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**Fine-scale variation in projected climate change presents opportunities for
biodiversity conservation in Europe**

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Fine-scale variation in projected climate change presents opportunities for biodiversity conservation in Europe

Abstract

Climate change is a major threat to global biodiversity, although projected changes show remarkable geographical and temporal variability. Understanding this variability allows for the identification of regions where the present-day conservation objectives may be at risk or where opportunities for biodiversity conservation emerge. We use a multi-model ensemble of regional climate models to identify areas with significantly high and low climate stability persistent throughout the 21st century in Europe. We then confront our predictions with the land coverage of three prominent biodiversity conservation initiatives at two scales. The continental-scale assessment shows that the most instable future climate in Europe is likely to occur at low and high latitudes, with the Iberian Peninsula and the Boreal zones identified as prominent areas of climatic instability. A follow-up regional scale investigation shows that robust climatic refugia exist even within the highly exposed southern and northern macro-regions. About 23-31 % of assessed biodiversity conservation sites in Europe coincide with these identified climatic refugia, we contend that these sites should be prioritised in the formulation of future conservation priorities as the stability of future climate is one of key factors determining their conservation prospects. Although such focus on climate refugia cannot halt the ongoing biodiversity loss, along with measures such as the resilience-based stewardship, it may improve the effectiveness of biodiversity conservation under climate change.

Key words: climate change, climatic stability, biodiversity conservation, adaptive conservation strategy

Introduction

Rapid climate change induced by human activity is already changing the environmental niche of a great number of species^{1,2}. Current commitments under the Paris COP21 agreement are unlikely to keep planetary warming below 2°C considered safe, plus several feedback mechanisms and climate tipping points threaten to exacerbate it further³. Climate change is thus one of the key threats to biodiversity at all levels; from genes to biomes⁴. On the one hand, effects of climate change range from local extinctions of species with narrow ecological niches, to profound ecosystem change at the trailing edge of the shifting climatic envelope⁵. On the other hand, we already see increased species richness in areas acting as refugia and effects such as the Northern Biodiversity Paradox⁶. Recent observations from Europe show a significant decrease in mountain species richness in the Mediterranean and a concurrent increase in the boreal–temperate zone⁷. Climatic processes driving these changes include the emergence of novel climates, rapid displacement of climatic isoclines or the divergence of temperature and precipitation vectors⁸, all resulting in significant niche shifts affecting species distribution.

Species extinctions and migration are likely to generate novel communities and thus challenge the contemporary conservation planning framework⁹, which relies on a fixed system of protected areas and conservation goals. Rapid climate change highlights the need for accommodating transient ecosystem dynamics into conservation planning^{9,10}, yet practical implementation of climate change adaptation into conservation management is still rare¹¹. Recent climate-adapted conservation concepts include an evaluation of species vulnerability by empirical niche models¹², use of climatic refugia to shelter species of conservation concern¹³, or the implementation of resilience-oriented ecosystem management¹⁴. Moreover, a broader shift in governance structures and improved coordination between land managers, politicians and conservation organisations appears critical to the implementation of adaptive biodiversity conservation¹⁵. To date, the theoretical understanding of these approaches, their trade-offs and interactions is not sufficiently advanced to support the formulation of robust and consistent conservation policies.

In Europe, Key Biodiversity Areas (KBA;¹⁶), Natura 2000 habitat network¹⁷ and European Primary Forests (EPF;¹⁸) represent examples of biodiversity conservation initiatives focused on preserving geographically well-defined areas of interest. Under climate change, some of these areas, and associated conservation goals, may be subject to greater climatic exposure than others. At the same time, conservation opportunities may emerge elsewhere due to future spatial or temporal variation of climate change effects. Focusing on areas with predicted stable climate,

relative to background climate change, is increasingly recognised as a viable conservation strategy¹⁹⁻²¹. Such climatic refugia are evident at multiple spatial scales, from small-scale poleward-facing slopes, sites affected by cold groundwater or deep snow drifts²², to the continental-scale refugia such as the Boreal zone in Europe⁶. Vital lessons about species migration and persistence in climatic refugia during glacial and interglacial periods may be applicable to present-day conservation effort¹⁹, if future climate can be resolved at appropriate scale. Climate models, which have an increasing ability to resolve the fine-scale atmospheric processes relevant for local and regional resource management and conservation planning, have thus become the central means for formulating the forward-looking adaptation policies²³.

We investigate how future climate change may affect present-day nature conservation initiatives in Europe by considering spatial coverage and temporal persistence of regions with significantly low or high climatic stability. This information may be vital for the transition from current static conservation framework to climate-adapted conservation strategies²⁴, deemed necessary to avoid the imminent biodiversity breakdown. At continental and regional scales, we confront climatic stability patterns with established biodiversity conservation initiatives, ranging in size from the Global Biodiversity Hotspots to small patches of primary forests. Representing the diversity of spatial scales at which atmospheric and biological processes operate²⁵, we (i) evaluate the patterns of projected climatic stability in Europe at two scales; (ii) indicate some of the existing biodiversity conservation sites initiatives as those at high or low risk of climatic instability, and (iii) discuss how identification of such sites can inform the formation of a climate-adapted biodiversity conservation strategy for Europe.

Results

Climatic instability

Our analysis of future climatic instability centres on projected changes of nine climate variables, selected to proxy key aspects of terrestrial ecosystem dynamics (Table 1). The cumulative change of all climate variables, termed Aggregate Climate Change (ACC), is used to identify regions of significantly high or low climatic stability (Getis-Ord G_i^* p -value < 0.05) across Europe, the former category typically referred to as climatic refugia. We carry out this assessment at the continental and regional scales by considering two RCP scenarios (RCP4.5 and RCP8.5) as drivers for five regional climate models (Table S1).

1. Continental-scale assessment

At this scale, the future climate variation in Europe displays a distinct latitudinal pattern. This pattern is robust and consistent across all three time periods and both RCP scenarios modelled in this study (Fig. 1). Temporal stability of climatic features and inter-model agreement were poorer at higher latitudes than in the rest of Europe (Fig. S4–S5). The Central Zone (CZ) with the most stable future climate is located across the centre of Europe (ca 45° – 55° N) and covers most of the Atlantic, Continental and Steppic biogeographical zones (Fig. S2). The Northern and the Southern Zones located at high and low latitudes of Europe are characterised by significantly instable future climate (NZ and SZ, respectively). The SZ extends over the Mediterranean and Anatolia, while the NZ takes in the Boreal and the Arctic regions.

Figure 1 Predicted zones with instable (red) and stable (blue) climate in Europe, relative to continental background climate change. Indication of climate stability zones during three separate time periods (a-c) and those persisting throughout the predicted time period 2041-2100 (d-e).

The magnitude of ACC, as well as the specific local combination of individual variable changes, form a unique climatic setting for each of the major zones and their subzones (Fig. S1 and Table S3). The magnitude of ACC in the CZ is more than 20% smaller than that predicted for the NZ or the SZ, and reaches 51-55 % of the maximum permissible change (i.e. change that would occur if the largest changes in all underlying climate variables predicted across Europe were to culminate in the same location). Looking at zones of instability predicted under RCP 8.5, the most distinct features of the NZ are increased precipitation (+95%), shorter dry periods (-9 days) and longer frost-free periods (+80 days, Table S3). The most striking climate features driving the instability in the SZ are a severe decrease of precipitation (-62 to 98%) and an accompanying increase of the Ellenberg climate quotient (+21 to 23 mm °C⁻¹).

2. Regional-scale assessment

After the extraction of the continental-scale trend, the residual variation of ACC (Fig. S3) indicates regionally relevant zones against the background of a block approximately 100 x 100 km, with minor differences in its size between climate projections and time periods. Regional-scale variation of ACC creates a mosaic of areas distributed all over Europe (Fig. 2). In contrast to the continental scale, the regional climatic features show poorer temporal stability and inter-RCP agreement (Fig. S4–S5). However, a number of areas characterised by residual ACC significantly different from background persist throughout the 21st century under the most conservative assessment (areas identified by four out of five RMS in each RCP, Fig. 2d-e and Table S3). Areas of persistently low residual ACC are henceforth interpreted as potential climatic refugia and we investigate their overlap with existing biodiversity conservation initiatives.

At this scale, the most distinct regional instability areas are located within the SZ (Fig. 1), emphasising the high regional variability of ACC in the Mediterranean. Looking at the central band identified as stable at the continental scale (CZ, Fig. 1), Eastern Alps and parts of Norway now show up as areas with regionally significantly instable climate. Crucially, areas with low and high climatic stability are often adjacent to each other, e.g. seashore to inland transitions or elevation differences in mountain ranges, generating rather unique pattern of climatic exposure potentially complicating the conservation effort.

Figure 2 Predicted zones with instable (red) and stable (blue) climate in Europe, relative to regional background climate change. Indication of climate stability zones during three separate time periods (a-c) and those persisting throughout the predicted time period 2041-2100 (d-e).

Spatial coincidence of conservation priorities and climate instability

To consider long-term implication of here identified patterns of low and high climatic stability for conservation efforts in Europe, in this section we confront the prominent biodiversity conservation networks in Europe (Fig. 3, Fig. S2) with continental and regional areas of climate (in)stability persisting between 2040 and 2100 (Fig. 1d-e and 2d-e).

Figure 3 Geographical coverage of investigated biodiversity sites classified as belonging to area of regionally significantly instable (red) or stable (blue) future climate as predicted under RCP 4.5 or RCP 8.5.

Modelling based on both RCP scenarios at the continental scale indicates a high probability of significant **northern zone** of climatic instability covering northern Finland and Karelia (Fig. 1). This trend represents a clear threat to Natura 2000 and KBA areas present in northern Finland. Currently only one forest has been identified as EPF in the country, not allowing us to draw conclusions in relation to this network. Looking at the predictions analysed at regional scale, it is possible to identify several current biodiversity sites likely to fall under a more stable future climate conditions than others (Fig. 3 and 4). Specifically, our data indicate that Natura 2000 and KBA sites in central Norway are significantly less exposed than those straddling the border between Norway and Finland.

Our continental-scale assessment shows that the **central zone** area of Europe stretching from the British Isles in the west to the Ukrainian steppe in the east is likely to experience significantly weaker climate change than the rest of the continent (Table S3). Regional-scale assessment shows that the greatest share of the KBA extent predicted to be in climatically instable areas is in the Pannonian, Steppic, Mediterranean and the Anatolian zones. The above-average share of the KBA sites in the climatically stable sites is in the Alpine North and Atlantic

zones, and Arctic and the Black Sea zones; in the latter two zones, however, the total area of the KBA sites is only minor (Fig. 4). The Alpine zone includes 119 out of the total of 257 primary forests in Europe, a continental-scale assessment shows that 100% of these are in a climatically instable zone. However, the finer-scale modelling shows that only 11% of these sites are threatened by significantly instable climate at regional scale.

The **southern zone** shows the highest climatic instability in Europe at the continental scale and largely overlaps with Europe's prominent global biodiversity hotspot – the Mediterranean Basin. It also covers the entire European parts of the Irano-Anatolian and the Caucasus zones (Fig. S6). The SZ thus affects all global biodiversity sub-hotspots embedded within the Mediterranean Basin: the Rif-Betique range, Maritime and Ligurian Alps, Tyrrhenian Islands, southern and central Greece, Crete, southern Turkey and Cyprus ²⁶. The model prediction at this scale thus delivers a very bleak message for biodiversity conservation sites in and around the Med.

Fig. 4 The proportion of Natura 2000 (a), Key Biodiversity Areas (b) and European primary forests (c) present in areas identified as climatically stable or instable relative to background climate change at continental scale (bars). Pie charts indicate the fraction of the three biodiversity initiatives in stable or instable areas at regional-scale embedded within the continent-scale pattern. Values in pie charts show area of Natura2000 and KBA sites (mil. of ha), or the number of EPF in each climate stability category. Climatic stability as predicted under RCP4.5 or RCP8.5 and persisting throughout 2041-2100.

The regional scale prediction, however, may offer some guidance. The most conservative prediction of regional-scale climate instability (the overlap between both RCPs) shows that it is the areas in the interior of Iberia, in southern Italy and away from the coasts of Turkey that are exposed the most (Figure 3). Interestingly, when comparing the indication of effects of

climate stability on biodiversity initiatives between the two scales, around 25-30% of areas indicated as under instable climate at the continental scale are confirmed as such by the regional assessment (Fig. 4). The same is not true for areas under stable climate. The ratio of Natura 2000 sites distributed in climatically instable areas is the least favourable in the Alpine North, Pannonian, Steppic and in the Mediterranean zones (Fig. S7). In these zones, the proportion of sites in climatically instable areas significantly exceeds the Europe-wide average, while the percentage of sites in climatically stable areas is average to below-average.

Discussion

Accelerating loss of biodiversity caused by climate change and other anthropogenic factors^{27,28} has highlighted the vulnerability of current conservation effort which historically did not take account of projected climate change⁹. Some areas of high biodiversity value in Europe are under increasing threat²⁹, the development of their conservation strategies requiring location-specific information on future viability³⁰. Emerging capability of climate models to identify macro-refugial features within the landscape³¹ and downscaled climate models to identify microclimatic refugia¹³ illustrates the potential of confronting conservation planning with climate stability. Whilst the conservation of biodiversity and its planning is clearly important at the global scale^{32,33}, most species are composed of local populations, the survival of which is driven by local climate and environment variation³⁴.

Continental scale

According to our continental-scale predictions for Europe, the most stable climate will persist in the Atlantic and Temperate zones, whilst the Mediterranean and the Boreal zones may be exposed to the least stable climate (Figure 1), confirming existing global or continental climatic assessments^{35,36}. Climatic changes indicating the onset of predicted trends have already been recorded, both in the Med and in the Boreal zone³⁷, with corresponding changes in biodiversity⁷. Although large-scale trends of climatic instability found in our study are unambiguous, matching them with a targeted effort to conserve biodiversity is fraught with difficulty. European regions such as the Med or Scandinavia are known to contain a range of diverse ecosystems, a result of the current climatic sub-zonation and a history of species migration driven by the glacial cycles.

European glacial maxima are typical for the prevalence of southern macrorefugia (The Med), while glacial minima lead to a build-up of biodiversity in the north (currently the Northern Biodiversity paradox⁶). Human-induced climate change resembles a shift to an interglacial period, typical for the presence of microrefugia in the south and a large area of increasing

species diversity in the north. The results of modelling studies correspond to this scaling of effects driven by the glacial cycles: continental-scale predictions might be relevant for some parts of the continent, while finer-scale climate patterns may drive biodiversity patterns in others. The key difference with past glacial minima is that European species now migrate across a very fragmented landscape and have to do so at increasing speed ³⁸.

Regional scale

Land-use zonation and associated ecosystem typology is well established in Europe and historically ingrained in the landscape. Within this context, areas of high conservation value are historically demarcated, but this does not necessarily reflect their ability to allow species to persist during future periods of unfavourable climate ³⁹. A large-scale climate change pattern may inform strategic conservation planning but may not be practical for informing nature conservation in Europe, where species are likely to have diminished capacity to respond by migration ⁴⁰. Conversely, protected areas are known to facilitate range shifts ⁴¹. We found that while most of the smaller-scale patterns of future climatic stability variation were ephemeral, some showed high temporal persistence and were consistently identified in the majority of climate projections. We suggest that such robust features should be factored into conservation planning and could be used for strategic positioning of conservation efforts. We also found that such smaller scale refugia exist even within the climatically highly exposed Mediterranean and Boreal macro-regions, providing a new perspective on biodiversity conservation there. Climate is not the only environmental factor affecting species distribution ⁴², the finer the scale of climate instability indication, the closer it comes to corresponding with the spatial representation of other factors such as land use, soils or topography ^{13,43}.

Implications for biodiversity conservation

Areas of high biodiversity value in Europe are under increasing threat ²⁹, location-specific information on their future viability is of critical importance ³⁰. We found that the three prominent European biodiversity initiatives considered here overlap with areas potentially serving as climate refugia to a different degree, with large geographical differences. For example, EPF typically are small remnants of natural vegetation, a number of which are found in the stable CZ at continental scale and some are within regional climate refugia. Our analysis suggests that these forests could be the target of priority protection due to better future prospects than other locations. In contrast, Natura2000 and KBA sites tend to have larger land coverage and be actively managed. Here, the indication of future climate stability can be used to plan *in-situ* conservation (e.g. measures to reduce risk and foster resilience), or even *ex-situ* conservation by expanding existing areas into neighbouring climate refugia ⁴⁴.

A different approach may be needed in areas of high conservation value located in predicted areas of low climatic stability. Following an assessment of climate risk for a species or a habitat (see future work below), a revision of the current conservation framework may include abandoning the conservation effort on sites where the prospects of future stability are poor, potentially deploy active measures to their restructuring and adaptation⁴⁵. A more detailed analysis of future climate stability and current conservation efforts would indicate areas potentially serving as climatic refugia across Europe. A potentially useful outcome could be a mosaic of areas with relatively stable future climate to serve as refugia or steppingstones aiding migration.

The provision of spatially explicit information on climatic exposure, such as that presented in this paper, is an effective tool for communicating the link between climate change and biodiversity to various actors⁴⁶. Identification of areas which are the most exposed to future climate change may then stimulate vulnerability studies and aid the targeting of adaptation effort and investment⁴⁷. Our analysis indicates the locations of conservation initiatives at risk and illustrates how ecosystems within a specific region may be better placed to withstand climate change than others. Zones with well-established land use and development processes, such as most of Europe, may use regional climate stability maps to move towards adaptive biodiversity conservation strategy by creating rules and interventions triggered when pre-determined climatic conditions are reached⁴⁸ or to guide current continental-scale re-naturalisation efforts⁴⁹. Regional climate stability information could then be overlaid with habitat maps to identify priority species or habitats.

Limitations and future work

The foremost area of improvement is the use of a limited number of RCP and model runs – the use of a wider ensemble might offer better robustness of predictions. The usefulness of our findings remains limited by the resolution and level of process detail of current RCMs, anticipated transition to convection-permitting modelling systems³¹ could be a breakthrough to detailed refugia mapping. We used an arbitrary threshold of 30% to assess residual variation of ACC, this value can be dynamically adjusted to address different social or ecological aspects. In addition, performing a sensitivity analysis of individual climate variables and their effect on ACC might improve prediction accuracy. The three biodiversity initiatives used as examples in this study are disparate in that some locations of interest are delineated as areas (KBA, Natura 2000), while others are just points (EPF), limiting the comparability of results (Table S2). In addition, the initiatives use different criteria for the identification of an area as important for biodiversity, including all three (or more) in a common assessment might thus approximate a

best-case scenario. Climate modelling needs to be joined with species distribution modelling (SDM) to better represent actual effects on biodiversity. For example, species are able to migrate at different speed or differ in their capacity to persist in-situ or ex-situ, both factors that can be assessed by SDM⁵⁰.

Conclusion

In this study, we provide a climatological assessment of the persistence of stable or instable climate in Europe throughout the 21st century. We show how this type of predictive modelling can be used to inform biodiversity conservation initiatives. We argue that the distribution of future climatic refugia should be considered in the formation of dynamic climate-adapted biodiversity conservation frameworks, for example via the strategic positioning of new sites across the landscape. We highlight the high spatial variability of future climate stability across Europe, presenting different level of risk to and opportunities for the present-day conservation objectives.

Methodology

1. Biodiversity indicators

We used the distribution of global biodiversity hotspots extending into Europe as an indicator of continental-scale biodiversity value of an area. Here, global hotspots are chiefly represented by the Mediterranean basin (MB), with small incursions from the Irano-Anatolian (IA) and Caucasus (CA) hotspots²⁶. To carry out a regional-scale analysis, we use data from three initiatives describing areas of high current biodiversity value in Europe (Fig. S2): Key Biodiversity Areas (KBA; ¹⁶), Natura 2000 habitat network¹⁷ and European Primary Forests (EPF; ¹⁸). Each initiative uses different criteria for site selection, these can be summarised as:

(1) **KBA** are sites holding biodiversity elements that are globally restricted, or at risk of disappearing. KBA selection criteria integrate evaluation of biodiversity at genetic, species and ecosystem levels. The KBA approach aims to support the identification of sites important for elements of biodiversity not considered in existing approaches. The KBA database builds on previous efforts and includes subsets of biodiversity such as birds, fungi, higher plants or butterflies.

(2) **Natura 2000** is one of the tools delivering EU Biodiversity Strategy, which aims to halt the loss of biodiversity and ecosystem services on its territory. Natura 2000 is a network of core breeding and resting sites, plus some rare natural habitat types. The aim of the network is to

ensure the long-term survival of Europe's most valuable and threatened species and habitats, listed under both the Birds Directive and the Habitats Directive. Natura 2000 covers both land and sea ecosystems, however this study focuses on terrestrial habitats only.

(3) **EPF** is the most comprehensive ground-truthed database of currently known naturally regenerated forests of native species in Europe, with no clearly visible signs of past human activity or significant disturbance of ecological processes. Excluding Russia, large patches of primary forest no longer exist in Europe, this database thus includes forests previously classified as primeval, virgin, near-virgin, old-growth and long-untouched, where empirical evidence suggests absence of direct human impact for at least 200 years.

2. Climate data

A reference climate covering the period 1961-1990 was calculated from the high-resolution gridded dataset E-OBS ⁵¹. We used the E-OBS 15.0 on $0.25^{\circ} \times 0.25^{\circ}$ grid, the most recent version of the database available at the time of the current study (December 2018). The dataset was constructed by interpolation of ECA&D ⁵² and contained daily minimum, maximum, mean temperature, precipitation, and sea level pressure time series.

We considered nine candidate bias-corrected regional climate models (RCM) for Europe, accessible in the EURO-CORDEX database and covering the period 1951–2100. We selected five climate models results, representing all combinations of global and regional climate models included in the original dataset (Table S1; see ⁵³ for more details on the selection criteria). The models were driven by two Representative Concentration Pathway scenarios: RCP4.5 and RCP8.5 ⁵⁴, giving us 10 climate projections in total (5 RCMs $\times$ 2 RCPs). The data covered the EUR-11 domain of the EURO-CORDEX project with $0.11^{\circ} \times 0.11^{\circ}$ horizontal resolution ⁵⁵. All selected simulations were bias-corrected using the distribution scaling method developed by the Swedish Meteorological and Hydrological Institute (SMHI-DBS45). We investigated three future time periods – 2041-2060, 2061-2080 and 2081-2100.

We initially considered 23 climate variables as indicators of the degree of future climate stability, the list of variables was refined by inspecting their correlation matrix for redundancy. Delta predictor (predicted future values minus reference value) was used to generate the correlation matrix to correspond with further analysis of climate instability which is based solely on differences between climate periods. Pearson coefficient >0.7 was used to discard one variable out of each pair of correlated variables (see Dormann et al. ⁵⁶ for rationale). Table 1 lists the final set of variables used in this study.

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Table 1. Climate variables used as predictors of future climate stability, all calculated on annual basis (T – temperature, Pr – precipitation, MCMT - mean coldest month temperature).

ID	Abbreviation	Description	Units	Calculation
1	MWMT	Mean warmest month temperature	°C	$MWMT = \max(T_{mon.mean})$
2	DDa5	Degree-days above 5°C	°C	$DDa5 = \sum_{day} \begin{cases} T - 5^{\circ}C, & T > 5^{\circ}C \\ 0^{\circ}C, & T < 5^{\circ}C \end{cases}$
3	FFP	Longest frost-free period	Days	The length of the longest period of consecutive days with daily minimum temperature above 0°C.
4	EQ	Ellenberg climatic quotient	°C mm ⁻¹	$EQ = \frac{MWMT}{Pr_{ann}} * 1000$
5	Cont	Gorczynski climatic continentality	—	$Cont = \left(1.7 * \frac{MWMT - MCMT}{\sin \varphi}\right) - 20.4$
6	NDP	Number of dry periods	—	$DryDay = \begin{cases} 1, & Pr < 5\text{ mm} \\ 0, & Pr > 5\text{ mm} \end{cases}$ <i>DryPeriod</i> : period of at least 10 consecutive DryDays <i>numDryPeriods</i> : the number of DryPeriods
7	LLDP	Length of the longest dry period	Days	Number of dry days of the longest <i>DryPeriod</i> .
8	T	Annual mean temperature	°C	Average of daily mean temperatures
9	P	Annual total precipitation	mm	Sum of daily precipitations

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3. Assessment of future climatic stability

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We identified areas with climatic stability significantly different from their surroundings⁵⁷ as follows: (i) for each grid cell in climate maps, we calculated Euclidean distance between past and future climates in an n-dimensional space defined by a set of climate variables to produce a continuous map of Aggregate Climate Change (ACC); (ii) we used the resulting ACC map to identify areas with significantly low and high climatic stability using the Getis-Ord Gi* statistics; (iii), we then subtracted the continent-wide trend from the ACC data to create a residual ACC map, and inspected it using Getis-Ord Gi* to uncover regional areas with contrasting climatic stability. This analysis was conducted for all climate projections and time periods, partial results were then aggregated to identify the most robust and temporally stable areas with low (refugia) and high (hotspots) climatic stability.

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3.1 Calculation of Aggregate Climate Change

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We first calculated Standard Euclidean Distance (SED,⁵⁸) to characterise ACC between present and future periods in a n-dimensional climate space:

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$$ACC = \sqrt{\left(\sum_{i=1}^n SED_v\right)}$$

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[1]

390 SED for the variable v is defined as:

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$$SED_v = (\Delta_v / \max[|\Delta_v|]_{xy})^2 \quad [2]$$

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where (Δ_v) is the change in climate variable v at each grid point between two time periods, and $\max[|\Delta_v|]_{xy}$ is the maximum value of the change in variable v over the entire study area. In our study, Δ_v is calculated for each pixel and each variable as the difference between a future period (2021-2040, 2041-2060 and 2061-2100) and the reference period (1961-1990). This analysis was conducted separately for 10 climate projections and 3 future time periods (i.e. 30 ACC maps were produced).

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To prevent the undesired effect of using $\max[|\Delta_v|]_{xy}$ to standardize the Δ_v , which can be affected by a single extreme value, we used the 95 % quantile instead:

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$$SED_v = (\Delta_v / Q_{95}[|\Delta_v|]_{xy})^2 \quad \left\{ \begin{array}{l} \text{if } SED_v > 1 \text{ then } SED_v = 1 \\ \text{if } SED_v < 1 \text{ then } SED_v = SED_v \end{array} \right\} \quad [3]$$

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Raw ACC values were expressed as percentage of the maximum permissible change to improve the clarity and interpretation of the assessment. The maximum change is defined as square root of the number of variables used for the ACC calculation ($n=9$ in this study):

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$$ACC_{\%} = \frac{ACC}{\sqrt{n}} * 100 \quad [4]$$

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While this type of ACC calculation may inform on large-scale patterns of climatic exposure relevant at the continental scale, it may obscure small-scale patterns of regional importance. We also carried out a regional scale study where patterns of climatic stability are identified from residual ACC% (rACC%) generated by subtracting the continental-scale trend from raw ACC% values. Europe-wide spatial trend to be subtracted from the ACC% was defined using the following generalized additive model:

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$$ACC_{\%} = \alpha + f(Lat, Long) + \varepsilon \quad [5]$$

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where f is the spline-on-the-sphere basis function⁵⁹, Lat is latitude and $Long$ is longitude in degrees, α is the intercept and ε is the error term.

Due to unequal goodness of fit to 30 ACC surfaces, we did not use the estimation of function parameters based on the automatized penalization procedure as it would hamper their comparison. Instead, we iteratively searched for the parameter k (number of knots of the spline) to reach 70 % fit of the function to the data in all ACCs, with a minor tolerance. All calculations were conducted in R 342 v.3.3.2⁶⁰ using the mgcv v. 1.8-23 library⁶¹.

3.2 Getis-Ord G_i^* statistics

We used a rigorous approach based on the Getis-Ord G_i^* statistics to identify discreet zones with significantly low and high climate stability both at continental (based on the original ACC) and regional (based on the residual ACC) scales. The procedure was developed to evaluate spatial data for clustering of high and low values, often referred to as hotspots and coldspots of a given phenomenon⁶². The procedure evaluates whether the sum of values surrounding each feature (grid-cell in the current study) differs significantly from the sum calculated for the spatial domain under investigation.

$$G_i^* = \frac{\sum_{j=1}^n w_{i,j} x_j - \bar{X} \sum_{j=1}^n w_{i,j}}{S \sqrt{\frac{[n \sum_{j=1}^n w_{i,j}^2 - (\sum_{j=1}^n w_{i,j})^2]}{n-1}}} \quad [6]$$

Where x_j is the ACC value for the grid-cell j , $w_{i,j}$ is the weight between grid-cells i and j , and n is the total number of grid-cells in the investigated spatial domain. $\bar{X}$ and S are calculated as:

$$\bar{X} = \frac{\sum_{j=1}^n x_j}{n} \quad [7]$$

$$S = \sqrt{\frac{\sum_{j=1}^n x_j^2}{n} - (\bar{X})^2} \quad [8]$$

$w_{i,j}$ is calculated on the basis of the conceptualized spatial relationship between samples. We used an inverse distance weighting to attach a larger influence to grid cells nearer to the target grid-cell compared to more distant grid-cells. This procedure generates z -values and thus allows for testing of the statistical significance of identified clusters. We used $\alpha = 0.05$ to identify clusters of grid-cells significantly different from the surrounding area. To account for the effects of multiple testing and spatial dependency of the data, a correction for the False Discovery Rate was applied⁶³. See Figure S3 for intermodal comparison. The analysis was conducted in ArcGis (Release 10.8. Redlands, CA).

3.3 Post-processing

The final evaluation constructed 30 categorical maps of areas with significantly low and high climatic stability obtained using the Getis-Ord G_i^* statistics; these maps correspond to 5 RCMs

443 driven by two RCP scenarios, and 3 future time periods. These maps were combined using a
444 set of criteria to identify the final locations of key continental or regional areas with high or low
445 climatic stability. First, the key areas had to be identified by at least four out of the five RCMs
446 used here, relative to each RCP scenario (Figure S2). Second, we evaluated whether the
447 locations of key areas were agreed under a single or both RCP scenarios. Third, we evaluated
448 the temporal persistence of the identified key areas. With respect to the needs of future
449 conservation planning, we opted to use a conservative approach, and considered only those
450 areas, which persisted in their location throughout the three future time periods.

451 We used the biogeographical zones of Europe (⁶⁴; Figure S1) to categorize the identified key
452 areas with respect to current biogeographical conditions in Europe. The analyses were
453 conducted using the R 342 v.3.3.2 ⁶⁰ using raster ⁶⁵, and rgdal ⁶⁶ libraries.

454

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598

Figures

Figure 1

Predicted zones with instable (red) and stable (blue) climate in Europe, relative to continental background climate change. Indication of climate stability zones during three separate time periods (a-c) and those persisting throughout the predicted time period 2041-2100 (d-e). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Predicted zones with instable (red) and stable (blue) climate in Europe, relative to regional background climate change. Indication of climate stability zones during three separate time periods (a-c) and those persisting throughout the predicted time period 2041-2100 (d-e). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 3

Geographical coverage of investigated biodiversity sites classified as belonging to area of regionally significantly instable (red) or stable (blue) future climate as predicted under RCP 4.5 or RCP 8.5. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 4

The proportion of Natura 2000 (a), Key Biodiversity Areas (b) and European primary forests (c) present in areas identified as climatically stable or instable relative to background climate change at continental scale (bars). Pie charts indicate the fraction of the three biodiversity initiatives in stable or instable areas at regional-scale embedded within the continent-scale pattern. Values in pie charts show area of Natura2000 and KBA sites (mil. of ha), or the number of EPF in each climate stability category. Climatic stability as predicted under RCP4.5 or RCP8.5 and persisting throughout 2041-2100.