UNIVERSITY OF MONTPELLIER – MONTPELLIER SUPAGRO

Master "Biodiversity, Ecology, Evolution, B2E"
Specialisation "EcoSystemS"

M2 Internship Research Project:

Assessment of the climatic connectivity of the protected area network in Austria

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Abstract
Species must track their suitable climatic envelopes in a changing environment to persist across time and space. Conservation areas may provide habitat suitable for colonization under altered conditions but may be hard to reach due to human influences on the landscape. A protected area (PA) network should thus ideally guarantee connectivity in the sense that it provides intact habitat along climatic gradients, in order to facilitate species migration to places with analogous climates in the future. Here, we assess the effectiveness of the current Austrian PA network regarding its climatic connectivity for its current endemic biodiversity in the face of future climate change, by using gradients of temperature. We further apply a cost-distance algorithm combined with temperature data and a map representing organisms' movement resistance to design new spatial corridors for facilitating species movement between PAs. Finally, we use indicators to quantify both current connectivity and its potential improvement by the new corridors. Overall climate connectivity of the Austrian PA network currently reaches 60% and corridors could further improve it by about 13%. 50 endemic species could additionally move to suitable future climates through new corridors, particularly in mountain areas. These results will support a potential revision of conservation strategies in Austria in the face of climate change.

Keywords: Austria, climate change, connectivity, corridor, protected area network

Acknowledgments
The success and final outcome of this project required a lot of guidance and support from many people and I am extremely privileged to have got this all along the completion of my Master thesis project.

I would like to express my gratitude to Professor Stefan Dullinger for providing me an opportunity to do this research work. His patient guidance and useful suggestions during the development of this research work helped me in successfully completing this project.

I would also like to thank Dr. Philipp Semenchuk, for his enthusiastic encouragement, advice and assistance in keeping my progress on schedule. His willingness to give his time so generously has been very much appreciated.

My grateful thanks are also extended to Dr. Dietmar Moser for his help in spatial analysis and to Mr. Andreas Gattringer, without whom I would not have been able to overcome the many computer difficulties.

I would not forget to remember Dr. Christoph Plutzar for providing such a nice support and assistance in mapping wilderness continuum.

Special thanks to the staff and also the master students of CVL department for their communicative cheerfulness and kindness.

1. Introduction

Climatic and physical environments shape the niche of species and are major determinants of species' geographical distribution, at least at a regional scale (Soberón, 2005). As a consequence, climate change forces species to adapt either their niches or their ranges to the altered distribution of suitable sites (Parmesan & Yohe, 2003; Jump & Peñuelas, 2005; Atkins & Travis, 2010; Hill *et al.*, 2011; Hoffmann & Sgró, 2011). Indeed, climate-driven range shifts have already become widespread during the recent decades (Maclean & Wilson, 2011; Chapman *et al.*, 2014) with movements to cooler environments, i.e. towards higher elevations and latitudes (Root *et al.*, 2003; Parmesan & Yohe, 2003; Pauchard *et al.*, 2016). For instance, Lenoir *et al.* (2008) have shown a significant upward shift (26 m/decade) of European forest plant species, which is even more pronounced in species of mountain forests. Considering that the rate of projected climate change is expected to accelerate in the future (IPCC, 2018), species will have to migrate even further and faster to avoid a decline in population size or even extinction (Schloss *et al.*, 2012). Whether such fast migration is possible will depend, among other things, on the occurrence and frequency of topographical, ecological and anthropogenic obstacles to movement (Keeley *et al.*, 2018). In other words, the spatial configuration of habitats will be of crucial importance for successful acclimatization of species ranges to the changing climate. Human habitat fragmentation reduces connectivity and is hence considered a major constraint on species range shifts (McGuire *et al.*, 2016; Keeley *et al.*, 2018).

Connectivity is a tricky concept as it is used for different purposes and at different scales (Hannah, 2011). Tischendorf and Fahrig (2000) give a broad definition of connectivity: the degree to which a landscape facilitates the movement of organisms. Authors distinguish between functional connectivity, i.e. the movement capability of an individual species, and structural connectivity resulting from landscape features (Uezu *et al.*, 2005; Fischer & Lindenmayer, 2007). It is generally agreed that connectivity is crucial for biological conservation (Taylor *et al.*, 1993) and that its improvement could prevent biodiversity loss if connectivity is achieved between habitats of conservation concern (McGuire *et al.*, 2016). In a climate change context, connectivity may become even more crucial as it not only facilitates the exchange of individuals and genes among habitats but also allows species to track their niches. Keeley *et al.* (2018) have highlighted that connectivity between protected areas could be particularly effective fostering climate-driven range adaptation as protected areas per se facilitate both colonization and movement of species (Thomas *et al.*, 2012). However, to be efficient when the climate warms, connectivity must not only overcome habitat fragmentation but also compensate for the increase of temperature, i.e. connected habitats should be arranged along a temperature gradient that allows species to move towards sites that will have a similar climate in the future as their current environment has today. This specific case of connectivity has been called 'climatic connectivity', defined as "whether the spatial configuration of natural lands allows species to track their current climatic conditions during projected climate change" by McGuire *et al.* (2016). In the context of spatial conservation planning, this definition can be reformulated as the requirement that PA network should be designed such that the protected species should be able to track their current climatic conditions via movement through this network. Where existing networks do not fulfil this requirement, adding appropriate corridors between them may be necessary.

Conservation policies set legal acts and standards for ecosystems (Penker, 2009) and are carried out within protected areas, at local, national and international scales (IUCN, 1994). PAs are geographical areas recognised, dedicated and managed through a legal framework to achieve the long-term conservation of ecosystems (Dudley, 2008). The International Union for Conservation of Nature (IUCN) classifies Protected areas (PAs) into six management categories, if at least 75% of their surface corresponds to the following definition: strict nature reserve (Ia), wilderness area (Ib), national park (II), natural monument or feature (III), habitat/species management area (IV), protected landscape or seascape (IV) and protected areas with sustainable use of natural resources (V). In Austria, over 28% of the terrestrial area, scattered across 1546 sites, is considered protected (UNEP-WCMC, 2018). These areas are mainly forest ecosystems, as 40% of the country is covered by forest, mostly in the western Alpine region of the country. However, whether this current network of protected areas is designed to maximise species survival in a climate change context is unknown.

This research project is part of a wider national 3-year program "Conservation under Climate Change: Challenges, Constraints and Solutions" funded by the Austrian Climate Research Programme (ACRP) – Climate and Energy Fund, and in partnership with the Environment Agency Austria. The aim of this program is to rethink conservation strategies and paradigms in the presence of climate change in order to suggest modifications to existing strategies to render them functional in future environmental conditions. In this context, my master thesis focuses on evaluating the climatic connectivity of the Austrian PA network. Austria is a suitable country for this type of analysis as it exhibits both regions with strong altitudinal gradients and flat regions. We first ask to what extent the spatial connectivity of the current PA network will allow species, in particular animal and plant species endemic to the country, to track their suitable climate in the face of climate change. Then, we evaluate whether and to which degree the design of new corridors among existing protected sites could improve the climatic connectivity of the network.

We determined connectivity among PAs by connecting land patches of analogous temperature, considering present and future climate projections. We run least-cost distance modelling combined with a resistance map to design efficient corridors and to estimate improvements made in achieving climate connectivity. Adopting a set of indicators based on cost, length and endemic species distribution, we finally identified areas in Austria where implementing ecological corridors would be most effective in improving climatic connectivity.

2. Methods

The study area includes all of Austria buffered by 27 km into all neighbouring countries (Switzerland, Slovenia, Germany, Italy, Hungary, Slovakia, Czech Republic and Liechtenstein) in order not to artificially increase the fragmentation of PAs that straddle several countries. The area is characterized by a set of climatically rather homogeneous ecological regions, ranging from humid continental in the eastern parts of the country, oceanic in the west and the east, to subarctic and glacial climates at high elevations, according to the Köppen classification updates (Peel *et al.*, 2007). Two-thirds of the country's area are occupied by the Alpine arc with elevations up to c. 3800 meters above sea level.

All spatial analyses were performed at a resolution of 100 m on ArcGIS software (ESRI, 2018) and R (R Core Team, 2018) with maps projected into European Terrestrial Reference System 1989 (ETRS89) Lambert azimuthal equal-area projection. An outline of all methods is provided in Appendix Fig. 1.

Temperature Data

The climatic niche of species is a multi-dimensional ecological space including various aspects of temperature and precipitation, the temporal distribution of these variables as well as the absolute value and timing of extremes (Littlefield *et al.*, 2017; Carroll *et al.*, 2018). Moreover, the importance of these different aspects for determining the geographical distribution of individuals varies from species to species. However, here, we do not want to characterize climatic connectivity in a species-specific way (Hunter *et al.*, 1988; Nuñez *et al.*, 2013) but rather want to provide a general framework applicable across a large number of species across taxonomic groups. Moreover, the approach should be comprehensible of for stakeholders and conservation managers. We hence decided to base climate connectivity calculations on one single variable that characterizes site-specific temperature regimes as comprehensively as possible and selected mean annual temperature for this purpose as current temperature map. We used the annual average temperature layer from WorldClim (Hijmans *et al.*, 2005) based on an interpolation of observed data from 1960 to 1990 and downscaled from 30-second resolution to 100-m resolution. Future temperature projections for every decade from 2030 to 2080 were provided by the EURO-CORDEX project, using the ALADIN-Climate regional climate model (Tramblay *et al.*, 2013) under three RCP scenarios (RCP2.6, RCP4.5 and RCP8.5). Original data provided by EUR-CORDEX were again statistically downscaled to 100-m resolution using the approach described in Dullinger et al. (2012), resulting in 18 different temperature grids (six decades x three scenarios).

Partitioning Protected Areas into Climatic Patches

The protected areas network encompasses all zones nominated for the Natura 2000 program and ICUN categories Ia, Ib, II and III (Dudley, 2008) encountered within the study area. Due to spatial processing, very small PAs (area below 0.01 km²) and PAs narrower than 100m have been deleted. In total, we thus worked with 1849 PAs covering 19% of the study area.

All PAs were subdivided into climatic patches, i.e. areas in which all 100 x 100 m pixels have the same temperature to deal with thermal variability within each PA (Appendix Fig. 2). Before building climatic patches, we smoothed the temperature values of individuals pixels by calculating, for each pixel, the average temperature of all neighbouring pixels in a 500 m radius window. This smoothing step prevents isolated extreme pixels from becoming very small patches containing only themselves. Smoothed temperature values were then rounded to the nearest integer, creating 7530 homogenous local patches with 1°C increment across all PAs within the study area. Rounding to next integer avoids undue influence of minor temperature differences that are unlikely to trigger species range shifts (Parmesan, 2006).

Connecting climate analogous patches

As the climate is predicted to warm (IPCC, 2018), species will have to move towards places which have their current temperature in the future (climate analogues). We sought to identify the coldest patch, subsequently called destination patch, from all those having an analogous or even colder climate in the future than the source patch has today. Destination patches could be reached by the source patches' organisms via migration, but only if the path from the source patch only includes adjacent patches with decreasing temperatures because this path would be the most likely path to take, i.e. organisms will most likely migrate along a catena of monotonically decreasing temperatures (Littlefield *et al.*, 2017). This ensures that the path to a destination patch only contains intermediate forms of the future climate analogue as climate change progresses. To identify the destination patch, we built a table of adjacent patches in ArcGIS and then applied the R script provided by McGuire et al. (2016) to perform a temperature propagation network.

Assessing climatic success

A source patch is considered as successfully-connected under a particular climate change scenario if it is linked to, through the temperature propagation network, a destination patch which will, in the future, have a temperature as cool or cooler than the source patch has today.

To measure climatic success, we calculated the difference between the current temperature of the source patch and the future temperature of the destination patch, called margin of success or failure ($Margin = T_o^c - T_d^f$) (McGuire *et al.*, 2016). As the future temperature of the destination patch is considered suitable only if it is equal or lower than the current temperature of the source patch ($T_d^f \leq T_o^c$) , a positive value means success, i.e. the source patch has access to a destination patch with a future climate analogue, whereas a negative value implies no success. We considered not only strictly equal but also lower temperatures as suitable because this implicitly ensures that the source patch will have access to a climate analogue, i.e. a site with equal climate, on its way to the destination patch as the path is monotonic.

We first measured climatic connectivity at the level of climatic patches and then weighted the resulting, patch-specific margin of success-values, by patch area to assess the percentage of the entire area within the PA network achieving climatic connectivity, under the three RCPs scenarios and for the six decadal time steps.

Landscape Resistance Surface

We sought to measure how much the ability to achieve climatic connectivity would be improved by implementing corridors between PAs, i.e. through areas outside of the PA network. These corridors were designed to connect source patches of one PA with future climatically analogous (or colder) destination patches within other PAs. They had to fulfil two basic criteria: temperature has to decrease monotonically along the corridor while simultaneously minimizing accumulated resistance. Resistance represents the difficulty or mortality risk associated with movement through the landscape (McRae *et al.*, 2012), determined mainly by anthropogenic alterations of natural conditions. Although this definition is not necessarily relevant for species adapted to urban or other man-made ecosystems (Menke *et al.*, 2011; McDonnell & Hahs, 2015), it is useful for most of the species protected through PAs as they are usually bound to remnants of semi-natural habitats. Moreover, human modifications are also relevant factors when establishing corridors of newly protected land in the landscape, e.g. highly productive farmland might be too valuable to be used as a corridor for species protection. Indeed, anthropized areas are not conducive to the building of wildlife corridors, as it is not easy displacing human populations and activities from a technical and economic point of view.

Based on these considerations, we decided to use the wilderness continuum map produced by Plutzar et al. (2013) to quantify a landscape's resistance to species movement. The map combines weighted path-distance models from anthropogenic point features characterizing three aspects of wilderness (remoteness from settlement, remoteness from access and apparent naturalness) and Corine landcover classes, an indicator of biophysical naturalness. All inputs were assigned weights based on their degree of wilderness, with values ranging from 1 to 5 (low to high) based on expert opinion. Knowing that combination of variables and weighting parameters were done without systematic methodology and may, therefore, be inappropriate (Wade *et al.*, 2015), a sensitivity test has been performed to assess the uncertainty of the model by adjusting the initial weights using a random re-sampling. In the final resulting map, the wilderness continuum is mapped on a scale from 0 to 1 (low to high) at a 100-m resolution across Austria but does not extend beyond its borders (i.e. into the 27 km buffer zone). Nevertheless, we were able to easily rebuild the map to adapt it to the dimensions of our study area since the input data were available for a larger geographical extent. We then reversed the index by subtracting values from 1 and multiplied them by 100 to get a map depicting human modifications and thus measuring how the movement of species is impeded (Appendix Fig. 3).

Corridor network creation

We applied a least cost-distance model through the Linkage Mapper Toolbox (Kavanagh *et al.*, 2013) in ArcGIS applying the “Climate Linkage Mapper” tool to build corridors between climatic patches. Climate Linkage Mapper assigns a cost to each pixel by considering a climatic layer and a surface representing the resistance to movement and finally identifies the link between two isolated patches with the lowest cumulative cost to create a network of least-cost corridors. Single pixel costs are defined by Nuñez et al. (2013) and take into account for neighbouring pixels, temperature and resistance values (detailed in Appendix Fig.4).

We used the first assessment of the ability to achieve climatic connectivity considering only adjacent patches (see *Assessment of climatic success* above) to identify climatic patches that fail at least once over time and climate scenario. We performed the corridor network creation process on those climatic patches (5295 out of the 7530 initial PAs pool), using the current temperature map and the adjusted wilderness continuum map (Appendix Fig. 3) as input data.

We restricted corridors to patches at least 200 m and no more than 10 km (in Euclidean distance) apart to guarantee consistency with the realities of conservation programs. Patches were allowed to become connected only if their temperature difference is greater than 1°C. We assigned a temperature-distance weight of 50km per 1°C following recommendations in Nuñez et al. (2013). The corridor network calculation delivered a network of 31743 corridors where corridors found exclusively within the same PA were removed, as there would be no physical sense in building a corridor in an already protected zone. We applied a filter through an R script to only retain corridors with strictly monotonically decreasing temperatures and which were shorter than 10 km (Appendix Fig. 5), ending up with a final set of 11086 corridors. We used an output table describing the source (warmest) and destination (coldest) patches for each corridor, as well as their cost and their length to update the temperature propagation network previously built (see *Connecting climate analogous patches* above). We finally repeated the calculation of climatic success including corridors. However, we did not account for corridor area when calculating the percentage of the PA network climatically connected with new corridors in places because (i) we did not set a corridor width and hence could not compute corridor area and (ii) to avoid an artificial increase in this percentage.

Assessing Corridor Efficiency

We sought to assess corridor efficiency in terms of ecological value and physical building realities. For this purpose, we overlaid the geographical and elevational distribution of plant and animal species endemic to Austria (Rabitsch & Essl, 2009) with a digital elevation model to identify the potential pool of endemic species in each individual PA (Appendix Fig. 6). As the initial species set was quite large, we preferred to keep only the species for which we had accurate, reliable and up-to-date knowledge. Consequently, we worked only on plants and insects (excluding *Apterygota* sub-class), resulting in a subset of 513 endemic species.

We determined to which PA a particular source patch belongs and assumed that the number of endemic species capable of taking a corridor that links this source to a climatically analogue destination patch in a different PA was equal to the number of endemic species present in the entire source PA. This assumption is quite coarse since all organisms living in the same PA may not be able to reach the corridor if they have to cross colder or warmer zones within the PA. We consequently defined this measure as the maximal number endemic species climatically connected via corridors.

We produced an overall corridors' ranking ranging from 1 to 11086 considering their length, their cost given in a table after running Climate Linkage Mapper, and their endemism content, i.e. the maximum number of endemic species they would climatically connect. The top corridors are short, cost-effective and can be used by many endemic species.

3. Results

Climatic connectivity success

Overall, more than 65% of the Austrian PAs network achieve climate connectivity without any conservation efforts being necessary in 2030, regardless of climate scenarios (Appendix Table S1). Nevertheless, this percentage gradually decreases over the years except for RCP2.6 to reach only 38% in 2080, under RCP8.5 (Fig. 1C and Appendix Table 1). Including corridors strengthens PAs network climate connectivity success by 12% overall (Table S1) over the years and across all RCP scenarios, to peak at 85% in 2030 for both scenarios RCP2.6 and 4.5. This is however not sufficient to maintain half of the network climatically connected by 2080 in the most pessimistic climate scenario RCP8.5 (Fig. 1C).

At a glance, there is a strong contrast between the Alpine arc region in the western parts of Austria, where climatic connectivity is achieved in most cases, and lower elevation and flat regions in the East, where corridors foster connectivity importantly or where connectivity is not achieved even with newly designed corridors (Fig. 1). In particular, the large mountainous PAs located in the Alpine arc and partitioned into several climatic patches do not need corridors to achieve climatic connectivity, regardless of climate scenarios. On its eastern border, the PAs of Wienerwald and Thermenregion are also successfully connected to future analogous climates as is the Boletice Natura 2000 in the northern continental climatic region, except for RCP8.5 (Fig. 1C). Many small PAs from Bavaria and Northern Tyrol, improve their climatic connectivity success through corridors connecting them to higher elevation and colder PAs towards the higher parts of the Alps south of them. Major improvements due to corridors especially occur in the eastern part of Austria, in the federal state of Burgenland and the buffer area shared with Hungary, Slovenia and Slovakia. Large PAs from this region, such as the Neusiedler See-Seewinkel National Park (Austria) or the Őrség National Park (Hungary), are able to reach suitable future temperatures since they are linked to Wienerwald – Thermenregion – Schneeberg – Rax areas, hosting a greater range of cold temperatures due to their higher elevation. However, these climatic connections decrease from 13% to 8% when moving from RCP2.6 (Fig. 1A) to RCP8.5 (Fig. 1C).

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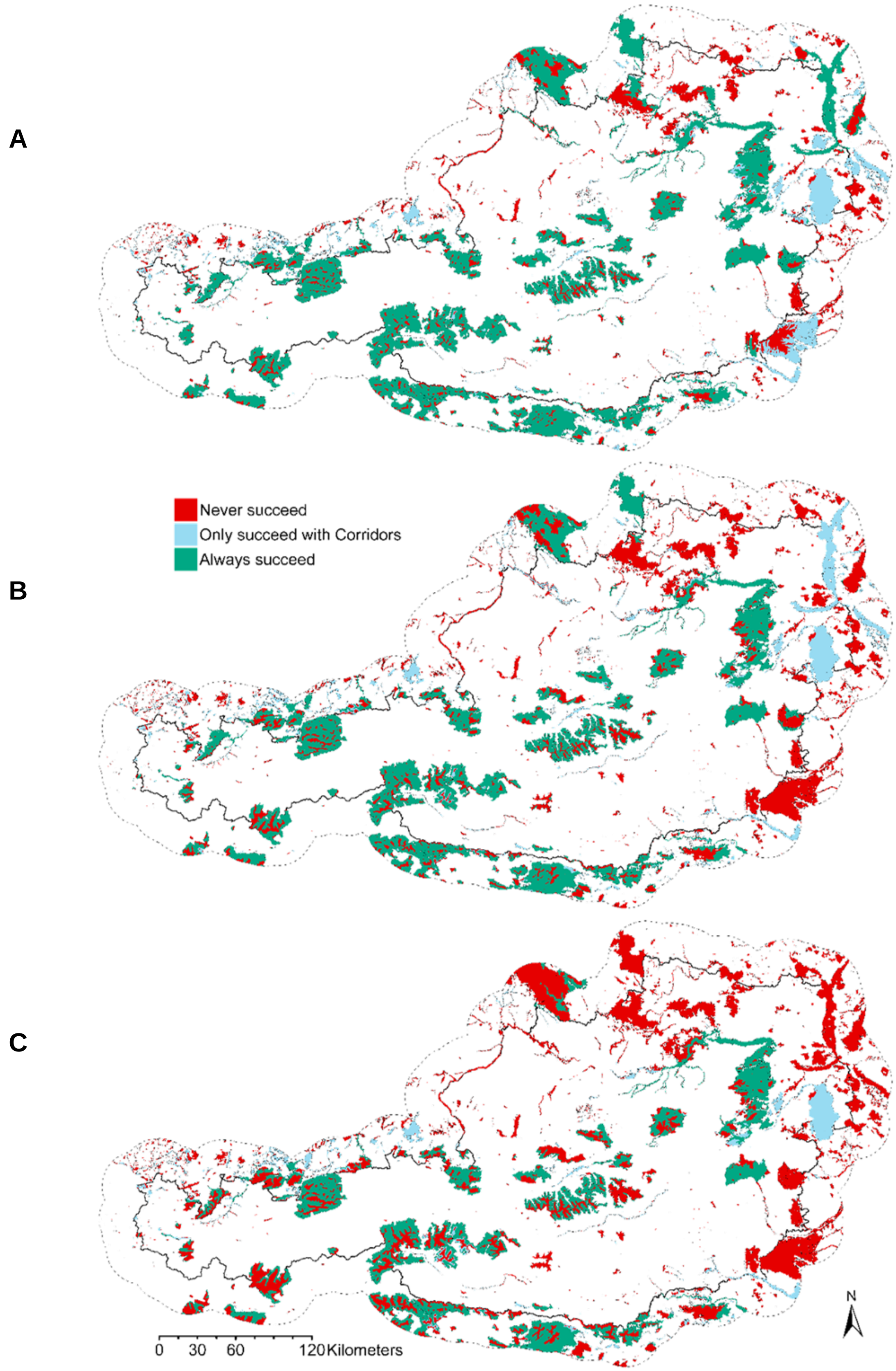

Figure 1: Climate connectivity of the Austrian protected area network with respect to the climate of the year 2080 and its improvement by newly designed corridors. Panels A, B and C represent results achieved under climate scenarios RCP2. 6, RCP4.5 and RCP8.5, respectively.

The low-elevation Burgenland region also hosts most PAs that never succeed in achieving climatic connectivity by 2080, even when including corridors. A more detailed look reveals that inside the coldest areas of the mountainous PAs in the Alpine, i.e. highest mountain tops, systematically fail. The failure zones widen by expanding to lower altitudes as the intensity of climate change increases (Fig. 1).

Quantitative values of the margin of success or failure metric are centred around 0°C (Fig. 2). Adding corridors induces a shift in the distribution towards the right, i.e. towards positive values (Fig. 2), thus increasing the frequency of success and overall climatic connectivity. Paired t-tests confirmed that this shift represents a significant increase in the mean margin of success value with corridors (0.92°C higher on average, p-value < 2.2e-16). High negative and positive values are also more frequent with corridors, resulting in a slightly more dispersed value distribution. With time, differences in the margin of success values between climate scenarios increase (Fig. 2 and Appendix Fig. 7) with peaks of value distribution shifting increasingly towards negative values under the more pronounced scenarios. Around 10% of the PAs network are connected to a patch having the exact same temperature in future (Fig. 2 and Appendix Fig. 7), regardless of the year and climate scenario considered. Those zero difference patches are most endangered of losing climatic connectivity under further warming and are particularly frequent in two types of regions: (i) the eastern part where corridors contribute most to improving climatic connectivity such as the Neusiedler See-Seewinkel National Park (Austria) or the Őrség National Park (Hungary), (Appendix Fig. 8A and C; Fig. 3) and (ii) within mountainous PAs, the second and/or third coldest zones, just below the summits (Appendix Fig. 8).

Corridor Efficiency

Corridor efficiency was evaluated by a combination of three different metrics, corridor length, corridor cost, and the (maximum) number of endemic species that become climatically connected via this corridor. Sorting corridors by length (Fig. 3A) does not reveal geographical grouping since short and long corridors are often co-occurring in neighbouring sites. Corridor cost here refers to a combination of temperature gradients and human-induced resistance to species movement combined into an arbitrary unit by the Climate Linkage Mapper algorithm. Although this indicator does not represent the financial cost at all, the metric is indicative of areas where corridors will be unlikely to become realized due to strong human impacts and hence competing interests. As shown in Fig. 3B, there are many small centres of high-cost corridors throughout the study area, corresponding to local high-resistance features such as roads and cities (Appendix Fig. 3). On the other hand, there is a homogenous distribution of low-cost corridors among the study area with no particular hot spots emerging (Fig. 3B). As expected, corridors conductive to most endemic species are those connecting mountainous PAs, such as the Hohe Tauern National Park, straddling Carinthia, Tyrol and Salzburg states or the Nordöstliche Randalpen Natura 2000 site, West of Vienna (Fig. 3C). Indeed, most endemic species of Austria are found at high elevation ranges (75% of endemic species have a minimum range margin of ≥ 1356m). Corridors found in the areas furthest from the Austrian border, e.g. south Bavaria (Fig. 3C), support the movement of very few endemic species. However, 14% of the total PA network (1087 PAs) mainly found in this buffer area did not have available endemic species distribution data. Despite the real preponderance of endemic range in the higher parts of the Alps, data deficiency may have additionally biased this indicator in disfavour of the marginal areas of the country.

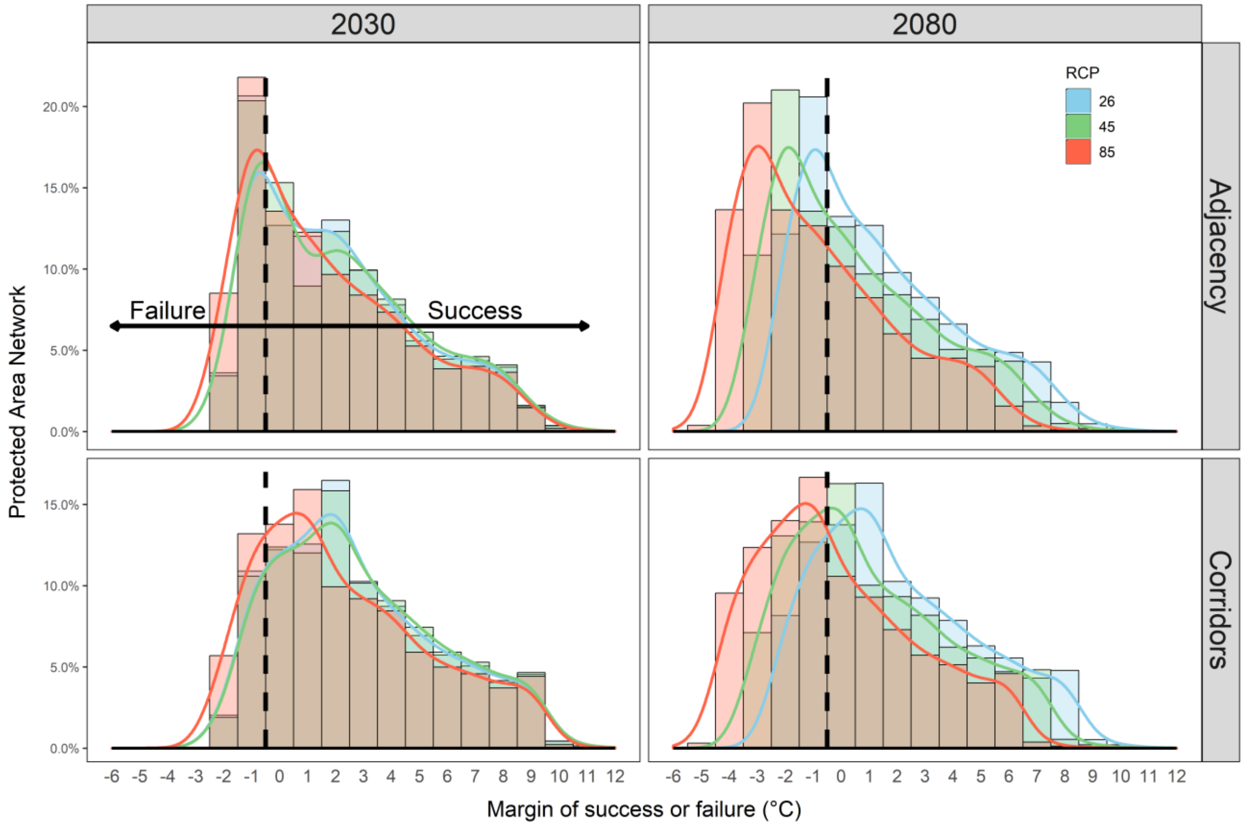

Figure 2: The margin of success or failure at achieving climate connectivity, given various climate scenarios, with and without corridors. The margin is defined as the difference between the current temperature of the origin patch and the future temperature of the destination patch ($Margin = T_o^c - T_d^f$) (McGuire *et al.*, 2016). Consequently, climate connectivity is achieved with positive margins, whereas negative margins are synonymous of failure. Margin distribution and density (A) are shown for years 2030 and 2080 under three climate scenarios (RCP2.6, 4.5 and 8.5) without ("Adjacency") and with ("Corridors") newly established corridors.

Most efficient corridors, based on a combination of criteria, seem to be mainly located in the central parts of Austria, especially in central Alpine region (Niedere Tauern, Hohe Tauern National Park) and its eastern border (Nordöstliche Randalpen). Incidence of efficient corridors is lower in the northern continental area (Waldviertel); in the west-southern region straddling with Slovenia (Pohorje); and finally, in southern Bavaria (Naturschutzgebiet Allgäuer Hochalper, Karwendek mit Isar). Interestingly, low-efficiency corridors can share location with very efficient corridors, e.g. in the south of Bavaria and Pohorje regions, supporting the importance of the actual and local path and delineation of the corridors.

Endemic Species and Climate Connectivity

We defined the number of endemic species per PA that achieve climate connectivity as the number of unique endemic species found in patches that achieve climate connectivity within a PA. On average across decades and scenarios, adding corridors increases the pool of endemic species that achieve climatic connectivity by at least one species in 15.2% of the PA network area distributed among 329 PAs (Appendix Table 2). The maximal gain is reached in 2080 under RCP4.5 where 23% of the PA network area fulfil the above criterion and corridors increase climate connectivity of the network by 12% up to 64% (Appendix Table 1). Again, corridors are most efficient in increasing climatic connectivity for endemic species in the flat eastern part of the study area. However, there are also several Alpine PAs, for both small and large PAs (Fig. 4 and Appendix Fig. 8) which profit from corridors in terms of linking more endemic species to analogous climates of the future. Obviously, these PAs largely correspond to those experiencing improvements of climatic connectivity with corridors independent of whether they harbour endemic species or not (Fig. 1B). Among the subset of PAs where corridors increase the number of endemic species climatically connected, those climatically homogeneous profit most from the corridors (Appendix Fig. 2). To pinpoint this trend, we performed a Poisson regression of species number climatically connected due to corridor establishment per PA as response variable, and the total and climatically connected number of climatic patches within the PA as well as decade and climate scenario as predictor variables. All terms had a significant influence on the gain (p-values < 0.05). The regression indicates that the estimated gain in climatically connected endemic species in a PA is multiplied by 0.96 (decrease of about 4%) when the PA has an additional climatic patch, while it increases by about 7% with each additional climatically connected patch.

On average, across all PAs, newly established corridors allow three additional endemics to achieve climate connectivity. However, 260 PAs (9% of the PA network area) only have one endemic in its current potential species pool (Appendix Fig. 6). To get around this calculation bias, we transformed counts in percentage, i.e. we calculated the number of endemic species that become climatically connected by corridors as a percentage of the total pool of endemics per PA. This transformation demonstrates that while the absolute number of species climatically "rescued" by corridors is often low (Appendix Fig. 9A) these species in several instances represent the entire endemic species pool of a PA (Appendix Fig. 9B). A more detail look at the absolute number of species gained (Box in Fig. 4) depicts that corridors have the greatest value when climatically connecting patches in the valleys of mountainous areas with up to about 50 endemic species "rescued" in Niedere Tauern mountain range.

We finally categorized Austrian PAs into size classes (large – medium – small – very small) with class limits based on logarithmic quantiles of the area (see Fig. 5). This distinction

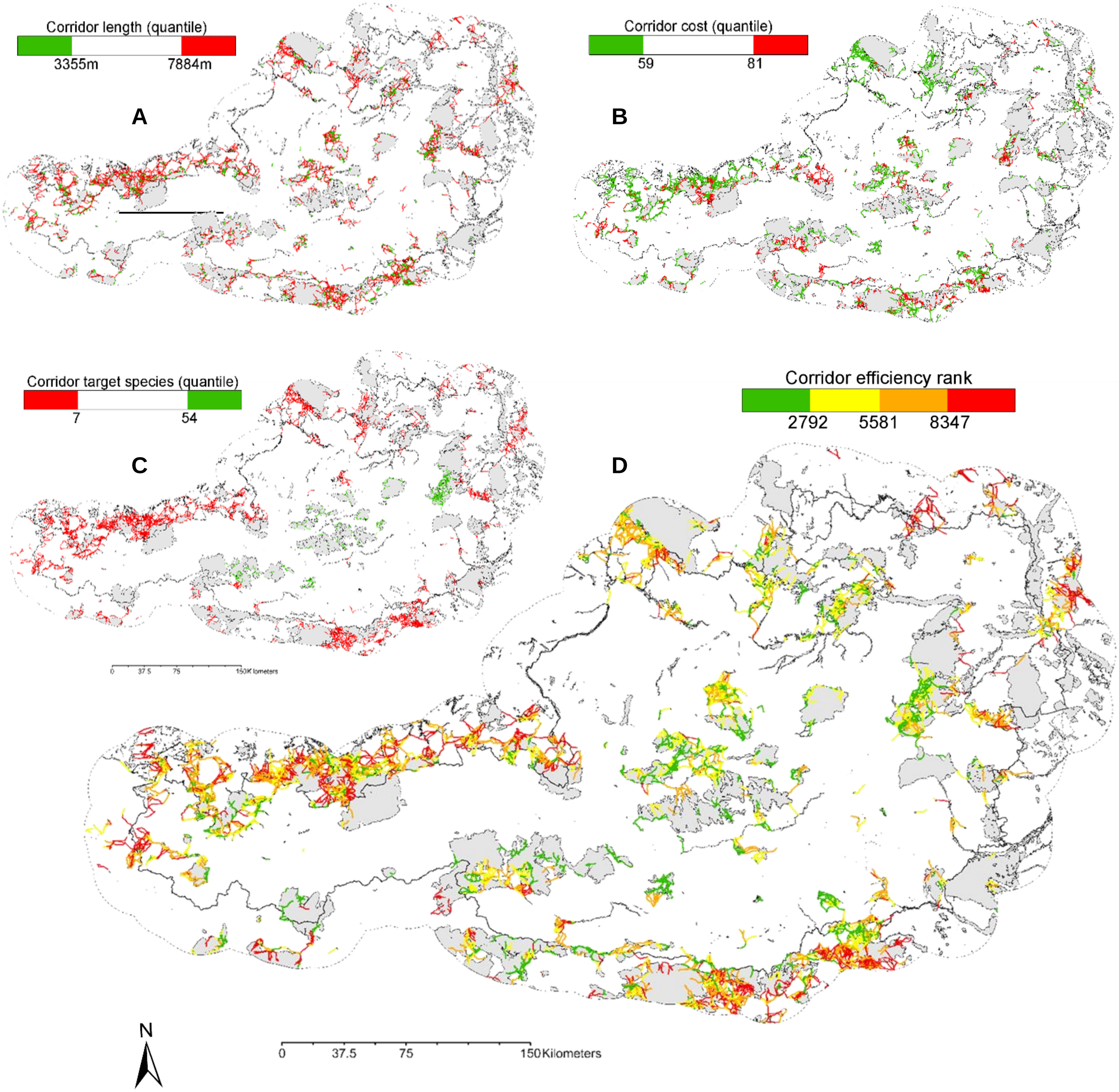

Figure 3: The efficiency of corridors, calculated based on their length (A), their cost (B) and the maximal number of endemic species that become climatically connected to future suitable habitat via these corridors (C). Only corridors belonging to the first and fourth quartiles are shown, to increase visibility. A ranking based on a combination of the three previous criteria (D) reveals shortest, least expensive corridors potentially crossed by many endemic species (in green), while the long corridors, accumulating a high cost and usable by few species are given in red. PAs are shown in grey.

demonstrates that very small and small PAs profit most from establishing new corridors in terms of the number of endemic species achieving climate connectivity, with up to more than 50 species getting climatically connected (Fig. 5). This trend is visible independent of which climate scenario or which decade in the future is considered. Large PAs tend to offer internal climatic connectivity to a greater absolute number of endemic species but do not profit much from corridors (Fig. 5). In 2030, corridors climatically rescue most species under the RCP8.5 scenario (Fig. 5). By contrast in 2080, corridors are most effective in rescuing endemic species under the RCP2.6 scenario. When converted into percentages, again low numbers of rescued species often represent the entire endemic species pool of PAs (Appendix Fig. 9B and Appendix Fig. 6).

4. Discussion

High climate connectivity success

Our results demonstrate that the climate connectivity of the Austrian PA network reaches a high level (60%) even without considering possible migrations between individual PAs. Indeed, a majority of PAs have an inherent large internal thermal variation, and hence provide analogous climates for most species in the future without the need for intervention. This situation, coupled with the fact that some areas may never be connected to an appropriate climate (because they are too isolated in space and/or elevation), implies that additional corridors have a limited potential of further improving climatic connectivity compared to previous studies (McGuire *et al.*, 2016). In addition, restrictions based on the length and monotony of temperature gradient within corridors may also have contributed to reducing the scope and ability of corridors to increase connectivity. This contribution may be assessed by using the same framework but setting different maximal length thresholds and performing a sensitivity analysis of the success of climate connectivity.

Mountain foothills, with a wide variety of altitudes and therefore temperatures, are privileged in terms of access to analogous climates range when the climate warms. By contrast, highest and coldest summits within mountainous regions are necessarily deprived of climate connectivity by nature and their climates will likely disappear regionally over the decades (Ohlemüller *et al.*, 2006; Williams & Jackson, 2007), being thus a dead end for the species they support (Littlefield *et al.*, 2017). Consequently, endemic species of high mountain habitats are most vulnerable to climate change (Spehn & Körner, 2006; Dirnböck *et al.*, 2011; Dobrowski & Parks, 2016) and no corridor design will likely be able to rescue them. Corridors will likely benefit those species which currently live in flat, low-elevation and warm regions of the Austrian east, by connecting them to landscape features sufficiently cold to ensure suitable climates in the future such as the easternmost parts of the Alpine arc. Nonetheless, if climate change is extremely severe as in RCP8.5 (between 2.6°C and 4.8°C rise by 2100 (IPCC, 2014)), even corridors may not be sufficient to guarantee climate connectivity because cold destination patches may become too rare, isolated or distant to be reached.

Although the overall percentage of the Austrian PA network that achieves climate connectivity is high and more than half of the network remains connected over the years, the margin of this success and its specific extent may be important to consider. The significant proportion of the network being on the verge of switching to the failure zone, i.e. whose destination will have exactly the same temperature in the future in 2080, allows us to extrapolate beyond the time limit of our study what will be the future of climate connectivity. It can thus be predicted that

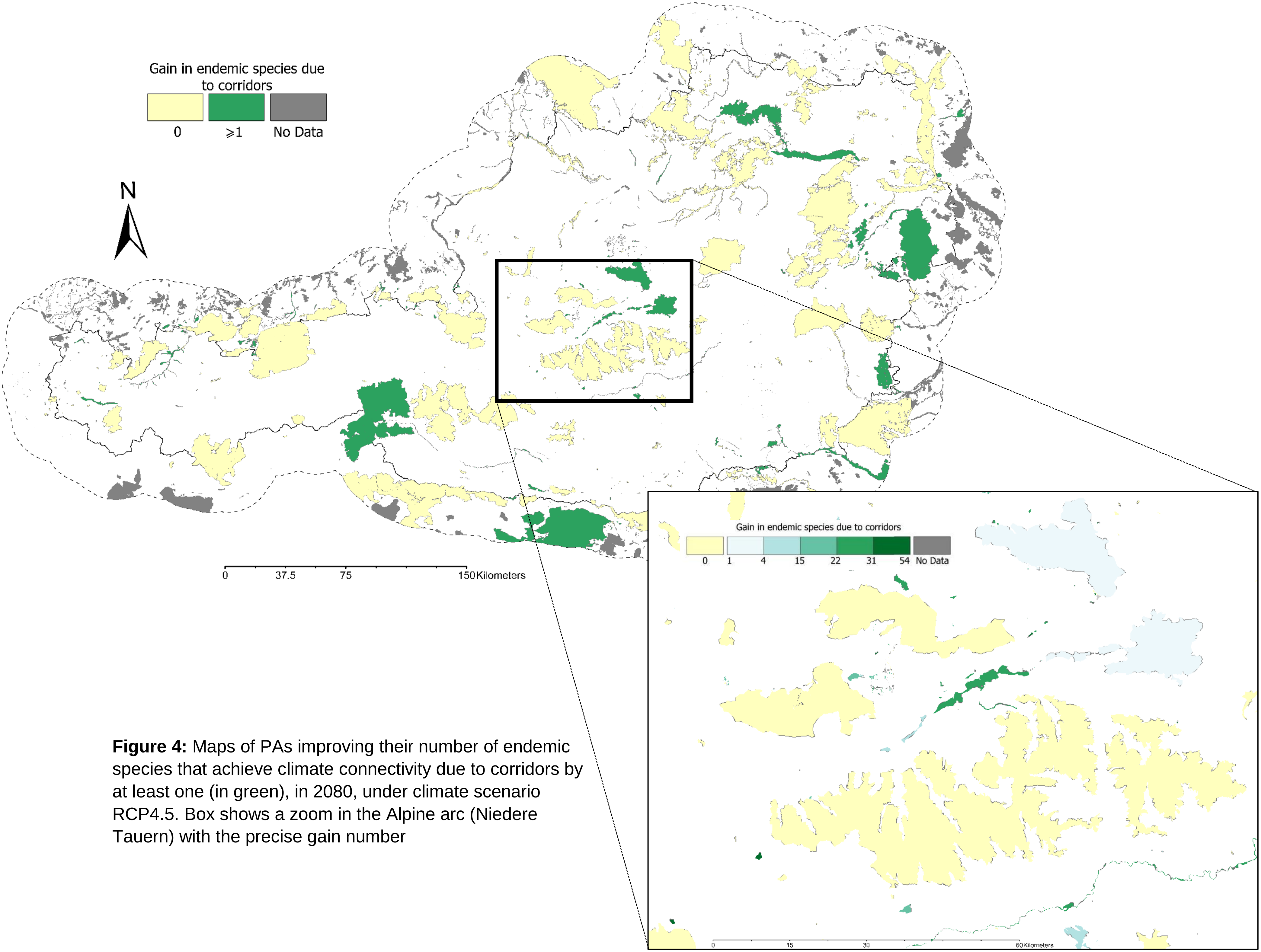

Figure 4: Maps of PAs improving their number of endemic species that achieve climate connectivity due to corridors by at least one (in green), in 2080, under climate scenario RCP4.5. Box shows a zoom in the Alpine arc (Niedere Tauern) with the precise gain number

it will continue to decline over the subsequent decades by about 10% to 15% depending on the scenario.

Corridor selection

The thousands of corridors calculated here can of course not all be truly built, because conservation has a limited fixed budget, and must, therefore, spend it on effective programmes and actions. This is why it is essential to be able to assess the value of a corridor. The indicators to be taken into account are set on the basis of the objectives of managers and conservationists and their relative weights can be adapted to the species or taxonomic group in question. In case of large carnivores, for example, avoidance of confrontations with human activities may have high priority while in case of less mobile species such as plants or snails, corridor length may be of particular importance. Further work should probably also focus on developing general-purpose corridors which facilitate migration of as many species as possible. Our endemic species indicator is a step towards this direction but needs integration in the sense of spatial prioritization of those areas where corridors usable to a particularly large number of species overlap and accumulate few resistances to movement.

Further improvement of our approach should tackle two different issues. First, in order for corridor construction to be the most sustainable over time, not only ecological determinants (dispersal capacity, suitable climate and habitats of species) must be taken into account, but also social and societal dimensions (Pecl *et al.*, 2017; Bonebrake *et al.*, 2018). Acting in concert with local human populations is vital for achieving not only legal but practical conservation and to respect the first goals set established by the Convention of Biological Diversity (CBD, 2010), which aims at addressing the biodiversity crisis by promoting biodiversity across government and society. Corridor solutions should hence be elaborated by an integrative socio-ecological approach.

Second, in this study, we modelled corridor using a least-cost paths algorithm, i.e. a pixel-based approach. As a result, the width of the corridors is not included in our analysis, although it is just as important as the length, shape and alignment (Soule & Gilpin, 1991). Some simulation studies have shown that dispersal ability and movement rate could decrease with decreasing corridor width (Baur & Baur, 1992; Haddad, 2017). Edge effects can also be relatively high on narrow corridors, and thus influence species mortality rate (Soule & Gilpin, 1991). We hence suggest that corridor width is a further dimension to be explicitly considered in any future development of our approach.

Any improvement matters

Although the overall progress in climate connectivity that corridors would allow is relatively low in most climatic scenarios, it matters from a conservation perspective. More than 15% of the PA network would benefit from corridors implementation in terms of species currently found, representing about 50 endemic plants and insects. High altitude habitats are experiencing and will continue to endure a massive reduction in their area as a result of climate change, mainly due to the expansion of tree line boundaries (Dirnböck *et al.*, 2011). Thereupon, endemic species in these habitats are more vulnerable to climate change and may see their risk of extinction increase in the coming years. This study also reaffirms the importance of small habitat patches, which have long been mistakenly believed to be of little use in preserving and restoring biodiversity (Wintle *et*

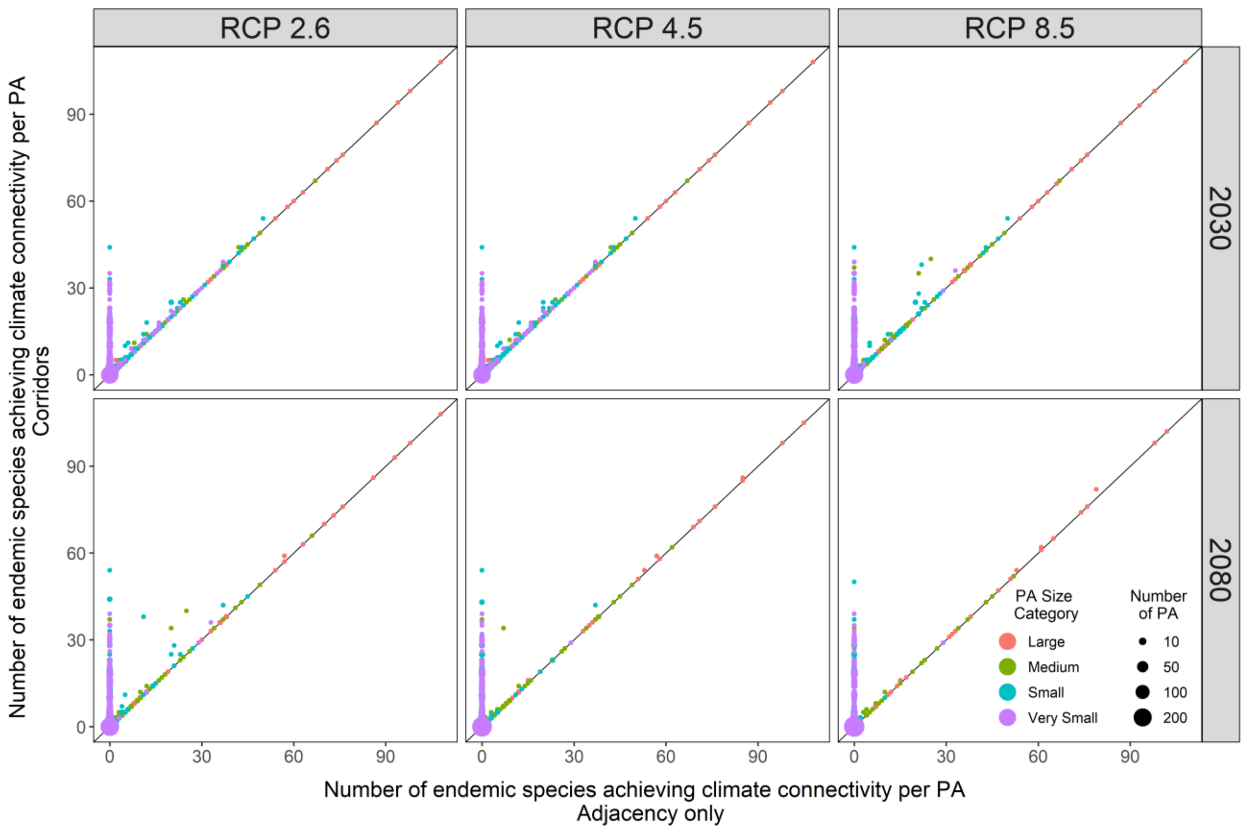

Figure 5: Comparison of the number of endemic species per PA that achieve climate connectivity with and without corridors, according to PA size, in 2030 and 2080 and three climate scenarios. PA classification is based on logarithmic quantiles of the area, where very small PAs have an area below 0.19 km²; small PAs are comprised between 0.2 and 3.65 km²; medium PAs between 3.66 and 69.71 km²; large PAs are above 69.71 km².

al., 2019). They act as reservoirs and stepping stones in heavily modified ecosystems.

Model assumptions, limitations and improvements

We here assumed that the geographical distribution of species in Austria is mainly determined by the temperature gradient, as suggested by recent shifts in species distribution (Rumpf *et al.*, 2018) and movement models (Dullinger *et al.*, 2012; Hülber *et al.*, 2016). Nevertheless, the mean annual temperature may not be the main climatic driver or the most appropriate predictor for at least part of the species considered. For instance, minimum temperature and growing degree days are commonly adopted and used in plants distribution modelling (Wang & Price, 2007). Further improvements of our model could be to substitute the temperature layer used during the corridors' building process by another climatic variable, or to define climate analogy by a combination of several parameters that may be reduced to a single dimension via a principal component analysis (Dobrowski & Parks, 2016; Carroll *et al.*, 2018).

We have also implicitly assumed that, regardless of the absolute values, the temperature gradients will remain of the same nature and magnitude in the future as the spatial climate is strongly shaped by terrain and water bodies at scales smaller than 10 km (Daly, 2006). However. others argue that fine-scale patterns of soil moisture content and vegetation cover may be driving microclimates at finer extent (Fridley, 2009), thus being possibly altered under climate change. To quantify the temporal stability of spatial thermal gradients, we could set as inputs the future temperature layers when running the Climate Linkage Mapper toolbox and subsequently, evaluate the proportion of spatial changes in corridors relative to those built using current climate.

Our third assumption, that organisms movement is impeded by human influences, may be coarse or even wrong for some species. For instance, Menke *et al.* (2011) found that urban areas may aid the persistence and movement of some dry-adapted ant species in North Carolina. In that case, cities however could act as corridors themselves between two warm and arid suitable habitats. Nevertheless, these examples are rare and as such, using a resistance surface based on human impacts on the landscape remains relevant for many areas where species in need of protection are actually those that cannot cope with the predominant, strongly altered landscape matrix. In addition, our approach is flexible and could easily be transformed to fit with species-specific requirements. The next steps of the project will involve a distinction between forest and non-forest species, by adjusting costs according to habitats types and land covers.

As human population and activities will still grow, areas that resist species movement may also expand or move in the near future, i.e. before corridors' construction. However, areas of conservation interest are often purchased by the state or municipalities well in advance of the start of development, thus ruling out the possibility of uncontrolled and unexpected urbanization.

Our approach assesses for the first time in Europe the connectivity in its climatic aspect for a network of protected areas, combining least-cost path analysis techniques, future climate projections and species distribution. However, despite the fact that this study highlights the theoretical potential for movement under climate change, it does not assure that organisms will be able to migrate, establish and colonize those new suitable environments (Littlefield *et al.*, 2017). Although we have tried to minimize inadequate climatic conditions by removing non-monotonous corridors, the path to the destination patch may still constrain movement due to geographical barriers (mountains, rivers) or inappropriate natural habitats for some species. Moreover, species persistence also dependents on population dynamics and multispecies interactions (Berg *et al.*, 2010). Novel destination patches as well as intermediate stepping-stone patches may or may not be large enough to allow gene flow to continue across sub-populations to maintain genetic diversity and viability (Shaffer, 1981).

Our model could be improved by integrating the notion of dispersion capacity. To this end, the corridors could be rebuilt with the same inputs but by increasing the maximum length limit to a large value, e.g. 500 km. Subsequently, the corridors thus created could be filtered according to several thresholds, corresponding to the dispersal abilities of particular species or taxonomic groups. We can also imagine taking time into account and thus vary the length of the corridors according to the time available to organisms to traverse them. Indeed, many authors (Lawler *et al.*, 2013; Keenan, 2015; Dobrowski & Parks, 2016; Keeley *et al.*, 2018) have pointed out that climate change is a dynamic phenomenon that fluctuates over time with an inherent velocity. If it is faster than the dispersal rate of the organisms, they would not be able to reach suitable climatic habitats in time (Dobrowski & Parks, 2016). Although we modelled climate change as a single event, taking into account the average annual temperature of different time slices, we attempted to address this concept by calculating the margin of success. Degrees above zero can be considered as spare degrees; species may be slow but still able to reach suitable habitats. However, this metric remains vague because we cannot compare it with the actual climate change speed, not studied here. Further improvements of the method should certainly elaborate on this issue as not considering climate change velocity may lead to inappropriate and ineffective conservation resources allocation (Gillson *et al.*, 2013).

Finally, we intentionally designed a general framework to assess climate connectivity rather than a species-specific model. We argue that our framework may be used as it stands by conservation planners to identify priority areas that are not likely to provide climate connectivity for the species they harbour and are thus more vulnerable in the face of climate change. Moreover, our framework is adaptable to species of interest. Indeed, all input data can be changed to match with species requirements: (i) another climatic variable could be used instead of the annual mean temperature; (ii) the resistance map could be aligned with habitats preferences and (iii) corridor length could be adjusted to dispersal distance and/or time.

Conclusion

In summary, this work demonstrates that the current Austrian protected area network provides relatively high climatic connectivity, at least under moderate to intermediate scenarios of climate change, and thus will probably allow many species to track their suitable climate. Nevertheless, the addition of corridors would be a highly valuable improvement in specific regions because they would climatically rescue a significant number of endemic species, which otherwise could be committed to extinction within the current state of the network.

The method applied does not guarantee the successful movement of organisms and has several limitations, but it does allow us to quantify connectivity under climate change by taking into account human influences and climate. In a world where habitat loss and fragmentation act as the major factors responsible for an unprecedented decline in global biodiversity (Díaz *et al.*, 2019), such methods appear relevant for other European countries as well as for the entire European Natura 2000 network for planning effective biodiversity conservation programmes. These actions must be coordinated at different levels (local, national and international) and must involve different actors, including especially citizens, in order to tackle this urgent crisis.

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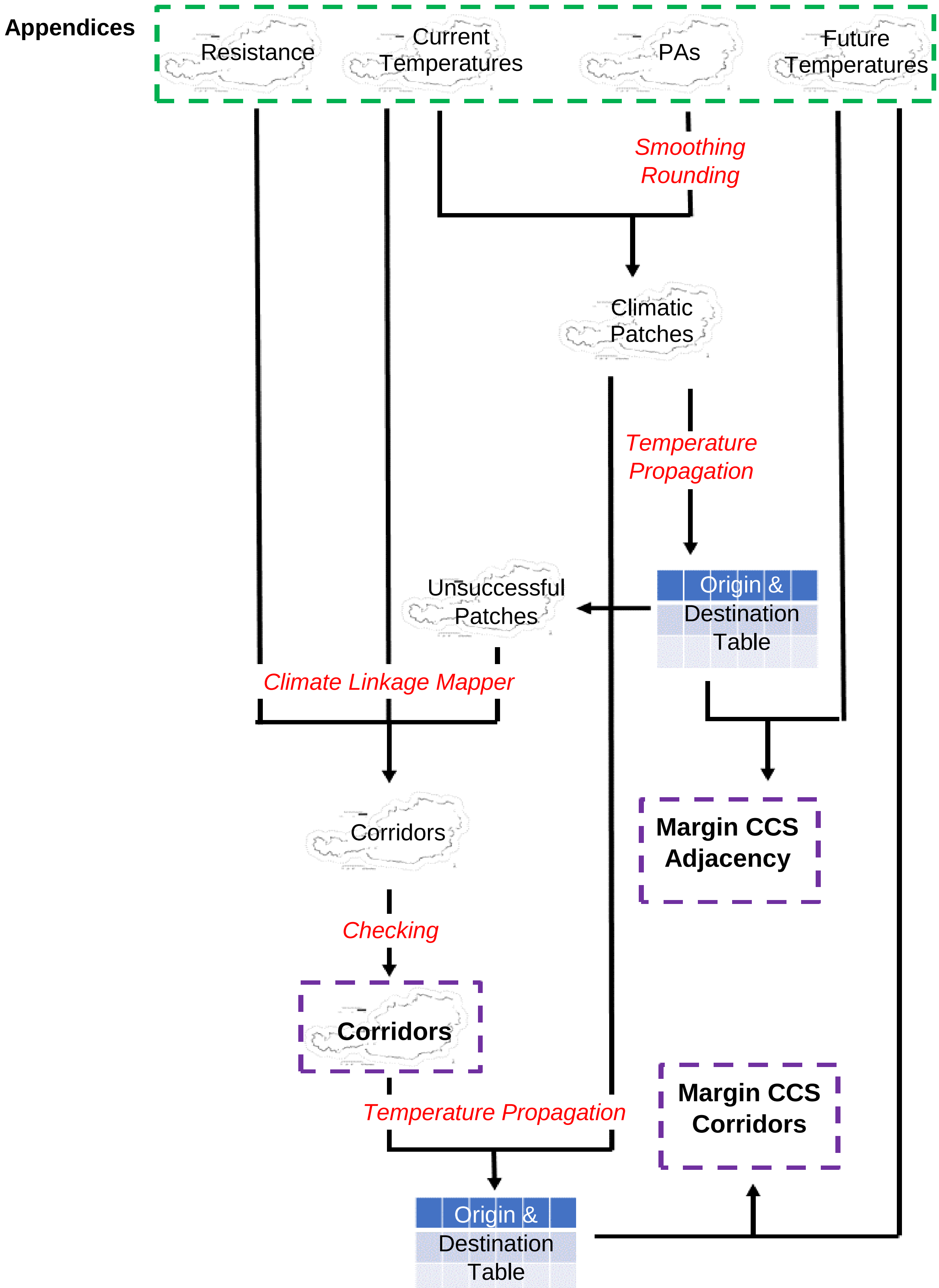
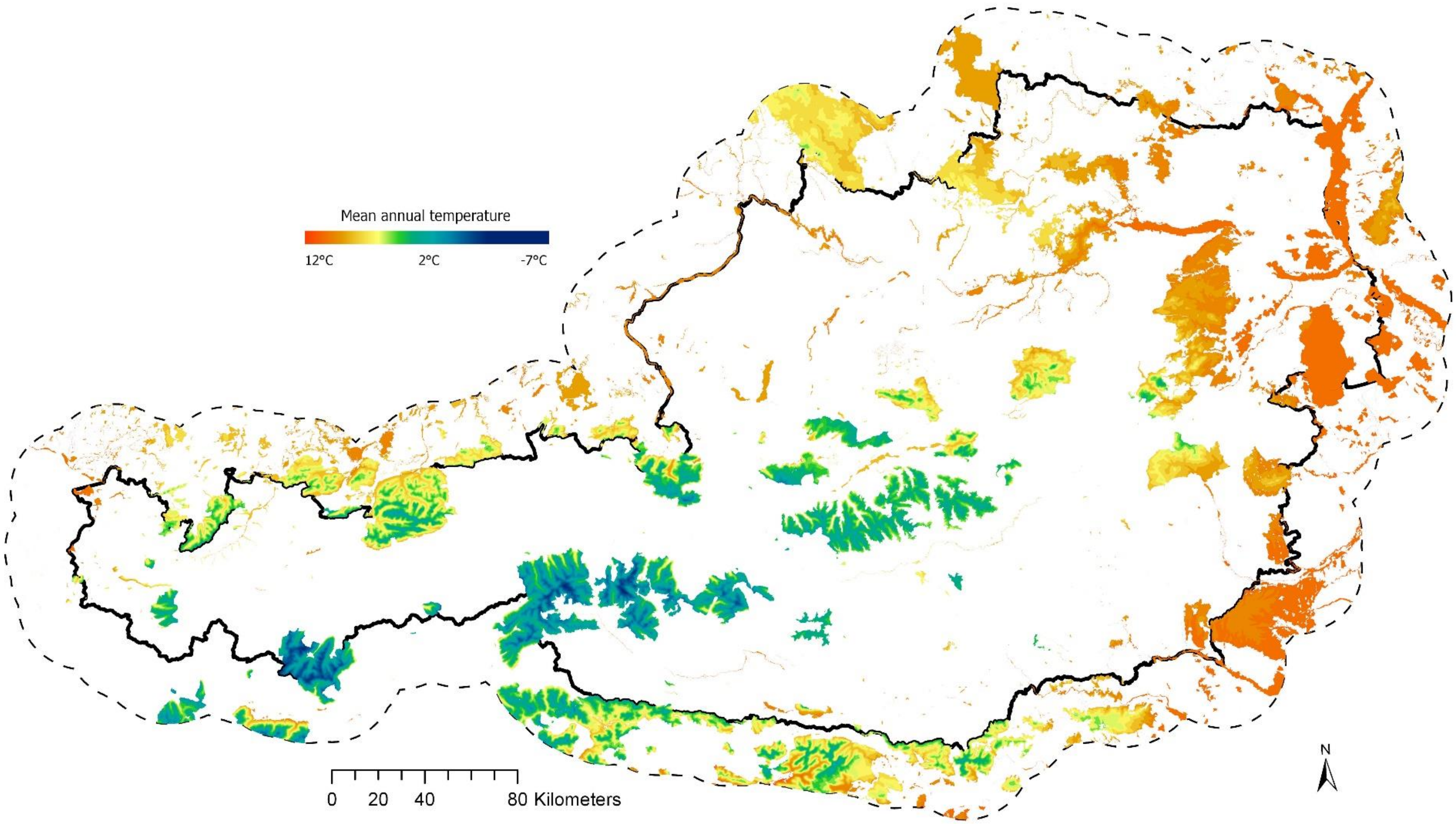
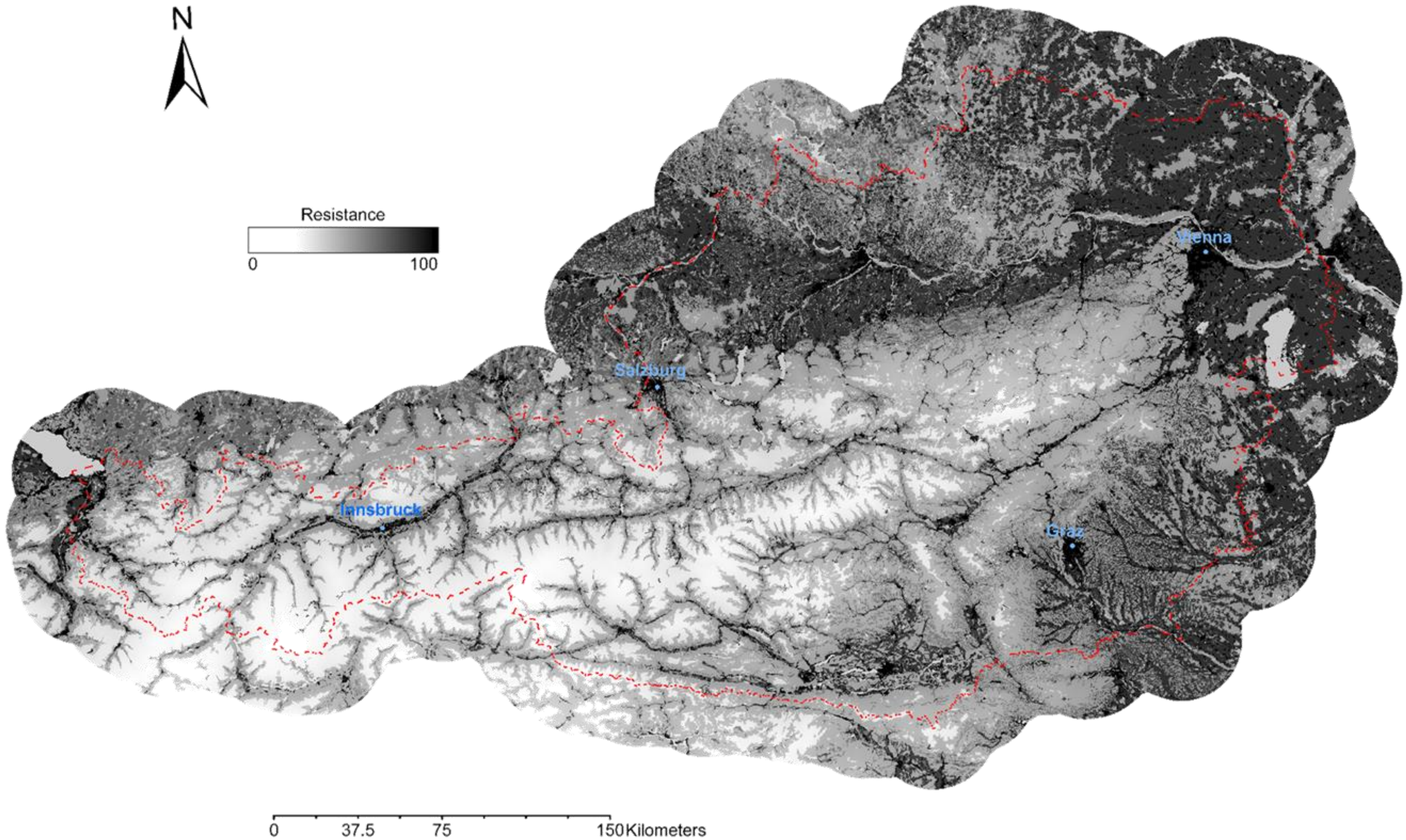


Appendix Figure 1: Flow chart of the methods applied. Inputs are in green boxes, processing in red and outputs in violet boxes. PAs: Protected Areas; CCS: Climate Connectivity Success.



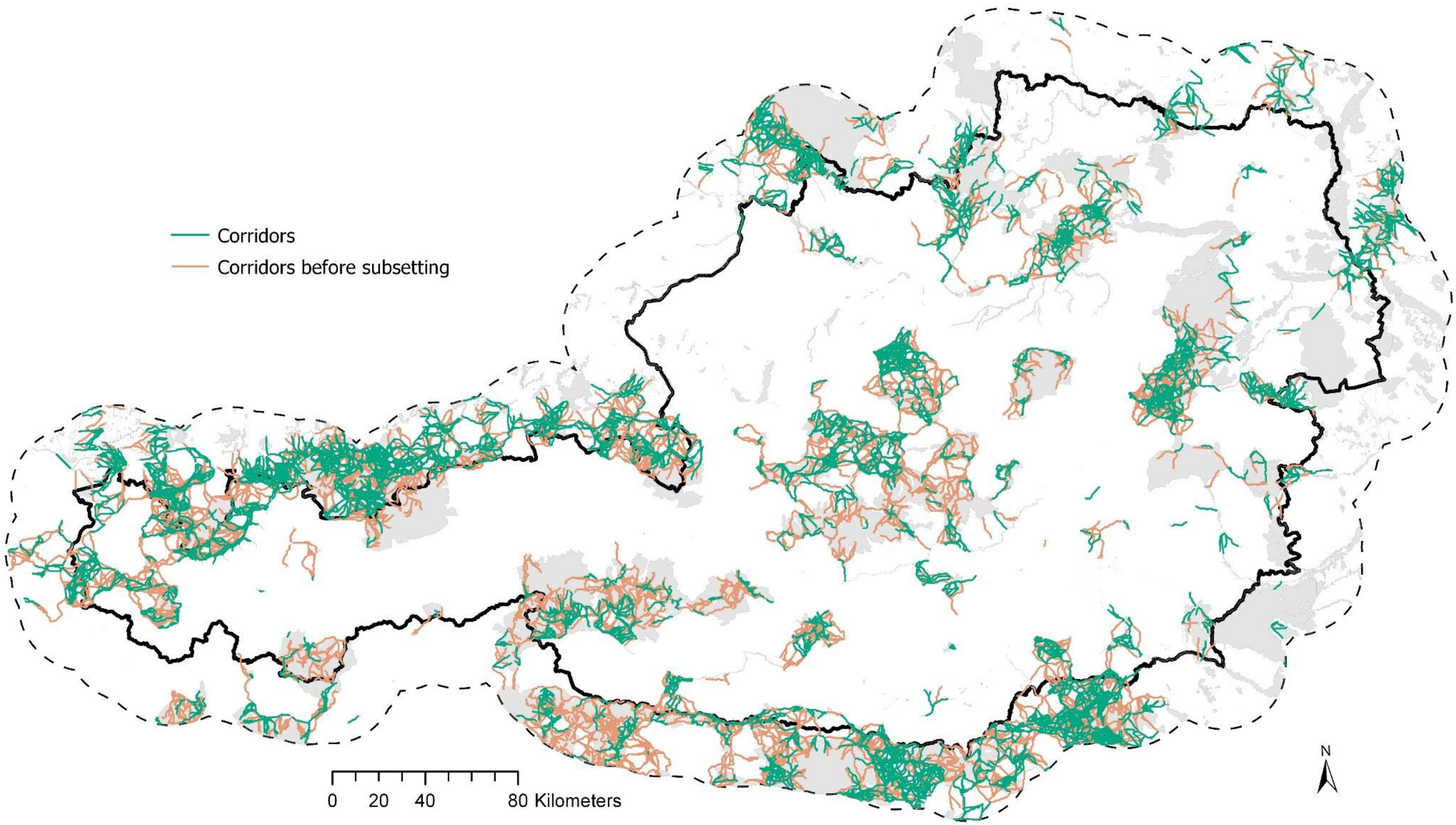
Appendix Figure 2: Climatic partitioning of the 1849 PAs of the study area into 7350 patches of equal temperature, after spatial smoothing of temperature values and rounding to the nearest integer.



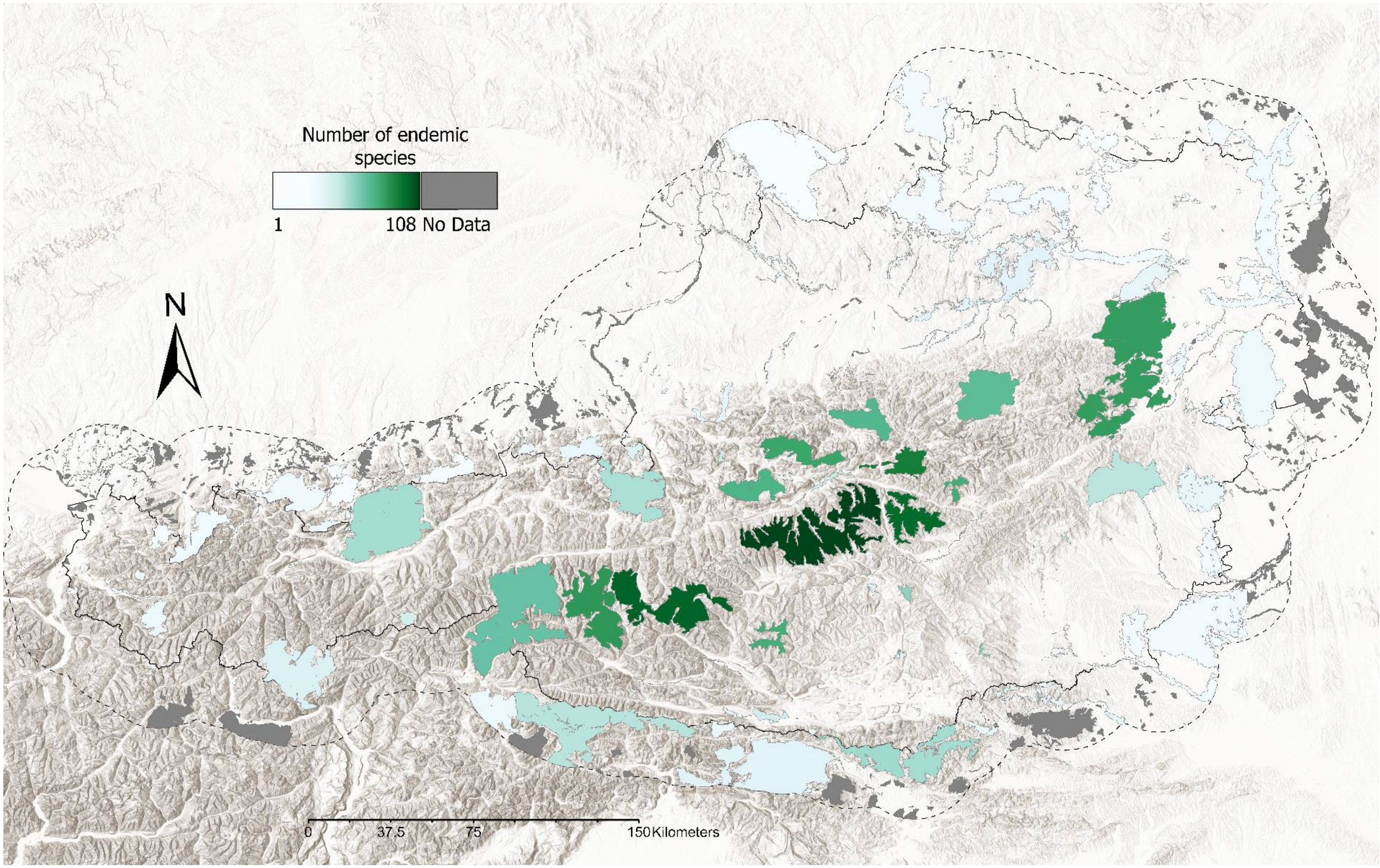
Appendix Figure 3: Adjusted wilderness continuum map, used as resistance surface. Zones with high values (in black) impede organisms' movement whereas low values (white) areas allow them to move more easily. Main cities are in blue and the Austrian border in red.

$$Cost\ distance = \left(\frac{Rfocal + Rneighbour}{2} \times Euclidean\ distance\right) + \left(temperature\ distance\ weight \times (Tfocal - Tneighbour)\right) \quad (1)$$

Appendix Figure 4: Equation defining single pixel costs by Nuñez et al. (2013). It takes into account for neighbouring pixels, temperature (T) and resistance (R). This formula ensures that corridors follow an approximative monotonic temperature gradient and minimises the resistance due to friction with anthropogenic features.



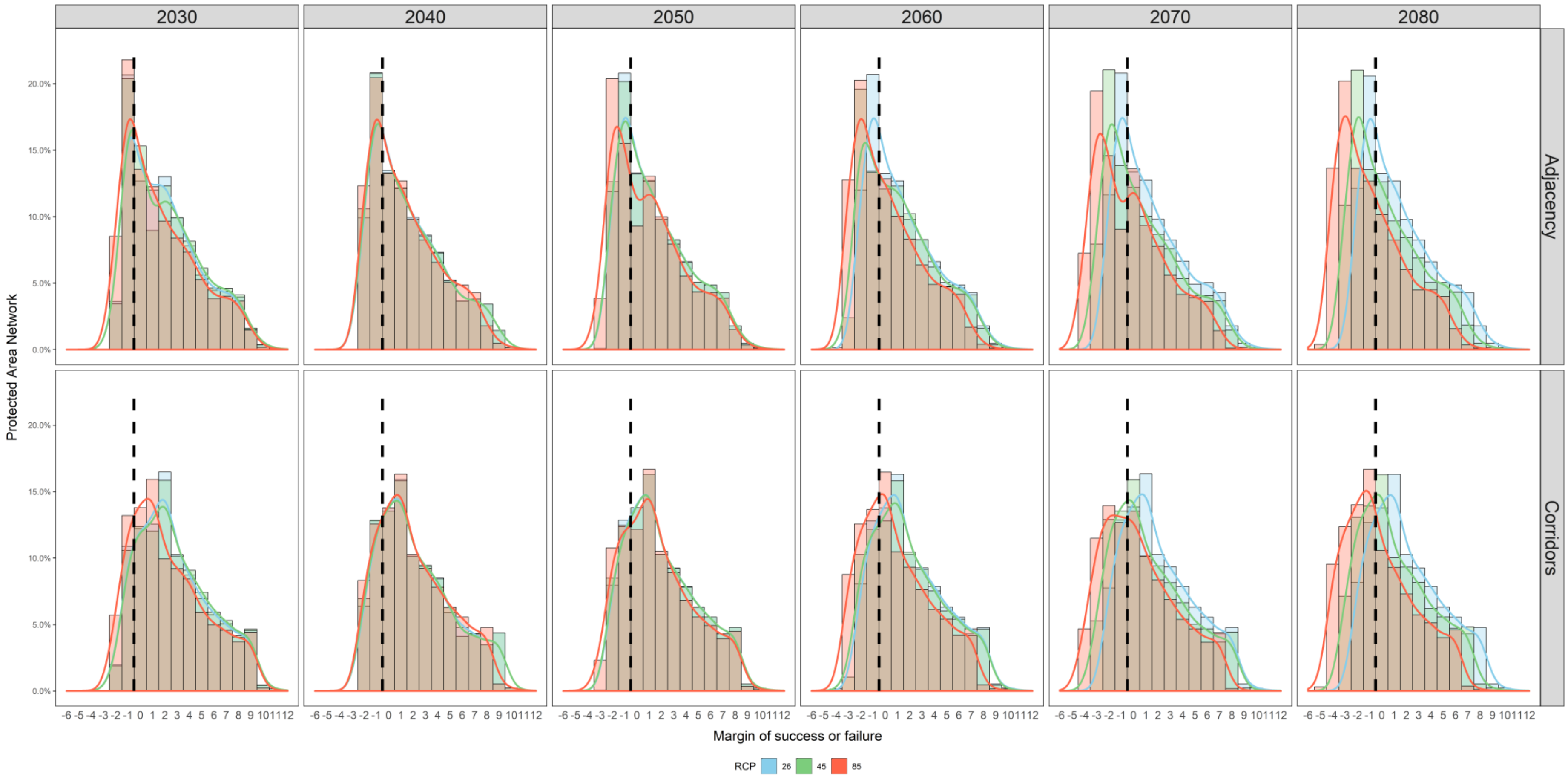
Appendix Figure 5: Climatic corridors, after checking for temperature monotony and length. Linkage Climate Mapper built 31739 corridors between climatic patches that did not achieve climate connectivity considering only their adjacent patches. 9938 of them were longer than 10 km and 10715 followed a non-monotonic temperature gradient, and were therefore removed from the initial pool, finally working with a subset containing 11086 corridors that met our criteria.



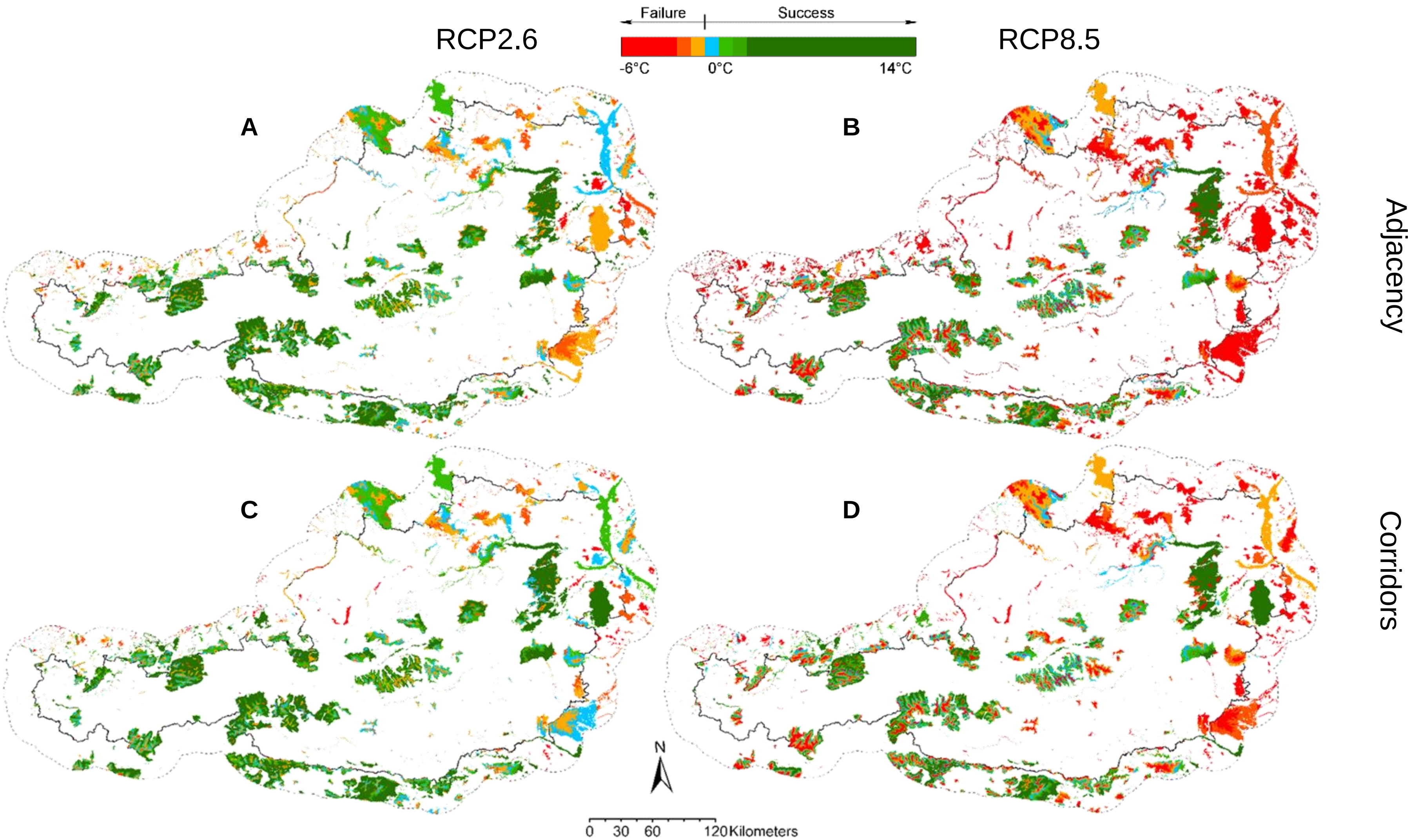
Appendix Figure 6: Current distribution of endemic species (plants and insects), by PA, projected onto a hillshade basemap. A total of 130 endemic plant species and 182 endemic insect species are found in the study area. PAs with a high richness are indicated in green. In grey, PAs for which no distribution data were available.

Appendix Table 1: Absolute values and success gains in climate connectivity when adding corridors, as a percentage of the total protected area network area, under various climate scenarios and over time. Low climate connectivity success values (below 50%) are shown in bold.

	Adjacency Only			**Corridors**			**Gain**		
	RCP2.6	RCP4.5	RCP8.5	RCP2.6	RCP4.5	RCP8.5	RCP2.6	RCP4.5	RCP8.5
2030	72	73	67	85	85	79	13	13	13
2040	66	66	64	79	78	77	13	13	13
2050	64	64	58	77	77	73	13	13	15
2060	64	62	51	77	75	63	13	13	12
2070	64	55	**47**	77	67	56	13	12	8
2080	64	52	**38**	77	64	**46**	13	12	8



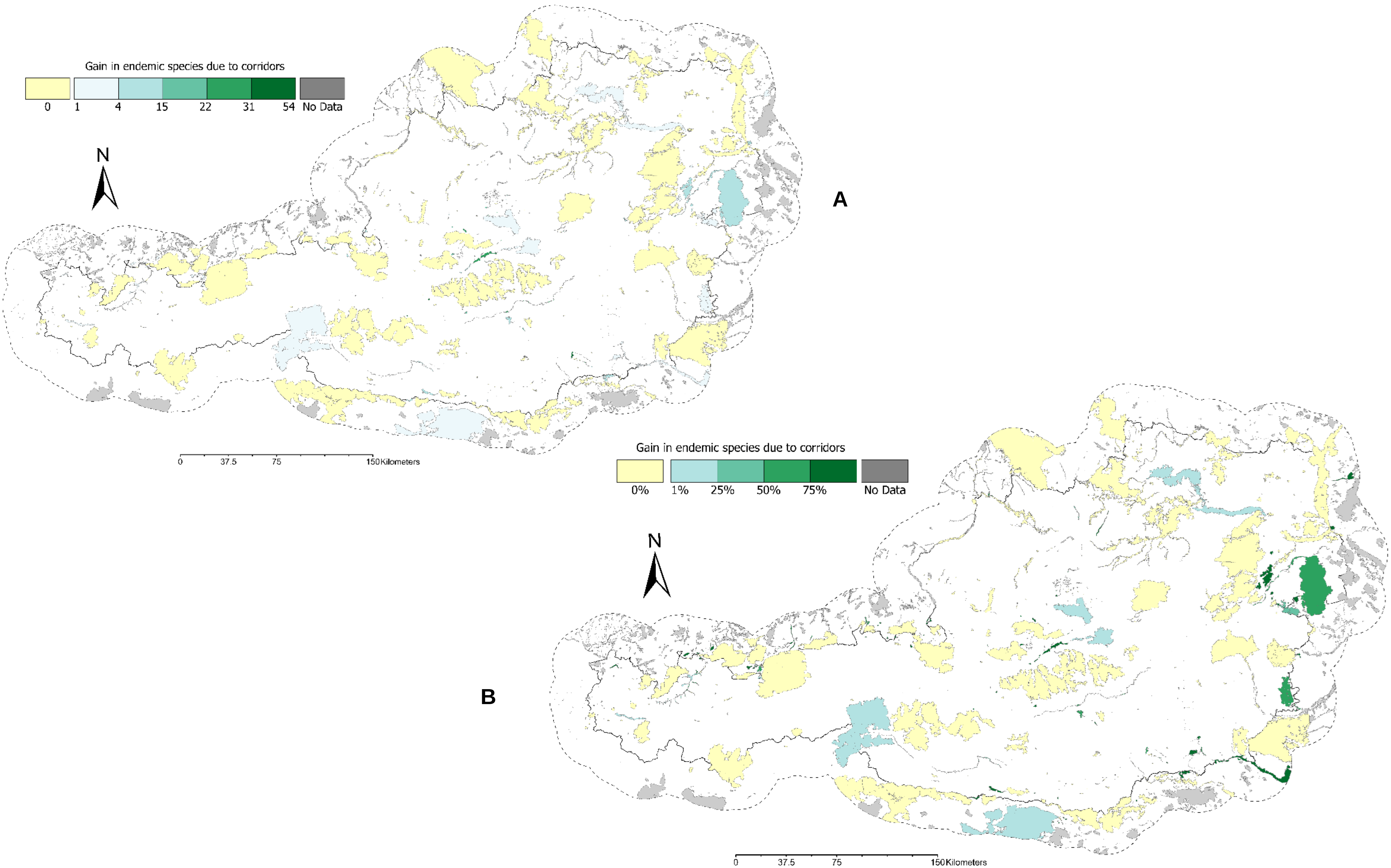
Appendix Figure 7: Margin of success or failure at achieving climate connectivity per percentage of area of Austrian PAs network, given various climate scenarios and dates, with and without corridors. Dashed lines delimit failure (on the left of it) and success (on the right) at achieving climate connectivity.



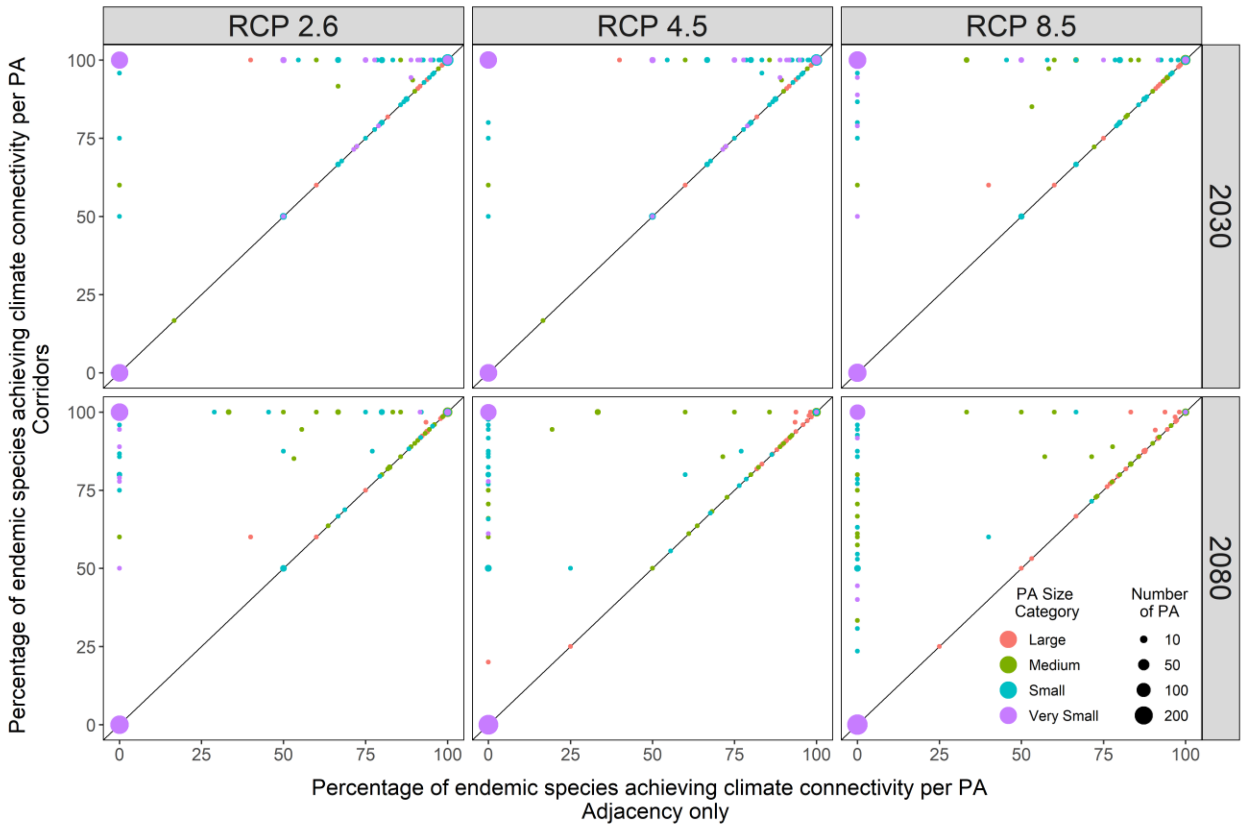
Appendix Figure 8: Maps of margin of success or failure at achieving climate connectivity in 2080, given the two extreme climatic scenarios (RCP2.6 and 8.5), with and without corridors. The margin is defined as the difference between the current temperature of the origin patch and the future temperature of the destination patch ($Margin = T_o^c - T_d^f$) (McGuire *et al.*, 2016). Consequently, climate connectivity is achieved with positive (green) or zero margin (blue), whereas negative margins (orange and red) are synonymous of failure.

Appendix Table S2: Summary of the percentages of PA network area and numbers of PAs that gain at least one endemic species that achieves climate connectivity by adding corridors, given various climate scenarios and years. On overall, 15.2% (standard deviation of 4.2%) of PA network area gain at least one species across all climate scenario and decades, corresponding to 329 PAs (standard deviation of 31).

RCP scenario	Year	% PA network area	Number of PAs
2,6	2030	11,0	312
	2040	11,8	351
	2050	12,5	358
	2060	12,6	361
	2070	12,5	358
	2080	12,6	361
4,5	2030	11,0	312
	2040	11,8	351
	2050	12,5	354
	2060	19,2	338
	2070	17,6	307
	2080	23,0	304
8,5	2030	11,8	349
	2040	12,5	355
	2050	22,0	321
	2060	22,3	307
	2070	17,6	273
	2080	19,0	254



Appendix Figure 9: Maps of gain in endemic species that achieve climate connectivity per PA due to corridors, in absolute value (A) and percentage of total endemic species per PA (B), in 2080 and scenario RCP4.5.



Appendix Figure 10: Comparison of the percentage of endemic species per PA that achieve climate connectivity with and without corridors, according to PA size, in 2030 and 2080, given various climate scenarios.