

Forest Connectivity

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Forest connectivity is critical for the long-term persistence and range shifts of forest-dependent species. In the face of contemporary climate change, the climate connectivity of forested areas is one of the most important factors that determine species' ability to track suitable climate niches. Climate connectivity is defined as the degree to which a landscape allows species to shift their ranges to suitable habitats that are the same or cooler than their current habitats as the climate warms. Improving climate connectivity is both a necessary action and a viable solution to reduce the likelihood of local extinctions and biodiversity loss. This is particularly urgent considering the rapid rate of climate change, which is expected to cause large shifts in the distributions of species in European forests.

climate change

species migration

landscape connectivity

European forests

1. Introduction

Forest connectivity is critical for the long-term persistence and range shifts of forest-dependent species [\[1\]\[2\]\[3\]](#). In the face of contemporary climate change, the climate connectivity of forested areas is one of the most important factors that determine species' ability to track suitable climate niches [\[4\]\[5\]\[6\]\[7\]\[8\]\[9\]\[10\]](#). Climate connectivity is defined as the degree to which a landscape allows species to shift their ranges to suitable habitats that are the same or cooler than their current habitats as the climate warms [\[11\]\[12\]\[13\]](#). Improving climate connectivity is both a necessary action and a viable solution to reduce the likelihood of local extinctions and biodiversity loss [\[14\]\[15\]](#). This is particularly urgent considering the rapid rate of climate change, which is expected to cause large shifts in the distributions of species in European forests.

Recent climate change has driven large shifts in the geographical ranges of species across Europe, especially for those inhabiting forested areas. However, such range shifts cannot guarantee their survival if the forests are not connected enough for species to track rapid climate change. In the Southern Scandes of Sweden, for example, tree lines were found to have shifted northward due to climate warming in the 20th century [\[16\]](#). Northward shifts have also been documented in the distributions of European birds and butterflies, which have moved 37 and 114 km, respectively, over two decades (1990–2008), lagging behind climate change by 212 and 135 km, respectively [\[17\]](#). In the Cantabrian Mountains (Spain), brown bear populations in temperate forested habitats are expected to decline considerably in the next 50 years, due to the potential impact of climate change on the distributions of their main food resources and shelter [\[18\]](#). Another study by Araujo et al. [\[19\]](#) suggested that, by the end of this century, more than half of the assessed plant and terrestrial vertebrate species will lose suitable climatic conditions in European protected areas. Given these circumstances, habitat-based conservation strategies are unable to support the long-term persistence of species in European forests under climate change [\[20\]\[21\]\[22\]](#). It is therefore

important to assess the climate connectivity of forested habitats for more effective conservation and management of biodiversity across Europe.

Recently, many methods have been proposed to assess climate connectivity at regional and continental scales. Some connectivity efforts have quantified climate connectivity as the paths or speed (also called climate velocity) at which species would need to shift their ranges to maintain climate conditions similar to those they experience today [23][24]. These climate connectivity methods require an identification of the closest future climate analogues based on geographical distances. For example, Dobrowski and Parks [25] and Parks et al. [14] quantified the climate velocity across North America along climate trajectories. Littlefield et al. [4] and Carroll et al. [26] delineated potential dispersal paths between current and future climate analogues across North America and identified climate connectivity areas where species range shifts are more likely to happen.

Some other studies have evaluated climate connectivity based on an identification of the coolest destination patch that can be reached from an origin patch by traversing a gradient of hotter to cooler adjacent patches. In these studies, climate connectivity was calculated as the temperature difference between the origin patch and its coolest destination. For instance, McGuire et al. [11] created climate-gradient corridors of natural lands along temperature gradients across the United States and assessed to what extent habitat fragmentation could limit species range shifts. More recently, Senior et al. [27] used a similar method to quantify the climate connectivity of tropical forests and changes in climate connectivity between 2000 and 2012. These studies offered a simple and rapid way to assess climate connectivity at global and regional scales.

2. Identify Forest Patches

The study area covered 43 European countries for which forest-cover data were obtained from Corine land-cover datasets for the year 2018 (<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>, accessed on 22 May 2021). Three forest types were taken into account: broad-leaved forests, coniferous forests, and mixed forests. We classified the raster data of land cover to either forested or non-forested cells and resampled the forest-cover map to a resolution of 1 km. As our study considered climate change the main driver of species range shifts, the forested cells were partitioned into forest patches based on their temperatures. Climate data were obtained from the WorldClim Version 2 database [28] (<https://www.worldclim.org>, accessed on 22 May 2021). We used the annual mean temperature data at a spatial resolution of 30 seconds for the years 1970–2000 as current temperature data. We then projected the temperature data in our study area to the projection of the land-cover data—the Lambert azimuthal equal-area (ETRS_1989_LAEA) projection—and resampled them to a resolution of 1 km, using bilinear interpolation.

By overlapping the current temperature map and the forest-cover map, the forested cells were assigned to their current temperature values, which were then reclassified to 1 °C increments over a full range of –3 to 20 °C. The resulting raster data were converted into polygons to aggregate neighbouring forested cells in the same temperature increment into forest patches (**Figure 1a**). To facilitate the following computation of inter-patch distances, we removed patches smaller than 10 km². These patches may be too small to allow sufficient population

sizes for long-term persistence and range shifts [\[1\]](#). The same patch-size threshold has been used in previous analyses on climate connectivity at regional and continental scales [\[11\]\[12\]\[27\]](#).

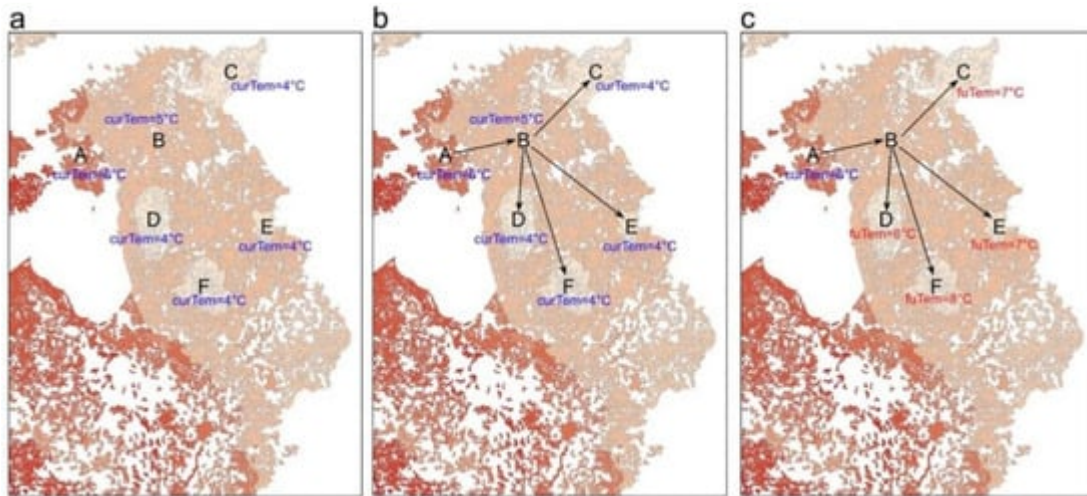


Figure 1. Illustration of our method to assess climate connectivity: (a) partitioning patches based on the current temperatures (curTem, in blue) of forest cells; (b) building directional paths from hotter to cooler patches; (c) the climate connectivity of Patch A ($-1\text{ }^{\circ}\text{C}$) was calculated as its current temperature ($6\text{ }^{\circ}\text{C}$) minus the future temperature (fuTem, $7\text{ }^{\circ}\text{C}$, in red) of its coolest destinations (Patches C and E). Therefore, patches A, B, C, and E were considered stepping stones for range shifts from Patch A to its coolest destinations along temperature gradients.

After that, each patch was also assigned a mean future temperature value for the years 2081–2100. Future temperature data were derived from the average of climate projections of eight CMIP6 Global Climate Models obtained from the WorldClim Version 2 database (namely BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0) at a spatial resolution of 2.5 min. Our study considered two emission scenarios, Shared Socio-Economic Pathways (SSPs): 245 and 585, which represent the moderate and the most severe ('business as usual') scenarios, respectively, to exhibit a likely range of future climate warming.

3. Evaluate Climate Connectivity

The distributions of terrestrial species have been found to be related to latitudinal shifts in isotherms [\[29\]](#). Therefore, our method assumed that species trace suitable climate conditions through directional paths traversing gradients of hotter to cooler patches. Patches within 2 km of each other are assumed to be connected enough for species to move across non-forest areas [\[11\]\[27\]](#). This assumption allows for an assessment of the structural connectivity between forested areas for terrestrial species to reach future habitats. In this way, the dispersal abilities of species are not considered in the study, in contrast to those studies that focus on functional connectivity [\[4\]\[12\]](#). Here, we used an ArcGIS extension, Conefor Input tool, to calculate the pairwise (Euclidean) distances between edges of forest patches within a distance threshold of 2 km.

Based on the current temperatures of forest patches, we identified directional paths between patches from hotter to cooler (**Figure 1b**), using the Python NetworkX package. We then built a directed graph with all the directional paths and used Dijkstra's method to compute the shortest directional paths between all patches in the graph. After that, we identified the coolest destination in the future that can be reached from each patch as a designated destination for the origin patch (**Figure 1c**). For patches that are not connected to cooler neighbours, their destinations were assigned as themselves.

According to the definition of climate connectivity, our study aimed to measure the extent to which European forest cover allows species to reach suitable habitats that are the same or cooler in the future than the temperatures they currently experience. To this end, climate connectivity can be measured as the maximum temperature difference between each patch and its destinations along temperature gradients. More specifically, the climate connectivity of each forest patch was calculated as its current temperature minus the future temperature of its coolest reachable patch. Higher values indicate better climate connectivity. Zero or positive values of climate connectivity suggest a success to achieve enough connectivity for climate-driven range shifts, while patches with negative values indicate a failure at achieving climate connectivity.

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