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Where will species on the move go? Insights from climate connectivity modelling across European terrestrial habitats

Sylvain Sonntag [a], Yoan Fourcade [a*]

[a] Univ Paris Est Creteil, Sorbonne Université, CNRS, IRD, INRAE, Institut d'écologie et des sciences de l'environnement, IEES, F-94010 Creteil, France

* Corresponding author:

Yoan Fourcade
61 avenue du Général de Gaulle
94010 Créteil, France
yoan.fourcade@u-pec.fr

Abstract

Climate change can induce species range shifts. However, the intensity of climate change, the intrinsic dispersal ability of species and the anthropization of landscapes are impeding species movements in most cases. In this context, preserving and promoting climate corridors for species to migrate from their current habitats to their future climatically similar habitats is an important strategy for preventing species extinction. Climate connectivity modelling is a tool that can identify these potential movement pathways. Here, we aimed to model connectivity between climate analogues across Europe under various ecological assumptions and climate change scenarios, in order to identify areas of high potential connectivity and to quantify variation in connectivity across a range of hypotheses. We also overlapped connectivity maps with protected areas to determine whether climate connectivity was sufficiently protected. We showed that climatic connectivity did not differ much between different scenarios of climate change, but was strongly dependent on species' dispersal assumptions. It was also relatively similar to a scenario of non-climatic connectivity. Therefore, it may be feasible to anticipate the effect of climate change on species movements regardless of the future trajectory of climate, but the implementation of protection strategies for multiple species will certainly prove complex. Overall, protected areas were located in the regions of high and stable connectivity, but some countries lack the appropriate protection schemes, especially regarding strong protections. Our results have the potential to serve in the construction of land cover change scenarios to identify the best strategies to improve climate connectivity.

Keywords

Climate change, climate connectivity, climate corridors, protected areas, movement.

1. Introduction

Knowing where species are distributed in space and how these distributions change under human pressure are key knowledge to acquire for conserving biodiversity (Santini et al., 2021). Species ranges are determined by both biotic (e.g. predation, pathogens, competition, resource availability) and abiotic factors (e.g. climate, soil properties, light availability) to which species are adapted and which determine their ecological niches. However, the large-scale distribution of species is generally thought to be mainly driven by their Grinnellian niche, which describes species' fundamental niche through the physicochemical properties of habitats (Soberón, 2007, Soberón & Nakamura, 2009). One of the main factors of the Grinnellian niche is climate, which largely determines the abiotic conditions that species experience at macro-ecological scale. Any long-term change in climate will thus modify the geographical areas that are suitable for a given species. However, abiotic factors are often not sufficient to describe species' realized niche, representing the conditions actually occupied by species. Indeed, dispersal also control the areas that can effectively be reached, independently of whether they are suitable otherwise (Soberón & Nakamura 2009). Therefore, area-based conservation strategies must take into account the interaction between physical environmental conditions, including climate, and dispersal opportunities of species with various intrinsic movement abilities, in a complex landscape of contrasted land use intensities.

Climate change has been recognized since the 1970s as one of the most severe anthropogenic environmental changes. This includes a global increase in the Earth's temperature, which could reach 1.5°C on average by 2040 (IPCC, 2018). In addition to the increase in average temperature, climate change may also lead to significant changes in the structure of habitats, for example by altering moisture regimes and causing initially wet areas to become dry (Raymond et al. 2019). Climate change is already having significant effects on terrestrial species, which have been widely observed in recent years. Among them are morphological changes of organisms through body-size shrinking (Sheridan & Bickford, 2011) and appendage lengthening (Ryding et al., 2021), changes in individuals' metabolic rate (Williams et al., 2015) and phenology (Macgregor et al., 2019), or acceleration of senescence (Le Roux et al. 2005). At the ecosystem-scale, climate change is expected to result into changes in species richness (Currie, 2001), modification of community composition and functionality (Mokany et al., 2015), shifts in biome distribution (Boonman et al., 2021), and to an overall increase in net primary production (Bergh et al. 2003). As a consequence of this profound alteration of their habitats, species may need to change their distributional areas to remain in suitable environmental conditions in order to limit the short and long term effects of climate change and to avoid extinction (Soberón and Nakamura, 2009; Caplat et al., 2016; Estrada et al., 2016). When species are able to tolerate temperature changes, climate change will likely lead to range expansion towards newly suitable habitat even if no range retraction occur at the trailing edge. In this context, predicting where and how species will carry out such range shifts appears as an important challenge for biodiversity conservation in a changing climate.

Empirical evidence shows that terrestrial species are moving primarily poleward and toward higher elevations in response to climate change (Parmesan, 2006, Chen et al., 2011). For example, a review of range shifts across several terrestrial taxa concluded that ca. 70% of species have migrated towards the poles over the last few decades (Thomas, 2010). However, not all species shift their range at the same pace, which can disrupt biological interactions. In some cases, mutualistic interactions can be altered because one of two interacting species is unable to shift its range (Pelini et al., 2009); alternatively, the arrival of range-shifting predators or competitors can disturb native ecosystems (Alexander et al., 2015; Kubelka et al., 2018). Species that are more sensitive to environmental changes are also more prone to move into new environments (Gilman et al., 2010). Importantly, species intrinsic dispersal ability influences range shifts opportunities, actively mobile species being generally favoured compared to species whose dispersal is achieved by the passive transport of propagules (Estrada et al., 2016). Trees' distributions, for example, may show a strong and growing disequilibrium with climate because their slow dispersal make them unable to respond as fast as climate changes (Vissault et al., 2020; Seliger et al., 2021). Therefore, fast and/or high changes in temperature compared to species migration ability may cause lags between temperature increase and community responses (Devictor et al., 2012).

Species' range shifts in response to climate change may be influenced by anthropogenic changes that impact species' ability to move. Occasionally, human activity can promote species' dispersal through the transport of individuals or the creation of new habitats. Still, habitat loss and fragmentation caused by anthropogenic land use often reduce the ability of species to disperse among habitats patches (Schtickzell et al. 2006). For example, infrastructures such as dams or roads frequently act as barriers for dispersal, preventing the movement of aquatic organisms along the river, and increasing mortality during crossing, respectively (Caplat et al. 2016). In addition to having a direct effect on the dispersal of non-synanthropic species, several studies have shown that habitat fragmentation can affect certain environmental variables, which can in return alter species' dispersal abilities. This includes changes in microclimatic conditions, with generally leads to an increase in mean temperature in fragmented habitats (Kuczynski et al., 2018). Changes in precipitation, on the other hand, was found to be context-dependent and could either increase (Kuczynski et al., 2018) or decrease (Platts et al., 2019) with fragmentation. Several studies conducted on bird, fish, and insect species have demonstrated that range shifts induced by changes in temperature can be impaired in highly fragmented areas (Jarzyna et al., 2015; Kuczynski et al., 2018; Platts et al., 2019; Fourcade et al., 2021). Enabling species' movement to allow them to track climate change is thus an important strategy for preventing species extinction.

Implementing conservation actions for promoting range shifts implies that we must be able to anticipate species' movement from their current habitats towards their future habitats (Krosby et al. 2010; Littlefield et al., 2019). In this context, the identification of climate corridors that species will use would allow targeting specific areas where connectivity networks could be strengthened to facilitate the movement of species in the landscape (Caplat et al., 2016). Several attempts have been made to identify the impact of land use, habitat fragmentation and climate on species movement (see Littlefield et al., 2019 for a review of climate connectivity modelling approaches). The simplest models assume that species movement in response to climate change occur based on temperature gradients (Nuñez et al., 2013; McGuire et al., 2016). However, considering more variables, including land cover and landscape fragmentation, may be more realistic (e.g. Littlefield et al., 2017). Climatic connectivity, corresponding to the capacity of a landscape to permit the movement of species that carry out range shifts in response to climate change, can be modelled explicitly between the current distribution of a focal species of conservation concern and its predicted distribution in future climate (Fitzpatrick and Dunn, 2019). In a broader context of landscape planning where all existing communities are to be protected against the deleterious impacts of climate change, connectivity can be alternatively modelled by identifying paths between climatic analogues, i.e., between two habitats where climatic conditions in future scenarios of climate change are similar to those in current climate (Littlefield et al., 2019). The identification of that path is a complex process that depends on various hypotheses. For example, it could be defined as the shortest distance between current habitat and its climatic analogue, or may be based on the least cost path following the geophysical properties of the environment (Carroll et al., 2018). Recent developments in connectivity modelling that are based on the analogy with electrical current provide an unvaluable tool to model climate connectivity at a large spatial scale (McRae et al. 2016; Leonard et al., 2017). Although several studies on the connectivity between climate analogues have already been conducted in the United States (Cushman et al., 2013; Littlefield et al., 2017; Carroll et al., 2018; Fitzpatrick and Dunn, 2019), few studies are available on a European scale. Moreover, whether the resulting models are stable to a range of hypotheses remains unknown. This information is crucial because there are many uncertainties regarding the way species will shift their range in the future, which could potentially modify the areas predicted to be used as climate corridors. For instance, climate-induced species movements will likely depend on the intensity of climate change (Nuñez et al., 2013); species with different ecological traits may also use different climate corridors (Littlefield et al., 2019). This uncertainty may hamper the implementation of efficient actions aiming at protecting climate corridors.

In the present study, we were interested in identifying the stability of climate corridors in Europe by modelling connectivity between climate analogues in relation to land use under various scenarios. An important expected outcome was to evaluate how mapping the stability of climate corridors in Europe would allow us to identify gaps in the current network of protected areas, which could potentially provide a good protection against the effect of climate change on biodiversity (Gillingham et al., 2015; Gaüzère et al., 2016; Haight and Hammill, 2020). To answer this question, we tested hypotheses about the dispersal ability of the species and their preferred habitat type (forests or semi-natural open habitats). Climate analogues were also identified between the current period and two future time periods (2050 and 2070) using bioclimatic variables calculated from two scenarios of climate change (RCP 2.6 and RCP 8.5). This strategy allows to test a range of realistic scenarios that can serve as a basis for biodiversity-friendly landscape planning at the European scale in a context of climate change. When species' movements are impaired by fragmentation and poorly managed land use (Jarzyna et al., 2015; Kuczynski et al., 2018; Platts et al., 2019; Fourcade et al., 2021), mapping climate corridors may help identifying areas of high connectivity that should be protected or restored, in such a way that species' and communities' climatic debt could be reduced (Devictor et al., 2012).

2. Material and methods

2.1. Data on climate, land use and protected areas

We based our modelling of climate connectivity on 19 bioclimatic variables, which correspond to biologically meaningful climate variables describing current and future climate. These variables represent annual average and extreme values of precipitation and temperature, as well as their seasonality, to which species are expected to respond. Current bioclimatic variables were produced by interpolating weather data between 1979 and 2013 from a global network of weather station (Karger et al, 2017), while future variables were derived from climate modelling under various scenarios (Karger et al, 2020). We selected future data from the Model for Interdisciplinary Research On Climate version 5 (MIROC5), which is one of the best atmospheric circulation models for representing the observed warming trend (Altamirano del Carmen et al, 2021). Climate data were downloaded from the CHELSA website (https://chelsa-climate.org/), which compiles global climate variables from several different models. Future bioclimatic variables were selected over two different time periods (2041-2060 and 2061-2080, hereafter referred to as 2050 and 2070) and under two scenarios (RCP 2.6 and RCP 8.5). The RCP 2.6 (Representative Concentration Pathway) scenario corresponds to a radiative forcing of +2.6 W/m^2 by 2100, resulting in an initial increase in the Earth's temperature followed by a decline. The second scenario (RCP 8.5) is the least optimistic and corresponds to an increase of +8.5 W/m^2 by 2100, associated to a strong temperature warming. Two contrasting scenarios were chosen to determine if large differences in movement pathways were observable depending on the severity of climate change.

To account for landscape resistance to movement (see ‘connectivity modelling’ section), we used land cover data from the CORINE land cover project (version 2018), obtained from the Copernicus website (https://land.copernicus.eu). It compiles pan-European land cover maps classified into 48 land cover types, allowing the classification of habitat types and the discrimination of highly anthropized areas against natural areas. The maps provided by the Corine Land Cover inventory are mainly produced by visual interpretation of high-resolution satellite images.

In order to overlap climate connectivity and protected areas, we used data from the World Database on Protected Areas (WDPA, https://www.protectedplanet.net/), which provides a nearly comprehensive global compilation of protected areas. Here, we used both the whole set of terrestrial protected areas in Europe, as well as a reduced dataset comprising only highly protected areas (IUCN category Ia) (Appendix A, Figure A1). These areas correspond to strict nature reserves set aside for the protection of biodiversity and where human visits and land use are strictly controlled.

All spatial data were reprojected in the ETRS89/LAEA Europe coordinate system and resolution was coarsened to 500 m × 500 m in order to speed-up computations that would otherwise be intractable at finer resolutions.

Throughout the text, the term "species" will refer to theoretical terrestrial species living on the European continent and adapted to the current climatic conditions. We expect our approach to be realistic enough to be applicable to real species affected by climate change.

2.2. Identifying climate analogues

To model habitat connectivity in a changing climate, we assumed that species movements will occur between a set of starting points and their climate analogues in the future. Therefore, we first identified climate analogues between current and future climates, i.e. locations that will share similar climatic conditions now and in each climate change scenario. We selected starting points in two different habitat types to simulate two groups of species differing by their ecological requirements: forested areas or open semi-natural habitats. Each species group was represented by 1000 randomly selected points in their respective habitats, defined according to the land cover map (categories with resistance = 1 in Table 1).

The identification of climate analogues was based on four climate change scenarios (two RCPs and two future time periods) and different ecological hypotheses. First, we considered that species do not change their ecological requirements, such that climate analogues had to be in the same habitat type as the initial points. Because of this, all the analogues of the forest points were searched in forests and all the analogues of the points located in semi-natural open environments were searched in semi-natural open environments. We then considered the application or not of a distance limit between climate analogues. To select a realistic dispersal, we referred to data from Littlefield et al. (2017) who used a similar method to model climate connectivity, and who reported that most species had an average dispersal rate of 0.5 to 5 km/yr. Here we retained an intermediate value such that maximum dispersal distance was rounded to 100 km in 35 years. Therefore, distance limit was set assuming a maximum dispersal distance of 2857.15 m yr-1, meaning that species would have travelled at most 100 km to reach their climatic analogue in 2050 (100 000 m / 35 yrs = 2857.15 m yr-1). Maximum movement distance in this hypothesis would thus be 157 km in 2070. In the case where no distance limit was defined, and providing that other biological and environmental conditions are fulfilled, species could migrate at infinite speed to reach their best possible climate analogues. This allows us to have an overview of the potential climate connectivity of species with a virtually infinite dispersal capacity (realistic for highly dispersing species such as some birds or large mammals that could easily travel hundreds of kms in this time frame) and, in the case where we impose a dispersal constraint, to determine the more realistic pathways for species with limited dispersal capacity. In total, eight scenarios per habitat type were used to identify the climate analogues of the 1000 random starting points. Each starting point (in blue on Figure 1) thus had 8 different climate analogues (in red or green on Figure 1). In addition, we selected for each starting point a random point that did not correspond to a climate analogue. These locations were defined according to the same set of rules (in the same habitat type – forest or open – and with or without dispersal limit) except that it did not correspond to a location with similar climate in future conditions. This was done to compare connectivity models built with the aim of simulating movements of range-shifting species to models representing a non-climatic ecological connectivity.

Analogue points were obtained by considering all 19 bioclimatic variables with the same weight. We calculated the climatic similarity of all grid cells to each 1000 random starting point using functions in the "analogues" R package. Each grid cell was given a value of climatic similarity and we defined the climate analogue as the one with the highest climate analogy, i.e. the value closest to 1 (100% similarity). In order to identify climate analogues within a distance limit, we defined a radius around the point and selected the most climatically similar point located within this radius.

In order to test whether the choice of 1000 points was sufficient to represent climate connectivity across Europe, we generated connectivity maps (produced with the method outlined below) consisting of the sum of the connectivity across random combinations of 100 to 1000 (by increments of 100) pairs of starting points and their analogues. We calculated the correlation between each subset and the connectivity map produced with the whole set of 100 points, and concluded that 1000 points were sufficient (Appendix A, Figure A2).

2.3. Connectivity modelling

In order to model connectivity between the initial random points and their respective climate analogues, it was first necessary to define the resistance of the environment to species movement. Resistance was defined according to land cover categories, using a geometric sequence of common ratio 4, where the lowest resistance value was set to 1, i.e. the easiest to cross. The highest resistance value corresponded to highly anthropized land cover types that we assumed to be highly unsuitable for species, while impassable areas (all aquatic environments) were set to NA, i.e. infinite resistance (Table 1). The use of a geometric sequence has been chosen because there is evidence that landscape resistance increases non-linearly with decreasing environmental suitability (Keeley et al., 2016). Here, the choice of a ratio of 4 allowed for strong differences between low resistance and high resistance land cover types. The land cover map was reclassified to obtain two resistance maps: one corresponding to the resistance of the landscape to the movement of forest species and another corresponding to the resistance of the landscape to the movement of species living in open semi-natural habitats.

We applied an electric circuit approach to compute connectivity between the initial points and their climate analogues (Figure 1). Circuit theory makes an analogy between the resistance to species movement in the environment and the resistance to current flow in electrical circuits (McRae et al. 2016). Contrary to other methods such as the identification of least-cost paths, circuit-based methods assign a value to each pixel of the resistance map, allowing to interpret the output in a probabilistic way. To model movement corridors from the initial random points to their future climate analogues across the resistance map, we used the Circuitscape software (Version 1.5.3, Anantharaman et al. 2019). To obtain each connectivity map, we provided Circuitscape with the coordinates of 1000 starting points, the coordinates of their analogues and a resistance map. We set the "connect_four_neighbors_only" parameter to false to allow each grid cell to be connected to eight contiguous grid cell, thus identifying all possible paths. Each pair of points was subjected to a virtual electric current representing the potential movement of the species (pairwise analysis). This approach results in a cumulative map that sums the connectivity between all 1000 pairs of points, highlighting the areas of potential passage. In total, 16 connectivity maps based on 1000 pairs of points were obtained, corresponding to each scenario and hypothesis (forest vs. open, RCP 2.6 vs. RCP 8.5, 2050 vs. 2070, unlimited vs. limited dispersal). The entire procedure was also carried out for non-analogue points.

2.4. Analysis of connectivity maps and analogues

First, we tested some prior hypotheses about the location of analogue points in response to the different scenarios. This was also a way to evaluate how those scenarios influenced the pairs of analogues used for modelling connectivity before analysing connectivity models themselves. Our hypotheses were that, in the furthest and most pessimistic scenario (RCP 8.5 in 2070), future climate analogues would be at greater distances, higher elevations, higher latitudes and have lower climatic similarity than their counterparts in current climate than in the closest and most optimistic scenario (RCP 2.6 in 2050). To do so, we extracted the elevation of each point from the elevation raster available on the Worldclim website (https://worldclim.org/), derived from the SRTM project. We calculated the geographical, latitudinal and altitudinal distance between pairs of analogues, and extracted their climate similarity as obtained at the stage of identification of climate analogues. We then determined which of the scenario, time interval, and dispersal hypothesis most influenced these variables by performing multi-factor analyses of variance (ANOVA) with two-way interactions.

Besides visual inspection of connectivity maps, we first examined the variability of connectivity depending on the climate scenario by calculating Pearson’s correlation between pairs of maps of the same habitat type, with and without dispersal limitations. Correlation was also calculated between each climate connectivity map and the corresponding connectivity model built from non-analogue points.

We then determined for each connectivity map the contribution of each country to the total, European-wide, connectivity, i.e. the amount of virtual current passing through each country. The purpose of this analysis was to determine which countries contributed the most to species’ potential movement under various hypotheses. To do this, we extracted the sum of connectivity within each 44 European countries represented in our models. We also extracted their total area, such that we could plot the relationship between connectivity and area. Countries above the regression line were thus countries that contributed disproportionally to

European climate connectivity compared to their area; reciprocally, countries below the connectivity / area regression line contributed less than expected to the total connectivity.

Additional analyses were conducted to assess the overlap between modelled climate connectivity and protected areas. All connectivity maps were combined into a single map to facilitate calculations, but we also report results for forest and open habitats separately. We conducted analyses for two different groups of protected areas: first considering all protected areas to determine the amount of connectivity through these areas, then considering only strict nature reserves (IUCN category Ia). As described above, we plotted total connectivity within protected areas per country against the amount of protected areas of each country to identify countries where protected areas overlapped particularly well or not with climate connectivity.

We synthesized results into a comprehensive bivariate map showing climate connectivity and its variation across hypotheses and scenarios. For this, we calculated the coefficient of variation of connectivity for three groups of connectivity maps: all scenarios, forest habitats only, and open semi-natural habitats only. In the three resulting bivariate maps, we partitioned connectivity and its coefficient of variation into three quantiles, therefore producing 9 categories. The proportion of each category, as a whole and within protected areas only, was extracted to identify the amount and stability of connectivity as a function of habitat type and environmental protection.

3. Results

3.1. Climate analogues

The first analysis revealed a significant effect of scenario, habitat, year, and distance limit on the elevation, climate analogy, distance, and latitude of analogue points (Appendix A, Table A1). On average, future climate analogues were located at higher elevation than in the present, especially in the RCP 8.5 scenario and in 2070 (Figure 2). Climate analogy, distance and latitude difference were influenced mainly by the climate scenario and the distance limit (Figure 2 and Appendix A, Table A1). Climate analogy appeared to be greater in the RCP 2.6 scenario and when no distance limit was imposed (Figure 2). Geographical and latitudinal distance between analogues were clearly higher in the RCP 8.5 scenario, although both distances were decreased by the introduction of a dispersal limit (Figure 2). The scenario × year factor was generally the most influential interaction, revealing that differences between 2050 and 2070 were exacerbated in the RCP 8.5 scenario (Appendix A, Table A1).

3.2. Climate connectivity per country

We found that climate connectivity was correlated positively to available area (Figure 3), with lower total climate connectivity in smaller countries and vice-versa. However, there were notable exceptions, such as Malta which had zero connectivity regardless of the area and surface considered. At the same time, the surface of protected areas also showed a clear positive correlation with country area. Still, we observed that some of the largest countries were not always the countries that protected their territory the most. Sweden and Norway were the two countries with the largest areas of Ia IUCN category protected areas, although they are only the 4th and 5th largest countries in Europe. On the contrary, although Turkey is the largest country covered by our maps (ca. 780,000 km^2 including its Asian part), its surface of protected areas was smaller than that of Denmark, which is only the 28th largest European country (ca. 44,000 km^2, Appendix A, Figure A4). Denmark, however, had lower than expected connectivity, regardless of the area considered (in total or within protected areas, Figure 3). Similarly, it appears that connectivity in Ia IUCN category protected areas was lower than expected in the United Kingdom. Despite being among the smallest European countries, Liechtenstein (137 km^2) had a connectivity comparable to that of Denmark, while the connectivity of Luxembourg (2,608 km^2) was close to that of Estonia (45,819 km^2). Focusing on forest and open semi-natural habitats, we observed again a strong correlation between total connectivity and country area (Appendix A, Figure A3). However, Ireland and Iceland had no connectivity in forested areas, regardless of the area considered. Another exception was Portugal, which had no connectivity in Ia IUCN category protected areas in forested areas.

3.3. Stability of climate connectivity

Overall, when looking at a broad European scale, climate connectivity maps highlighted the same main areas in all hypotheses and scenarios (Appendix A, Figure A5). However, finer examination revealed differences, mostly depending on the type of habitat considered and the existence of a dispersal limit. Correlation analyses showed that, for a given dispersal and habitat type, connectivity maps for the different scenarios and years of future climate change were highly correlated with each other (Pearson's correlation > 0.8), with a slightly stronger correlation without dispersal limits (Appendix A, Figure A5). Looking at the bivariate maps, we observed high connectivity, although with some variations, in a large part of the mountainous areas of Central Europe. The Bosphorus Strait (Turkey) also seemed to be associated with a high climatic connectivity but with an important variation depending of the habitat type and dispersal hypothesis. A strong, moderately variable, connectivity extended from northern Turkey to Poland, along the Balkan peninsula and the Alpine massif (Figure 4). Fennoscandian countries, although strongly connected under some hypotheses, also exhibited very variable connectivity, especially Sweden and Finland that were located in areas of high connectivity for forest species but not for those using open habitats. On the opposite, Turkey and Ireland showed high connectivity for open semi-natural areas but less for forest habitats. In addition, some areas exhibited high and stable connectivity, such as in the Carpathians in Romania, the Massif Central in France and central Portugal (Figure 4).

When considering both habitat types together, the most frequently observed areas were those of low connectivity and high variation in connectivity (13.6%), while the low-connectivity associated with low-variation areas were the least frequent (9.0%, Table 2). This was the case also when looking at open semi-natural habitats only, but not for forests where medium connectivity with low variation was the most frequent (Table 2). Protected areas appeared to be mostly located in highly connected and very stable areas (21.9%). In total, 46.6% of the surface of all protected areas were located in high-connectivity regions. Looking at each habitat separately, we observed that climate connectivity remained predominantly high in protected areas located in forest and semi-natural open habitats. More than half of strongly protected areas (Ia IUCN category) were highly connected, including 30.8% with high variation. This result remained observable in forested areas but appeared to be different in semi-natural open habitats, where 35% of the strongly protected areas were in low-connectivity regions; the distribution of connectivity and its variation was also more homogeneous.

3.4. Climate connectivity vs. non-climatic connectivity

To identify whether connectivity between climate analogues differed from a more general definition of ecological connectivity in Europe, we produced connectivity maps between random locations. In the case of a forested habitat and without distance limitation, the climate and random connectivity maps were correlated at more than 75% and were therefore very similar. The maps of semi-natural open spaces showed correlations of more than 85% with the connectivity maps obtained from the climate analogue. Looking at the maps produced with distance limits, we observed that, in the case of forest as in the case of open semi-natural habitats, correlations that did not exceed 60%. Thus, the climate analogue and the non-analogue maps appeared in this case distinctly different (Table 3).

4. Discussion

In a context of climate change, conservation planning must take into account species movements between their current habitat and the habitats they will need to reach in the future to keep pace with temperature warming. Modelling climate connectivity according to different scenarios of climate change and ecological hypotheses allows producing predictions of the most likely pathways for species range shifts, and thus aid in the design of biodiversity-friendly landscapes. Several climate connectivity modelling studies have already been conducted to identify species movement and facilitate species range change in increasingly fragmented habitats (Littlefield et al., 2019). Such approach has been particularly carried out for species-specific needs, or at the continental scale in America only (e.g. Littlefield et al., 2017; Carroll et al., 2018). Here, for the first time, we provide a mapping of climate connectivity across Europe under various scenarios of climate change, landscape resistance and dispersal. We used these results to assess the coverage of climate connectivity by each European country and their protected areas, providing a first step for future enhancements of the network of protected areas within Europe.

First of all, the process of identifying climate analogues showed that none of the "analogues" we selected for modelling connectivity were 100% climatically similar to the initial locations. This is certainly due to the fact that we computed climate analogy based on a large set of variables (19); however, this also shows that climate change will favour the emergence of novel climates (Williams et al., 2007) that do not currently exist in Europe. True climate analogues may exist further than the extent of Europe that we analysed here; however, since species cannot realistically travel at infinite distances, this suggests that many organisms will face climatic conditions that they did no experience before, even if they are capable of long-distance movements. In reality, species are not adapted to a single climate, but possess a more or less wide climatic niche (Quintero and Wiens, 2013). Therefore, the likelihood for species to find suitable climatic conditions in the future will likely depend on their niche properties (Thuiller et al., 2005) and on their ability to reach the areas harbouring these climatic conditions (Estrada et al, 2016). In this regard, our modelling scenario where we set a maximum dispersal distance highlighted further the impact that species' intrinsic movement ability may have on their response to climate change. Here, the diminishing climatic analogy shows that species with reduced movement capacity will have to cope with future climatic conditions that can be very different from now. Species with a narrow niche breadth and limited dispersal ability are thus expected to be particularly sensitive to climate change (Thuiller et al. 2005; Ofori et al., 2017). This result, however, is partly dependent on the coarse resolution we used here; microclimate refugia may exist at a smaller scale that could help species persist longer in their current habitats (Suggitt et al., 2011).

Our study demonstrated that difference in elevation, climate analogy, as well as geographical and latitudinal distances between climate analogues, were influenced by the scenario of future climate change. Specifically, it could be observed that the distance species will have to travel to find the closest possible climate analogue is maximum in the case of RCP 8.5; in this scenario, climate analogy will also be lower. The most environmentally impactful scenarios thus appear to impose greater displacement to more distant and less climatically similar analogues (Littlefield et al. 2017), likely increasing the vulnerability of little mobile species. Similarly, differences in elevation and latitude were also larger in the case of RCP 8.5. This was expected as this is the most severe scenario of climate change (IPCC, 2018); our results confirm that species will most likely be impacted more strongly by the most extreme changes in climate, accelerating extinction risk for many species (Urban, 2015).

The fact that elevation is higher and climate analogy is lower in 2070 than in 2050 shows that climate change will continue to alter species' habitats over time regardless of the scenario and habitat type considered. The movement of species to higher elevations as a response to an increase in temperature conditions has already been shown, for example in bird species (Flousek et al., 2015). Species movement to higher elevations and latitudes, however, depends on the species under consideration, with greater shifts in meridional areas (Chen et al., 2011). This result has been proven in particular on bumblebee species, which moved to higher altitudes in the southern limits but decreased in distribution in the septentrional limits (Kerr et al., 2015). Plant species, especially herbaceous, also follow a shift to higher elevations in response to climate change (Lenoir et al., 2008). However, moving to higher altitudes is not always effective, especially since the topographical configuration of mountains leads to decreasing available area at higher elevations (Elsen and Tingley, 2005). This has resulted, for example, in large losses of butterfly diversity in mountainous areas of Spain (Wilson et al., 2007). Poleward range shifts are not necessarily an easier way for species to track their climatic niche. Indeed, latitudinal range shifts often involve long-distance movements in a fragmented landscape and require all ecological requirements to be present in novel habitats (Chen et al., 2011; Devictor et al., 2012). It will therefore be important to preserve existing habitats to slow down the extirpation of cold-adapted species and to promote the migration and settlement of species in new habitats.

The synthesis of climate connectivity at the country level allowed us to determine which countries contributed the most to the predicted movements across Europe. Since we determined that the amount of climate connectivity within countries is directly related to their size, efforts directed towards assisting species' range shifts must be mainly accomplished in the largest European countries such as France, Spain, Sweden, Norway and Germany, which together host a large part of the predicted climate connectivity. Differences can be observed in some countries, though. For example, we observed a remarkable lack of connectivity in Malta that is clearly due to its geographical location and size, Malta being an island at the very southern European limit. The choice of points may also have influenced this result since the probability of obtaining one out of 1000 random points in the smallest countries was low. There was also a complete lack of connectivity in forested areas in Ireland and Iceland, which is easily explained by the fact that very few forest areas are identifiable in these two countries. The probability of getting one initial location in the forest of Ireland or Iceland out of 1000 points is therefore low; the probability that its future climate analogue is also located in the same country is even lower. To overcome the lack of connectivity in small- to medium-sized islands, a small but non-null connectivity could have been allowed across seas to simulate long-distance dispersers that can cross large water bodies.

The effectiveness of protected areas in mitigating the effects of climate change has already been demonstrated for some species, such as breeding birds (Gaüzère et al., 2016). Generally, protected areas appear to be a good way of providing protection and climate refugia for climate-sensitive species at their trailing edge, as well as favouring the colonisation of expanding species at their leading edge (Thomas et al. 2012; Gillingham et al. 2015). Here, we assessed whether European protected areas were placed in locations with high climate connectivity, effectively protecting species experiencing range shifts. We first observed that some countries have significantly fewer protected areas than others, despite their large size. For example, Turkey had a much smaller surface of protected areas, compared to its total size, than most other countries (Appendix A, Figure A1). Regrettably, the Bosphorus was also the area with the largest sum of connectivity in several scenarios. There, connectivity was very strong in all scenarios without dispersal limit, but also appeared unstable because the assumption of a dispersal limit could prevent passage across the strait. Looking closely at land cover in this region, we noticed that predicted movement occurred through heavily anthropized areas. Despite the high resistance values assigned to these land cover types, it appeared to be the only possible way to go from Asia to Europe in search of climate analogues. In fact, other corridors may exist around the Black Sea that could not be modelled here because our land cover data did not encompass this region. Moreover, even if we did not consider this possibility in our models, some species could disperse through water, swimming or transported by the current; flying or wind-dispersing species may also be able to cross the short distance separating the European and Asian parts of Turkey (see e.g. Waisel et al., 2008; Martínez-López et al., 2020). However, it is likely that crossing the Bosphorus will be necessary for some species tracking their preferred climate, from Anatolia to Balkans for example. Therefore, it seems important that Turkey acknowledges its leading role in this regard, for instance by increasing its network of protected areas to promote the climatic connectivity of habitats. This could also be done by prohibiting the construction of human infrastructure in the residual natural areas, by limiting urban expansion along the coast, or by promoting the development of green spaces in the existing urban areas. The construction of ecoducts across the strait could also be a solution to remedy the difficulty of passage in this area.

We detected in other areas such as in the vicinity of Zagreb in Croatia, in Liguria (north-western Italy) and around the Haut-Languedoc Regional Nature Park (southern France) a high variation in the modelled connectivity. The dispersal limit was mostly responsible for this variation because it determines whether some relatively distant natural areas, separated by highly anthropized land cover, could be connected or not. The largest region where variation in connectivity was high is in Sweden and Finland. The instability in these areas is also partly due to the establishment of a distance limit, but is mainly caused by variation among habitats. Indeed, Sweden and Finland show almost no connectivity in semi-natural open habitats, in contrast to forest that is the dominant land cover in these countries. There, the maintenance and expansion of efficient climate corridors will thus largely depend on the development of a sustainable management of forested areas, which are currently mostly privately owned for wood production (Chapin et al., 2007). This prominent importance of the dispersal limit in our connectivity models also highlights that, on the opposite, the actual scenario and period of climate change matters a lot less, making it easier to anticipate the effect of climate change on species movements whatever the socio-economical trajectory society will follow.

It was visible from our connectivity maps that much of Central Europe has strong connectivity and stability, highlighting the high likelihood of climate-driven movements connecting southern to northern Europe. Spain and Portugal are also two countries with strong and very stable connectivity. Many protected areas are present in these regions and, generally, we showed that protection overlapped more often with areas of stable connectivity (with the exception of strict nature reserves, probably because they are mostly located in Fennoscandia, where connectivity differs a lot between habitats). However, despite some positive signs (e.g. Gaüzère et al., 2016), the ability of protected areas to truly protect climate-tracking species remains uncertain. For example, there are contrasting empirical evidence of the effectiveness of the Natura 2000 network for biodiversity conservation, with demonstrated positive effect in birds (Princé et al. 2021) but not in butterflies (Rada et al., 2019). In the context of climate change, it is also important to ensure that spatial connectivity between protected areas is effectively capable of providing continuous corridors for species on the move (Caplat et al., 2016; Santini et al., 2016). It is noticeable that the number of strict nature reserves is overall very low, and even non-existent in some of the most connected areas (e.g. all central Europe). In order to fully protect these areas, it could be interesting to increase the level of protection, including more wilderness areas and national parks that we did not consider separately in our study but that confer a relatively strong protection for biodiversity. An interesting strategy could also be to deliberately implement protected areas in regions of high variation in connectivity in order to protect these areas from future, uncertain, changes. Issues regarding the location of protected areas were also observed in the United States, where most regions of high climate connectivity were not located in protected areas (Carroll et al., 2018). This is therefore a complex challenge to identify the areas that must be protected in a context where climate change drives spatial dynamics of biodiversity, especially when resources are not infinite and must be allocated carefully.

Comparing maps of connectivity between climate analogues with non-climatic connectivity maps allowed us to determine whether areas of high connectivity were strongly dependent on the exact location of connected points. In our results, climate and non-climatic connectivity maps were very similar when no distance boundary was defined. Indeed, the main areas of predicted movement remain broadly the same, regardless of the habitat considered. This reinforces the idea that the areas we have identified are indeed areas of high probability of passage to be preserved in the future, but also for ensuring ecological continuity regardless of climate change. However, we also noted significant dissimilarities between climate and non-climate connectivity maps in the case where we imposed a distance limit. It can be explained by the fact that, while long-distance connectivity always follows the same main European corridors, connectivity within a smaller distance is highly dependent on the exact location of the points. This is another confirmation that species' dispersal ability is one of the main factors to consider when predicting movements in a fragmented landscape, which makes complex the implementation of protection strategies for multi-species aims.

5. Conclusion

We know that global change has a major impact on the movement of species. Limiting the ongoing warming – which undoubtedly involves considerable changes in human activities – is thus crucial to limit the need for species to engage in long-distance movements to higher latitudes and elevations. The lower climate analogies between current and future habitats under the more pessimistic scenario reveals the importance of preserving climate refugia. We also demonstrated that species with limited dispersal capacity may face in the near future climatic conditions that no longer match the ones they are currently adapted to. In addition, our study showed that species living on islands will be more vulnerable to climate change because of the difficulty of dispersing to the continent. Long-term predictions of climate change are also characterised by an increase in the distance between current and future analogue climates. Reducing our impact in the coming decades could therefore help species to reach their climatic analogue more easily. Our approach also identified the most important climate corridors, in part to determine which regions should be subject to the establishment of protected areas if they are lacking such. Interestingly, we showed that pan-European climatic connectivity did not differ much between different scenarios of climate change, or between connectivity modelled from now to 2050 or from now to 2070. This implies that modelling climate connectivity may be an efficient tool to predict where species could go during range shift whatever the path we take – rapid mitigation of climate change or worst-case scenario with a severe increase in temperature – and the time period considered. However, models showed important differences depending on the dispersal hypothesis. Here, we tested only two assumptions of dispersal limit (unlimited or ca. 3 km yr^{-1}); in reality each species will disperse at its own pace, hence restructuring communities and complicating the modelling of multi-species connectivity. We also proved that even when considering no climatic connectivity between random locations, the areas of high connectivity remained broadly the same as in climate connectivity models. The protection of climate corridors is therefore an important issue both to help species reach their climate analogue and to limit extinction risk in their initial habitats. It would be possible to go further by comparing our results with historical data of bioclimatic and land use variables to determine if the climate corridors we have identified could have been identified with past data. Our results could also be compared with actual species movement data in Europe, to determine whether the identified climate corridors will actually be used in the future. Finally, the framework we used here has the potential to serve in the construction of land cover change scenarios to identify the best strategies to improve climate connectivity.

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Tables

Table 1: Resistance values according to land cover categories. The resistance values are scaled from 1 (low resistance) to 16348 (high resistance). NA values represent infinite resistance. Land cover categories were classified according to the habitat group considered. Initial random points and their analogues were selected within habitats with resistance = 1.

Resistance value	Forests	Semi-natural open habitats
1	Agro-forestry areas, Broad-leaved forest, Coniferous forest, Mixed forest	Pastures, Natural grasslands, Moors and heathland, Sclerophyllous vegetation
4	Green urban areas, Fruit trees and berry plantations, Olive groves, Sclerophyllous vegetation	Green urban areas, Sport and leisure facilities, Non-irrigated arable land, Annual crops associated with permanent crops, Complex cultivation patterns, Land principally occupied by agriculture, with significant areas of natural vegetation, Transitional woodland-shrub, Sparsely vegetated areas
16	Complex cultivation patterns, Natural grasslands, Moors and heathland, Transitional woodland-shrub	Permanently irrigated land, Inland marshes
64	Vineyards, Pastures, Annual crops associated with permanent crops, Land principally occupied by agriculture, with significant areas of natural vegetation	Peat bogs, Salt marshes, Salines
256	Sport and leisure facilities, Non-irrigated arable land, Permanently irrigated land, Rice fields, Inland marshes, Peat bogs	Rice fields, Vineyards, Fruit trees and berry plantations
1024	Sparsely vegetated areas	Olive groves, Agro-forestry areas, Broad-leaved forest, Coniferous forest, Mixed forest
4096	Road and rail networks and associated land, Beaches, dunes, sands, Bare rocks, Burnt areas, Glaciers and perpetual snow, Salt marshes, Salines, Intertidal flats	Beaches, dunes, sands, Bare rocks, Burnt areas, Glaciers and perpetual snow, Intertidal flats
16384	Continuous urban fabric, Discontinuous urban fabric, Industrial or commercial units, Port areas, Airports, Mineral extraction sites, Dump sites, Construction sites	Continuous urban fabric, Discontinuous urban fabric, Industrial or commercial units, Road and rail networks and associated land, Port areas, Airports, Mineral extraction sites, Dump sites, Construction sites
NA	Water courses, Water bodies, Coastal lagoons, Estuaries, Sea and ocean, NODATA, UNCLASSIFIED LAND SURFACE, UNCLASSIFIED WATER BODIES, UNCLASSIFIED	Water courses, Water bodies, Coastal lagoons, Estuaries, Sea and ocean, NODATA, UNCLASSIFIED LAND SURFACE, UNCLASSIFIED WATER BODIES, UNCLASSIFIED

Table 2: Summary table of the sum and variation of connectivity in Europe. Each cell in the table represents the proportion (in %) of grid cells of each quantile of connectivity value and connectivity variation in Europe, in the whole Europe, in total protected areas and in highly protected areas.

		All Europe			**All protected area**			**Strong protected area**		
		Sum of connectivity								
		Low	Medium	High	Low	Medium	High	Low	Medium	High
Variation of connectivity	**Total**									
	High	13.6	10.0	9.7	9.7	6.5	7.5	15.3	13.5	30.8
	Medium	9.8	11.3	12.1	6.9	9.4	17.2	6.2	6.8	13.4
	Low	9.0	12.5	12.0	7.9	13.0	21.9	3.0	3.1	7.9
	Forests									
	High	11.4	10.0	11.9	8.5	9.9	13.9	7.0	9.8	28.3
	Medium	9.8	11.7	11.9	5.8	11.0	17.1	3.7	6.9	14.6
	Low	8.3	13.5	11.5	6.0	12.4	15.4	4.9	8.0	16.8
	Open semi-natural habitat									
	High	14.8	9.4	9.1	9.8	7.9	12.9	12.9	8.9	8.2
	Medium	9.4	11.5	12.5	7.2	10.2	19.4	12.9	11.9	13.7
	Low	7.8	13.1	12.4	6.0	9.7	16.9	11.7	7.6	12.2

Table 3: Pearson's correlation coefficients between climate connectivity maps and random connectivity maps. A value of 1 represents perfect similarity, and a value of 0 represents no similarity.

		Limited dispersal	**Full dispersal**
Forest			
RCP 2.6	2050	0.79	0.58
	2070	0.84	0.59
RCP 8.5	2050	0.81	0.58
	2070	0.75	0.60
Open semi-natural habitats			
RCP 2.6	2050	0.85	0.49
	2070	0.85	0.55
RCP 8.5	2050	0.85	0.49
	2070	0.87	0.52

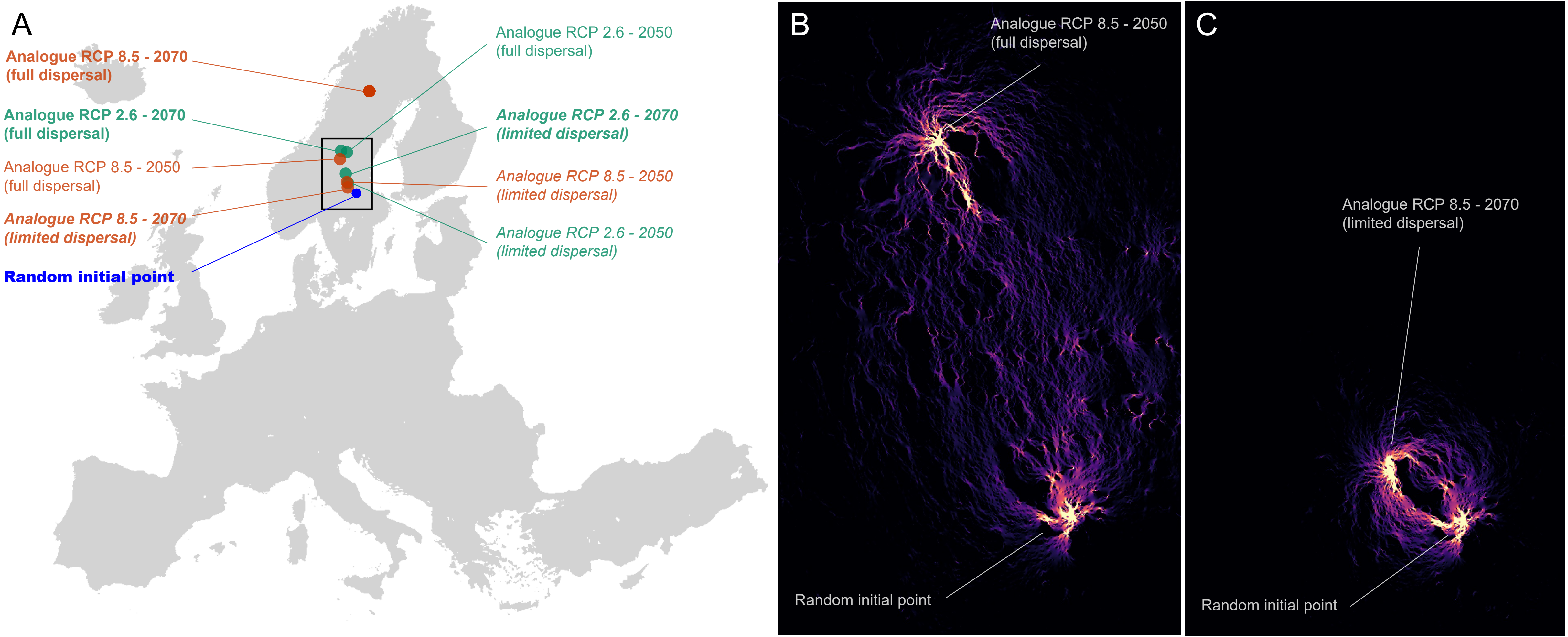
Figure captions

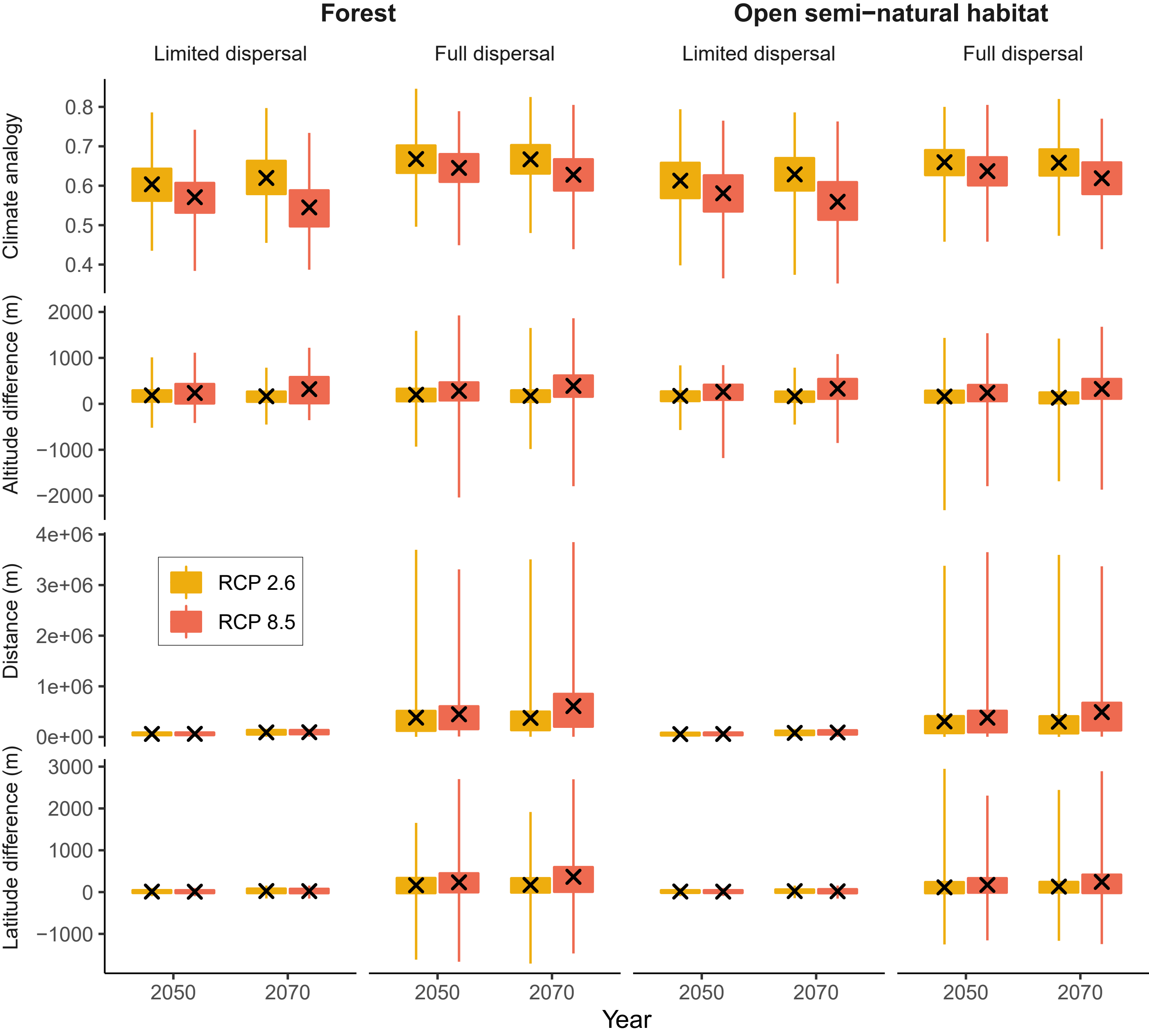
Figure 1: Illustration of the methods used for modelling climatic connectivity. A randomly chosen point (blue) and its different climate analogues (red and green) are shown in A. Connectivity modelled using Circuitscape between the initial point and its analogue in 2050 in the RCP 8.5 scenario with full dispersal is shown in B, and with its analogue in 2070 in the RCP 8.5 scenario with no dispersal in C. We produced in total 16 European-scale connectivity maps by modelling connectivity between 1000 pairs of points for forest and open species, with or without dispersal limit, for two climate change scenarios and two future time periods.

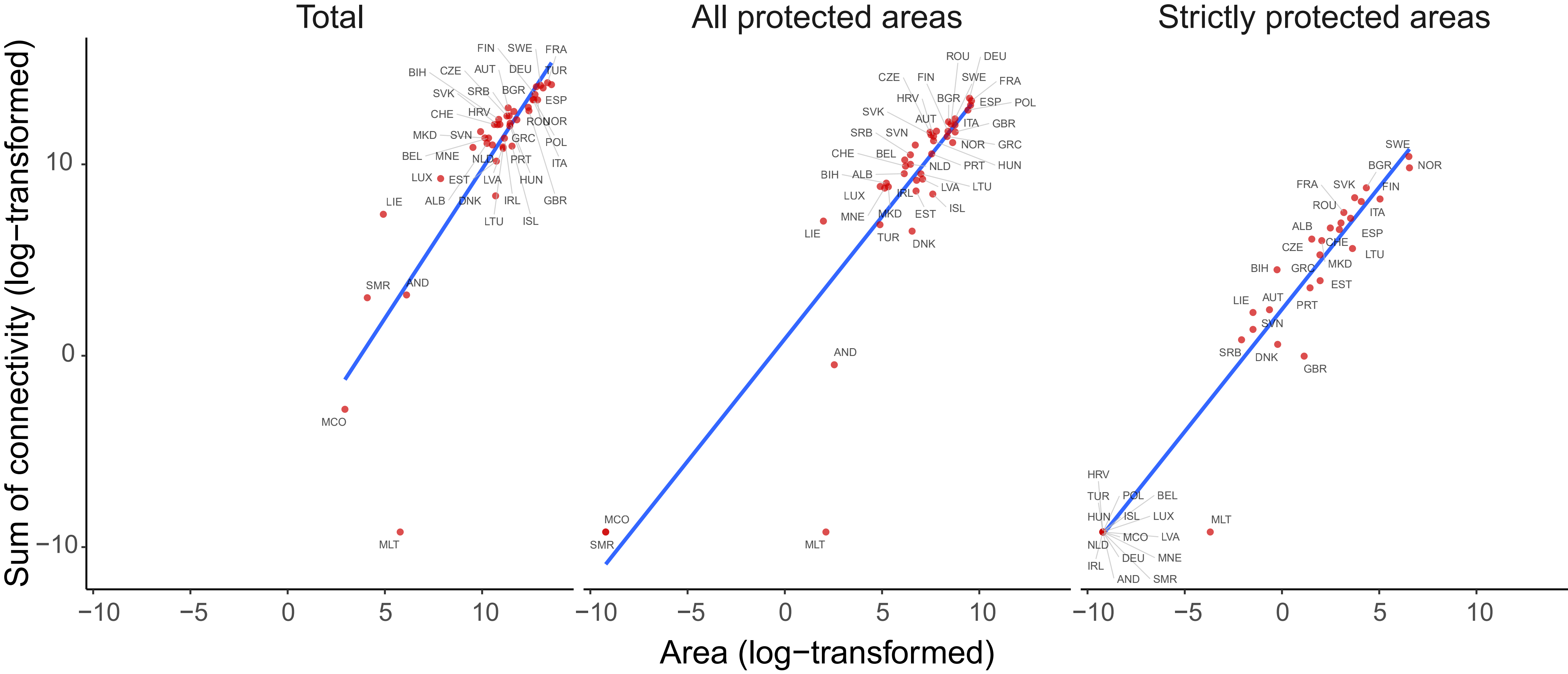
Figure 2: Difference between the 1000 random points and their future climate analogues. Box-and-whisker plots show the altitudinal and latitudinal difference, as well as the geographical distance and climate analogy, between the initial points and their analogues, for forest and open semi-natural habitats, for both RCP 2.6 and 8.5 scenarios, and with or without dispersal limits. Mean values are shown as black crosses within boxplots.

Figure 3: Relationship between the sum of climate connectivity within each European country and their total area (left), within protected areas (middle), and within strictly protected areas only (IUCN category Ia) (right). Countries are represented by three letters from the ISO standard. Both connectivity and area were log-transformed.

Figure 4: Bivariate maps representing the sum of connectivity and its variation (coefficient of variation), calculated for all connectivity maps merged together or for connectivity maps in forests or in open semi-natural habitats only. Areas represented in grey have no connectivity value.


A
Analogue RCP 8.5 - 2070
(full dispersal)
Analogue RCP 2.6 - 2070
(full dispersal)
Analogue RCP 8.5 - 2050
(full dispersal)
Analogue RCP 8.5 - 2070
(limited dispersal)
Random initial point
Analogue RCP 2.6 - 2050
(full dispersal)
Analogue RCP 2.6 - 2070
(limited dispersal)
Analogue RCP 8.5 - 2050
(limited dispersal)
Analogue RCP 2.6 - 2050
(limited dispersal)
B
Analogue RCP 8.5 - 2050
(full dispersal)
Random initial point
C
Analogue RCP 8.5 - 2070
(limited dispersal)
Random initial point


Forest
Open semi−natural habitat
Limited dispersal
Full dispersal
Limited dispersal
Full dispersal
Climate analogy
0.8
0.7
0.6
0.5
0.4
Altitude difference (m)
2000
1000
0
−1000
−2000
Distance (m)
4e+06
3e+06
2e+06
1e+06
0e+00
RCP 2.6
RCP 8.5
Latitude difference (m)
3000
2000
1000
0
−1000
2050
2070
Year


Total
All protected areas
Strictly protected areas
Sum of connectivity (log−transformed)
Area (log−transformed)
10
0
−10
−10
−5
0
5
10
FIN
SWE
FRA
BIH
CZE
AUT
DEU
TUR
SVK
SRB
BGR
ESP
CHE
HRV
ROU
NOR
MKD
SVN
GRC
POL
BEL
MNE
NLD
PRT
ITA
LUX
EST
LVA
HUN
LIE
ALB
DNK
IRL
GBR
LTU
ISL
SMR
AND
MCO
MLT
ROU
DEU
CZE
FIN
SWE
FRA
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ESP
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SVK
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ITA
GBR
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BIH
ALB
LVA
LTU
LUX
IRL
ISL
MNE
MKD
EST
LIE
TUR
DNK
AND
MCO
SMR
MLT
SWE
BGR
NOR
FRA
SVK
FIN
ROU
ITA
ALB
ESP
CZE
CHE
LTU
BIH
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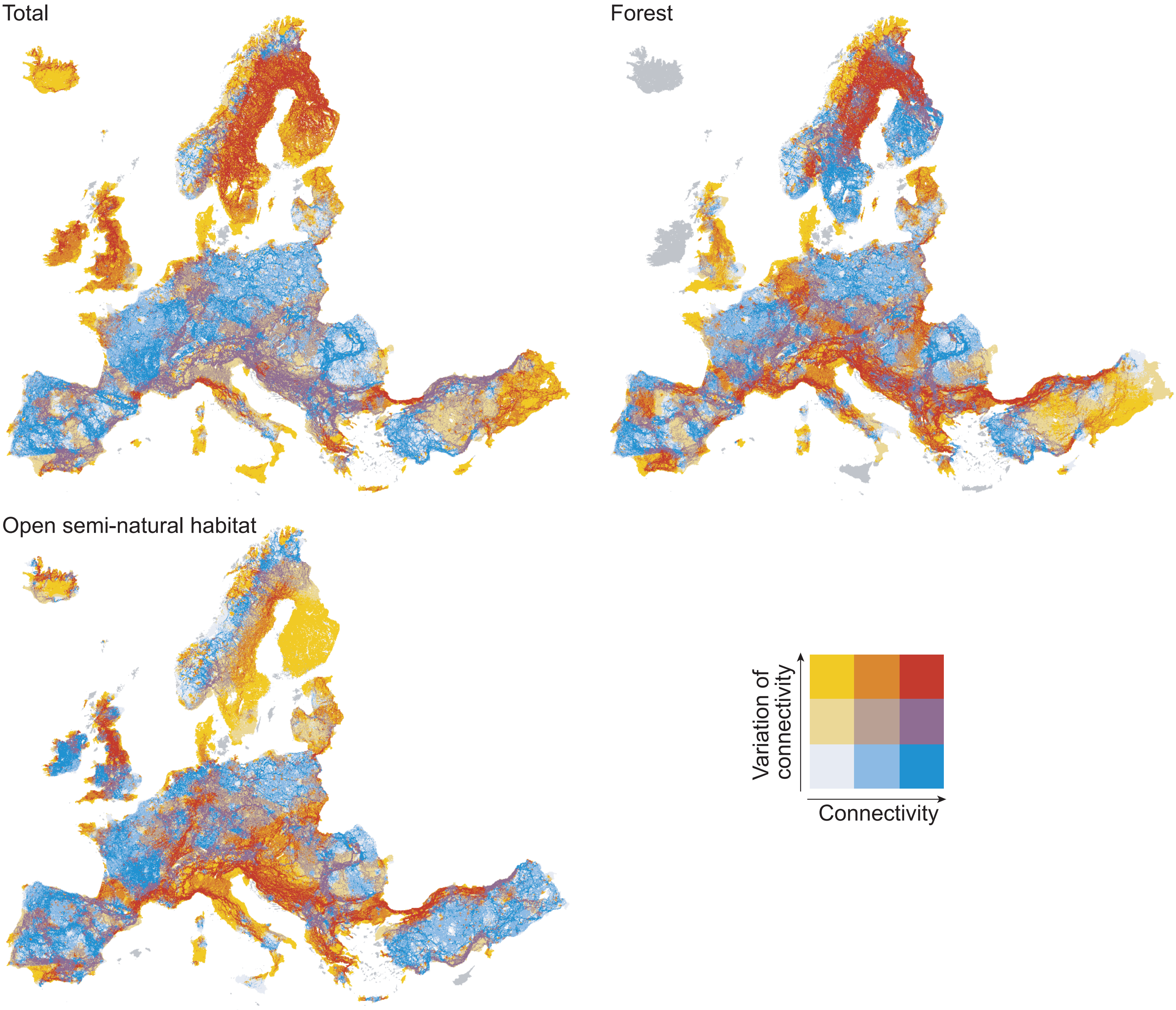
Total
Forest
Open semi-natural habitat
Variation of connectivity
Connectivity