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

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

4

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15

## 16 **Abstract**

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

## 37 **Keywords**

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

## 39 1. Introduction

40 Knowing where species are distributed in space and how these distributions change under  
41 human pressure are key knowledge to acquire for conserving biodiversity (Santini et al.,  
42 2021). Species ranges are determined by both biotic (e.g. predation, pathogens, competition,  
43 resource availability) and abiotic factors (e.g. climate, soil properties, light availability) to  
44 which species are adapted and which determine their ecological niches. However, the large-  
45 scale distribution of species is generally thought to be mainly driven by their Grinnellian  
46 niche, which describes species' fundamental niche through the physicochemical properties of  
47 habitats (Soberón, 2007, Soberón & Nakamura, 2009). One of the main factors of the  
48 Grinnellian niche is climate, which largely determines the abiotic conditions that species  
49 experience at macro-ecological scale. Any long-term change in climate will thus modify the  
50 geographical areas that are suitable for a given species. However, abiotic factors are often not  
51 sufficient to describe species' realized niche, representing the conditions actually occupied by  
52 species. Indeed, dispersal also control the areas that can effectively be reached, independently  
53 of whether they are suitable otherwise (Soberón & Nakamura 2009). Therefore, area-based  
54 conservation strategies must take into account the interaction between physical environmental  
55 conditions, including climate, and dispersal opportunities of species with various intrinsic  
56 movement abilities, in a complex landscape of contrasted land use intensities.

57 Climate change has been recognized since the 1970s as one of the most severe  
58 anthropogenic environmental changes. This includes a global increase in the Earth's  
59 temperature, which could reach 1.5°C on average by 2040 (IPCC, 2018). In addition to the  
60 increase in average temperature, climate change may also lead to significant changes in the  
61 structure of habitats, for example by altering moisture regimes and causing initially wet areas  
62 to become dry (Raymond et al. 2019). Climate change is already having significant effects on  
63 terrestrial species, which have been widely observed in recent years. Among them are  
64 morphological changes of organisms through body-size shrinking (Sheridan & Bickford,  
65 2011) and appendage lengthening (Ryding et al., 2021), changes in individuals' metabolic rate  
66 (Williams et al., 2015) and phenology (Macgregor et al., 2019), or acceleration of senescence  
67 (Le Roux et al. 2005). At the ecosystem-scale, climate change is expected to result into  
68 changes in species richness (Currie, 2001), modification of community composition and  
69 functionality (Mokany et al., 2015), shifts in biome distribution (Boonman et al., 2021), and  
70 to an overall increase in net primary production (Bergh et al. 2003). As a consequence of this  
71 profound alteration of their habitats, species may need to change their distributional areas to  
72 remain in suitable environmental conditions in order to limit the short and long term effects of  
73 climate change and to avoid extinction (Soberón and Nakamura, 2009; Caplat et al., 2016;  
74 Estrada et al., 2016). When species are able to tolerate temperature changes, climate change  
75 will likely lead to range expansion towards newly suitable habitat even if no range retraction  
76 occur at the trailing edge. In this context, predicting where and how species will carry out  
77 such range shifts appears as an important challenge for biodiversity conservation in a  
78 changing climate.

79 Empirical evidence shows that terrestrial species are moving primarily poleward and  
80 toward higher elevations in response to climate change (Parmesan, 2006, Chen et al., 2011).  
81 For example, a review of range shifts across several terrestrial taxa concluded that ca. 70% of  
82 species have migrated towards the poles over the last few decades (Thomas, 2010). However,  
83 not all species shift their range at the same pace, which can disrupt biological interactions. In  
84 some cases, mutualistic interactions can be altered because one of two interacting species is  
85 unable to shift its range (Pelini et al., 2009); alternatively, the arrival of range-shifting  
86 predators or competitors can disturb native ecosystems (Alexander et al., 2015; Kubelka et al.,

87 2018). Species that are more sensitive to environmental changes are also more prone to move  
88 into new environments (Gilman et al., 2010). Importantly, species intrinsic dispersal ability  
89 influences range shifts opportunities, actively mobile species being generally favoured  
90 compared to species whose dispersal is achieved by the passive transport of propagules  
91 (Estrada et al., 2016). Trees' distributions, for example, may show a strong and growing  
92 disequilibrium with climate because their slow dispersal make them unable to respond as fast  
93 as climate changes (Vissault et al., 2020; Seliger et al., 2021). Therefore, fast and/or high  
94 changes in temperature compared to species migration ability may cause lags between  
95 temperature increase and community responses (Devictor et al., 2012).

96 Species' range shifts in response to climate change may be influenced by anthropogenic  
97 changes that impact species' ability to move. Occasionally, human activity can promote  
98 species' dispersal through the transport of individuals or the creation of new habitats. Still,  
99 habitat loss and fragmentation caused by anthropogenic land use often reduce the ability of  
100 species to disperse among habitats patches (Schtickzell et al. 2006). For example,  
101 infrastructures such as dams or roads frequently act as barriers for dispersal, preventing the  
102 movement of aquatic organisms along the river, and increasing mortality during crossing,  
103 respectively (Caplat et al. 2016). In addition to having a direct effect on the dispersal of non-  
104 synanthropic species, several studies have shown that habitat fragmentation can affect certain  
105 environmental variables, which can in return alter species' dispersal abilities. This includes  
106 changes in microclimatic conditions, with generally leads to an increase in mean temperature  
107 in fragmented habitats (Kuczynski et al., 2018). Changes in precipitation, on the other hand,  
108 was found to be context-dependent and could either increase (Kuczynski et al., 2018) or  
109 decrease (Platts et al., 2019) with fragmentation. Several studies conducted on bird, fish, and  
110 insect species have demonstrated that range shifts induced by changes in temperature can be  
111 impaired in highly fragmented areas (Jarzyna et al., 2015; Kuczynski et al., 2018; Platts et al.,  
112 2019; Fourcade et al., 2021). Enabling species' movement to allow them to track climate  
113 change is thus an important strategy for preventing species extinction.

114 Implementing conservation actions for promoting range shifts implies that we must be  
115 able to anticipate species' movement from their current habitats towards their future habitats  
116 (Krosby et al. 2010; Littlefield et al., 2019). In this context, the identification of climate  
117 corridors that species will use would allow targeting specific areas where connectivity  
118 networks could be strengthened to facilitate the movement of species in the landscape (Caplat  
119 et al., 2016). Several attempts have been made to identify the impact of land use, habitat  
120 fragmentation and climate on species movement (see Littlefield et al., 2019 for a review of  
121 climate connectivity modelling approaches). The simplest models assume that species  
122 movement in response to climate change occur based on temperature gradients (Nuñez et al.,  
123 2013; McGuire et al., 2016). However, considering more variables, including land cover and  
124 landscape fragmentation, may be more realistic (e.g. Littlefield et al., 2017). Climatic  
125 connectivity, corresponding to the capacity of a landscape to permit the movement of species  
126 that carry out range shifts in response to climate change, can be modelled explicitly between  
127 the current distribution of a focal species of conservation concern and its predicted  
128 distribution in future climate (Fitzpatrick and Dunn, 2019). In a broader context of landscape  
129 planning where all existing communities are to be protected against the deleterious impacts of  
130 climate change, connectivity can be alternatively modelled by identifying paths between  
131 climatic analogues, i.e., between two habitats where climatic conditions in future scenarios of  
132 climate change are similar to those in current climate (Littlefield et al., 2019). The  
133 identification of that path is a complex process that depends on various hypotheses. For  
134 example, it could be defined as the shortest distance between current habitat and its climatic  
135 analogue, or may be based on the least cost path following the geophysical properties of the

136 environment (Carroll et al., 2018). Recent developments in connectivity modelling that are  
137 based on the analogy with electrical current provide an invaluable tool to model climate  
138 connectivity at a large spatial scale (McRae et al. 2016; Leonard et al., 2017). Although  
139 several studies on the connectivity between climate analogues have already been conducted in  
140 the United States (Cushman et al., 2013; Littlefield et al., 2017; Carroll et al., 2018;  
141 Fitzpatrick and Dunn, 2019), few studies are available on a European scale. Moreover,  
142 whether the resulting models are stable to a range of hypotheses remains unknown. This  
143 information is crucial because there are many uncertainties regarding the way species will  
144 shift their range in the future, which could potentially modify the areas predicted to be used as  
145 climate corridors. For instance, climate-induced species movements will likely depend on the  
146 intensity of climate change (Nuñez et al., 2013); species with different ecological traits may  
147 also use different climate corridors (Littlefield et al., 2019). This uncertainty may hamper the  
148 implementation of efficient actions aiming at protecting climate corridors.

149 In the present study, we were interested in identifying the stability of climate corridors in  
150 Europe by modelling connectivity between climate analogues in relation to land use under  
151 various scenarios. An important expected outcome was to evaluate how mapping the stability  
152 of climate corridors in Europe would allow us to identify gaps in the current network of  
153 protected areas, which could potentially provide a good protection against the effect of  
154 climate change on biodiversity (Gillingham et al., 2015; Gaüzère et al., 2016; Haight and  
155 Hammill, 2020). To answer this question, we tested hypotheses about the dispersal ability of  
156 the species and their preferred habitat type (forests or semi-natural open habitats). Climate  
157 analogues were also identified between the current period and two future time periods (2050  
158 and 2070) using bioclimatic variables calculated from two scenarios of climate change (RCP  
159 2.6 and RCP 8.5). This strategy allows to test a range of realistic scenarios that can serve as a  
160 basis for biodiversity-friendly landscape planning at the European scale in a context of  
161 climate change. When species' movements are impaired by fragmentation and poorly  
162 managed land use (Jarzyna et al., 2015; Kuczynski et al., 2018; Platts et al., 2019; Fourcade et  
163 al., 2021), mapping climate corridors may help identifying areas of high connectivity that  
164 should be protected or restored, in such a way that species' and communities' climatic debt  
165 could be reduced (Devictor et al., 2012).

166

## 167 **2. Material and methods**

### 168 *2.1. Data on climate, land use and protected areas*

169 We based our modelling of climate connectivity on 19 bioclimatic variables, which  
170 correspond to biologically meaningful climate variables describing current and future climate.  
171 These variables represent annual average and extreme values of precipitation and temperature,  
172 as well as their seasonality, to which species are expected to respond. Current bioclimatic  
173 variables were produced by interpolating weather data between 1979 and 2013 from a global  
174 network of weather station (Karger et al, 2017), while future variables were derived from  
175 climate modelling under various scenarios (Karger et al, 2020). We selected future data from  
176 the Model for Interdisciplinary Research On Climate version 5 (MIROC5), which is one of  
177 the best atmospheric circulation models for representing the observed warming trend  
178 (Altamirano del Carmen et al, 2021). Climate data were downloaded from the CHELSA  
179 website (<https://chelsa-climate.org/>), which compiles global climate variables from several  
180 different models. Future bioclimatic variables were selected over two different time periods  
181 (2041-2060 and 2061-2080, hereafter referred to as 2050 and 2070) and under two scenarios  
182 (RCP 2.6 and RCP 8.5). The RCP 2.6 (Representative Concentration Pathway) scenario

183 corresponds to a radiative forcing of +2.6 W/m<sup>2</sup> by 2100, resulting in an initial increase in the  
184 Earth's temperature followed by a decline. The second scenario (RCP 8.5) is the least  
185 optimistic and corresponds to an increase of +8.5 W/m<sup>2</sup> by 2100, associated to a strong  
186 temperature warming. Two contrasting scenarios were chosen to determine if large  
187 differences in movement pathways were observable depending on the severity of climate  
188 change.

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

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

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

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

## 209 *2.2. Identifying climate analogues*

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

218 The identification of climate analogues was based on four climate change scenarios (two  
219 RCPs and two future time periods) and different ecological hypotheses. First, we considered  
220 that species do not change their ecological requirements, such that climate analogues had to  
221 be in the same habitat type as the initial points. Because of this, all the analogues of the forest  
222 points were searched in forests and all the analogues of the points located in semi-natural  
223 open environments were searched in semi-natural open environments. We then considered the  
224 application or not of a distance limit between climate analogues. To select a realistic  
225 dispersal, we referred to data from Littlefield et al. (2017) who used a similar method to  
226 model climate connectivity, and who reported that most species had an average dispersal rate  
227 of 0.5 to 5 km/yr. Here we retained an intermediate value such that maximum dispersal

228 distance was rounded to 100 km in 35 years. Therefore, distance limit was set assuming a  
229 maximum dispersal distance of 2857.15 m yr<sup>-1</sup>, meaning that species would have travelled at  
230 most 100 km to reach their climatic analogue in 2050 (100 000 m / 35 yrs = 2857.15 m yr<sup>-1</sup>).  
231 Maximum movement distance in this hypothesis would thus be 157 km in 2070. In the case  
232 where no distance limit was defined, and providing that other biological and environmental  
233 conditions are fulfilled, species could migrate at infinite speed to reach their best possible  
234 climate analogues. This allows us to have an overview of the potential climate connectivity of  
235 species with a virtually infinite dispersal capacity (realistic for highly dispersing species such  
236 as some birds or large mammals that could easily travel hundreds of kms in this time frame)  
237 and, in the case where we impose a dispersal constraint, to determine the more realistic  
238 pathways for species with limited dispersal capacity. In total, eight scenarios per habitat type  
239 were used to identify the climate analogues of the 1000 random starting points. Each starting  
240 point (in blue on Figure 1) thus had 8 different climate analogues (in red or green on Figure  
241 1). In addition, we selected for each starting point a random point that did not correspond to a  
242 climate analogue. These locations were defined according to the same set of rules (in the same  
243 habitat type – forest or open – and with or without dispersal limit) except that it did not  
244 correspond to a location with similar climate in future conditions. This was done to compare  
245 connectivity models built with the aim of simulating movements of range-shifting species to  
246 models representing a non-climatic ecological connectivity.

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

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

### 260 *2.3. Connectivity modelling*

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



273 another corresponding to the resistance of the landscape to the movement of species living in  
274 open semi-natural habitats.

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

#### 293 *2.4. Analysis of connectivity maps and analogues*

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

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

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

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

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

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

337

### 338 **3. Results**

#### 339 *3.1. Climate analogues*

340 The first analysis revealed a significant effect of scenario, habitat, year, and distance limit on  
341 the elevation, climate analogy, distance, and latitude of analogue points (Appendix A, Table  
342 A1). On average, future climate analogues were located at higher elevation than in the  
343 present, especially in the RCP 8.5 scenario and in 2070 (Figure 2). Climate analogy, distance  
344 and latitude difference were influenced mainly by the climate scenario and the distance limit  
345 (Figure 2 and Appendix A, Table A1). Climate analogy appeared to be greater in the RCP 2.6  
346 scenario and when no distance limit was imposed (Figure 2). Geographical and latitudinal  
347 distance between analogues were clearly higher in the RCP 8.5 scenario, although both  
348 distances were decreased by the introduction of a dispersal limit (Figure 2). The scenario ×  
349 year factor was generally the most influential interaction, revealing that differences between  
350 2050 and 2070 were exacerbated in the RCP 8.5 scenario (Appendix A, Table A1).

#### 351 *3.2. Climate connectivity per country*

352 We found that climate connectivity was correlated positively to available area (Figure 3), with  
353 lower total climate connectivity in smaller countries and vice-versa. However, there were  
354 notable exceptions, such as Malta which had zero connectivity regardless of the area and  
355 surface considered. At the same time, the surface of protected areas also showed a clear  
356 positive correlation with country area. Still, we observed that some of the largest countries  
357 were not always the countries that protected their territory the most. Sweden and Norway  
358 were the two countries with the largest areas of Ia IUCN category protected areas, although  
359 they are only the 4<sup>th</sup> and 5<sup>th</sup> largest countries in Europe. On the contrary, although Turkey is  
360 the largest country covered by our maps (ca. 780,000 km<sup>2</sup> including its Asian part), its surface  
361 of protected areas was smaller than that of Denmark, which is only the 28<sup>th</sup> largest European  
362 country (ca. 44,000 km<sup>2</sup>, Appendix A, Figure A4). Denmark, however, had lower than

363 expected connectivity, regardless of the area considered (in total or within protected areas,  
364 Figure 3). Similarly, it appears that connectivity in Ia IUCN category protected areas was  
365 lower than expected in the United Kingdom. Despite being among the smallest European  
366 countries, Liechtenstein (137 km<sup>2</sup>) had a connectivity comparable to that of Denmark, while  
367 the connectivity of Luxembourg (2,608 km<sup>2</sup>) was close to that of Estonia (45,819 km<sup>2</sup>).  
368 Focusing on forest and open semi-natural habitats, we observed again a strong correlation  
369 between total connectivity and country area (Appendix A, Figure A3). However, Ireland and  
370 Iceland had no connectivity in forested areas, regardless of the area considered. Another  
371 exception was Portugal, which had no connectivity in Ia IUCN category protected areas in  
372 forested areas.

### 373 *3.3. Stability of climate connectivity*

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

392 When considering both habitat types together, the most frequently observed areas were  
393 those of low connectivity and high variation in connectivity (13.6%), while the low-  
394 connectivity associated with low-variation areas were the least frequent (9.0%, Table 2). This  
395 was the case also when looking at open semi-natural habitats only, but not for forests where  
396 medium connectivity with low variation was the most frequent (Table 2). Protected areas  
397 appeared to be mostly located in highly connected and very stable areas (21.9%). In total,  
398 46.6% of the surface of all protected areas were located in high-connectivity regions. Looking  
399 at each habitat separately, we observed that climate connectivity remained predominantly  
400 high in protected areas located in forest and semi-natural open habitats. More than half of  
401 strongly protected areas (Ia IUCN category) were highly connected, including 30.8% with  
402 high variation. This result remained observable in forested areas but appeared to be different  
403 in semi-natural open habitats, where 35% of the strongly protected areas were in low-  
404 connectivity regions; the distribution of connectivity and its variation was also more  
405 homogeneous.

### 406 *3.4. Climate connectivity vs. non-climatic connectivity*

407 To identify whether connectivity between climate analogues differed from a more general  
408 definition of ecological connectivity in Europe, we produced connectivity maps between

409 random locations. In the case of a forested habitat and without distance limitation, the climate  
410 and random connectivity maps were correlated at more than 75% and were therefore very  
411 similar. The maps of semi-natural open spaces showed correlations of more than 85% with the  
412 connectivity maps obtained from the climate analogue. Looking at the maps produced with  
413 distance limits, we observed that, in the case of forest as in the case of open semi-natural  
414 habitats, correlations that did not exceed 60%. Thus, the climate analogue and the non-  
415 analogue maps appeared in this case distinctly different (Table 3).

416

## 417 **4. Discussion**

418 In a context of climate change, conservation planning must take into account species  
419 movements between their current habitat and the habitats they will need to reach in the future  
420 to keep pace with temperature warming. Modelling climate connectivity according to  
421 different scenarios of climate change and ecological hypotheses allows producing predictions  
422 of the most likely pathways for species range shifts, and thus aid in the design of biodiversity-  
423 friendly landscapes. Several climate connectivity modelling studies have already been  
424 conducted to identify species movement and facilitate species range change in increasingly  
425 fragmented habitats (Littlefield et al., 2019). Such approach has been particularly carried out  
426 for species-specific needs, or at the continental scale in America only (e.g. Littlefield et al.,  
427 2017; Carroll et al., 2018). Here, for the first time, we provide a mapping of climate  
428 connectivity across Europe under various scenarios of climate change, landscape resistance  
429 and dispersal. We used these results to assess the coverage of climate connectivity by each  
430 European country and their protected areas, providing a first step for future enhancements of  
431 the network of protected areas within Europe.

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

453 Our study demonstrated that difference in elevation, climate analogy, as well as  
454 geographical and latitudinal distances between climate analogues, were influenced by the  
455 scenario of future climate change. Specifically, it could be observed that the distance species

456 will have to travel to find the closest possible climate analogue is maximum in the case of  
457 RCP 8.5; in this scenario, climate analogy will also be lower. The most environmentally  
458 impactful scenarios thus appear to impose greater displacement to more distant and less  
459 climatically similar analogues (Littlefield et al. 2017), likely increasing the vulnerability of  
460 little mobile species. Similarly, differences in elevation and latitude were also larger in the  
461 case of RCP 8.5. This was expected as this is the most severe scenario of climate change  
462 (IPCC, 2018); our results confirm that species will most likely be impacted more strongly by  
463 the most extreme changes in climate, accelerating extinction risk for many species (Urban,  
464 2015).

465 The fact that elevation is higher and climate analogy is lower in 2070 than in 2050 shows  
466 that climate change will continue to alter species' habitats over time regardless of the scenario  
467 and habitat type considered. The movement of species to higher elevations as a response to an  
468 increase in temperature conditions has already been shown, for example in bird species  
469 (Flousek et al., 2015). Species movement to higher elevations and latitudes, however, depends  
470 on the species under consideration, with greater shifts in meridional areas (Chen et al., 2011).  
471 This result has been proven in particular on bumblebee species, which moved to higher  
472 altitudes in the southern limits but decreased in distribution in the septentrional limits (Kerr et  
473 al., 2015). Plant species, especially herbaceous, also follow a shift to higher elevations in  
474 response to climate change (Lenoir et al., 2008). However, moving to higher altitudes is not  
475 always effective, especially since the topographical configuration of mountains leads to  
476 decreasing available area at higher elevations (Elsen and Tingley, 2005). This has resulted, for  
477 example, in large losses of butterfly diversity in mountainous areas of Spain (Wilson et al.,  
478 2007). Poleward range shifts are not necessarily an easier way for species to track their  
479 climatic niche. Indeed, latitudinal range shifts often involve long-distance movements in a  
480 fragmented landscape and require all ecological requirements to be present in novel habitats  
481 (Chen et al., 2011; Devictor et al., 2012). It will therefore be important to preserve existing  
482 habitats to slow down the extirpation of cold-adapted species and to promote the migration  
483 and settlement of species in new habitats.

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

501 The effectiveness of protected areas in mitigating the effects of climate change has  
502 already been demonstrated for some species, such as breeding birds (Gaüzère et al., 2016).  
503 Generally, protected areas appear to be a good way of providing protection and climate  
504 refugia for climate-sensitive species at their trailing edge, as well as favouring the

505 colonisation of expanding species at their leading edge (Thomas et al. 2012; Gillingham et al.  
506 2015). Here, we assessed whether European protected areas were placed in locations with  
507 high climate connectivity, effectively protecting species experiencing range shifts. We first  
508 observed that some countries have significantly fewer protected areas than others, despite  
509 their large size. For example, Turkey had a much smaller surface of protected areas, compared  
510 to its total size, than most other countries (Appendix A, Figure A1). Regrettably, the  
511 Bosphorus was also the area with the largest sum of connectivity in several scenarios. There,  
512 connectivity was very strong in all scenarios without dispersal limit, but also appeared  
513 unstable because the assumption of a dispersal limit could prevent passage across the strait.  
514 Looking closely at land cover in this region, we noticed that predicted movement occurred  
515 through heavily anthropized areas. Despite the high resistance values assigned to these land  
516 cover types, it appeared to be the only possible way to go from Asia to Europe in search of  
517 climate analogues. In fact, other corridors may exist around the Black Sea that could not be  
518 modelled here because our land cover data did not encompass this region. Moreover, even if  
519 we did not consider this possibility in our models, some species could disperse through water,  
520 swimming or transported by the current; flying or wind-dispersing species may also be able to  
521 cross the short distance separating the European and Asian parts of Turkey (see e.g. Waisel et  
522 al., 2008; Martínez-López et al., 2020). However, it is likely that crossing the Bosphorus will  
523 be necessary for some species tracking their preferred climate, from Anatolia to Balkans for  
524 example. Therefore, it seems important that Turkey acknowledges its leading role in this  
525 regard, for instance by increasing its network of protected areas to promote the climatic  
526 connectivity of habitats. This could also be done by prohibiting the construction of human  
527 infrastructure in the residual natural areas, by limiting urban expansion along the coast, or by  
528 promoting the development of green spaces in the existing urban areas. The construction of  
529 ecoducts across the strait could also be a solution to remedy the difficulty of passage in this  
530 area.

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

546 It was visible from our connectivity maps that much of Central Europe has strong  
547 connectivity and stability, highlighting the high likelihood of climate-driven movements  
548 connecting southern to northern Europe. Spain and Portugal are also two countries with strong  
549 and very stable connectivity. Many protected areas are present in these regions and, generally,  
550 we showed that protection overlapped more often with areas of stable connectivity (with the  
551 exception of strict nature reserves, probably because they are mostly located in Fennoscandia,  
552 where connectivity differs a lot between habitats). However, despite some positive signs (e.g.  
553 Gaüzère et al., 2016), the ability of protected areas to truly protect climate-tracking species

554 remains uncertain. For example, there are contrasting empirical evidence of the effectiveness  
555 of the Natura 2000 network for biodiversity conservation, with demonstrated positive effect in  
556 birds (Princé et al. 2021) but not in butterflies (Rada et al., 2019). In the context of climate  
557 change, it is also important to ensure that spatial connectivity between protected areas is  
558 effectively capable of providing continuous corridors for species on the move (Caplat et al.,  
559 2016; Santini et al., 2016). It is noticeable that the number of strict nature reserves is overall  
560 very low, and even non-existent in some of the most connected areas (e.g. all central Europe).  
561 In order to fully protect these areas, it could be interesting to increase the level of protection,  
562 including more wilderness areas and national parks that we did not consider separately in our  
563 study but that confer a relatively strong protection for biodiversity. An interesting strategy  
564 could also be to deliberately implement protected areas in regions of high variation in  
565 connectivity in order to protect these areas from future, uncertain, changes. Issues regarding  
566 the location of protected areas were also observed in the United States, where most regions of  
567 high climate connectivity were not located in protected areas (Carroll et al., 2018). This is  
568 therefore a complex challenge to identify the areas that must be protected in a context where  
569 climate change drives spatial dynamics of biodiversity, especially when resources are not  
570 infinite and must be allocated carefully.

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

585

## 586 **5. Conclusion**

587 We know that global change has a major impact on the movement of species. Limiting the  
588 ongoing warming – which undoubtedly involves considerable changes in human activities – is  
589 thus crucial to limit the need for species to engage in long-distance movements to higher  
590 latitudes and elevations. The lower climate analogies between current and future habitats  
591 under the more pessimistic scenario reveals the importance of preserving climate refugia. We  
592 also demonstrated that species with limited dispersal capacity may face in the near future  
593 climatic conditions that no longer match the ones they are currently adapted to. In addition,  
594 our study showed that species living on islands will be more vulnerable to climate change  
595 because of the difficulty of dispersing to the continent. Long-term predictions of climate  
596 change are also characterised by an increase in the distance between current and future  
597 analogue climates. Reducing our impact in the coming decades could therefore help species to  
598 reach their climatic analogue more easily. Our approach also identified the most important  
599 climate corridors, in part to determine which regions should be subject to the establishment of  
600 protected areas if they are lacking such. Interestingly, we showed that pan-European climatic

601 connectivity did not differ much between different scenarios of climate change, or between  
602 connectivity modelled from now to 2050 or from now to 2070. This implies that modelling  
603 climate connectivity may be an efficient tool to predict where species could go during range  
604 shift whatever the path we take – rapid mitigation of climate change or worst-case scenario  
605 with a severe increase in temperature – and the time period considered. However, models  
606 showed important differences depending on the dispersal hypothesis. Here, we tested only  
607 two assumptions of dispersal limit (unlimited or ca. 3 km yr<sup>-1</sup>); in reality each species will  
608 disperse at its own pace, hence restructuring communities and complicating the modelling of  
609 multi-species connectivity. We also proved that even when considering no climatic  
610 connectivity between random locations, the areas of high connectivity remained broadly the  
611 same as in climate connectivity models. The protection of climate corridors is therefore an  
612 important issue both to help species reach their climate analogue and to limit extinction risk in  
613 their initial habitats. It would be possible to go further by comparing our results with  
614 historical data of bioclimatic and land use variables to determine if the climate corridors we  
615 have identified could have been identified with past data. Our results could also be compared  
616 with actual species movement data in Europe, to determine whether the identified climate  
617 corridors will actually be used in the future. Finally, the framework we used here has the  
618 potential to serve in the construction of land cover change scenarios to identify the best  
619 strategies to improve climate connectivity.

620

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628

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853 **Tables**

854

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

859

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

860

861

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

866

		All Europe			All protected area			Strong protected area		
		Sum of connectivity								
		Low	Medium	High	Low	Medium	High	Low	Medium	High
Variation of connectivity	<b>Total</b>									
	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
	<b>Forests</b>									
	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
	<b>Open semi-natural habitat</b>									
	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

867

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

871

		Limited dispersal	Full dispersal
<b>Forest</b>			
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
<b>Open semi-natural habitats</b>			
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

872

873



## 874 **Figure captions**

875

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

883

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

889

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

894

895 **Figure 4:** Bivariate maps representing the sum of connectivity and its variation (coefficient of  
896 variation), calculated for all connectivity maps merged together or for connectivity maps in  
897 forests or in open semi-natural habitats only. Areas represented in grey have no connectivity  
898 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)

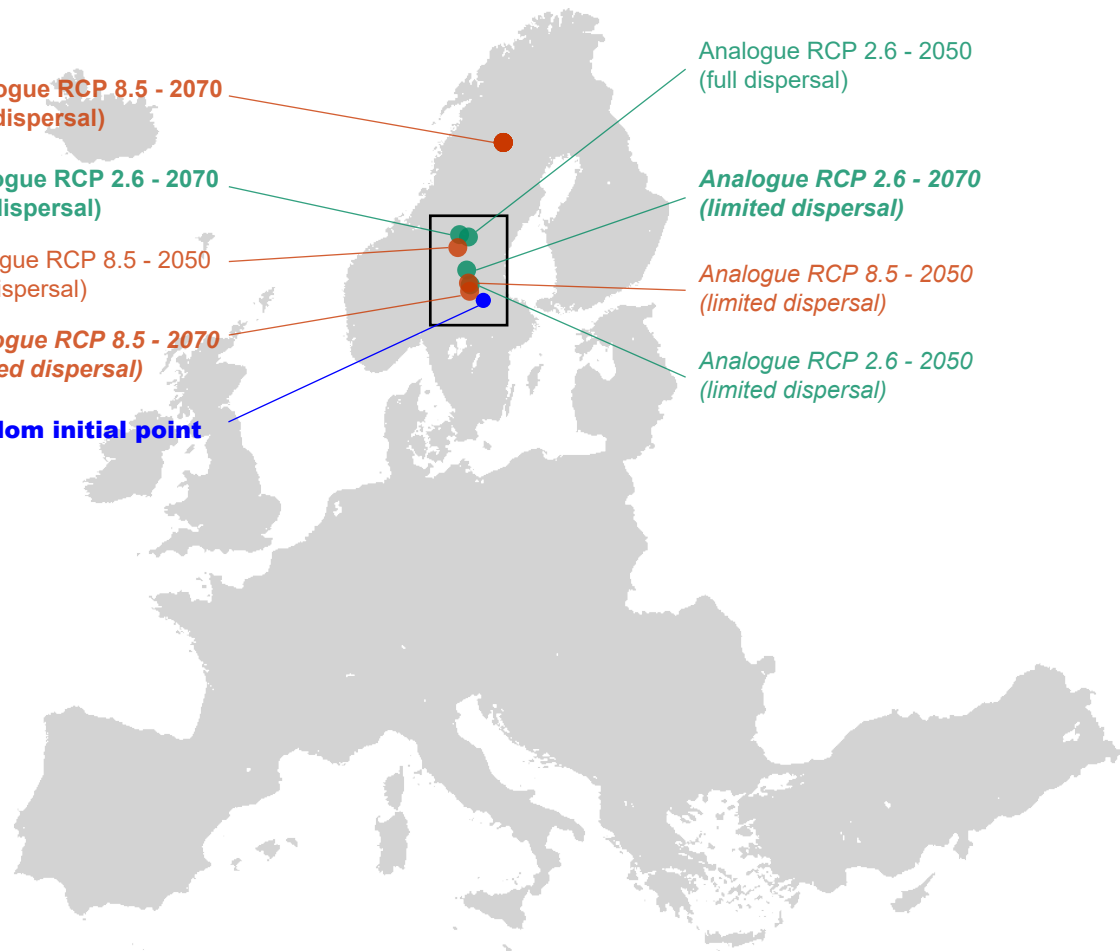
Random initial point

Analogue RCP 2.6 - 2050  
(full dispersal)

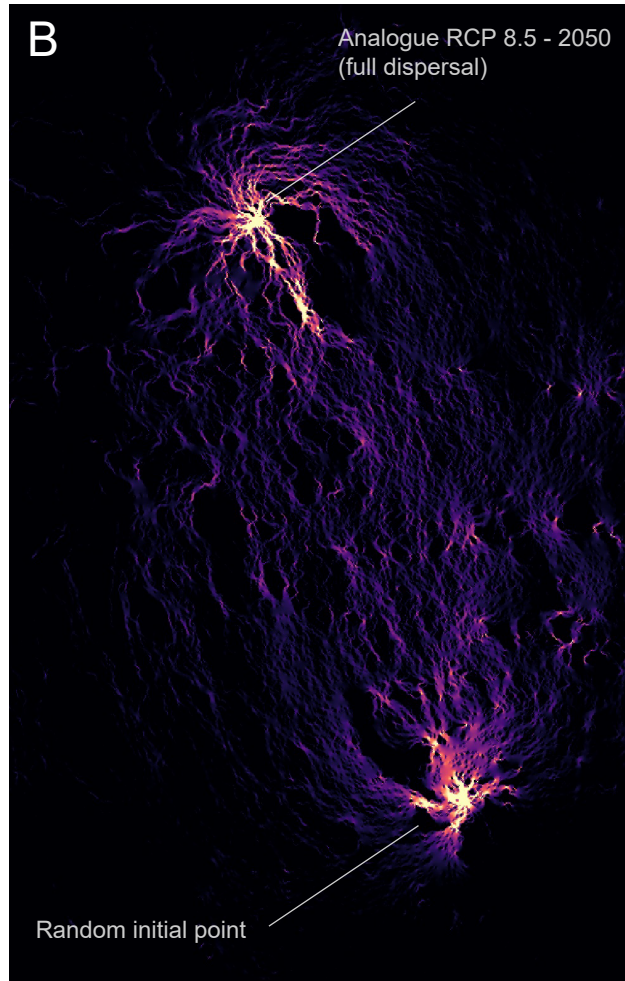
Analogue RCP 2.6 - 2070  
(limited dispersal)

Analogue RCP 8.5 - 2050  
(limited dispersal)

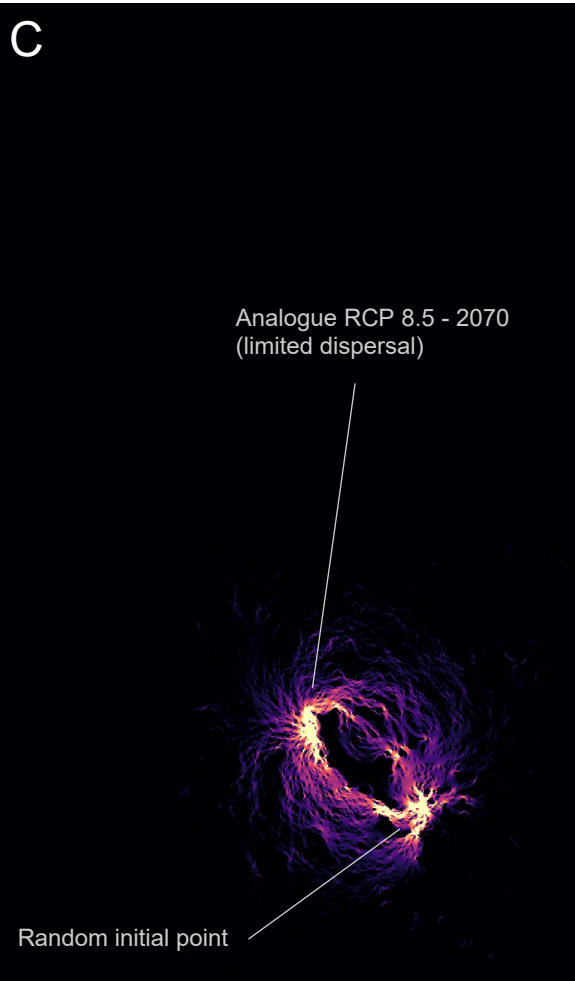
Analogue RCP 2.6 - 2050  
(limited dispersal)

**B**

Analogue RCP 8.5 - 2050  
(full dispersal)

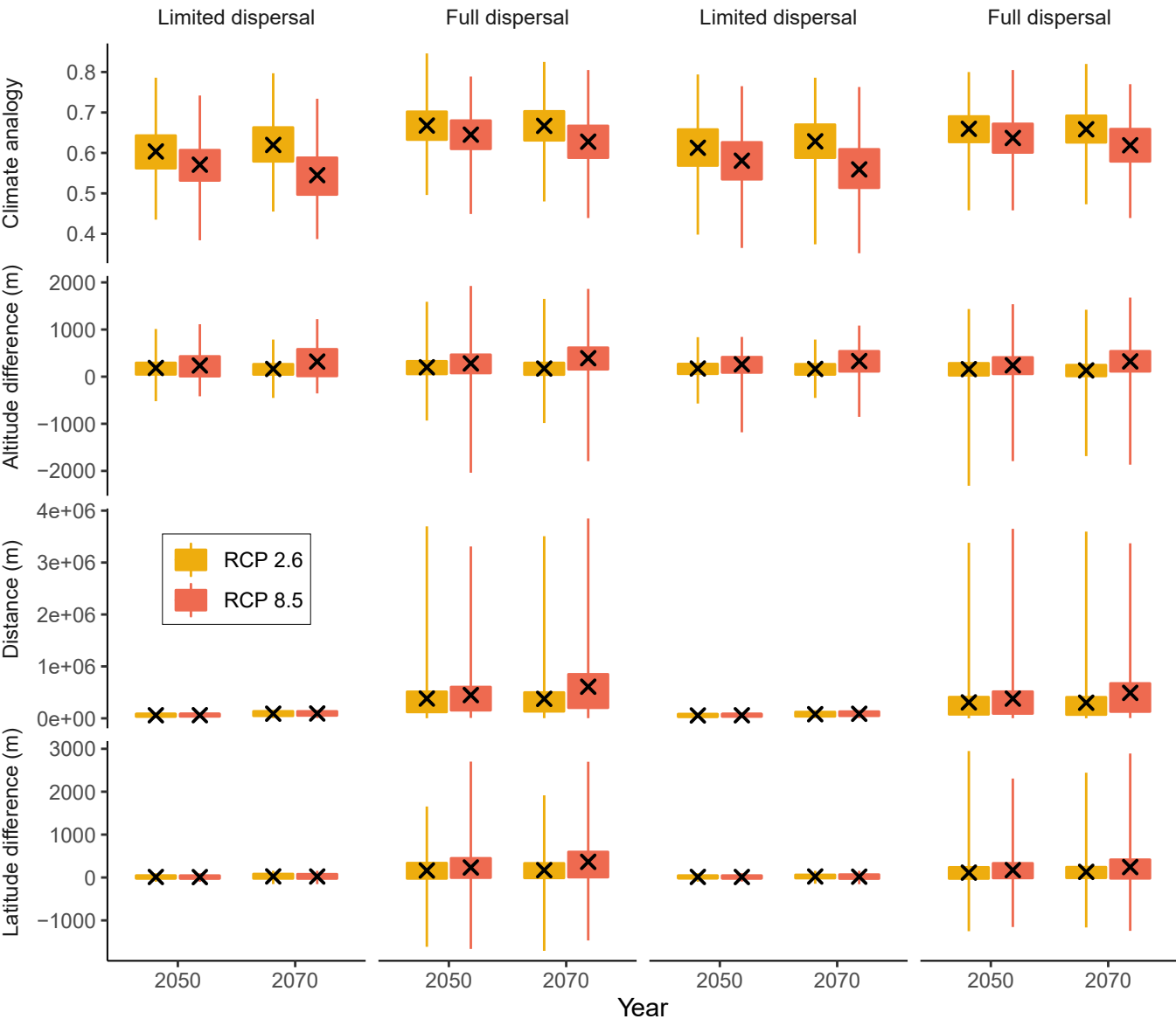
**C**

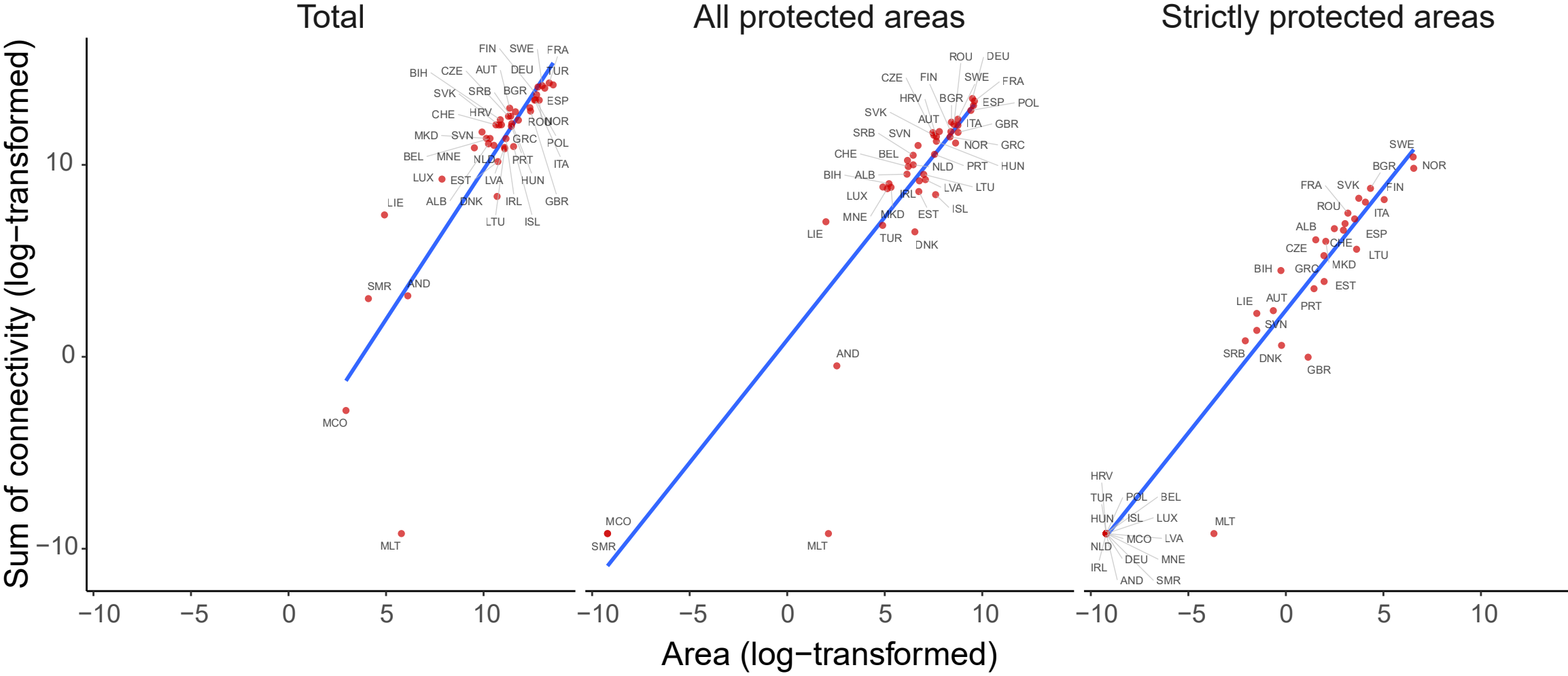
Analogue RCP 8.5 - 2070  
(limited dispersal)



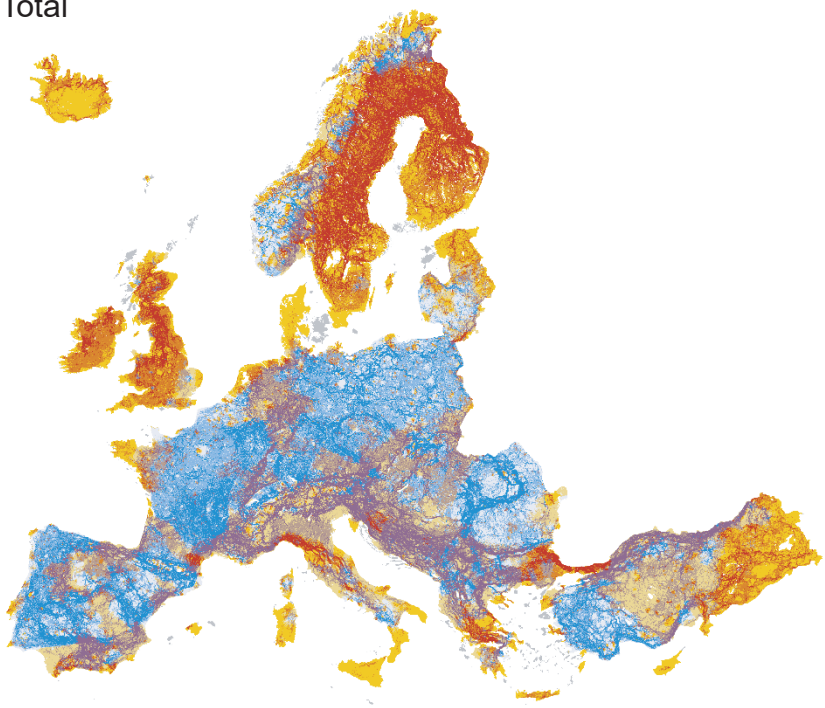
# Forest

# Open semi-natural habitat

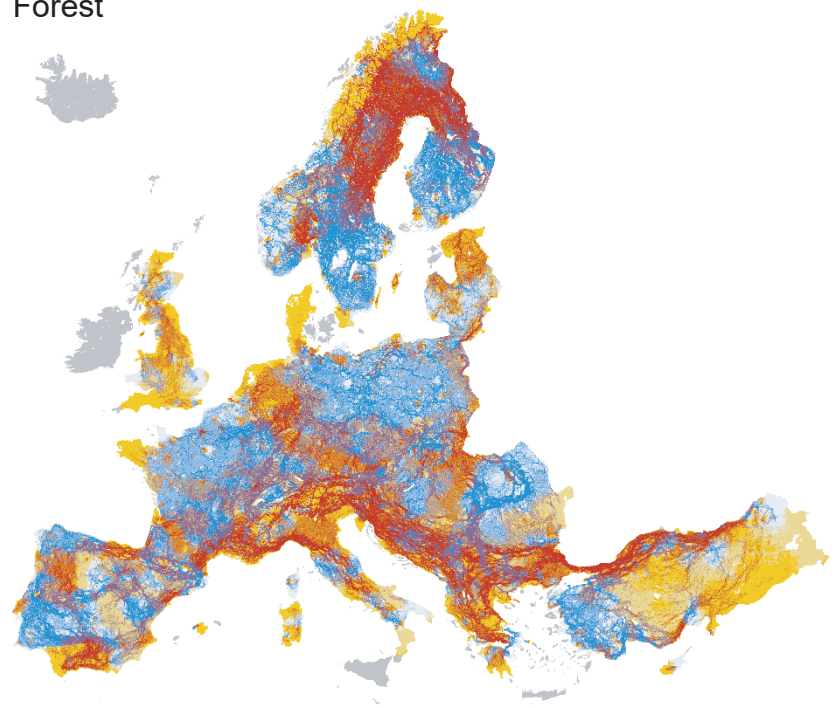




Total



Forest



Open semi-natural habitat

