considered important sites for species conservation. We therefore suggest considering climate change hotspots and coldspots within Natura

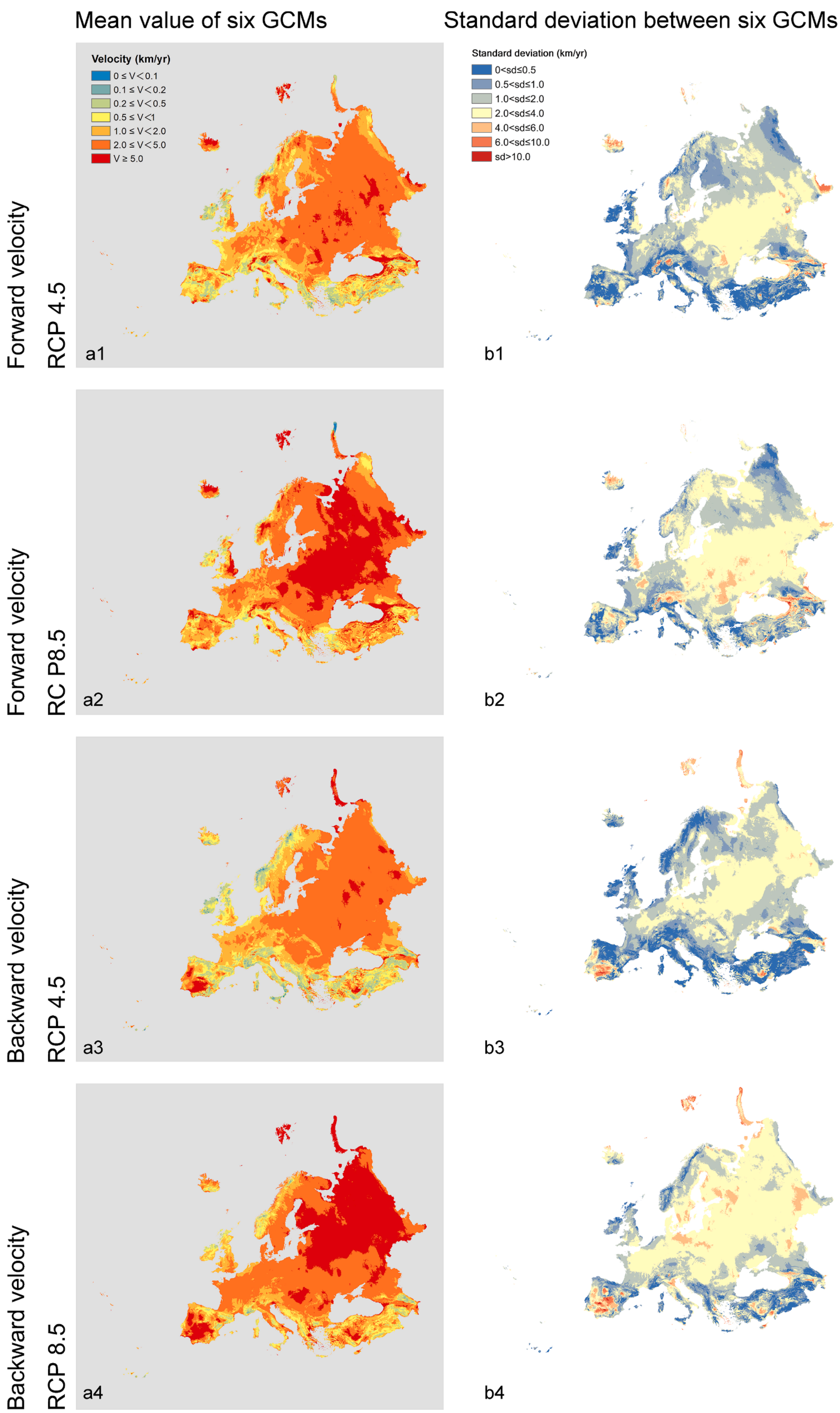

Fig. 4. Mean (a1-4) and standard deviation (b1-4) of forward and backward climate change velocity values across six GCMs for the year 2070 under RCP 4.5 and RCP 8.5.

2000 network as priority conservation sites now and in future.

3. Results

3.1. Forward and backward climate change velocity

The area with high mean velocity values across the six GCMs is larger under RCP 8.5 compared to RCP 4.5, in both forward velocity and backward velocity (Fig. 4). High forward velocity values are widely present in inland Europe, where the Boreal and the Continental biogeographical regions are located. High forward velocity values also occur in the Arctic region, the east coast of the Black Sea, and particularly in high-elevation areas of the Alpine region.

Coastal areas and the Mediterranean region show lower forward

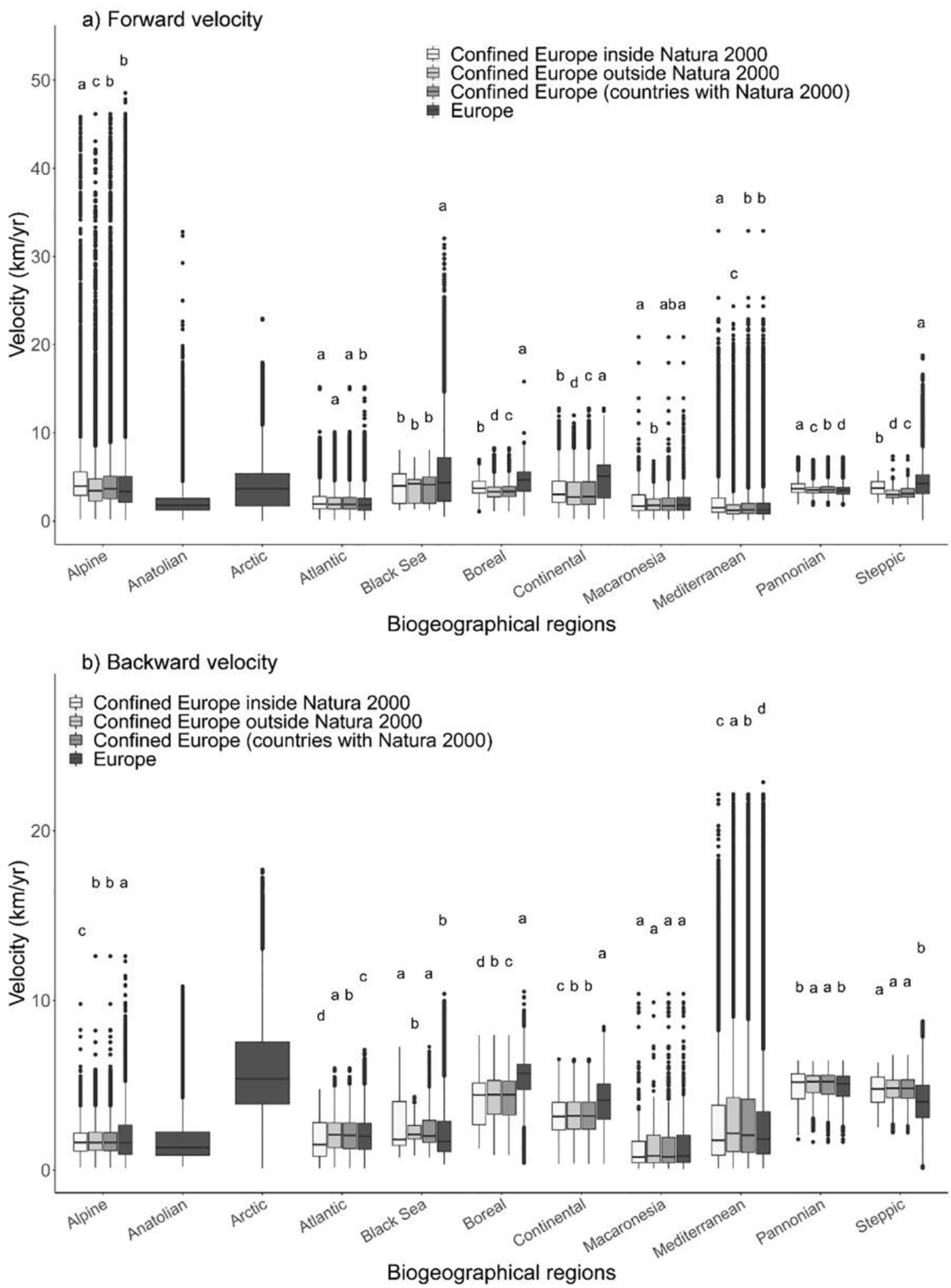

Fig. 5. Mean climate change velocity values across six GCMs for the year 2070 inside and outside Natura 2000 sites per biogeographical region under RCP 8.5. a) Forward climate change velocity, b) Backward climate change velocity. Letters above boxplots indicate significant differences from Least Significant Difference (LSD) tests; p values were adjusted using Bonferroni method. The limits of the boxes show the lower and upper quartiles, i.e., the interquartile range. The horizontal black line within boxes shows the median. The whiskers extend to the lowest and highest values within 1.5 times the interquartile range. The black dots indicate outliers beyond the whiskers. "Confined Europe" stands for countries with Natura 2000 sites.

velocity values. High backward velocity values are mainly distributed in the Continental and Boreal regions of Europe, which is consistent with the distribution of high forward velocity values. In contrast to forward velocity values, backward velocity values are relatively high in the Iberian Peninsula and relatively low in large parts of the Alpine region. Climatic velocities of individual GCMs and RCP scenarios are given in the Appendix (Appendix II and III).

Areas with high mean values generally coincide with areas of high standard deviation (SD) values, i.e., with high variation or uncertainty among climate models (Fig. 4). The area with lower variation of velocity values across the six GCMs is larger under RCP 4.5 compared to RCP 8.5, in both forward velocity and backward velocity. Lowest SD values are mainly found at the margins of Europe, in the Mediterranean, Anatolian, Atlantic, Boreal and Arctic regions. Intermediate SD values are mainly located at inland Europe, in the Continental and Boreal regions. Patches of highest SD values can be found all over Europe, particularly in the Artic, Alpine and Mediterranean regions. Spatial patterns of the SD of forward and backward velocity do not coincide all over Europe such as seen in the Artic, Alpine and Mediterranean regions.

3.2. Climate change velocity inside and outside the Natura 2000 network per biogeographical region

The highest median forward velocity values occur in the Continental

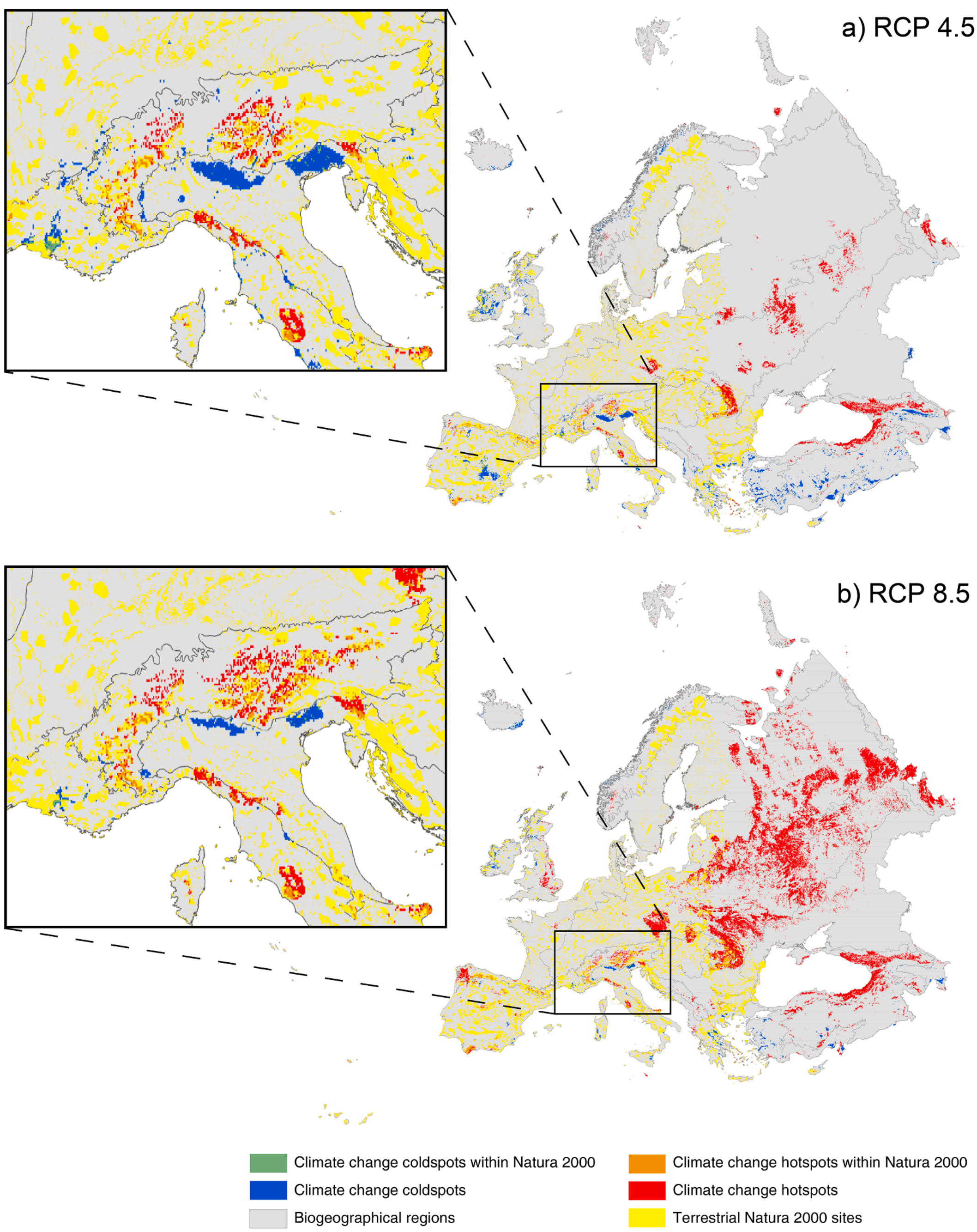

Fig. 6. Climate change exposure of terrestrial Europe based on mean forward and backward climate change velocity across six GCMs for the year 2070 under a) RCP 4.5 and b) RCP 8.5. The red category involves the highest forward and backward velocity values and marks climate change hotspots. The blue category involves the lowest forward and backward velocity values and marks climate change coldspots. The terrestrial Natura 2000 network is marked in yellow, climate change hotspots within the Natura 2000 network in orange and climate change coldspots within the Natura 2000 network in green. Grey lines indicate biogeographical regions.

region, followed by the Boreal, Black Sea, Steppic, Arctic, Pannonian, Alpine, Macaronesia, Atlantic, Anatolian and Mediterranean region (Fig. 5a). The highest single forward velocity value across Europe is approaching 50 km/yr and found in the Alpine region. The LSD tests indicate that there is no significant difference between forward velocity values inside and outside the Natura 2000 network in the Atlantic and Black Sea region. In other biogeographical regions, the forward velocity values inside Natura 2000 are notably higher than of outside Natura 2000.

The highest median backward velocity values occur in the Boreal region, followed, by the Arctic, Pannonian, Steppic, Continental, Atlantic, Mediterranean, Black Sea, Alpine, Anatolian, and Macaronesia region (Fig. 5b). The backward velocity values are overall lower than the forward velocity values. The highest single backward velocity value is approaching 30 km/yr and found in the Mediterranean region. According to the LSD test, there is no significant difference between backward velocities inside and outside the Natura 2000 network in the Macaronesia region and the Steppic region. In the Atlantic region, the backward velocity values inside Natura 2000 are significantly lower than outside Natura 2000. This difference is also notable in other biogeographical regions besides the Black Sea region, where the backward velocity value inside Natura 2000 is significantly higher than outside Natura 2000. The forward and backward velocity values per biogeographical region for RCP 4.5 can be found in the Appendix (Appendix V).

3.3. *Climate change velocity-based hotspots, coldspots and priority conservation sites*

Areas with velocity values higher than 5 km/yr in both backward and forward velocity (red category) were identified as climate change hotspots (Fig. 6). Such hotspots are mainly located in the Boreal, Black Sea, Continental and Alpine regions. More grid cells were identified as hotspots than coldspots, and more hotpots were calculated under RCP 8.5 (Fig. 6b) than under RCP 4.5 (Fig. 6a), notably in the Boreal region. Cells with coldspots (blue) are more frequent under RCP 4.5 and spread across the Mediterranean, Alpine, Anatolian and Atlantic regions, often in mid-elevation zones and close to the coast. The bivariate choropleth colour map of forward and backward climate velocity can be found in the Appendix (Appendix VI).

Climate change hotspots (marked in red in Figs. 6, 7 and 8) and coldspots (blue) partly overlap with the Natura 2000 network (yellow) and thus form the climate-based priority conservation sites (orange and green, respectively). More climate change hotspots and less coldspots are forecasted under RCP 8.5 than RCP 4.5 (Figs. 6 and 7). 2.0% (RCP 4.5) to 6.5% (RCP 8.5) of confined Europe's land area (i.e., countries with Natura 2000 sites) are projected to become climate change hotspots (Fig. 7). Only 1.9% (RCP 4.5) to 0.6% (RCP 8.5) of confined Europe will likely remain climate change coldspots. While Natura 2000 sites cover more than 17% (Aichi Target 11) of confined Europe (18.5%), only a minor proportion of Natura 2000 sites are considered priority conservation sites according to projected climate change hotspots and coldspots. 0.9% (RCP 4.5) to 2.1% (RCP 8.5) of confined Europe is covered by Natura 2000 sites that are predicted to become climate change hotspots. 0.2% (RCP 4.5) to 0.1% (RCP 8.5) of confined Europe is covered by Natura 2000 sites that are predicted to become climate change coldspots.

In the Atlantic, Boreal and Continental region of confined Europe (countries with Natura 2000 sites), Natura 2000 sites do not yet cover 17% (Aichi Target 11) of land area (Fig. 8). Across RCP scenarios (Fig. 8), the Alpine, Continental, Mediterranean and Pannonian regions hold largest proportions of climate change hotspots, whereas biogeographical regions adjacent to the sea (Mediterranean, Atlantic, Macaronesia, Continental) hold highest proportions of climate change coldspots. Under RCP 8.5 (Fig. 8b), the proportion of hotspots in the Alpine region is larger than 17%. However, a relatively large proportion of predicted hotspots in the Alpine region is already covered by Natura 2000 sites. In contrast, the coverage of coldspots by Natura 2000 sites is very low in each biogeographical region. Under RCP 4.5 (Fig. 8a), no hotspots are predicted for the Macaronesia, Pannonian and Steppic regions; and no coldspots for the Black Sea, Boreal, Pannonian and Steppic regions. Under RCP 8.5 (Fig. 8b), hotspots are predicted for each biogeographical region; and no coldspots for the Black Sea, Boreal, Macaronesia, Pannonian and Steppic regions. The land area proportions considering entire terrestrial Europe including countries without Natura 2000 sites are shown in the Appendix (Appendix VII).

4. Discussion

4.1. *Forward and backward climate change velocity*

Our hypothesis assuming high climate change velocity for the continental lowland regions of Europe and low values for the coastal and mountain regions can be largely confirmed. In terms of forward climate change velocity, the Continental and Boreal regions in lowland Europe showed on average highest values. Interestingly, we also calculated high forward velocity values for high-elevation parts of the Alpine region. The findings for the Alpine region contradict our hypothesis but are likely generated by the most extreme climatic conditions of the highest-elevation zones. We consequently suppose that the nearest analogous future climates of high-elevation areas are located in other potentially even higher-elevation areas that are very distant. High forward velocity expresses climate change exposure of present biodiversity at a given location because present organisms would have to emigrate or disperse long distances to reach analogous climate habitat in future. Hence, a considerable proportion of inland Europe could be prone to local extinctions due to rapid climate change. In contrast, regions with low forward velocity values are found in coastal areas of the Mediterranean, Anatolian, Atlantic and Macaronesia regions. In these areas, the oceanic influence might buffer climatic changes (Sutton et al., 2007). However, the coastal biodiversity might suffer from other impacts of climate change such as the sea-level rise and extreme weather events (Ameca y Juárez et al., 2013; Harter et al., 2015; Walls et al., 2019).

In terms of backward climate change velocity, values are relatively low in the Macaronesia, Anatolian, Alpine, Black Sea, Mediterranean and Atlantic regions, what we also expected. Low backward velocity values in coastal regions can be explained by the oceanic buffer effect as well. In regions with elevational gradients such as the Alpine region, low backward velocity is probably because analogous current climates can be found at nearby downslope locations, except low-elevation valley bottoms (Carroll et al., 2015, 2017). In contrast, large areas of lowland Europe such as in the Boreal, Arctic, Pannonian, Steppic and Continental regions have high backward velocity values, which is in line with the spatial pattern of forward velocity. High backward velocity reflects the climate change exposure of potentially immigrating species at a given location in future, because immigrating species would have to migrate long distances from their current climate habitat. Consequently, locations with high backward velocity are potentially threatened because species are insufficiently adapted to the locations' future climate, which could affect ecosystem functioning and services (Carroll et al., 2015, 2017; Hamann et al., 2015).

Surprisingly, we found several areas with high forward velocities but low backward velocities and vice-versa, such as on the Iberian Peninsula. Such contrasting patterns of forward and backward velocity indicate that current climates will locally disappear (i.e., high forward velocity) or locally novel climates will occur in future (i.e., high backward velocity). Thus, such areas seem to be located at the extremes of the region's climate space.

4.2. *Climate change velocity inside and outside the Natura 2000 network*

Although Natura 2000 sites were established without considering the

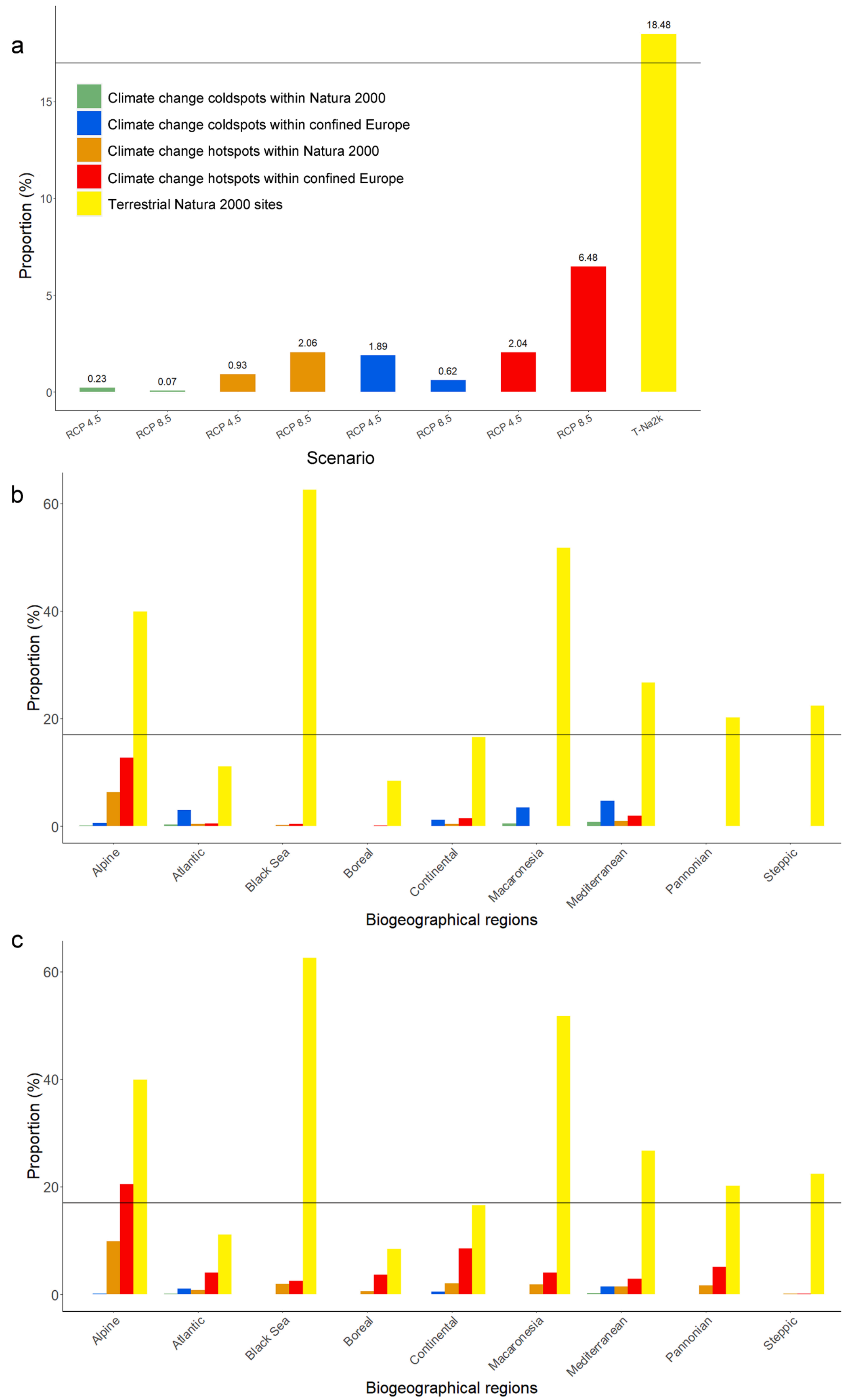

Fig. 7. Mean proportions of land area of confined Europe (i.e., countries with Natura 2000 sites) covered by climate change hotspots, coldspots, Natura 2000 sites, and priority conservation sites (i.e., hotspots and coldspots within the Natura 2000 network) across six GCMs under emission scenarios RCP 4.5 and RCP 8.5 for the year 2070; a) for entire confined Europe, b) for each biogeographical region under RCP 4.5 and c) for each biogeographical region under RCP 8.5.

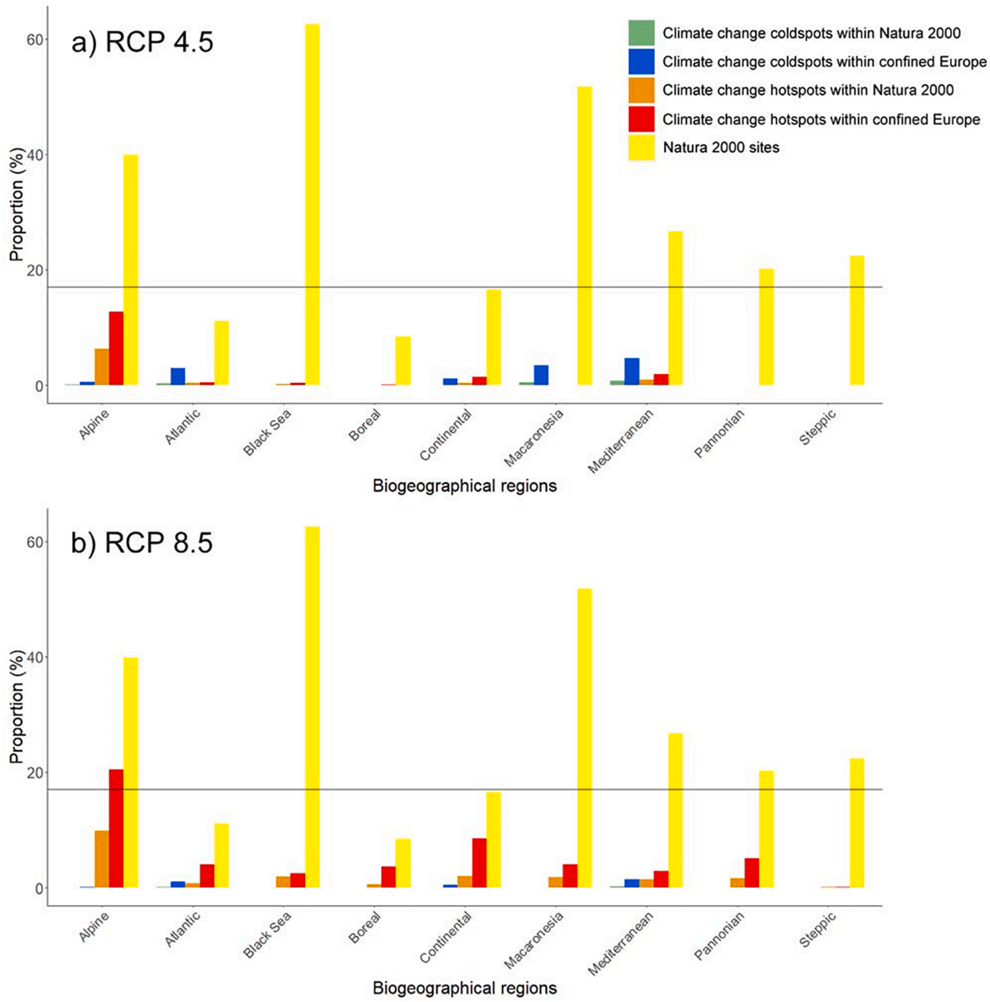

Fig. 8. Mean proportions of land area covered by climate change hotspots, coldspots, Natura 2000 sites, and priority conservation sites (i.e., hotspots and coldspots within the Natura 2000 network) across six GCMs under emission scenarios RCP 4.5 and 8.5 for the year 2070. a) Proportion of land area of confined biogeographical regions (i.e., biogeographical regions inside confined Europe) under RCP 4.5. b) Proportion of land area of confined biogeographical regions under RCP 8.5. The horizontal black lines indicate 17% corresponding to Aichi Target 11 on global protected area coverage.

dynamic impacts of climate change on biodiversity, they are expected to safeguard species and habitats in the long term. As we showed, climate change velocity was found higher inside Natura 2000 sites in more than half of the biogeographical regions. In Natura 2000 sites of these biogeographical regions, we recommend monitoring climate change impacts and to extend the network by climate change refugia. Natura 2000 is the largest protected area network on Earth, but not safe from climate change. Nevertheless, the Natura 2000 network is only one part of the EU's protected area estate (Hoffmann et al., 2018). There are more established protected areas that we did not consider here but could serve as complements to the Natura 2000 network to effectively safeguard biodiversity under climate change in Europe.

4.3. Climate change velocity-based hotspots, coldspots and priority conservation sites

By combining forward and backward velocity, we could identify areas holding both high forward and backward velocity values, i.e., climate change hotspots. In terms of proportion land area, hotspots predominantly cover the Alpine region, followed by the Continental region, which only partly conforms to our hypothesis stating high velocities in lowlands. The reason for hotspots in Alpine regions might be that particularly geographically isolated high-elevation parts of the Alpine region were identified as climate change hotspots, where climate analogs can only be found in very distant and even higher elevation mountains. High forward and backward velocity at a given location means severe climate change threat to present and potentially colonizing species, which will likely decrease local biodiversity, ecosystem functioning and services (Carroll et al., 2015, 2017; Hamann et al., 2015).

In terms of proportion land area, climate change coldspots, i.e., areas of lowest forward and backward velocity, are mostly covering biogeographical regions adjacent to the sea (Mediterranean, Atlantic, Macaronesia), which is in line with our hypothesis. Coldspots can be rather small patches scattered across topographically complex areas such as in the Mediterranean, Alpine, Anatolian, and Atlantic region. In the Alpine region, climate velocity coldspots are found in the mid-elevation zones. In contrast to the low and high-elevation zones, in the mid-elevation zone, current and future analogous climate can be found downslope and upslope, respectively. Coldspots are considered as climatic refugia, i.e., areas where current and future analogs are close by. In coldspots, less changes in local biodiversity, ecosystem functioning, and services are expected (Carroll et al., 2015, 2017; Hamann et al., 2015).

Consequently, areas that are more geographically isolated, with lower topographic complexity, and with more extreme climate conditions seem to be more exposed to climate change. Areas less geographically isolated, with higher topographic complexity and intermediate climate conditions seem to be less exposed to climate change. Low climatic diversity – that means low topographical complexity – and high geographical isolation indicate high climate change exposure (Lawrence et al., 2021). The oceanic influence might also buffer climate change exposure. These results are in line with comparable studies on the geography of climate change in Europe (De Castro et al., 2007; Ohlemüller et al., 2006) and North America (Belote et al., 2018; Carroll et al., 2015;

Dobrowski and Parks, 2016; Haight and Hammill, 2020).

Topographic complexity is associated with climate diversity, which decreases climate change velocity. Therefore, the velocity of climate change is higher in flat terrain than in mountain areas (Carroll et al., 2015, 2017; Dobrowski and Parks, 2016; Hamann et al., 2015; Loarie et al., 2009). Yet, topographical resistance for migrating species can be less in flat terrain. In steep terrain, temperature and precipitation change within a short distance. Accordingly, species may find analogous future climate within a short distance in mountain ranges. However, unlike in flat terrain where the climate trajectory tends to be a straight line (Euclidean distance), in mountainous terrain, species might need to move over or around mountains to reach their analogous future climate niche. The actual length of climate trajectories and thus climate change exposure may thus be underestimated in mountain regions (Dobrowski and Parks, 2016). However, potential movement trajectories under climate change depend not only on climate trajectories and topography, but also on land use and cover (Carroll et al., 2018; Costanza and Terando, 2019). In mountain regions, for instance, species migrating upwards from foothills and lower montane zones may even find larger habitat area that is less pressured by humans (Elsen et al., 2020b). Potential migration paths due to climate change, topography and land use change has not been investigated in terrestrial Europe and the Natura 2000 network yet.

Climate change coldspots suggest locations in which current biodiversity and ecosystem functioning will likely persist under climate change. Climate velocity hotspots suggest locations where enormous alterations of biodiversity are expected such as population declines, local extinctions, novel biotic interactions, and communities (Ordonez et al., 2016). Novel communities are generated, because organisms vary in their ability to react to climate change through adaptation, migration, and dispersal (Williams and Jackson, 2007). Novel communities, their functioning and services are barely predictable (Hobbs et al., 2006; Scheffers et al., 2016). Physiological, morphological, and behavioural changes of individuals and demographic changes of populations are likely if individuals do not migrate from hotspots (Peñuelas et al., 2013). Organisms that have low adaptation capacity and live close to their climatic tolerance limits will be most affected by climate change (Garcia et al., 2014). Under climate change, species richness and functioning of ecosystems can also increase (Kueffer and Kaiser-Bunbury, 2014; Mascaro et al., 2012).

Particularly in the Alpine region, many Natura 2000 sites overlap with climate change hotspots. In all other regions, the proportion area of Natura 2000 sites overlapping with hotspots is much lower and far from the Aichi 17% target. The deficiency of hotspots not included in the Natura 2000 network suggests biogeographical regions where conservation action is required, since biodiversity in hotspots will be prone to highest climate change velocities. The coverage of coldspots by Natura 2000 sites is even lower than for hotspots in each biogeographical region. However, establishing new protected areas at climate change coldspots is also important because these sites will likely act as climate refugia where species can find relatively constant climate conditions over time. Identifying conservation priority areas such as climate change refugia and hotspots are analogous strategies with a common purpose, to help guide climate-smart conservation planning. It is not trivial to decide whether climate change hotspots or coldspots should receive conservation priority. This decision is context dependent. The local climate change vulnerability of biodiversity is not only determined by climate change exposure. The adaptive capacity, ecological importance, resistance, and resilience of biodiversity varies, also between locations (Dawson et al., 2011; Li et al., 2018a). Climate change velocity is therefore a complement, but not a substitute for biodiversity vulnerability assessments. Climate-induced changes interact with other threats to biodiversity, e.g., habitat degradation and fragmentation (Lawrence et al., 2021b), or the spread of invasive species (Schulze et al., 2018). These threats can accumulate (Bowler et al., 2019). Subsequently, vulnerability assessments were developed to estimate climate change threat of specific biodiversity components (Foden et al., 2019). However, this specificity comes at the expense of limited generality, since only a limited amount of biodiversity components can be considered by such metrics.

Given the spatial and temporal complexity of biotic and abiotic factors determining vulnerability of biodiversity to climate change, management recommendations for individual protected areas cannot be given in this study. Climate-smart management plans should be developed in the context of individual protected areas because the climate predictions, their uncertainties, ecosystem intactness, conservation targets, the conservation capacity of land, the management resources available and the risks of management actions differ between protected areas (Hoffmann, 2021b). Conservation management is more difficult in climate velocity hotspots, all other factors being equal. Climate-smart management responses can vary from low intensity interventions, e.g., monitoring, to high intensity applications, e.g., assisted migration and restoration (Dawson et al., 2011; Gillson et al., 2013). Another climate-smart management approach is to enhance habitat connectivity to foster migration and dispersal under climate change (Heller and Zavaleta, 2009). Reducing human pressures and expanding protected area is always beneficial to biodiversity preservation. If climate change hotspots and coldspots are already protected, existing management plans can be adapted according to our findings about climate change velocity.

4.4. Limitations and further considerations

Climate change velocity is a fundamental climate change metric (Brito-Morales et al., 2018; Garcia et al., 2014). However, there are many more facets of climate change that are not reflected by climate change velocity, e.g., changes in climate extremes, seasonality, and area. To reveal the entire spectrum of potential climate change impact, future studies are required that consider multiple dimensions of climate change.

To represent complementary future climate change scenarios, the forward and backward climatic velocities were calculated for an intermediate and extreme RCP including projected climate data from six GCMs (Knutti et al., 2013). The standard deviation of the six GCMs is an indicator of the variation among climate models, which can be considered as the uncertainty of climate predictions. The predictive performance of GCMs varies in space (Bring et al., 2019). The WorldClim climate data quality decreases in regions with less climate stations such as remote mountain ranges (Hijmans et al., 2005). In our analysis, areas with high mean velocity values generally coincide with areas of high standard deviation values, i.e., with variation or uncertainty among climate models. Lowest variation among GCMs can be found at the margins of Europe, in the Mediterranean, Anatolian, Atlantic, Boreal and Arctic regions. Increasing variation can be located at inland Europe, in the Continental and Boreal regions. High variation can be found all over Europe, but particularly in the Artic, Alpine and Mediterranean regions.

User choices have been made throughout the climate velocity calculation process, including the threshold settings to create climate classes. While the relative patterns of climate change velocity do not change by different thresholds (Carroll et al., 2015; Hamann et al., 2015), the absolute climate change velocity values will change. Therefore, the absolute velocity values should not be taken for granted when comparing them to migration and dispersal rates of species. Through our sensitivity analysis we tried to balance over- and underestimation of climate change velocity. Our results thus represent intermediate velocity values.

Individual climate variables offer limited information about climatic changes in general. Hence, multiple climate variables were used in the climate velocity calculation. The application of a PCA to generate independent climate variables is to avoid collinearity between climate variables. However, the impacts of individual climate variables were not resolved although it would be useful to know which thermal and hydrological variables will change.

The nearest-neighbour search algorithm makes isolated islands, peninsulas and border areas holding higher velocity values, because isolated areas have less grid cells – and therefore analogous climate – in close vicinity (Hamann et al., 2015). To compensate this bias on the Eastern boarders of terrestrial Europe, we calculated climate change velocity for terrestrial Europe but focus on confined Europe, i.e., countries containing Natura 2000 sites.

We selected a recently revised classification of European biogeographical regions (Cervellini et al., 2018) as operational units for summarising predicted climatic changes. It should be mentioned that there are many other map products on biogeographical regions that can differ to a significant degree. While we used a map product that was originally provided by the European Environmental Agency, other biogeographical delimitations could potentially result in different biogeographical regions being most or least affected by projected climatic changes.

5. Conclusion

This study was set out to analyze the geographical distribution of climate change velocity across terrestrial Europe and the Natura 2000 network. Our straightforward approach makes this study easy to understand for conservationists and stakeholders. The study is aimed toward guiding conservation planning. A substantial proportion of terrestrial Europe and the Natura 2000 network is exposed to severe climate change. The geographical locations of identified priority conservation sites can serve as a guidance for future conservation action at the continental scale of Europe.

Enduring efforts are needed to make conservation management and protected areas climate-proof. Climate-smart conservation management is required that does not only account for predicted climate change exposure, but also for potential climate change impacts on the various components of biodiversity, from genetic diversity to ecosystem services. Moreover, these plans are urgently needed for local conservation management worldwide. Most importantly, conservation action must be taken, but since resources for nature conservation are limited, the focus on priority sites can serve as a first orientation.

CRediT authorship contribution statement

Qi Lai: Conceptualization, Methodology, Formal analysis, Software, Data curation, Visualization, Writing – original draft. **Samuel Hoffmann:** Conceptualization, Methodology, Formal analysis, Visualization, Writing – review & editing, Supervision. **Anja Jaeschke:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Carl Beierkuhnlein:** Writing – review & editing, Supervision, Funding acquisition.

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.

Acknowledgement

The study was supported by the ECOPOTENTIAL project, grant agreement No. 641762, and e-shape project, grant agreement No. 820852, both funded by EU Horizon 2020 research and innovation programme. Open access funding was enabled and organized by the Open Access Fund of the University of Bayreuth, funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 491183248.

Appendix

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108829.

References

Ameca y Juárez, E.I., Mace, G.M., Cowlishaw, G., Cornforth, W.A., Pettorelli, N., 2013. Assessing exposure to extreme climatic events for terrestrial mammals. Conserv. Lett. 6 (3), 145–153. https://doi.org/10.1111/j.1755-263X.2012.00306.x.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecol. Lett. 14 (5), 484–492. https://doi.org/10.1111/j.1461-0248.2011.01610.x.

Belote, T.R., Carroll, C., Martinuzzi, S., Michalak, J., Williams, J.W., Williamson, M.A., Aplet, G.H., 2018. Assessing agreement among alternative climate change projections to inform conservation recommendations in the contiguous United States. Sci. Rep. 8 (1), 9441. https://doi.org/10.1038/s41598-018-27721-6.

Bowler, D.E., Bjorkman, A.D., Dornelas, M., Myers-Smith, I.H., Navarro, L.M., Niamir, A., Bates, A.E., 2019. Mapping human pressures across the planet uncovers anthropogenic threat complexes. BioRxiv 432880. https://doi.org/10.1101/432880.

Bring, A., Goldenberg, R., Kalantari, Z., Prieto, C., Ma, Y., Jarsjö, J., Destouni, G., 2019. Contrasting Hydroclimatic Model-Data Agreements Over the Nordic-Arctic Region. Earth's. Future 7 (12), 1270–1282. https://doi.org/10.1029/2019EF001296.

Brito-Morales, I., García Molinos, J., Schoeman, D.S., Burrows, M.T., Poloczanska, E.S., Brown, C.J., Ferrier, S., Harwood, T.D., Klein, C.J., McDonald-Madden, E., Moore, P. J., Pandolfi, J.M., Watson, J.E.M., Wenger, A.S., Richardson, A.J., 2018. Climate velocity can inform conservation in a warming world. Trends Ecol. Evol. 33 (6), 441–457. https://doi.org/10.1016/j.tree.2018.03.009.

Carroll, C., Lawler, J.J., Roberts, D.R., Hamann, A., 2015. Biotic and climatic velocity identify contrasting areas of vulnerability to climate change. PLoS One 10 (10), e0140486. https://doi.org/10.1371/journal.pone.0140486.

Carroll, C., Parks, S.A., Dobrowski, S.Z., Roberts, D.R., 2018. Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. Glob. Change Biol. 24 (11), 5318–5331. https://doi.org/10.1111/gcb.14373.

Carroll, C., Roberts, D.R., Michalak, J.L., Lawler, J.J., Nielsen, S.E., Stralberg, D., Hamann, A., Mcrae, B.H., Wang, T., 2017. Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. Glob. Change Biol. 23 (11), 4508–4520. https://doi.org/10.1111/gcb.13679.

Cervellini, M., Zannini, P., Di Musciano, M., Fattorini, S., Jiménez-Alfaro, B., Rocchini, D., Field, R., Vetaas, O.R., Irl, S.D.H., Beierkuhnlein, C., Hoffmann, S., Fischer, J.-C., Casella, L., Angelini, P., Genovesi, P., Nascimbene, J., Chiarucci, A., 2018. A grid-based map for the biogeographical regions of Europe. Biodivers. Data J. 8 https://doi.org/10.3897/BDJ.8.e53720.

Compo, G.P., Sardeshmukh, P.D., 2009. Oceanic influences on recent continental warming. Clim. Dyn. 32 (2-3), 333–342. https://doi.org/10.1007/s00382-008-0448-9.

Costanza, J.K., Terando, A.J., 2019. Landscape connectivity planning for adaptation to future climate and land-use change. Current Landscape Ecology Reports 4 (1), 1–13. https://doi.org/10.1007/s40823-019-0035-2.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: Biodiversity conservation in a changing climate. Science 332 (6025), 53–58. https://doi.org/10.1126/science.1200303.

De Castro, M., Gallardo, C., Jylha, K., Tuomenvirta, H., 2007. The use of a climate-type classification for assessing climate change effects in Europe from an ensemble of nine regional climate models. Clim. Change 81 (SUPPL. 1), 329–341. https://doi.org/10.1007/s10584-006-9224-1.

Dobrowski, S.Z., Parks, S.A., 2016. Climate change velocity underestimates climate change exposure in mountainous regions. Nat. Commun. 7 (1), 12349. https://doi.org/10.1038/ncomms12349.

EEA. (2019). Natura 2000 data – the European network of protected sites. Retrieved from https://www.eea.europa.eu/data-and-maps/data/natura-10.

Elsen, P.R., Monahan, W.B., Dougherty, E.R., Merenlender, A.M., 2020a. Keeping pace with climate change in global terrestrial protected areas. Sci. Adv. 6 (25), eaay0814. https://doi.org/10.1126/sciadv.aay0814.

Elsen, P.R., Monahan, W.B., Merenlender, A.M., 2020b. Topography and human pressure in mountain ranges alter expected species responses to climate change. Nat. Commun. 11 (1), 1974. https://doi.org/10.1038/s41467-020-15881-x.

European Commission. (2013). Guidelines on Climate Change and Natura 2000. Dealing with the impact of climate change. On the management of the Natura 2000 Network of areas of high biodiversity value. https://doi.org/10.2779/29715.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Foden, W.B., Young, B.E., Akçakaya, H.R., Garcia, R.A., Hoffmann, A.A., Stein, B.A., Thomas, C.D., Wheatley, C.J., Bickford, D., Carr, J.A., Hole, D.G., Martin, T.G., Pacifici, M., Pearce-Higgins, J.W., Platts, P.J., Visconti, P., Watson, J.E.M., Huntley, B., 2019. Climate change vulnerability assessment of species. Wiley Interdiscip. Rev. Clim. Change 10 (1). https://doi.org/10.1002/wcc.551.

Fuentes-Castillo, T., Scherson, R.A., Marquet, P.A., Fajardo, J., Corcoran, D., Román, M. J., Pliscoff, P., Holmgren, M.(OE)., 2019. Modelling the current and future biodiversity distribution in the Chilean Mediterranean hotspot. The role of protected

areas network in a warmer future. Divers. Distrib. 25 (12), 1897–1909. https://doi.org/10.1111/ddi.12988.
García Molinos, J., Schoeman, D.S., Brown, C.J., Burrows, M.T., 2019. VoCC: An R package for calculating the velocity of climate change and related climatic metrics. Meth. Ecol. Evol. https://doi.org/10.1111/2041-210X.13295.
Garcia, R.A., Cabeza, M., Rahbek, C., Araujo, M.B., 2014. Multiple dimensions of climate change and their implications for biodiversity, 1247579 Science 344 (6183), 1247579. https://doi.org/10.1126/science.1247579.
Gaston, K.J., Jackson, S.F., Nagy, A., Cantú-Salazar, L., Johnson, M., 2008. Protected areas in Europe. Ann. N. Y. Acad. Sci. 1134 (1), 97–119. https://doi.org/10.1196/annals.1439.006.
Gillson, L., Dawson, T.P., Jack, S., McGeoch, M.A., 2013. Accommodating climate change contingencies in conservation strategy. Trends Ecol. Evol. 28 (3), 135–142. https://doi.org/10.1016/j.tree.2012.10.008.
Haight, J., Hammill, E., 2020. Protected areas as potential refugia for biodiversity under climatic change. Biol. Conserv. 241, 108258. https://doi.org/10.1016/j.biocon.2019.108258.
Hamann, A., Roberts, D.R., Barber, Q.E., Carroll, C., Nielsen, S.E., 2015. Velocity of climate change algorithms for guiding conservation and management. Glob. Change Biol. 21 (2), 997–1004. https://doi.org/10.1111/gcb.12736.
Harter, D.E.V., Irl, S.D.H., Seo, B., Steinbauer, M.J., Gillespie, R., Triantis, K.A., Fernández-Palacios, J.-M., Beierkuhnlein, C., 2015. Impacts of global climate change on the floras of oceanic islands - Projections, implications and current knowledge. Perspect. Plant Ecol. Evol. Syst. 17 (2), 160–183. https://doi.org/10.1016/j.ppees.2015.01.003.
Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biol. Conserv. 142 (1), 14–32. https://doi.org/10.1016/j.biocon.2008.10.006.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25 (15), 1965–1978.
Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P. R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob. Ecol. Biogeogr. 15 (1), 1–7. https://doi.org/10.1111/j.1466-822X.2006.00212.x.
Hoffmann, S., 2021a. Advances in conservation biogeography: towards protected area effectiveness under anthropogenic threats. Front. Biogeogr. 13 (2) https://doi.org/10.21425/F5FBG49679.
Hoffmann, S., 2021b. Challenges and opportunities of area-based conservation in reaching biodiversity and sustainability goals. Biodiv. Conser. https://doi.org/10.1007/s10531-021-02340-2.
Hoffmann, S., Beierkuhnlein, C., 2020. Climate change exposure and vulnerability of the global protected area estate from an international perspective. Divers. Distrib. 26 (11), 1496–1509. https://doi.org/10.1111/ddi.13136.
Hoffmann, S., Beierkuhnlein, C., Field, R., Provenzale, A., Chiarucci, A., 2018. Uniqueness of protected areas for conservation strategies in the European Union. Sci. Rep. 8 (1), 6445. https://doi.org/10.1038/s41598-018-24390-3.
Hoffmann, S., Irl, S.D.H., Beierkuhnlein, C., 2019. Predicted climate shifts within terrestrial protected areas worldwide. Nat. Commun. 10 (1), 4787. https://doi.org/10.1038/s41467-019-12603-w.
Hole, D.G., Huntley, B., Arinaitwe, J., Butchart, S.H.M., Collingham, Y.C., Fishpool, L.D. C., Willis, S.G., 2011. Toward a management framework for networks of protected areas in the face of climate change. Conserv. Biol. 25 (2), 305–315. https://doi.org/10.1111/j.1523-1739.2010.01633.x.
Holsinger, L., Parks, S.A., Parisien, M., Miller, C., Batllori, E., Moritz, M.A., 2019. Climate change likely to reshape vegetation in North America's largest protected areas. Conserv. Sci. Pract. 1 (7), e50 https://doi.org/10.1111/csp2.50.
Knutti, R., Masson, D., Gettelman, A., 2013. Climate model genealogy: Generation CMIP5 and how we got there. Geophys. Res. Lett. 40 (6), 1194–1199. https://doi.org/10.1002/grl.50256.
Kueffer, C., Kaiser-Bunbury, C.N., 2014. Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. Front. Ecol. Environ. 12 (2), 131–137. https://doi.org/10.1890/120201.
Laurance, W.F., Koster, H., Grooten, M., Anderson, A.B., Zuidema, P.A., Zwick, S., Zagt, R.J., Lynam, A.J., Linkie, M., Anten, N.P.R., 2012. Making conservation research more relevant for conservation practitioners. Biol. Conserv. 153, 164–168. https://doi.org/10.1016/j.biocon.2012.05.012.
Lawrence, A., Hoffmann, S., Beierkuhnlein, C., 2021a. Topographic diversity as an indicator for resilience of terrestrial protected areas against climate change. Global Ecol. Conserv. 25, e01445. https://doi.org/10.1016/j.gecco.2020.e01445.
Lawrence, A., Friedrich, F., Beierkuhnlein, C., 2021b. Landscape fragmentation of the Natura 2000 network and its surrounding areas. PLoS One 16 (10), e0258615. https://doi.org/10.1371/journal.pone.0258615.
Li, D., Wu, S., Liu, L., Zhang, Y., Li, S., 2018a. Vulnerability of the global terrestrial ecosystems to climate change. Glob. Change Biol. 24 (9), 4095–4106. https://doi.org/10.1111/gcb.14327.
Li, Q., Kou, X., Beierkuhnlein, C., Liu, S., Ge, J., 2018b. Global patterns of non-analogous climates in the past and future derived from thermal and hydraulic factors. Glob. Change Biol. 24 (6), 2463–2475. https://doi.org/10.1111/gcb.14104.
Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. Nature 462 (7276), 1052–1055. https://doi.org/10.1038/nature08649.
Mascaro, J., Hughes, R.F., Schnitzer, S.A., 2012. Novel forests maintain ecosystem processes after the decline of native tree species. Ecol. Monogr. 82 (2), 221–228. https://doi.org/10.1890/11-1014.1.
Mazaris, A.D., Papanikolaou, A.D., Barbet-Massin, M., Kallimanis, A.S., Jiguet, F., Schmeller, D.S., Pantis, J.D., Hérault, B., 2013. Evaluating the connectivity of a protected areas' network under the prism of global change: The efficiency of the European Natura 2000 network for four birds of prey. PLoS ONE 8 (3), e59640. https://doi.org/10.1371/journal.pone.0059640.
Nila, M.U.S., Beierkuhnlein, C., Jaeschke, A., Hoffmann, S., Hossain, M.L., 2019. Predicting the effectiveness of protected areas of Natura 2000 under climate change. Ecol. Process. 8 (1), 13. https://doi.org/10.1186/s13717-019-0168-6.
Ohlemüller, R., Gritti, E.S., Sykes, M.T., Thomas, C.D., 2006. Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100. Glob. Ecol. Biogeogr. 15 (4), 395–405. https://doi.org/10.1111/j.1466-822X.2006.00245.x.
Ordonez, A., Williams, J.W., Svenning, J.-C., 2016. Mapping climatic mechanisms likely to favour the emergence of novel communities. Nat. Clim. Change 6 (12), 1104–1109. https://doi.org/10.1038/nclimate3127.
Orlikowska, E.H., Roberge, J.M., Blicharska, M., Mikusiński, G., 2016. Gaps in ecological research on the world's largest internationally coordinated network of protected areas: A review of Natura 2000. Biol. Conserv. 200, 216–227. https://doi.org/10.1016/j.biocon.2016.06.015.
Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A., Rivas-Ubach, A., Llusià, J., Garbulsky, M., Filella, I., Jump, A.S., 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. Glob. Change Biol. 19 (8), 2303–2338. https://doi.org/10.1111/gcb.12143.
Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R. T., Butchart, S.H.M., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W.B., Martin, T.G., Mora, C., Bickford, D., Watson, J.E.M., 2016. The broad footprint of climate change from genes to biomes to people. Science 354 (6313).
Schulze, K., Knights, K., Coad, L., Geldmann, J., Leverington, F., Eassom, A., Marr, M., Butchart, S.H.M., Hockings, M., Burgess, N.D., 2018. An assessment of threats to terrestrial protected areas. Conserv. Lett. 11 (3) https://doi.org/10.1111/conl.12435.
Sutton, R.T., Dong, B., Gregory, J.M., 2007. Land/sea warming ratio in response to climate change: IPCC AR4 model results and comparison with observations. Geophys. Res. Lett. 34 (2), L02701. https://doi.org/10.1029/2006GL028164.
Thomas, C.D., Gillingham, P.K., 2015. The performance of protected areas for biodiversity under climate change. Biol. J. Linn. Soc. 115 (3), 718–730. https://doi.org/10.1111/bij.12510.
van Teeffelen, A., Meller, L., van Minnen, J., Vermaat, J., Cabeza, M., 2015. How climate proof is the European Union's biodiversity policy? Reg. Environ. Change 15 (6), 997–1010. https://doi.org/10.1007/s10113-014-0647-3.
Velazco, S.J.E., Villalobos, F., Galvão, F., De Marco Júnior, P., Serra-Diaz, J., 2019. A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. Divers. Distrib. 25 (4), 660–673. https://doi.org/10.1111/ddi.12886.
Walls, S.C., Barichivich, W.J., Chandler, J., Meade, A.M., Milinichik, M., O'Donnell, K. M., Owens, M.E., Peacock, T., Reinman, J., Watling, R.C., Wetsch, O.E., 2019. Seeking shelter from the storm: Conservation and management of imperiled species in a changing climate. Ecol. Evol. 9 (12), 7122–7133. https://doi.org/10.1002/ece3.5277.
Walther, G.R., 2010. Community and ecosystem responses to recent climate change. Philos. Trans. R. Soc. B: Biol. Sci. 365 (1549), 2019–2024. https://doi.org/10.1098/rstb.2010.0021.
Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5 (9), 475–482. https://doi.org/10.1890/070037.
Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., Moritz, C., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol. 6 (12), e325. https://doi.org/10.1371/journal.pbio.0060325.