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„Habitats' climate connectivity within the Austrian protected area network"

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Contents

Abstract

With the advancement of climate change, species that are unable to adapt to the ecological modifications of their environment need to migrate to track their ideal niche. The successful movement of these species might be dependent on how well connected the area they are coming from and their destination are. Protected areas (PAs) are conservation tools used to safeguard species and their environment, however, as they are usually planned based on current factors such as temperature and species distribution, they might fail to preserve areas needed by the species in the future. In the present study the climate connectivity of eight habitats of conservation concern and covered by the Austrian protected area network was assessed. We analyzed how well connected the patches of each habitat were and, based on a least-cost distance, we run corridor calculations to identify the best areas in Austria to implement efficient corridors in order to improve connectivity where adjacency is not met. Climate connectivity varies between habitats but, overall, most habitats have more than 50% of their area achieving climate connectivity by 2060 in an intermediate climatic scenario. The improvements provided by corridor were relatively higher in grasslands habitats and the number of endemic species profiting from them was higher in high altitude habitats. These results support potential amendments in conservation strategies in the Austrian territory.

Zusammenfassung

Mit dem Fortschreiten des Klimawandels müssen Arten, die sich nicht an die ökologischen Veränderungen ihrer Umgebung anpassen können, migrieren, um ihre ideale ökologische Nische zu finden. Die erfolgreiche Migration dieser Arten hängt davon ab, wie gut das Gebiet, aus dem sie kommen und ihr Zielort miteinander verbunden sind. Naturschutzgebiete sind Instrumente, die zum Schutz von Arten und ihrer Umwelt eingesetzt werden und werden in der Regel auf der Grundlage aktueller Faktoren, wie Temperatur und Artenverteilung geplant. Deshalb können Gebiete, die von den Arten in der Zukunft benötigt werden, nicht unter Schutz gestellt werden. In der vorliegenden Studie wurde die Klimakonnektivität von acht schützenswerten Lebensräumen, die vom österreichischen Schutzgebietsnetzwerk abgedeckt werden, bewertet. Wir analysierten, wie gut die Schutzgebiete des jeweiligen Lebensraums miteinander verbunden sind und führten auf Basis einer *Least-Cost-Distanz* Korridorberechnungen durch. Das Ziel der Studie war es, die geeignetsten Gebiete in Österreich zu identifizieren, in denen effiziente Korridore implementiert werden können, um die Konnektivität von nicht angrenzenden Gebieten zu verbessern. Grundsätzlich variiert die Klimakonnektivität zwischen den Lebensräumen. Die meisten Lebensräume erreichen jedoch Klimakonnektivität auf mehr als 50 % ihrer Fläche in einem mittleren Klimaszenario bis 2060. Die Verbesserungen durch Korridore waren in Grasland-Habitaten relativ höher und die Anzahl der endemischen Arten, die davon profitieren, war in hoch gelegenen Habitaten höher. Diese Ergebnisse unterstützen mögliche Änderungen in den Naturschutzstrategien auf dem österreichischen Staatsgebiet.

Introduction

In the last decades, climate change has become a topic which concerns different fields of studies, from economics to biodiversity research. The impacts of a changing climate are getting more noticeable, with direct consequences on human well-being, food sovereignty and security and ecosystem functions (IPCC 2014). Ecosystems provide different goods and services to the human population, such as disease control, food production, carbon sequestration and water quality (Boon and Ahenkan 2011). Climate change impacts tend to affect poor communities more negatively since their livelihoods depend on food production, water supply and biodiversity, factors that are intricately dependent on climate systems (Boon and Ahenkan 2011). A projected increase in temperature and a decrease in precipitation, for example, can strongly contribute to a decrease in water yield, one of the main hydrological ecosystem services (Natalia et al. 2020). On top of that, biodiversity distribution has been changing, as species migrate towards higher elevations (Dullinger et al. 2012) and higher latitudes to track their ideal climate (Chen et al. 2011). According to a meta-analysis done by Chen et al (2011), species range has recently shifted to higher elevations at a median rate of 11m per decade, and to higher latitudes at a median rate of 16.9km. This change in distribution leads to consequences to the aforementioned factors and to the dynamics of climate change itself (Pecl et al. 2017).

One of the main biodiversity conservation efforts is the implementation and management of protected areas (PAs). According to the IUCN (Dudley 2008), "a protected area is a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values." This conservation strategy has the potential to safeguard species and their habitats, and might usually present a higher abundance and species richness when compared to non-protected areas, specially to areas with human-dominated land uses (Gray et al. 2016). However, there are some caveats to the representativeness of PAs. Firstly, there are some biases not only on the location of current PAs — specially located toward higher altitudes and away from human settlements and infrastructure — but also on the types of climate they represent (Elsen et al. 2020). Moreover, PAs are mostly planned based on current species' distributions and habitat conditions (Heller & Zavaleta 2009). As species' ranges are shifting due to climate change, these protected sites could possibly, in the future, fail to afford the intended protection to those species (Hole et al. 2009). The implementation and management of PAs usually face a limited amount of financial and human resources (Armsworth et al. 2011; Watson et al. 2014). Therefore, this conservation strategy should be well planned to use the limited resources in the best way and to best achieve its conservation goals. Considering climate change projections when implementing a PA is a fundamental prerequisite to tackle species' needs and to conserve them successfully.

Different authors suggest the expansion of the PA network as a strategy to address climate change (Heller & Zavaleta 2009; Maxwell S.L. et al. 2020). There are mainly two recommendations on how to expand this network: by creating new PAs or by increasing the size of existing ones. The first approach has the potential to increase the coverage of different facets of biodiversity and to facilitate movement of species to track suitable climatic conditions across larger geographical domains; the second one allows species' regional populations to grow and to track suitable conditions at a smaller scale, within existing reserved areas (Lawler et al. 2019). Simply protecting a larger area might, however, not necessarily mean that species will be able to migrate. Matrix quality and anthropogenic intervention are factors that influence the capability of species' migration and their speed. On average, movement is greater when the matrix is more similar to the area where the species is coming from (Eycott et al. 2012). Moreover, species movement might be delayed when habitat connectivity is interrupted by human land use in the landscape matrix (Miller & McGill 2017). Therefore, one of the most frequent recommendations in the literature to address species conservation in the face of climate change is to increase habitat connectivity and hence the permeability of landscapes for migrating species (Heller & Zavaleta 2009).

Landscape connectivity is the degree to which the movement of species is facilitated or impeded (Taylor et al. 1993). A higher connectivity means that species can move between their source and their destination more easily. The lack of connectivity results in isolated habitat patches, potentially leading to less gene flow, pollination, seed dispersal, wildlife migration and other important spatial ecological processes (Saura et al. 2011). The ability of a species to move in response to climate change depends on the suitability of a destination patch in terms of its local climate — which should be similar in the future to the current local climate of the patch the species migrates from (climate analogues) — and on the existence of a suitable connection between these two patches, in terms of both climate and habitat quality (Senior et al. 2019). Climate connectivity hence measures the connectedness of habitat patches to their future climate analogues. As climate warms, and isotherms shift across the planet (Loarie et al.

2009) climate connectivity may decrease or increase over time (Senior et al. 2019), and proper integration of climatic connectivity into the design of PA expansion should hence be a priority (Maxwell et al. 2020). This implies that conservation planning should focus particularly on climate analogues of currently protected habitat patches and reduce pressure from human land use in both potential destination patches and the corridors that link them to source patches (Parks et al. 2019).

The implementation of wildlife corridors is one of the most popular tools used in conservation planning to improve landscape connectivity (Gilbert-Norton et al. 2010; Haddad et al. 2011). By connecting isolated areas, corridors can increase the effective size of reserves and the rate of exchange of individuals and genes, ultimately reducing the risk of local extinction (Newmark 1993). Corridors can be planned based on different approaches, such as a focal species approach, a method more focused on the ecological integrity or the degree of "naturalness" (Krosby et al. 2015) or other structural properties of landscapes (Keeley et al. 2018). Their success depends on the specific corridor design and on the taxonomic group it is designed for (Lindenmayer & Nix 1993). In general, corridors can increase the movement of species between habitat patches by up to 50% when compared to areas without them (Gilbert-Norton et al. 2010). The implementation of an appropriate corridor design is hence a potentially effective tool to increase climate connectivity of PAs, or of any vulnerable habitats, in a warming world.

Analyzing and implementing climate connectivity is still a relatively new challenge in biological conservation and only a few real PAs have been studied in this respect (Keeley et al. 2018). Here, we present a structural connectivity analysis sensu Keeley et al. (2018), i.e. an analysis of structural landscape properties meant to facilitate species movement independent of a focal species or species group. We concentrate the analysis on eight habitat types of conservation concern in Central Europe, using the PA network of Austria as a case study. In particular, we (i) assess to which degree the Austrian PAs containing patches of these habitats are climatically connected by adjacency, i.e. without any need of expanding or connecting existing PAs; and, (ii) calculate corridors between the areas that are not adjacent to assess how they could improve their connectivity. Finally, (iii) we measure corridor success by evaluating the number of species endemic to Austria – for which Austria hence has a particular conservation responsibility – that would be potentially connected by them.

Methods

The study area comprises the whole Austrian territory (83,879km²) surrounded by a 27km buffer zone, making a total area of 133,540km². The buffer zone includes parts of Germany, Czech Republic, Slovakia, Hungary, Slovenia, Italy, Lichtenstein and Switzerland and is included to avoid the fragmentation of protected areas that cross international borders. According to the Köppen climate classification (Beck et al. 2018), the study area has mostly a humid continental climate, with oceanic climate to the far west and subarctic and tundra climates in the alpine regions.

All spatial analyses were performed with 100m resolution maps through ArcGIS software 10.8 (ESRI 2020) and R 4.0.2 (R Core Team 2020) and projected into the European Terrestrial Reference System 1989 (ETRS89) Lambert azimuthal equal-area projection.

Temperature data

The climatic niche of species can be determined by various biologically relevant climatic features related e.g. to heat sums, water availability or solar radiation income and the distribution of these features across the year (Soberón 2007; Rodrigues et al. 2019). The most relevant features are specific to each species. As we here focus on a structural connectivity analysis rather than on a focal species (Nuñez et al. 2013), we use mean annual temperature (hereafter temperature) as a generic descriptor of local climates. We extracted the mean annual temperature of the study area from WorldClim (Hijmans et al. 2005). The values are based on an interpolation of observed data for the climatic period 1960 to 1990 onto a 1 km² grid. 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 representative concentration pathway (RCP) scenarios (RCP2.6, RCP4.5 and RCP8.5). Both WorldClim and EURO-CORDEX datasets were statistically downscaled to 100-m resolution using the approach described in Dullinger et al. (2012). We thus produced 18 different temperature grids (six decades x three scenarios) of the study area.

Habitat selection

Habitat selection was based on the high-resolution Central European Habitat map (CEH; Kuttner et al. 2015) that includes the distribution of small patches of semi-natural habitat types that often are of high conservation value (Wintle et al. 2019). From the 19 habitat types of the map, we selected eight terrestrial ones (Coniferous Forest; Broad Leaved Forest, Shrub

Lands, Extensive Grasslands, Alpine Grasslands, Wetlands, Dry Grasslands and Rocks) based on their ecological importance and conservation value. The habitat gravel banks was excluded due to very low area coverage.

The eastern part of the buffer zone covering Czech Republic, Slovakia, Hungary and Slovenia is not part of the CEH. Therefore, we used the CORINE land cover map (CLC; European Environment Agency 2012) to cover the distribution of focal habitat types in this part of the buffer zone (with a somewhat lower spatial resolution). The CEH habitat types are tied to the CLC classifications, but they are not identical. We hence had to assign some CEH-types to ecologically most similar CLC classes.

Partitioning Protected Areas into Climatic Patches

The PA network included all areas nominated for the Natura 2000 program (DG Environment of the European Commission 2008) and the IUCN PA categories Ia, Ib, II and III (Dudley 2008). PAs with a total area below 0.01km² and narrower than 100m were deleted due to spatial processing. After all, there were 1849 PAs covering 19% of the study area. Each PA was further subdivided into climatic patches (hereafter patches), namely areas in which all 1 ha (= 100 x 100m) pixels have the same mean annual temperature. Before subdividing the areas into patches, the temperature values of individual pixels were smoothed by calculating, for each pixel, the average temperature of all neighboring pixels in a 500m radius. This avoids extremely isolated pixels from becoming very small patches. The smoothed temperature values were rounded to the nearest integer to avoid undue influence of minor temperature differences that are unlikely to trigger species range shifts (Parmesan 2006). In total, there were 7530 final patches.

In a next step, we filtered, for each habitat type separately, the subset of these 7530 climatic patches that contain a certain minimum area of the focal habitat type. To account for high variability in area coverage among the eight habitat types we did not use an absolute, but a relative definition of the minimum area. We therefore calculated a 4 km² (2 x 2 km) raster map of the density (= percentage area within a raster cell) of each habitat type in the entire study area. We used this coarser resolution to avoid excessive 100 % values of the more widespread habitat types, especially the forests. We then selected the subset of the 7530 climatic patches which contained at least one 1 ha pixel with a focal habitat density within the upper 95th percentile of this density map.

Subdividing PAs into patches and further filtering them into high density patches prevents unrealistic connectivity and corridor suggestions. These easily may arise when large PAs encompasses a variety of habitats, with the focal habitat developed only in one or several small patches somewhere within the larger area.

All the further steps were done separately for each habitat type.

Connecting climate analogues

Climate analogues are here defined as patches that, in the future, will have at most the same temperature as the source patch has in the present, but not a warmer one. To reach their climate analogues, species are assumed to preferentially migrate along a path of monotonically decreasing temperature (Littlefield et al. 2017). Therefore, to identify each patch's destination, a table of all adjacent patches was created through ArcGIS. Using the script of McGuire et al. (2016) we created from this table a patch network that linked patches to adjacent ones with lower temperature values.

Assessing connectivity success

Patches were considered successfully connected under a particular climate change scenario if the destination patch they were connected to was their climate analogue (in the sense just defined, i.e. including sites that are cooler in the future than the destination patch is today). A margin of success or failure was calculated by subtracting the future temperature of the (coolest reachable) destination patch from the current temperature of the source patch (Margin = T^{c}_{s} - T^{f}_{d}) (McGuire et al. 2016). If the margin of success or failure is positive ($T^{f}_{d} \leq T^{c}_{s}$), climate connectivity is achieved, i.e. the (coolest) destination patch will have an analogous or cooler temperature as the source. If the margin is negative ($T^{c}_{s} \leq T^{f}_{d}$), climate connectivity is unsuccessful, as the (coolest) destination patch will, in the future, be warmer than the source patch in the present. We considered not only equal but also lower temperatures as suitable because patch network creation rules imply that species normally pass a patch with an equivalent temperature before the reach the cooler one (McGuire et al. 2016).

The climate connectivity of each patch was analyzed for the three RCP projections and for the six future decades, totalizing 18 different scenarios. A patch was considered always successfully connected to its climate analogue only if it was connected to it in all 18 scenarios.

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 PA network achieving climatic connectivity, under the three RCPs scenarios and for the six decadal time steps.

Resistance layer

After assessing how well connected patches were through adjacency, and hence mainly within PAs, we analyzed how their climate connectivity could improve by implementing corridors where connectivity through adjacency was not met. Corridors aim to connect habitat patches placed in different PAs and, to do so, they need to cross unprotected areas. Therefore, the maps of each habitat's density in the entire study area was also used as a resistance layer for corridor calculation. Thereby, higher habitat density represents a lower movement resistance, so species are more likely to migrate through these areas to reach their climate analogues. The density map was inverted to a scale between 0 and 100, where 100 means maximum resistance (minimum habitat density). Therefore, ideal corridors are the ones that have monotonically decreasing temperature while minimizing cumulative resistance (McGuire et al. 2016).

Corridor network creation

Corridor creation was based on a least-cost model which calculates the least-cost distance between two areas in function of the distance and the costs necessary for the traversal (Etherington 2016). In ArcGIS, the Climate Linkage Mapper from the Linkage Mapper toolbox (Kavanagh et al. 2012) was used to build corridors as this tool calculates least-cost links between locations considering, in addition to the resistance layer, the climate range the links have to cross. Considering climate fluctuations as a cost when calculating corridors might increase the likelihood that these corridors are the ones used by wildlife, especially the ones that are sensitive to climate (Kavanagh et al. 2012).

Although the aim of the corridors in our study is to connect the unsuccessful patches (the ones that are not climatically linked by adjacency), we used all the patches as an input considering that an unsuccessful patch can be connected to a successful one. As a consequence, patches connected by adjacency are also available as destination option to be reached through corridors from other patches. The current temperature raster and the habitat density map (resistance layer) were used as additional inputs for corridor calculation.

We set the following restrictions on corridor creation: the minimum distance between two patches to have a corridor built was 200m while the maximum was 10km, both in Euclidean distance. Moreover, corridors were only built when the (current) temperature difference between two patches was greater than 1°C. As corridors should ideally follow a monotonic path, temperature changes were also translated into cost-distance units within the tool (climate cost variable). Therefore, we established a temperature–distance weight of 50 km/1°C according to the suggestion of Nuñez et al. (2013). These authors selected the weight of 50 km/1°C because it maintained an unidirectional change in temperature when moving between pixels in most cases and nevertheless resulted in corridors not longer than three times the Euclidean distance between patches.

From the resulting set of corridors, the ones that were placed within PAs were excluded, as there is no reason to build a corridor inside an area already protected. In an *a posteriori* step, we moreover filtered suitable corridors that were shorter than 10km and strictly monotonic. We set the 10km limit because many of the species that PAs aim to protect are unlikely to achieve migration rates of 100 m / year (i.e. 10 km in 50 years, the approximate time horizon of our analysis if one accounts for time until corridors might be implemented) (Svenning & Sandel 2013). This is particularly true for most of the endemic species we use for the evaluation of corridor success (see below) (e.g. Essl et al. 2011). The final set of corridors was then used to update the adjacency-based propagation network in order to assess how much the corridors could improve the habitats' climate connectivity (McGuire et al. 2016). It is important to point that corridor area was not accounted for when calculating the percentage of PA connected by the corridors because corridor width was not included, therefore impeding the calculation of corridor area.

Corridor Efficiency

All the suitable corridors were then analyzed to assess how efficient they were. As conservation actions are limited by many different factors, most importantly time and budget, it is very important to select which actions are more efficient in achieving the conservation goals and therefore prioritize them. Corridor efficiency was assessed based on three criteria, namely corridor length, corridor cost and how many endemic species might be connected through them. Shorter corridors should be prioritized because by crossing shorter paths species might have higher chances of surviving and reaching their destination. Lower cost is also an important factor as it increases the likelihood of implementation and means less modified areas, more density of the habitat in question and less changes in temperature, which are all crucial aspects in determining the likelihood of the corridor being used. Lastly, the more species using a corridor, the more relevant it is as it has the potential to conserve more species with less costs (budget and time). We focused on endemics in this calculation because their distribution is particularly well documented (Rabitsch & Essl 2009) and the Austrian PA network has a particular responsibility to conserve endemics of the study area. Corridors were ranked based on their efficiency and the best ones were shorter, with lower cost and connecting more species. To calculate a one dimensional rank based on three criteria, first we ranked each criteria separately (species rank was descending, in opposite to cost and length, i.e. the more species, the lower the number in the rank). Then we added the three ranks and this final sum was the value used in the final corridor rank.

Only endemic plant species were used for the analysis and to determine how many of them are connected by a corridor, we considered that all species present in a PA from where a source patch is connected to another PA through a corridor have the potential to use this corridor, even though corridors have been built considering climatic patches only (and many PAs encompass more than one climatic patch). This assumption is quite broad since not all species might take the same corridor, as some might have to cross areas without their ideal habitat or with changes in temperature. For this reason, this number is considered the maximum number of species climatically connected by the corridor in question. By doing so, we also determined how many additional species could be reached by the corridors. Ultimately meaning how many additional species have their distribution overlapping with patches that achieve climate connectivity through corridors. Since the species distribution maps are fairly coarse compared to the habitat distribution maps, we additionally restricted the species' distribution by their affiliation to the habitat in question in order to refine the distribution maps and have a more reliable species count.

Results

The filtering of total climatic patches into patches that enclosed at least one of the eight habitat types with significant density resulted in an area of 13285.07km² (termed focal area henceforth), which is 9.9% of the study area and 53.23% of the protected areas. On average across all eight habitat types, more than 50% of the focal area is climatically connected through adjacency, i.e. without any further conservation effort, until 2040, independent of the climate scenario (Table 1). In the longer run, however, climate connectivity through adjacency strongly depends on the scenario. In RCP2.6, connectivity is still reached for 55.7% of the focal area (SD across the eight habitat types =19.9) in 2080. In the intermediate scenario (RCP4.5), the average drops to 35.3% (SD=16.89) in 2080. And in RCP8.5, the most extreme scenario, the average focal area climatically connected through adjacency is only 13.3% (SD=8.22) in 2080 (Table 1). About 11 % of the focal area is always successfully connected, meaning that it achieves climate connectivity in all years and scenarios.

Shrub Lands are the habitat type with the most successfully connected area, followed by Extensive Grasslands, Coniferous Forest, Rocks, Alpine Grasslands, Broad Leaved Forest, Dry Grasslands and lastly Wetlands (Appendix Table 1). Only in RCP2.6, the ranking is slightly different, with Alpine Grasslands having a higher share of connected areas than Rocks.

Overall, corridors can improve climate connectivity of the habitat types, although the average increase in connectivity is low. In RCP2.6, this increase amounts to c. 3.4% of the focal area, with little variation across time. In RCP4.5, the increase also is c. 3.4% over most decades, but eventually drops to 1% in 2080. In RCP8.5, the initially similar 3.4% already start to decrease in 2060 and drop to only 0.7% in 2080. There is, however, considerable variation among habitat types in the contribution of corridors to climatic connectivity. For example, Dry Grasslands have gains of up to 17% (in RCP2.6) while Shrub Lands do not substantially profit from corridors under any scenario. The ranking of gains is Dry Grasslands, followed by Alpine Grasslands, Extensive Grasslands, Coniferous Forest, Wetlands, Broad Leaved Forest, Rocks and Shrub Lands (RCP4.5; the last two tied, with zero gain). In the other scenarios, the ranking slightly differs, with Wetlands in third place in RCP2.6 and with Shrub Lands in seventh place in RCP8.5.

As the intermediate RCP4.5 scenario is currently considered the most likely one (Hausfather & Peters 2020), the following more detailed descriptions will mainly refer to it, pointing out other scenarios when necessary.

One additional result from the available data is the relative amount of area that is protected of each habitat. Wetlands was the habitat with most relative area protected, with 54.27% of its total area under protection. The following ones were Rocks (47.49%), Shrub lands (40.52%), Dry Grasslands (38.77%), Broad Leaved Forest (29.49%), Alpine Grasslands (24.42%), Extensive Grasslands (19.56%) and lastly Coniferous Forest (16.52%; Appendix Table 1). It is important to note that there is a significant difference in the habitats size, e.g.

Table 1: Habitats' percentage area achieving climate connectivity through adjacency, corridors and the percentage gain due to corridors (CFO: Coniferous Forest; BLFO: Broad Leaved Forest; SHRUBS: Shrub Lands; EXTGR: Extensive Grasslands; ALPGR: Alpine Grasslands; WET: Wetlands; DRY: Dry Grasslands and ROCKS: Rocks)

RCP26

%protected habitat area connected by adjacency

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	85.2	75.3	69.8	68.8	69.9	64.9	72.32	6.51
BLFO	67.9	56.8	54.9	54.7	54.9	54.7	57.32	4.79
SHRUBS	89.1	79.2	73.1	72.6	73.1	72.6	76.62	6.05
WET	14.7	14.1	9.3	9.3	9.4	9.3	11.02	2.40
ROCK	82.8	70.5	67.7	67.7	67.7	67.5	70.65	5.53
ALPGR	88.6	65	62.6	62.2	62.2	62.2	67.13	9.65
EXTGR	80.8	77.8	69.6	68.6	70	68.6	72.57	4.87
DRY	50.8	48	41.6	41.6	41.6	40.6	44.03	3.90
Average through habitat	69.8	61.513	56.688	56.35	56.763	55.713		
Standard Deviation	23.98	20.56	20.38	20.18	20.39	19.99		

%protected habitat area connected by corridor

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	85.7	76.2	70.6	69.6	70.7	65.7	73.08	6.42
BLFO	69	57.2	55.3	55.1	55.3	55.1	57.83	5.05
SHRUBS	89.1	79.2	73.1	72.6	73.1	72.6	76.62	6.05
WET	16	14.9	10.1	10.1	10.1	10.1	11.88	2.54
ROCK	82.8	70.5	67.7	67.7	67.7	67.5	70.65	5.53
ALPGR	90.7	69.4	67.8	67.4	67.4	67.4	71.68	8.53
EXTGR	86.4	83.4	72.7	71.7	73.1	71.7	76.50	6.02
DRY	68.1	65.2	58	58	58	57	60.72	4.29
Average through habitat	73.5	64.5	59.4	59.0	59.4	58.4		
Standard Deviation	23.17	20.26	19.62	19.40	19.64	19.17		

%gain from corridor

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	0.5	0.9	0.8	0.8	0.8	0.8	0.77	0.12
BLFO	1.1	0.4	0.4	0.4	0.4	0.4	0.52	0.26
SHRUBS	0	0	0	0	0	0	0.00	0.00
WET	1.3	0.8	0.8	0.8	0.7	0.8	0.87	0.20
ROCK	0	0	0	0	0	0	0.00	0.00
ALPGR	2.1	4.4	5.2	5.2	5.2	5.2	4.55	1.13
EXTGR	5.6	5.6	3.1	3.1	3.1	3.1	3.93	1.18
DRY	17.3	17.2	16.4	16.4	16.4	16.4	16.68	0.40
Average through habitat	3.5	3.7	3.3	3.3	3.3	3.3		
Standard Deviation	5.49	5.49	5.22	5.22	5.23	5.22		

RCP45

%protected habitat area connected by adjacency

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	85.2	73.9	60.5	59.5	53.3	51.6	64.00	11.89
BLFO	68.2	56	54.6	51.1	27.4	26.5	47.30	15.32
SHRUBS	89.5	78.8	72.3	70	65.9	55.8	72.05	10.46
WET	16.3	14.1	9.1	9.1	8.6	7.1	10.72	3.30
ROCK	83.1	70.5	67.5	61.4	44.4	39.4	61.05	15.07
ALPGR	88.6	66.9	62.2	55.2	37.7	32.3	57.15	18.75
EXTGR	80.9	75.8	68.5	68.5	67.9	53.3	69.15	8.52
DRY	50.9	44.8	40.6	40.6	39.4	16	38.72	10.87
Average through habitat	70.3	60.1	54.4	51.9	43.1	35.3		
Standard Deviation	23.71	20.33	19.47	18.45	18.44	16.89		

%protected habitat area connected by corridor

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	85.7	74.7	61.3	61.2	55	53.8	65.28	11.37
BLFO	69.3	56.4	55	51.6	27.6	26.5	47.73	15.62
SHRUBS	89.5	78.8	72.3	70	65.9	55.8	72.05	10.46
WET	17.1	14.9	10	9.6	9.6	8	11.53	3.28
ROCK	83.1	70.5	67.5	61.4	44.4	39.4	61.05	15.07
ALPGR	90.7	70.4	67.4	60.4	42	36.5	61.23	18.13
EXTGR	86.4	81.4	71.7	71.7	70.9	53.4	72.58	10.34
DRY	68.1	62	56.9	56.9	55.9	16.2	52.67	16.84
Average through habitat	73.7	63.6	57.8	55.4	46.4	36.2		
Standard Deviation	22.88	19.97	19.02	18.33	18.96	16.92		

%gain from corridor

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	0.5	0.8	0.8	1.7	1.7	2.2	1.28	0.61
BLFO	1.1	0.4	0.4	0.5	0.2	0	0.43	0.34
SHRUBS	0	0	0	0	0	0	0.00	0.00
WET	0.8	0.8	0.9	0.5	1	0.9	0.82	0.16
ROCK	0	0	0	0	0	0	0.00	0.00
ALPGR	2.1	3.5	5.2	5.2	4.3	4.2	4.08	1.07
EXTGR	5.5	5.6	3.2	3.2	3	0.1	3.43	1.84
DRY	17.2	17.2	16.3	16.3	16.5	0.2	13.95	6.16
Average through habitat	3.4	3.5	3.4	3.4	3.3	1.0		
Standard Deviation	5.48	5.49	5.18	5.15	5.18	1.42		

RCP85

%protected habitat area connected by adjacency

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	77.4	63.8	58.3	41.9	33.5	12.2	47.85	21.41
BLFO	57	54.6	32.5	25.8	12	9.9	31.97	18.54
SHRUBS	83.3	72.3	68.9	48.2	42.9	27.8	57.23	19.13
WET	14.4	9.2	8.6	7.1	6.7	6.7	8.78	2.69
ROCK	72.5	67.5	46	36.7	20.1	10.1	42.15	22.81
ALPGR	74.2	62.2	49.4	27.2	9.9	9.3	38.70	25.01
EXTGR	78.4	68.6	68.3	49.6	44.3	26	55.87	17.75
DRY	48.6	40.6	40	14.4	13.7	4	26.88	16.76
Average through habitat	63.2	54.9	46.5	31.4	22.9	13.3		
Standard Deviation	21.44	19.60	18.71	14.49	14.20	8.22		

%protected habitat area connected by corridor

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	78.2	64.6	60.3	44.3	36.2	14.4	49.67	20.83
BLFO	57.4	55	32.9	25.8	12.1	9.9	32.18	18.70
SHRUBS	83.3	72.3	68.9	48.6	43.3	28.2	57.43	18.95
WET	15.1	10	9.6	8	7.2	7	9.48	2.75
ROCK	72.5	67.5	46	36.7	20.1	10.3	42.18	22.76
ALPGR	76.3	67.4	54.6	31.4	12.1	11.5	42.22	25.55
EXTGR	84	71.7	71.4	49.7	44.4	26	57.87	19.67
DRY	65.8	56.9	56.5	14.6	13.9	4.1	35.30	24.85
Average through habitat	66.6	58.2	50.0	32.4	23.7	13.9		
Standard Deviation	21.16	19.13	19.12	14.49	14.23	8.14		

%gain from corridor

	2030	2040	2050	2060	2070	2080	Average through years	Standard Deviation
CFO	0.8	0.8	2	2.4	2.7	2.2	1.82	0.75
BLFO	0.4	0.4	0.4	0	0.1	0	0.22	0.19
SHRUBS	0	0	0	0.4	0.4	0.4	0.20	0.20
WET	0.7	0.8	1	0.9	0.5	0.3	0.70	0.24
ROCK	0	0	0	0	0	0.2	0.03	0.07
ALPGR	2.1	5.2	5.2	4.2	2.2	2.2	3.52	1.39
EXTGR	5.6	3.1	3.1	0.1	0.1	0	2.00	2.11
DRY	17.2	16.3	16.5	0.2	0.2	0.1	8.42	8.25
Average through habitat	3.4	3.3	3.5	1.0	0.8	0.7		
Standard Deviation	5.51	5.19	5.18	1.41	0.99	0.89		

Wetlands have a total 1084.84km² while Coniferous Forest has 41621.51km², meaning that even though Coniferous Forest is the habitat with least relative area protected, its area under protection (6876.54km²) is still bigger than the whole Wetlands area.

Coniferous Forest

Most of the 3916.75km² focal area of Coniferous Forest is successfully connected until 2080, while only 0.8% of the habitat is isolated (Isolated patches are geographically isolated patches, meaning that in all years and scenarios they could not be connected to any other patch; Appendix Figure 1). From 434 suitable corridors, around 26 were responsible for increasing connectivity on average by 1.3%, with a peak of 2.2% in 2080 (Figure 1; Table 1). Gains in climatically connected area through corridors increased over time (Table 1) while the amount of area losing connectivity almost doubled from 2040 to 2080 (Appendix Table 3). In 2080, most of the Coniferous Forest in Lower Tauern will not achieve climate connectivity under whatever climate scenario while some areas in Lower Austria remain successfully connected, e.g. Wachau, Vienna Woods and "Nordöstliche Randalpen" (Appendix Figure 2). Most of the habitat within Slovenian buffer territory is also failing to achieve climate connectivity.

The distribution of 18 endemic plants overlaps with the focal area of Coniferous Forest. Corridors have the potential to increase the number of endemic plant species achieving climate connectivity in 13 protected areas. They are spread throughout the central and eastern part of the study area and the gain in climatically connected endemics ranges from 1 to 6 (Figure 2). The most efficient corridors are based in Styria (High altitudes of the eastern Wölzer Tauern and Seckauer Alps) and in Lower Austria (Appendix Figure 3).

Broad Leaved Forest

The 2610.69km² focal area of this habitat type is more concentrated in the northeastern part of the study area (Appendix Figure 4) and has 68.2% of its area connected by 2030, however this value drops dramatically to only 26.5% in 2080 (Table 1; Appendix Figure 5). Most of the area in Donau-Auen are always successful until 2080, while Neusiedlersee National Park and half of the Vienna Woods area does not achieve climate connectivity by the same year, even with corridors (Appendix Figure 4). Corridors provide a maximum of 1.1% gain in 2030 and by 2080 they do not connect any additional area (Table 1).

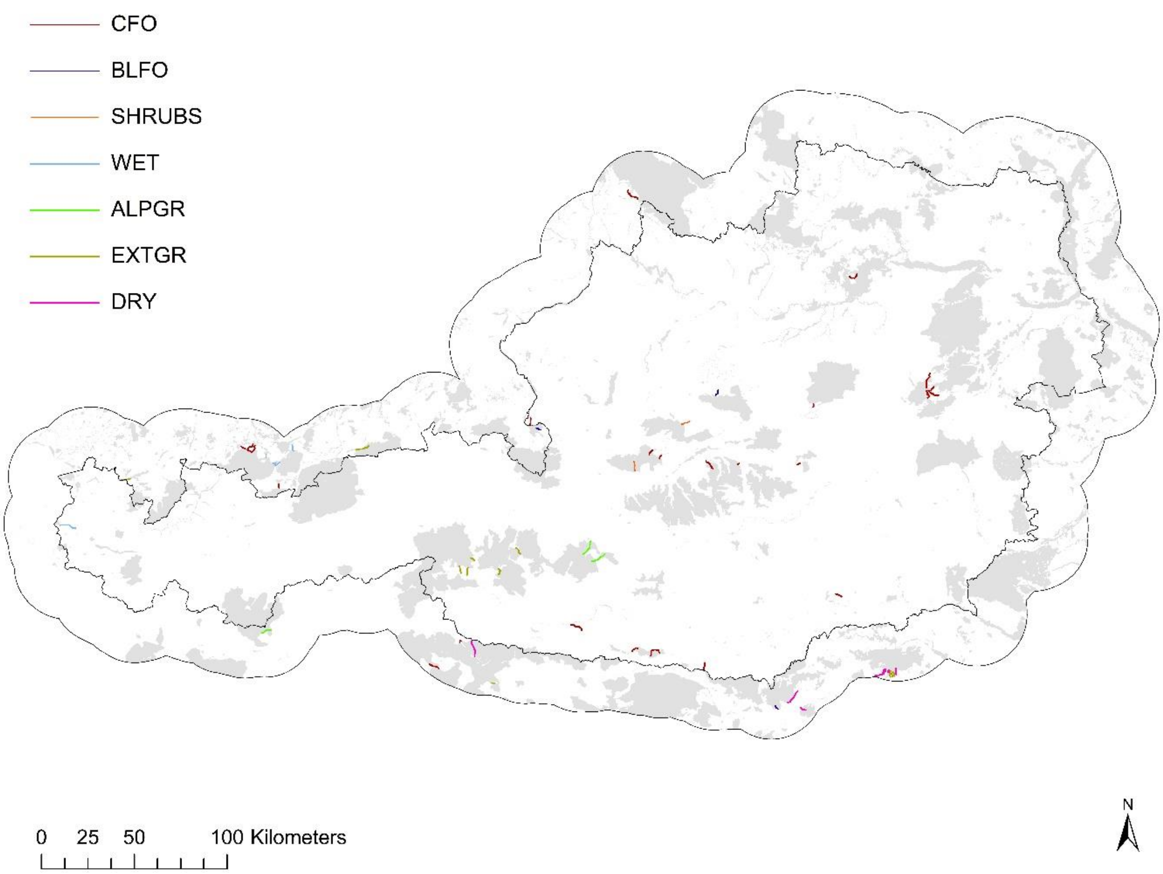

Figure 1: Corridors improving climatic connectivity of different habitat types in the Austrian protected area network under the RCP4.5 climate scenario in the year 2080. CFO: Coniferous Forest; BLFO: Broad Leaved Forest; SHRUBS: Shrub Lands; EXTGR: Extensive Grasslands; ALPGR: Alpine Grasslands; WET: Wetlands; DRY: Dry Grasslands and ROCKS: Rocks.

The ranges of only five endemic plant species overlap with the focal area of this habitat type, while corridors have the potential to increase the amount of species achieving climate connectivity of two Natura 2000 sites (Appendix Figure 6). “Schluchtwälder der Steyr- und Ennstaler Voralpen” in Upper Austria presents no species in successfully connected areas and corridors can reach two species. “Nordöstliche Randalpen”, in Lower Austria benefits with one more successfully connected species, while without them already 2 were achieving climate connectivity. In 2040, from 17 corridors, the 10 most efficient ones are located mostly in Upper Austria (mostly “Schluchtwälder der Steyr- und Ennstaler Voralpen” and Kalkalpen). In 2080, however, there are only 3 important corridors in total, located in at Kalkalpen, Untersberg (Germany) and Grintovec (Slovenia; Appendix Figure 7).

Shrub lands

Climatic patches with sufficient density of this habitat encompass a focal area of 1737.14km², of which more than 50% might be successfully connected until 2080 (Table 1, Appendix Figure 8). Three corridors add only 0.08km² of successfully connected focal area, with no substantial change over the years (Appendix Table 3; Appendix Figure 9). They are located in Upper Austria, at Dachstein and Schluchtwälder der Steyr- und Ennstaler Voralpen, a Natura 2000 site. A few patches located in the border with Slovakia and Hungary are isolated, accounting to 1.8% of the total area. Higher density of this habitat is found in the Central Eastern Alps, at the border with Germany and within the buffer area of Italy, Slovenia and Czech. Shrub lands patches that will lose connectivity through years are spread through the study area, with no particular concentration (Appendix Fig. 10).

The distribution of 20 endemic plant species overlaps with the focal area of this habitat. Corridors increase the pool of species achieving climate success in both PAs connected by corridors and the gains are of 5 and 8 species, respectively (Appendix Figure 11).

Wetlands

The 478.26km² of focal wetland area was concentrated in the buffer zones outside the Austrian territory (Figure 3). While around 5 corridors, out of 67 suitable ones, improved connectivity by an average of 0.82%, 59% of the focal area remains isolated at any time with and without corridors (Appendix Table 3). Also, most of the non-isolated area never reaches climate connectivity, neither through adjacency nor corridors: on average, only 11.5% of the habitat achieves climate connectivity, even with the addition of corridors (Table 1; Appendix Figure 12). The few successful areas are located in the Bavarian region, more specifically in the Ester Mountains, Murnauer Moos and Chiemgau Alps (Figure 2; Appendix Figure 13).

Only three endemic species have ranges that overlap with the focal area of Wetlands. Corridors do not increase the number of successfully connected species of any protected area. From the 132 protected areas where Wetlands are located, 12 overlap with endemic species' ranges and only two (Penkensee in Carinthia and Šumava National Park in Czech) have species in successfully connected areas.

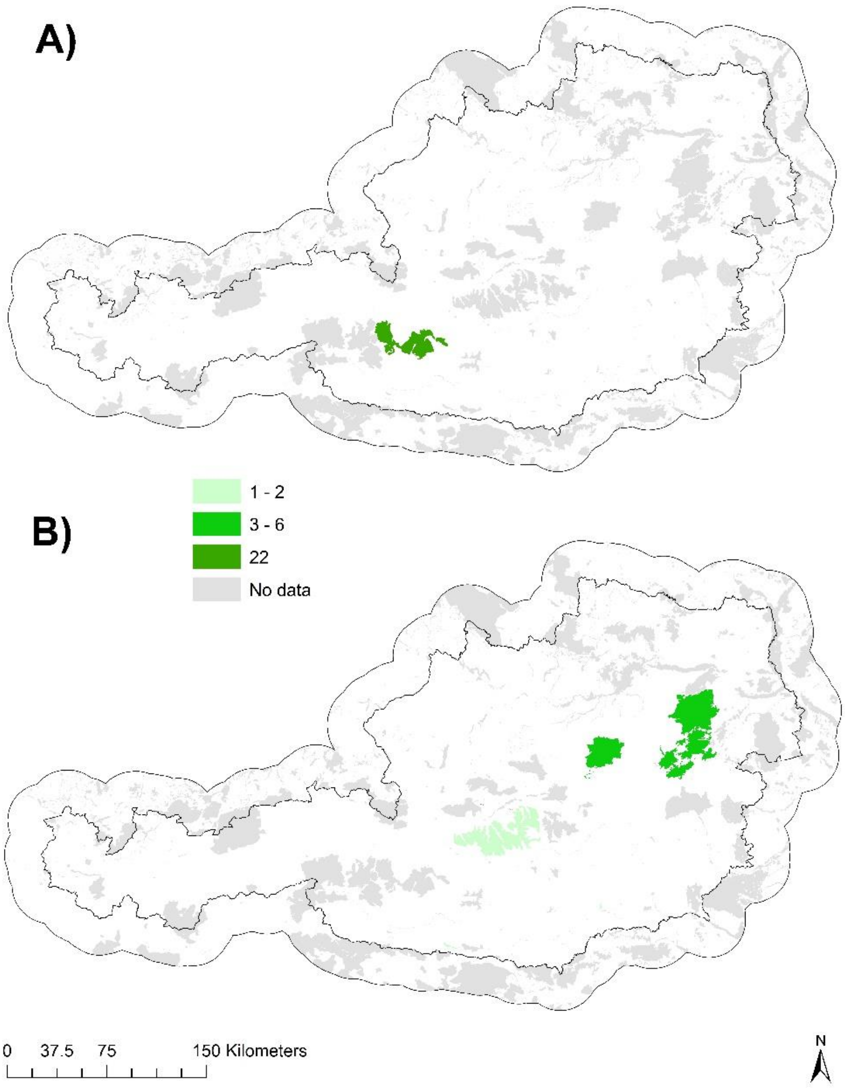

Figure 2: Absolute gain, due to corridors, in endemic plant species of particular habitat types which achieve climate connectivity in the Austrian protected area network under the RCP4.5 climate scenario in the year 2040, the year with highest gains. A) Alpine Grasslands and B) Coniferous Forest.

Rocks

This habitat was one of the few that did not have any isolated area. An average of 61% of the focal area is climatically successfully connected through adjacency, the 4th most successful habitat. However, corridors did not increase the amount of successfully connected area in any year for all scenarios (Appendix Figure14). The only exception is found in 2080 in RCP8.5, when one corridor, located in Germany (Wetterstein mountains), provides an increase of 0.2% in successfully connected area (Table 1). This habitat was absent in northeastern parts of the study area like Lower and Upper Austria, and more located in central-western parts where altitude is higher, such as Salzburg, Tyrol and South Tyrol in Italy (Appendix Figure

15). By 2080 most of the habitat will not achieve climate connectivity, with no specific hotspot. The focal area of this habitat overlaps with the distribution of 42 endemic species, of which many are located in areas successfully connected through proximity.

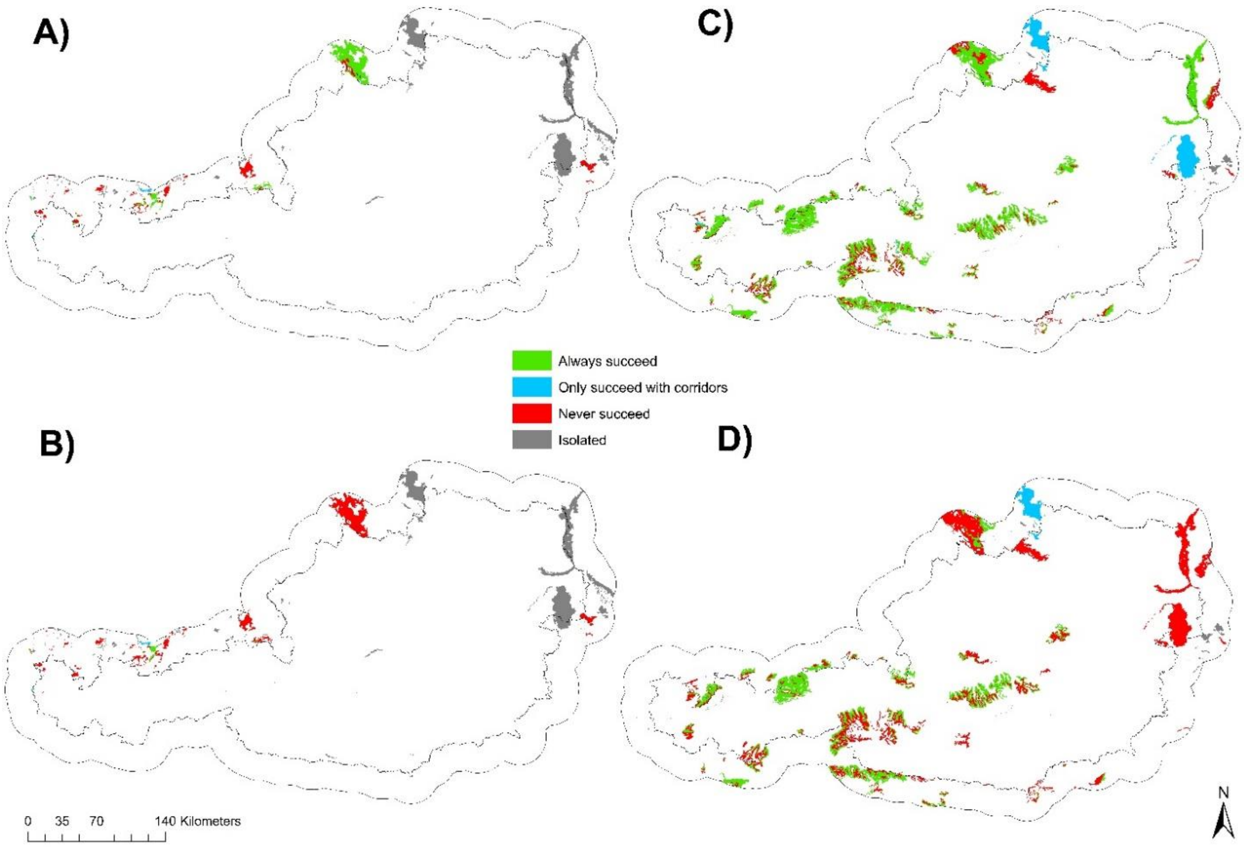

Figure 3: Climate connectivity assessment of climatic patches containing Wetlands under the RCP4.5 scenario in A) 2040 and B) 2080; and of those containing Extensive Grasslands under the same scenario and for the same years (B, D).

Alpine Grasslands

In 2030, Alpine Grasslands will still have more than 85% of their 734.09km² of focal area connected, but connectedness declines over time, mostly from 2030 to 2040, reaching a total of 32.3% of connected area in 2080 (Table 1; Appendix Figure 16). The number of corridors with potential to expand climate connectivity increases over the years, reaching a maximum of six corridors in 2080, when they provide a gain of 4.2% in successfully connected area (Figure 1; Table 1). Rocks and Alpine Grasslands are the only habitats with no isolated areas (Appendix Figure 17).

With 46 endemic plant species, this habitat is the one the focal area of which overlaps with the highest number of endemic plant species. Regarding gain in successfully connected species, corridors could reach 22 more species in one PA (High Tauern; Figure 2). When only adjacency is considered, 23 species are able to achieve climate connectivity. This means that, despite the few amount of corridors, they have the potential to almost double the amount successfully connected species (Appendix Figure 18).

Extensive Grasslands

Until 2080, from 1703.25km² of Extensive Grasslands in the focal area, more than half might be successfully connected (Table 1; Appendix Figure 19). Around 12 corridors were important to add an average of 3.4% gain in connected focal area through the years (Figure 1; Table 1). 109.9km² are climatically isolated, accounting to 6.5% of the total habitat area. At a glance, the northeastern region of the study area is more affected by climate warming, where patches fail to connect in 2080 even with corridors (Figure 3).

The distribution of 14 different endemic plant species overlaps with this habitat types' focal area. Corridors increased the number of species that achieve climate connectivity in two different protected areas. At Fertő-Hanság National Park, in Hungary in the vicinity of Neusiedlersee National Park, there are no endemic species in successfully connected patches. However, the establishment of a corridor might enable the movement of one endemic species from this protected area, but only in the initial years 2030 and 2040. Two more species at High Tauern National Park can also benefit from the construction of a corridor in the area, while adjacency connects only one species (Appendix Figure 20). The 11 most efficient corridors in 2080 include the corridors in these 2 PAs, High Tauern, Dolomites and Verwall in Vorarlberg (Appendix Figure 21).

Dry Grasslands

Dry Grasslands, with a total focal area of 713.67km², was one of the most endangered habitats, its connectivity dropping from 50.9% in 2030 to 16% in 2080 (Appendix Figure 22). In RCP8.5, for example, only 4% of the habitat area will be climatically connected by 2080 (Table 1). However, corridors present a relatively high improvement compared to the other habitats. Until 2070, corridors provide a 16.5% gain in connected areas, while in 2080, the gain drops considerably to 0.2% (Tables 1). Essentially all the habitat area within the Austrian territory fails to achieve climate connectivity by 2080, even with corridors (Appendix Figure 23).

Twelve endemic species have ranges that overlap with the focal area of this habitat type. However, none of them benefit from any corrido that can increase connectivity. In 2080, all the twelve corridors are outside of the Austrian territory, being distributed in Italy and Slovenia (Appendix Figure 24).

Discussion

Our results point out that under the RCP4.5 scenario most habitats (6 out of 8) have more than half of their high-density area connected to climate analogues (or colder) through proximity by 2060, without any extra conservation effort. From 2060, the percentage of climatically connected area drops rapidly for some habitat types, such as Broad Leaved Forest, Dry Grasslands or Alpine Grasslands. By 2080, only Coniferous Forest, Shrub lands and Extensive Grasslands still have more than 50% of their high-density area achieving climate connectivity. Under the RCP2.6 scenario more than 50% of the area remains climatically connected until 2080 in case of all habitat types except Wetlands and Dry Grasslands. By contrast, under the RCP8.5 scenario, all habitat types experience dramatic losses of climatic connectivity, with less the 15% of the area still connected in 2080 except for Shrub lands and Extensive Grasslands.

The impact of corridors on climate connectivity varies considerably between different habitats, demonstrating the importance of analyzing habitats separately. Dry Grasslands, the second last habitat with lowest amount of successful area, and Alpine Grasslands are the ones that benefit the most from corridors, with an average gain in area of 14% and 4.1%, respectively. On the other hand, the establishment of corridors to connect Shrub Lands' area do not seem a priority, as they do not add any gain in climatically connected areas. The only increase in area is in RCP8.5 from 2060 onwards, however just 0.4% of the area is added. Most of the habitat patches are already near to their climate analogues (72% of the area, on average) and the ones that are not are either isolated solely by distance (no monotonic corridor shorter than 10km can reach them) or the corridors that reach them do not connect them to their analogues, meaning that they would be connected to areas with temperature above the current one in the source patch. Another habitat which corridors provide substantially no gain in connected areas is Rocks. This habitat has no isolated area, meaning that all patches are somehow reached by a corridor. However, the corridors either connect areas that were already connected by adjacency (meaning that they do not strictly depend on them to achieve climate connectivity) or they do not connect climate analogues. Even though corridors do not increase the amount of successful areas, on average 61.05% of the habitat achieves climate connectivity, which is still a significant amount of area. Analyzing the three habitats that profit most and the two that least profit from corridors, we can see that corridors play a more important role in grassland types, regardless of elevation, while for the other habitats, elevation might have a stronger impact when it comes to achieving climate connectivity, since Rocks and Shrub lands are located in higher altitudes. For these habitats, high elevations might have "climate islands" that are harder to reach.

Although Wetlands, compared to the other biomes, is the habitat with most relative area protected, it is the one that has the most isolated area, as almost 60% of the habitat cannot be reached by any of the calculated corridors. From the non-isolated areas, most of it never achieves climate connectivity, neither through adjacency nor through corridors. By 2080, only 7.1% of the habitat will be climatically connected to an analogue (or colder area). Wetlands are especially susceptible to climate change as it will change both temperature regimes and the water supply on which this habitat depend more than other ones (Erwin 2009). Besides playing an important role in the provision of ecosystem services to humans, such as flood mitigation and water quality improvement, Wetlands additionally serve as net carbon sink (even when methane emissions are considered), and their decline is hence connected to climate change via a positive feedback loop (Mitsch et al. 2013).

We also analyzed how many endemic plant species could be added, as a consequence of corridor creation, to the pool of species located in successfully connected areas. Just species from a few PAs profited from corridors, and the amount varied across time as well as across habitat types. No additional species from Wetlands, for example, are reached by corridors, while only one Wetland-PA has an endemic species in an area that achieves climate connectivity until 2070. Other two PAs have only one successfully connected species until 2030 and 2040. The absolute gain in species connected via corridors is usually small, with exception of Alpine Grasslands and Shrub Lands (up to 22 and 8 species, respectively). However, as some areas had one or did not have any species in successfully connected areas, the percentage gain of successfully connected endemic species through corridor creation was nevertheless often considerable. When interpreting these results three relevant points are important to recall. First, we only looked at endemic species of plants, but corridors also have the potential to reach non endemic plants and also different taxa, their conservation values is hence potentially much larger. Second, the addition of species able to achieve climate connectivity due to corridors through the years is based on the current distribution of species. If the distribution changes over the years, optimal corridors for linkage to climatic analogues in 2080 may also change. Third, there is of course no guarantee that species would use these corridors to migrate to their climate analogues. Traditionally, focal species are used to design and implement corridors in connectivity planning approaches (Lambeck 1997). However, some studies have shown that corridors based on “naturalness”, or focal habitat density used here, may present a partial proxy to a focal species approach while demanding a lower analytical effort (Krosby et al. 2015; Theobald et al. 2012). Despite naturalness based corridors performing better for large vagile species than for smaller and locally dispersing species, this approach is relatively efficient when there is the need of an initial assessment of connectivity of a landscape and when there is a lack of data regarding the movement of biological taxa (Krosby et al. 2015).

On top of the aforementioned considerations, it is essential to outline that although the majority of alpine and sub-arctic species of European concern are projected to lose climatic suitability (Araújo et al. 2011) we might underestimate the ability of species to adapt and resist to changes in climate, as the sensitivity and adaptive capacity of many species to climate change are unknown (Elsen et al. 2020). Apart from phenotypic and evolutionary plasticity species might also persist in smaller scale refugia where their current climatic niche is preserved (Hannah et al. 2014). It is also relevant to note that, although we analyzed the core of the habitats’ area within PAs, there are still lower habitat density areas not accounted for in the analysis. Moreover, the assessed area was less than half of the total habitats’ range across the study area, as the total range encompasses protected and unprotected land. Unprotected areas also have a conservation potential, as they can guard high degrees of biodiversity that can, sometimes, exceed those of protected lands (Elsen et al. 2020).

Other than we assumed in our calculations, the amount of area that achieves climate connectivity could also be increased by designing corridors longer than 10km and/or by incorporating additional unprotected land into existing or new PAs to expand the network. Both approaches may suffer from competing land use interests, lack of compliance of residential people and resource availability. Moreover, depending on the species, longer distances might not be realized (Haddad 2000). Expanding PAs might moreover not be efficient in connecting the physically and climatically isolated patches to their analogues if these aspects are not taken into consideration during PA planning. A recent study has shown that the proportion of protected land has no impact on retaining the current climate conditions protected in the future (Elsen et al. 2020). On the other hand, considering a high representation of ecosystems, habitats, elevations, ecological processes and climatic conditions when planning conservation strategies such as the establishment of PAs is highly correlated with protection retention (Elsen et al. 2020). Some types of climate and ultimately biomes are projected to suffer a reduction of their protected land in future climates, like montane grasslands and boreal forests. Therefore, this kind of approach is also important to foresee the necessity of species that might populate these areas (Elsen et al. 2020).

Although the corridors calculated in this study have the potential to improve climate connectivity, it is very important to indicate some limitations on their calculation that could be improved. The first limitation worth mentioning is that we did not include corridor width in the calculations. Width of corridors can have impact both on humans and on wildlife and ecological processes. For humans, the corridors' width can have impacts on policies and economic activities by restricting land use, which can in turn impact economic opportunities (Ford et al. 2020). On the other hand, corridor width can have a great impact on the edge effect between different ecosystems. Edge effect are changes in biotic and abiotic processes that happen on the border of two different ecosystems (van Schalkwyk et al. 2020). Although recognized as a very important factor determining corridor quality, researches have struggled to determine an optimal corridor width (Beier 2018; Gilbert-Norton et al. 2010; Haddad et al. 2011). Ford and colleagues (2020) proposed a conceptual approach called effective corridor width to design and assess the effectiveness of corridors. While their concept illustrates the importance of different types of human occupation near corridors and how the effective width depends more specifically on the animal species, Beier (2018) proposed a more general rule of thumb that corridors should be at least 2km wide. As our corridor calculation method was not species specific and was based on the "naturalness" of the landscape, a more general approach like the one proposed by Beier (2018) might reduce some possible edge effects.

A second possible limitation from our method is the habitat density which we used as a resistance layer on the least cost model. The critique is not to the least cost model itself, although some authors indicate a few uncertainties when it comes to its effectiveness regarding wildlife linkages (Beier et al. 2009; Sawyer et al. 2011), but rather to the density map. Firstly, it was necessary to assume that the amount of habitat among PAs will not change, meaning that their density will more or less stay the same until 2080, which is unrealistic given that specially these areas are unprotected and can suffer human alterations and also changes due to climate change itself. Secondly, depending on the habitat, a 2km grid scale might be too coarse to capture its effective density. Moreover, for habitats closer to human occupations, an additional resistance layer based on human settlements might play an important role as its higher weight could indicate a stronger resistance on top of the lower habitat's density in the area.

A third limitation in our corridor calculations is that their location is based on the current temperature. We connected areas that have 1°C difference and then defined the source (warmest) and destination (colder) patches, while also using the climate projections to assess their climate connectivity success in the future. Ideally, corridor planning should account for transient climatic change and species migration as it may affect the optimal destination patches and migration routes (Littlefield et al. 2019). However, this process computationally highly demanding, and would ideally be coupled with species movement models which are notoriously difficult to parameterize even for small sets of species (Hülber et al. 2016).

Our model could also be further improved by considering dispersion capacity and climate change velocity. As climate change is a dynamic phenomenon that involves more than shifts in temperature, taking into account the velocity which species might need to move to maintain their climatic conditions could be a very important element when planning corridors (Corlett and Westcott 2013). Furthermore, many sessile species face the problem of migration lag, as their dispersion capacity struggles to keep up with the velocity of climate change, leaving them in locations that might be unsuitable in the future, resulting in an extinction debt. This process is especially critical to alpine plants, as they are experiencing a range loss coupled with their limited seed dispersal capacity (Morgan and Venn 2017: Dullinger et al. 2012). Therefore, an inclusion of both components is suggested for a more precise and robust model. Lastly, it is important to recall that we also assumed that ecological conditions other than climate as well as temperature gradients will remain the same, and that existing PAs are going to be well managed, focusing on their conservation goals.

Conclusion

The climate connectivity of the Austrian protected area network strongly depends on the habitat in question, but overall, most habitats' areas remain fairly well connected to climate analogues over the next 60 years even without additional conservation efforts as long as climate change will not become more pronounced as predicted by the RCP4.5 scenario used here. Corridors provide improvement in connectivity especially in grasslands areas, while also potentially rescuing species that were located in previously unsuccessful areas. Some habitats are highly vulnerable even under moderate climate change, in particular Wetlands. The example of Wetlands clearly illustrates that protecting large parts of a habitat's current range does not guarantee climatic connectivity.

Despite the limitations, this study presents a valuable first assessment of how current Austrian and bordering protected areas are able to preserve important climate refugia and to which extent their location can favor the connectivity of different habitats. Both protected areas and corridors planning and implementation should be done considering future climate projections, species dispersion and other socio ecological aspects, as different stakeholders should be consulted for the establishment of effective conservation plans. Moreover, all these measures must be done together with climate mitigation efforts, such as reduction and capturing of greenhouse gases emission, as their aim is not to halt climate, but rather adapt to it.

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Appendices

Appendix Table 1: descending order of habitats with most successful area connected through adjacency, corridors and with higher gain from corridors. Values are the averages through 2030-2080 for each RCP.

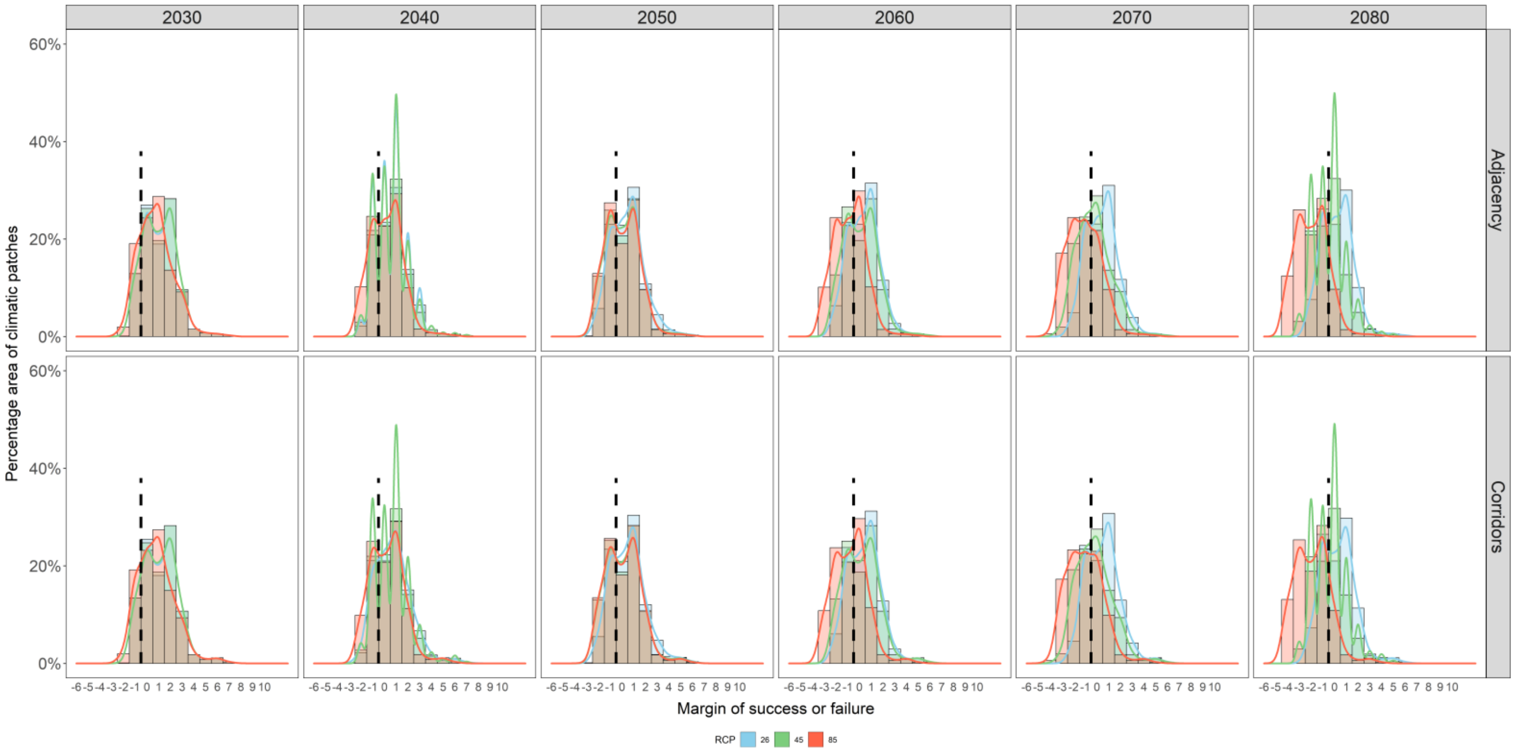
%protected habitat area connected by adjacency			%protected habitat area connected by corridor			%gain from corridor		
RCP26								
	Average through years	Standard Deviation		Average through years	Standard Deviation		Average through years	Standard Deviation
SHRUBS	72.32	6.05	**SHRUBS**	76.62	6.05	**DRY**	16.7	0.4
EXTGR	72.57	4.87	**EXTGR**	76.50	6.02	**ALPGR**	4.6	1.1
CFO	72.32	6.51	**CFO**	73.08	6.42	**EXTGR**	3.9	1.2
ROCK	70.65	5.53	**ALPGR**	71.68	8.53	**WET**	0.9	0.2
ALPGR	67.13	9.65	**ROCK**	70.65	5.53	**CFO**	0.8	0.1
BLFO	57.32	4.79	**DRY**	60.72	4.29	**BLFO**	0.5	0.3
DRY	44.03	3.90	**BLFO**	57.83	5.05	**ROCK**	0.0	0.0
WET	11.02	2.40	**WET**	11.88	2.54	**SHRUBS**	0.0	0.0
RCP45								
	Average through years	Standard Deviation		Average through years	Standard Deviation		Average through years	Standard Deviation
SHRUBS	72.05	10.46	**EXTGR**	72.58	10.34	**DRY**	14.0	6.2
EXTGR	69.15	8.52	**SHRUBS**	72.05	10.46	**ALPGR**	4.1	1.1
CFO	64.00	11.89	**CFO**	65.28	11.37	**EXTGR**	3.4	1.8
ROCK	61.05	15.07	**ALPGR**	61.23	18.13	**CFO**	1.3	0.6
ALPGR	57.15	18.75	**ROCK**	61.05	15.07302	**WET**	0.8	0.2
BLFO	47.30	15.32	**DRY**	52.67	16.84	**BLFO**	0.4	0.3
DRY	38.72	10.87	**BLFO**	47.73	15.62	**ROCK**	0.0	0.0
WET	10.72	3.30	**WET**	11.53	3.28	**SHRUBS**	0.0	0.0
RCP85								
	Average through years	Standard Deviation		Average through years	Standard Deviation		Average through years	Standard Deviation
SHRUBS	57.23	19.13	**EXTGR**	57.87	19.67	**DRY**	8.4	8.3
EXTGR	55.87	17.75	**SHRUBS**	57.43	18.95	**ALPGR**	3.5	1.4
CFO	47.85	21.41	**CFO**	49.67	20.83	**EXTGR**	2.0	2.1
ROCK	42.15	22.81	**ALPGR**	42.22	25.55	**CFO**	1.8	0.7
ALPGR	38.70	25.01	**ROCK**	42.18	22.76	**WET**	0.7	0.2
BLFO	31.97	18.54	**DRY**	35.30	24.85	**BLFO**	0.2	0.2
DRY	26.88	16.76	**BLFO**	32.18	18.70	**SHRUBS**	0.2	0.2
WET	8.78	2.69	**WET**	9.48	2.75	**ROCK**	0.0	0.1

Appendix Table 2: summary information about each habitats' area. The values in bold were the ones used in the study, accounting as total area.

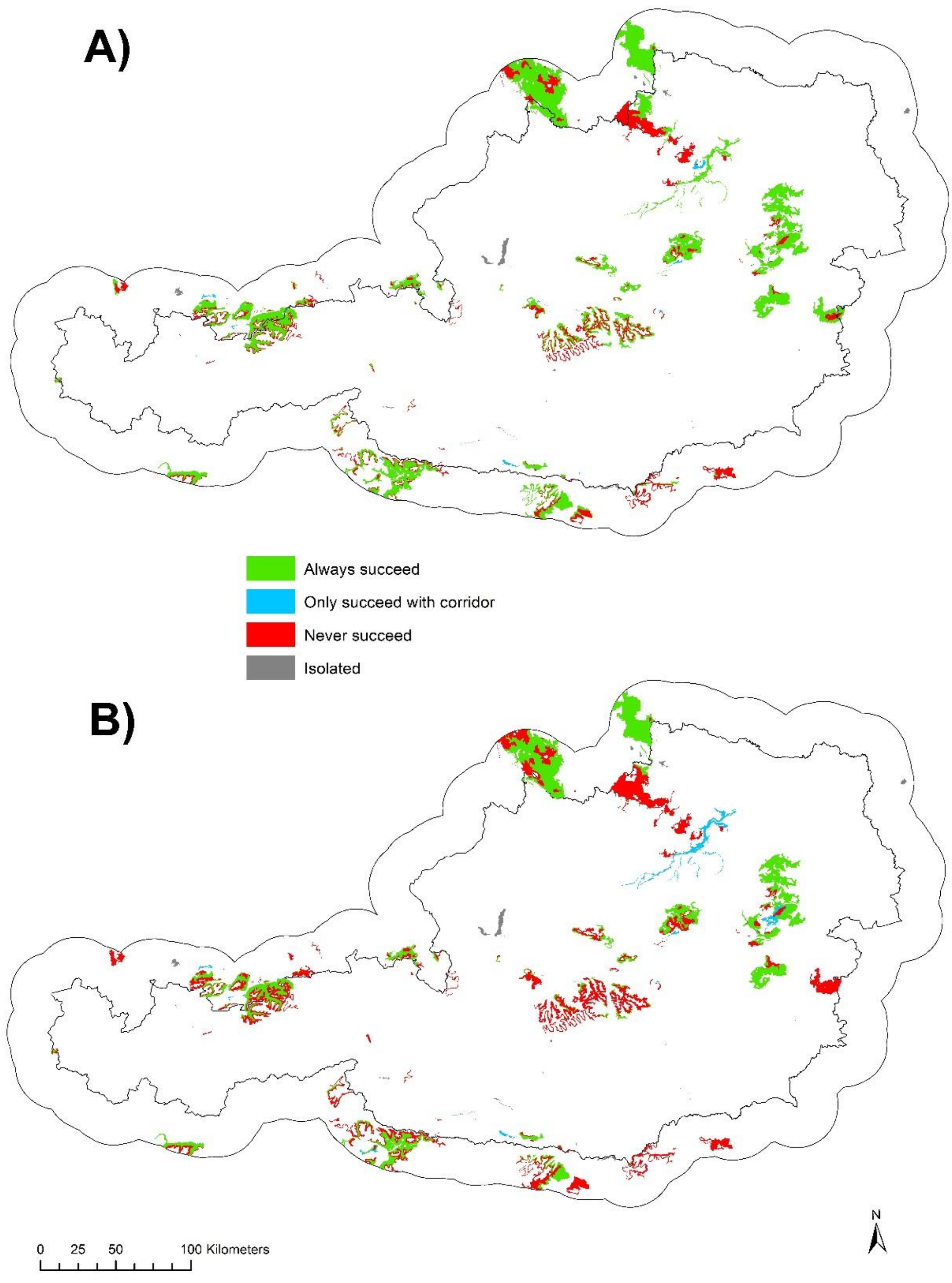
Total Study Area (km²)	133540.06							
Total Protected Area (km²)	24959.34							
	Habitat							
	CFO	**BLFO**	**SHRUBS**	**WET**	**ROCKS**	**ALPGR**	**EXTGR**	**DRY**
Total Habitat Area (km²)	41621.51	11340.04	5875.98	1084.84	4034.73	4695.65	12961.55	2494.47
%in total study area	31.17	8.49	4.40	0.81	3.02	3.52	9.71	1.87
Total Habitat Area within PAs (km²)	6876.54	3343.77	2381.17	588.69	1916.16	1146.61	2535.07	967.11
%of protected habitat	16.52	29.49	40.52	54.27	47.49	24.42	19.56	38.77
%in total PA area	27.55	13.40	9.54	2.36	7.68	4.59	10.16	3.87
%in total study area	5.15	2.50	1.78	0.44	1.43	0.86	1.90	0.72
Area within PA and above 95th percentile of density across study area	**3916.75**	**2610.69**	**1737.14**	**478.26**	**1391.22**	**734.09**	**1703.25**	**713.67**
%total habitat	9.41	23.02	29.56	44.09	34.48	15.63	13.14	28.61
%of total protected habitat	56.96	78.08	72.95	81.24	72.60	64.02	67.19	73.79
%in PA area	15.69	10.46	6.96	1.92	5.57	2.94	6.82	2.86
%in total study area	2.93	1.95	1.30	0.36	1.04	0.55	1.28	0.53

Appendix Table 3: Climate connectivity assessment of the focal area of each habitat under the RCP 4.5 climate scenario for the years 2040 and 2080. Always succeed: area that is connected to a climate analogue, either through adjacency or corridor. Only succeed with corridors: area that before was connected to non-analogue and then was connected to climate analogue through corridor. Never succeed: area that does not connect to climate analogue, neither through adjacency nor corridor. Isolated: area that is not connected to any other area, being climate analogue or not. CFO: Coniferous Forest; BLFO: Broad Leaved Forest; SHRUBS: Shrub Lands; EXTGR: Extensive Grasslands; ALPGR: Alpine Grasslands; WET: Wetlands; DRY: Dry Grasslands and ROCKS: Rocks.

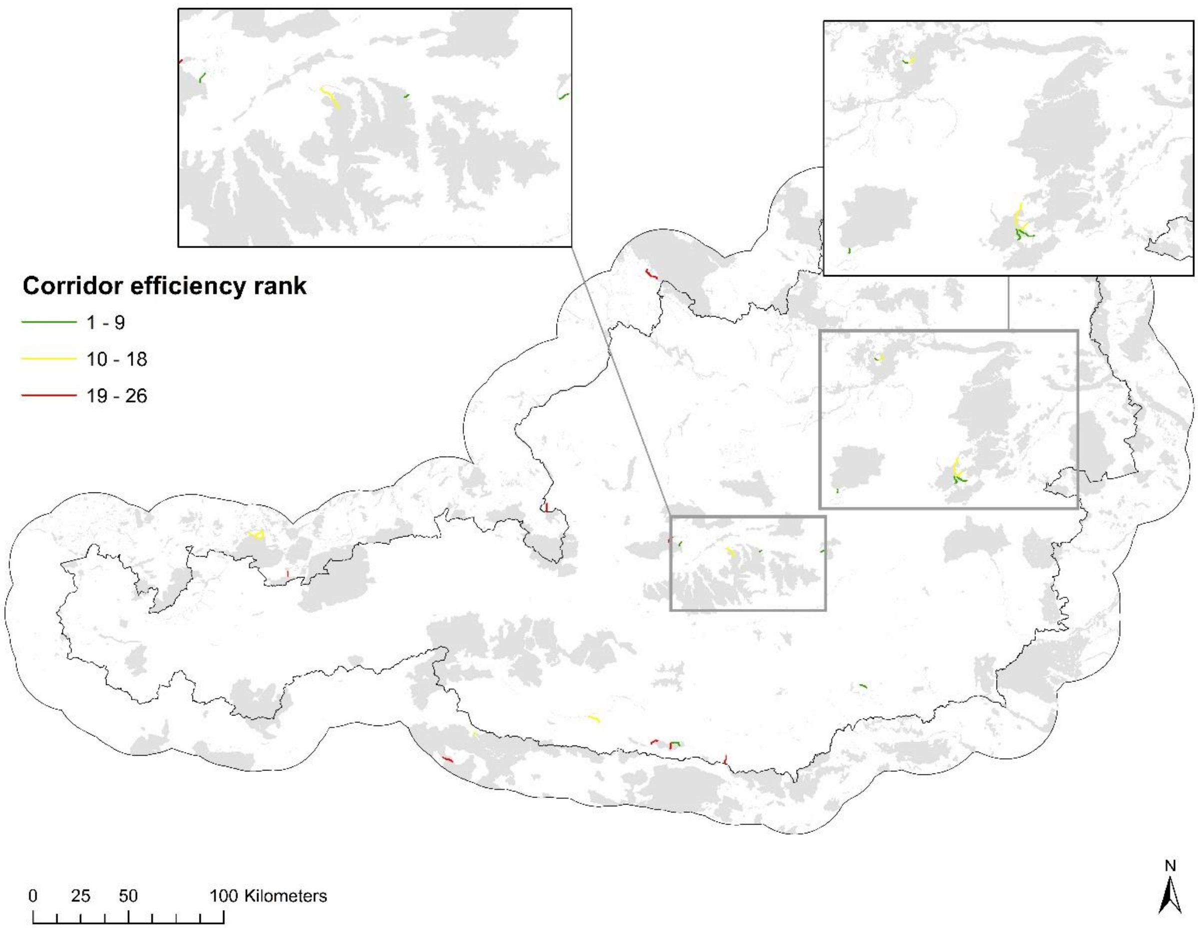
			Always succeed	**Only succeed with corridors**	**Never succeed**	**Isolated**	**Total area**
CFO	**2040**	**km²**	2892.65	32.96	958.37	32.77	3916.75
		%	73.9	0.8	24.5	0.8	
	2080	**km²**	2019.85	88.11	1776.02	32.77	3916.75
		%	51.6	2.2	45.3	0.8	
BLFO	**2040**	**km²**	1461.44	10.96	866.41	271.88	2610.69
		%	56.0	0.4	33.2	10.4	
	2080	**km²**	690.62	0.22	1647.97	271.88	2610.69
		%	26.5	0.0	63.1	10.4	
SHRUBS	**2040**	**km²**	1368.71	0.08	337.31	31.04	1737.14
		%	78.8	0.0	19.4	1.8	
	2080	**km²**	969.63	0.08	736.39	31.04	1737.14
		%	55.8	0.0	42.4	1.8	
WET	**2040**	**km²**	67.61	3.64	124.63	282.38	478.26
		%	14.1	0.8	26.1	59.0	
	2080	**km²**	33.87	4.27	157.74	282.38	478.26
		%	7.1	0.9	33.0	59.0	
ROCK	**2040**	**km²**	980.32	0	410.9	0	1391.22
		%	70.5	0.0	29.5	0.0	
	2080	**km²**	547.83	0	843.39	0	1391.22
		%	39.4	0.0	60.6	0.0	
ALPGR	**2040**	**km²**	491.44	25.72	216.93	0	734.09
		%	66.9	3.5	29.6	0.0	
	2080	**km²**	237.42	30.23	466.44	0	734.09
		%	32.3	4.1	63.5	0.0	
EXTGR	**2040**	**km²**	1291.88	94.94	206.54	109.89	1703.25
		%	75.8	5.6	12.1	6.5	
	2080	**km²**	908.34	1.9	683.12	109.89	1703.25
		%	53.3	0.1	40.1	6.5	
DRY	**2040**	**km²**	319.82	122.99	147.94	122.92	713.67
		%	44.8	17.2	20.7	17.2	
	2080	**km²**	113.86	1.63	475.26	122.92	713.67
		%	16.0	0.2	66.6	17.2	



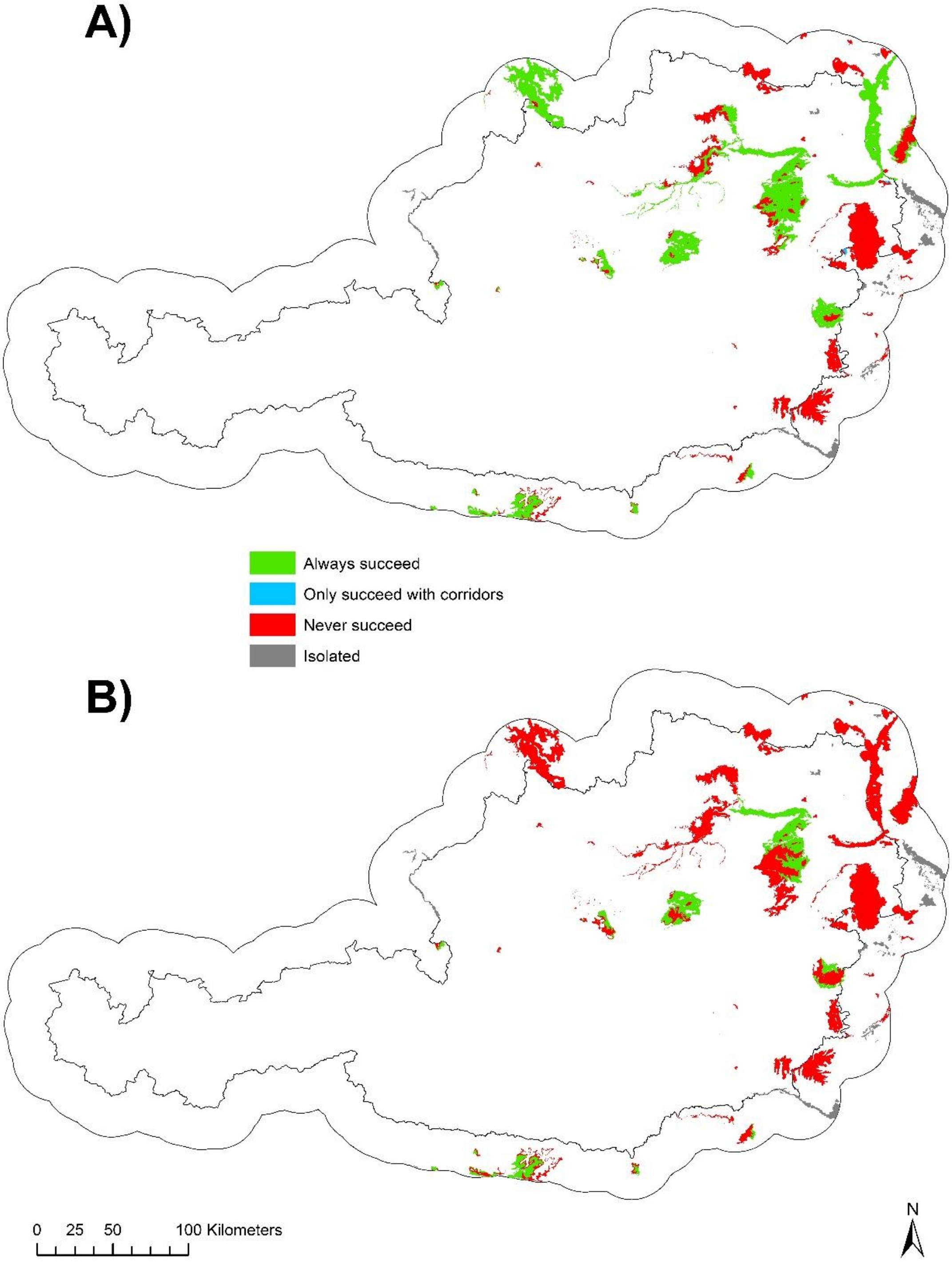
Appendix Figure 1: Percentage area and density curves of climatic patches with Coniferous Forest that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



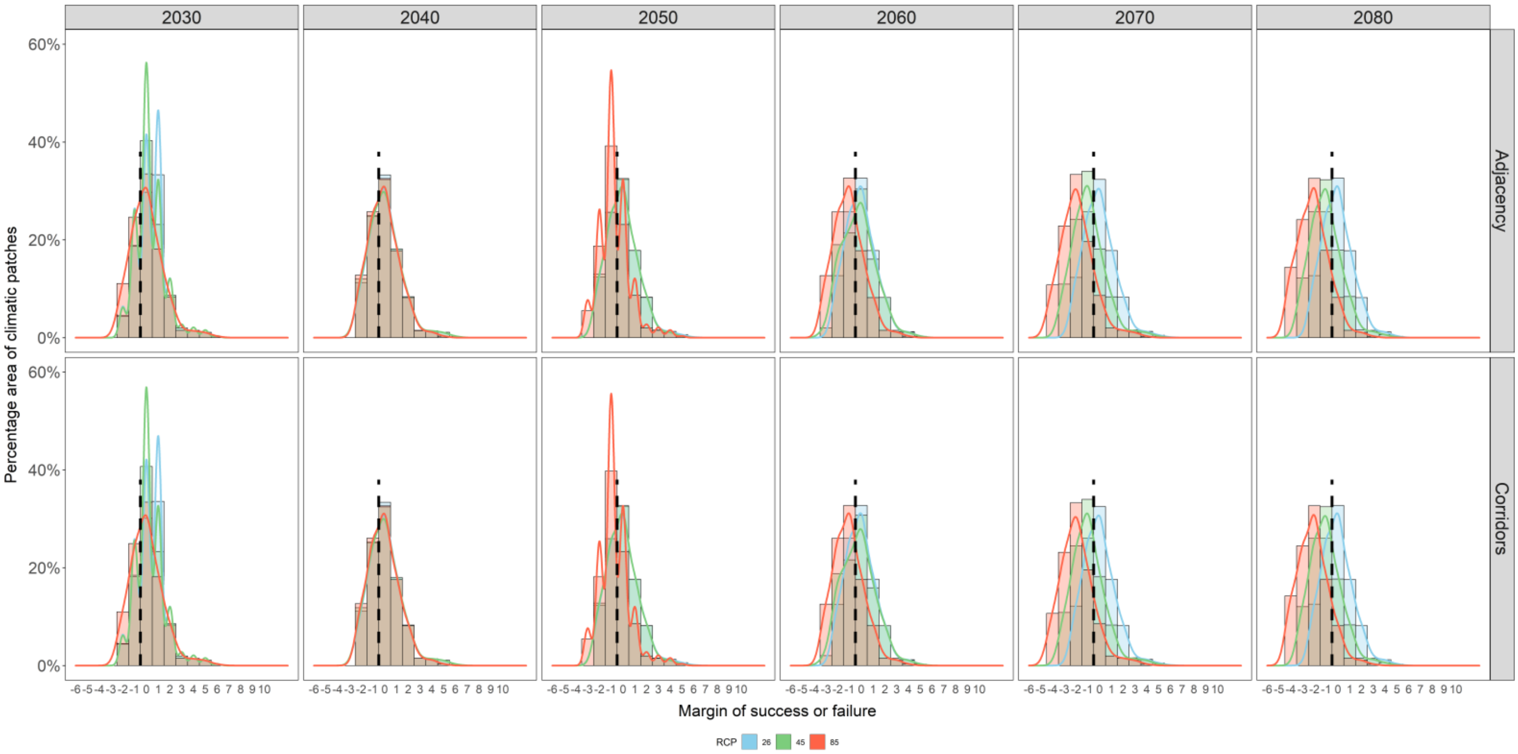
Appendix Figure 2: Climate connectivity assessment of climatic patches containing Coniferous Forest under the RCP4.5 scenario in A) 2040 and B) 2080.



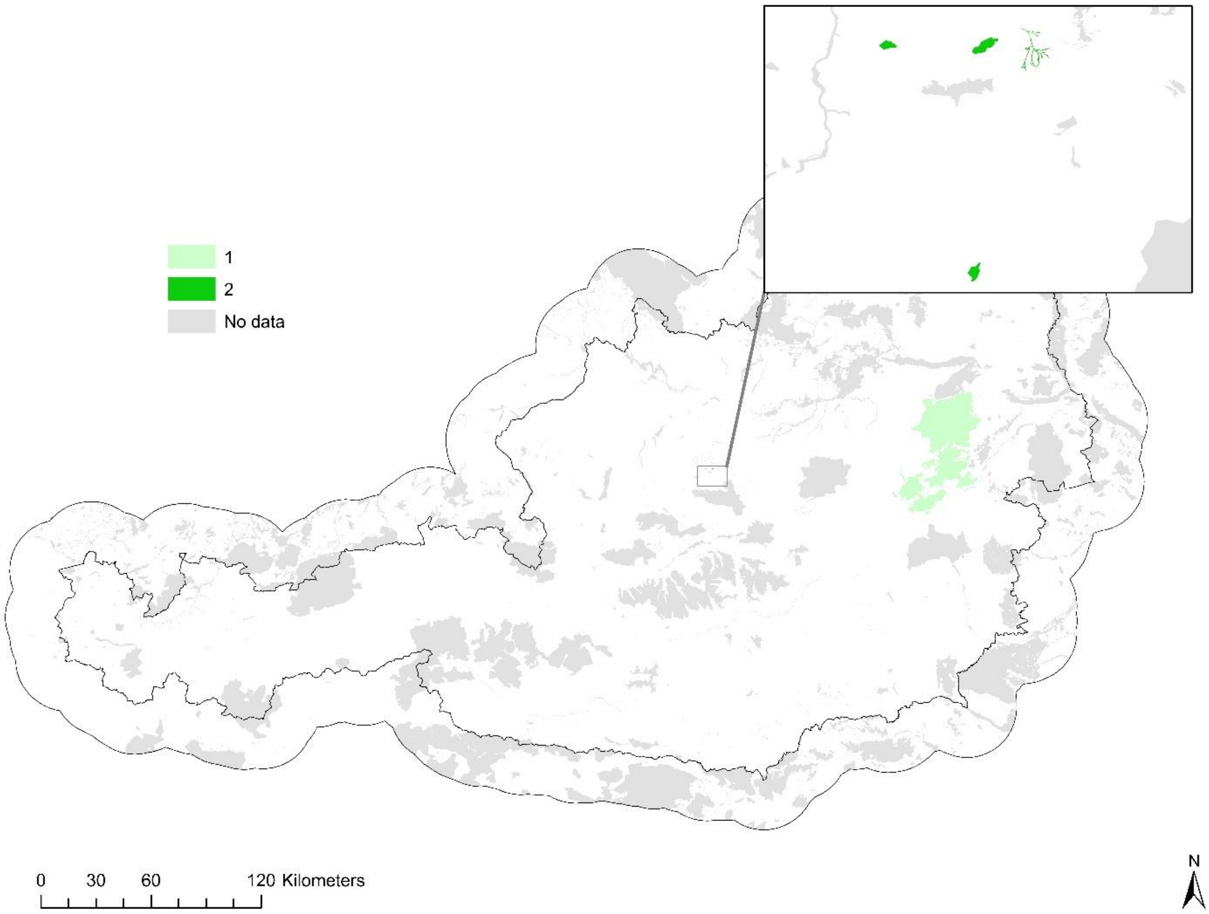
Appendix Figure 3: Corridors improving the climate connectivity of Coniferous Forest in 2080 under the RCP4.5 scenario, ranked by their efficiency.



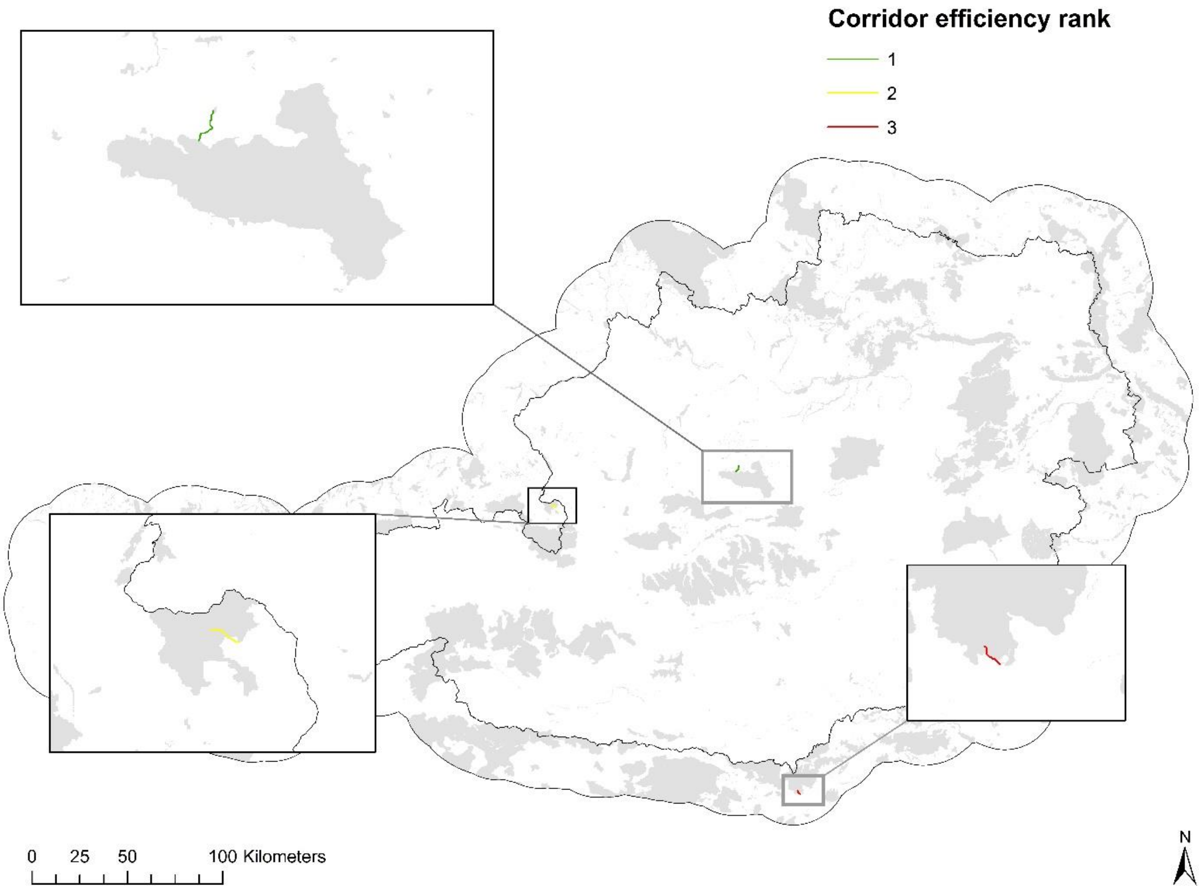
Appendix Figure 4: Climate connectivity assessment of climatic patches containing Broad Leaved Forest under the RCP4.5 scenario in A) 2040 and B) 2080.



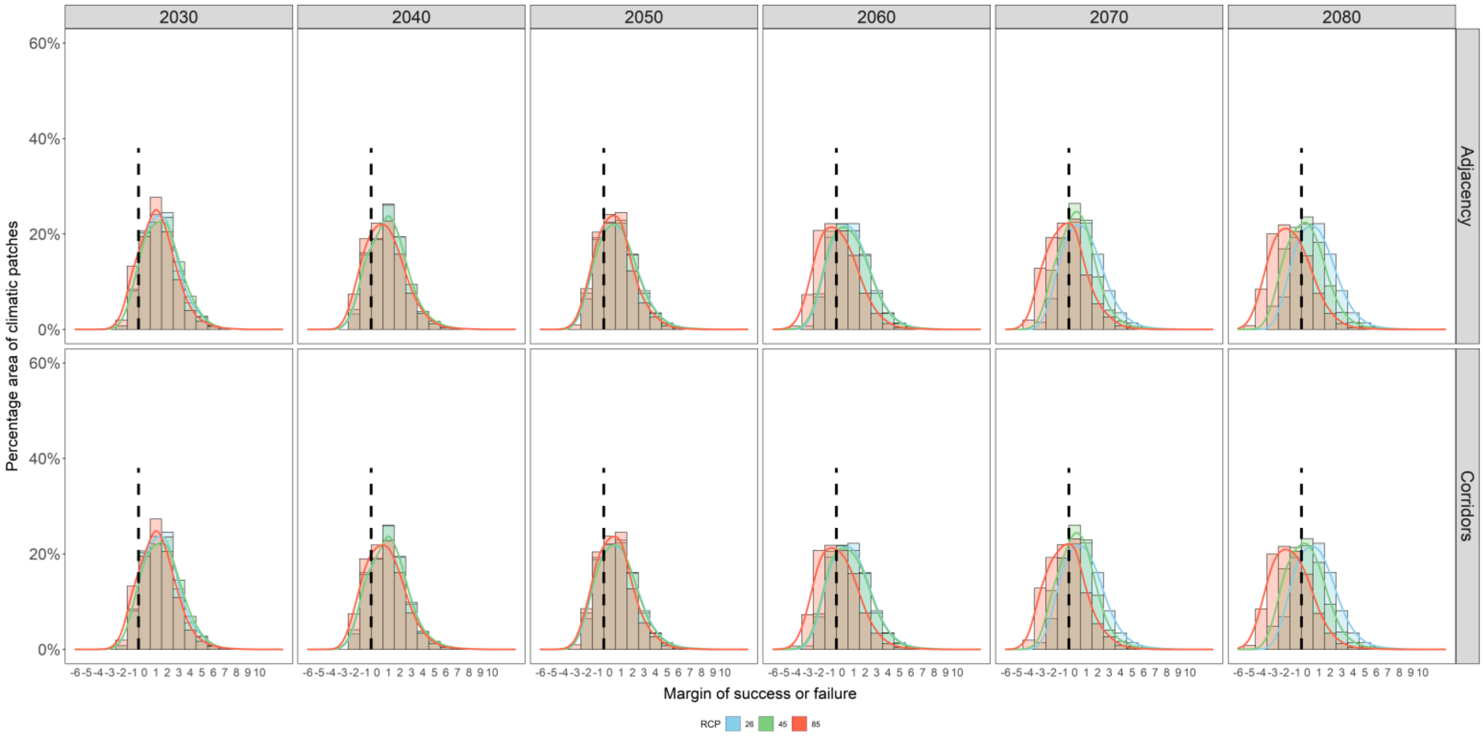
Appendix Figure 5: Percentage area and density curves of climatic patches with Broad Leaved Forest that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



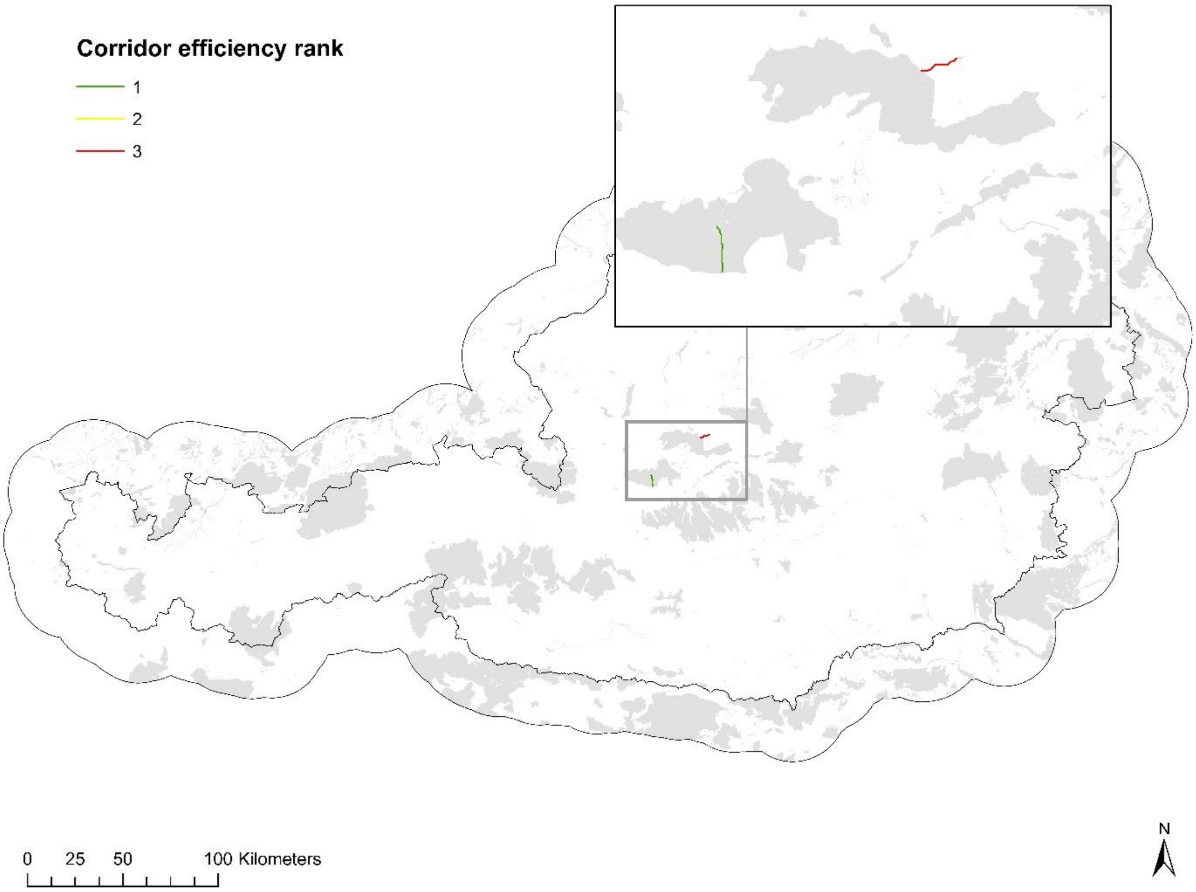
Appendix Figure 6: Absolute gain, due to corridors, in endemic species of Broad Leaved Forest achieving climate connectivity under the RCP4.5 climate scenario for the year 2040.



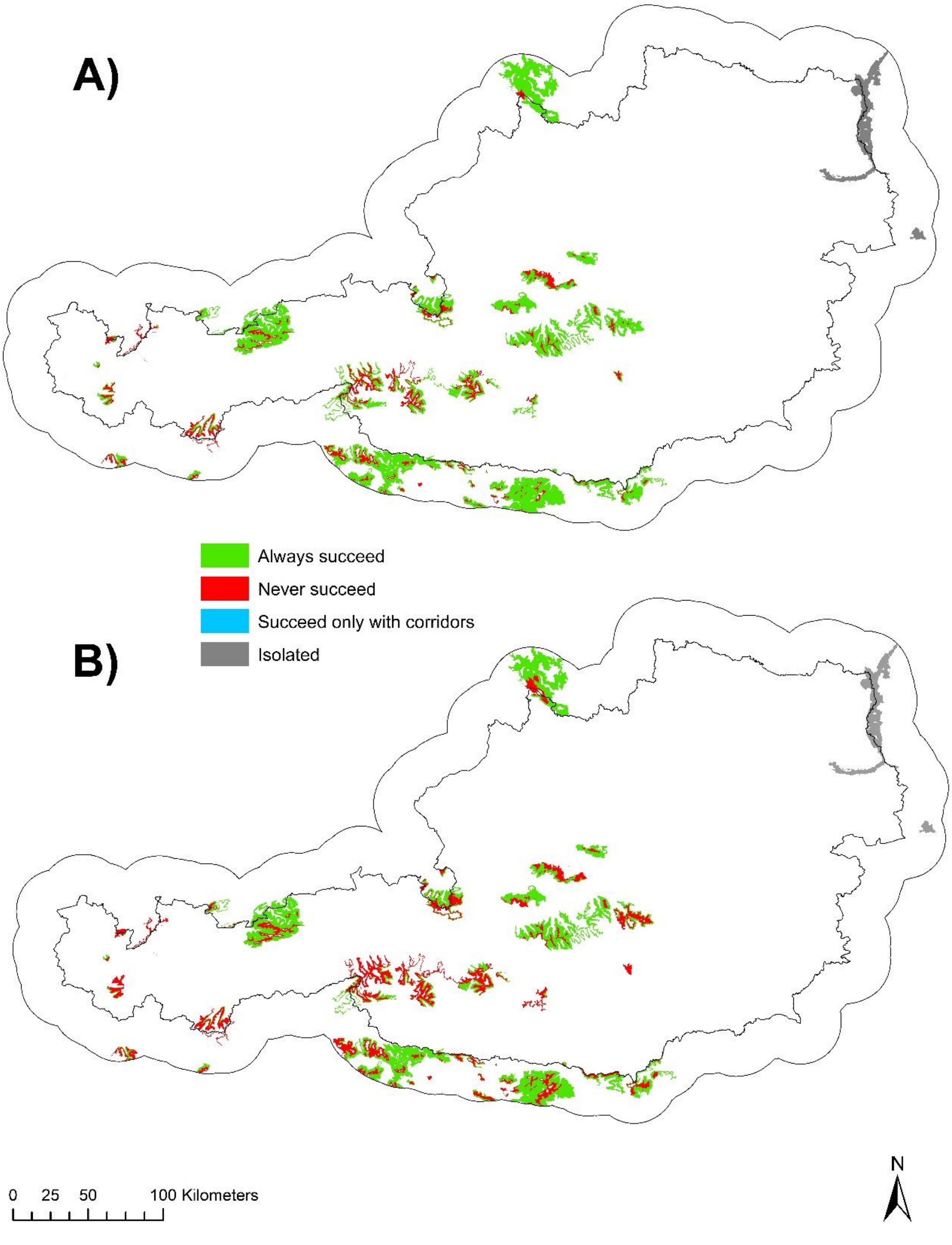
Appendix Figure 7: Corridors improving the climate connectivity of Broad Leaved Forest in 2080 under the RCP4.5 scenario, ranked by their efficiency.



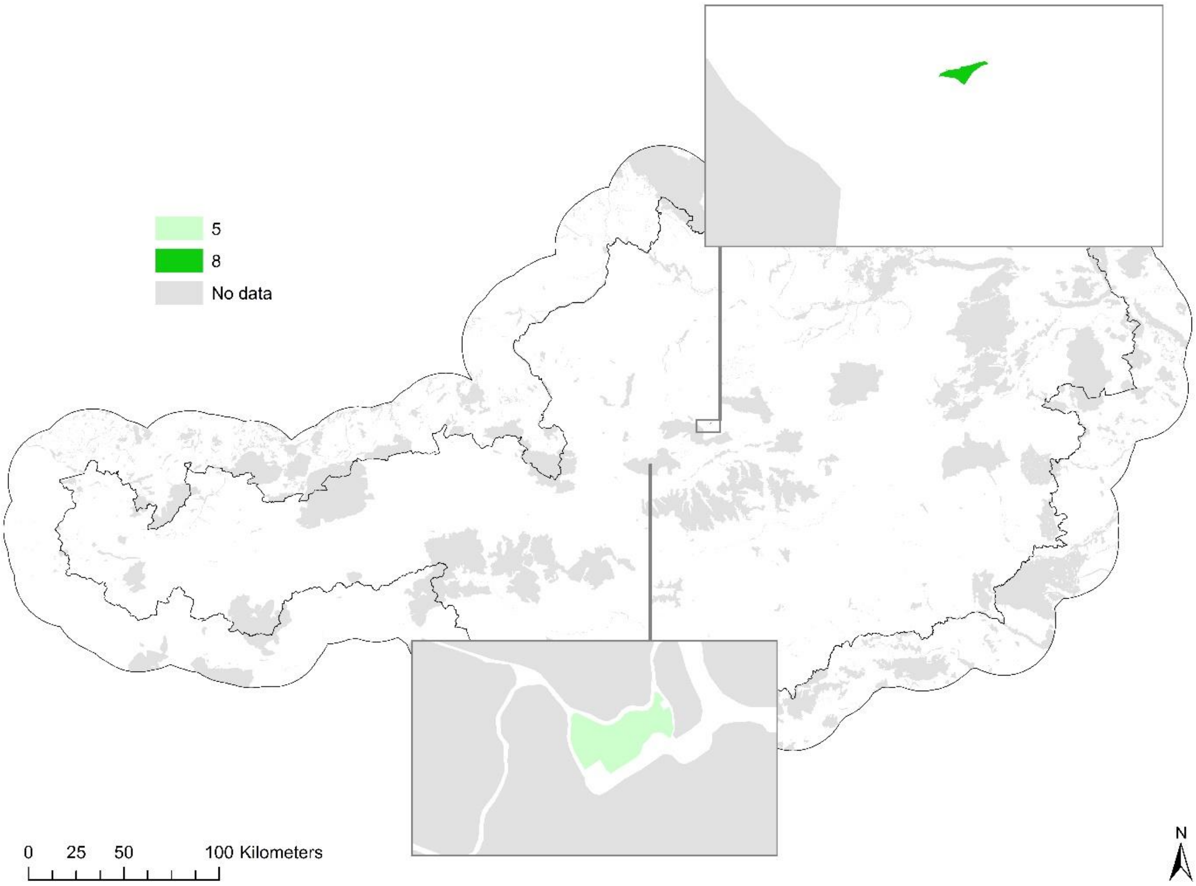
Appendix Figure 8: Percentage area and density curves of climatic patches with Shrub Lands that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



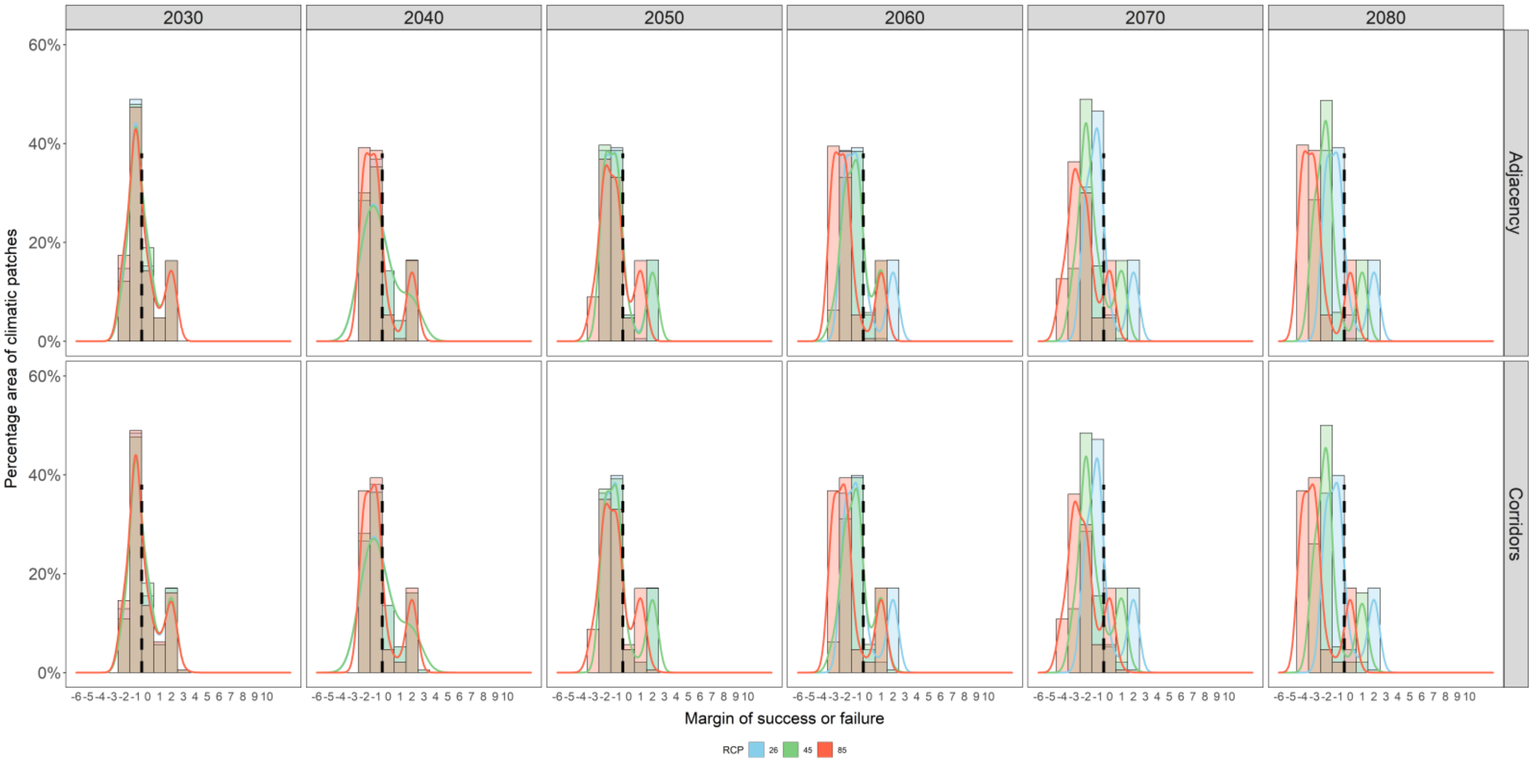
Appendix Figure 9: Corridors improving the climate connectivity of Shrubs Lands in 2080 under the RCP4.5 scenario, ranked by their efficiency (4 of top 6 corridors being shown).



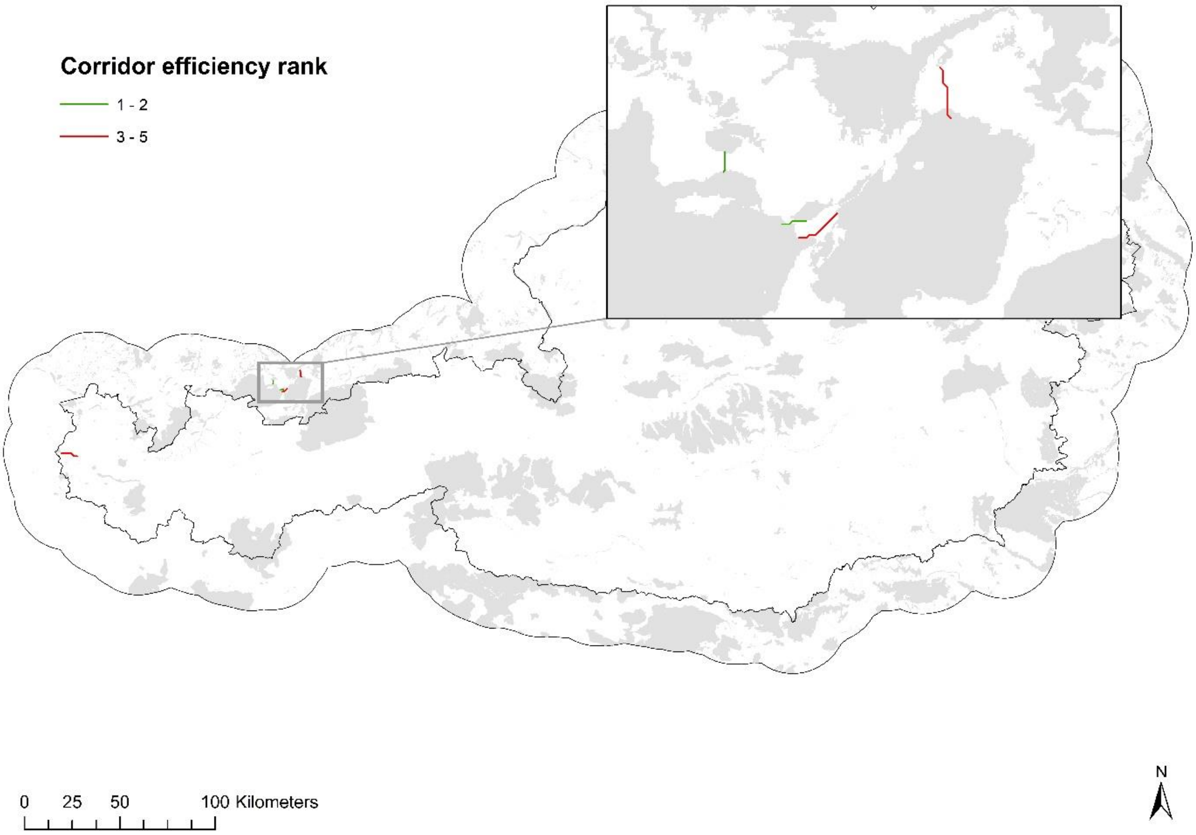
Appendix Figure 10: Climate connectivity assessment of climatic patches containing Shrub Lands under the RCP4.5 scenarios in A) 2040 and B) 2080.



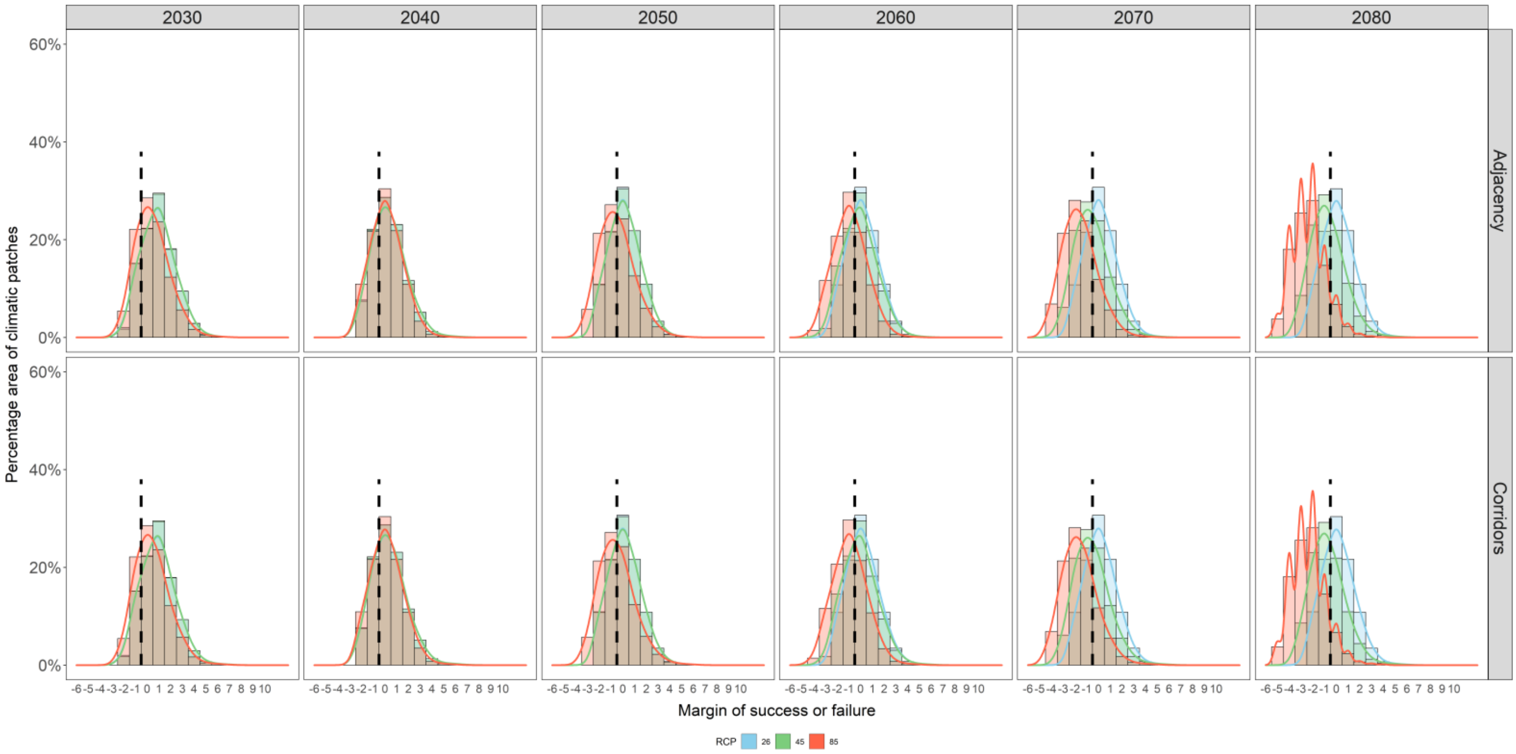
Appendix Figure 11: Absolute gain, due to corridors, in endemic species of Shrub lands achieving climate connectivity under the RCP4.5 climate scenario for the year 2040.



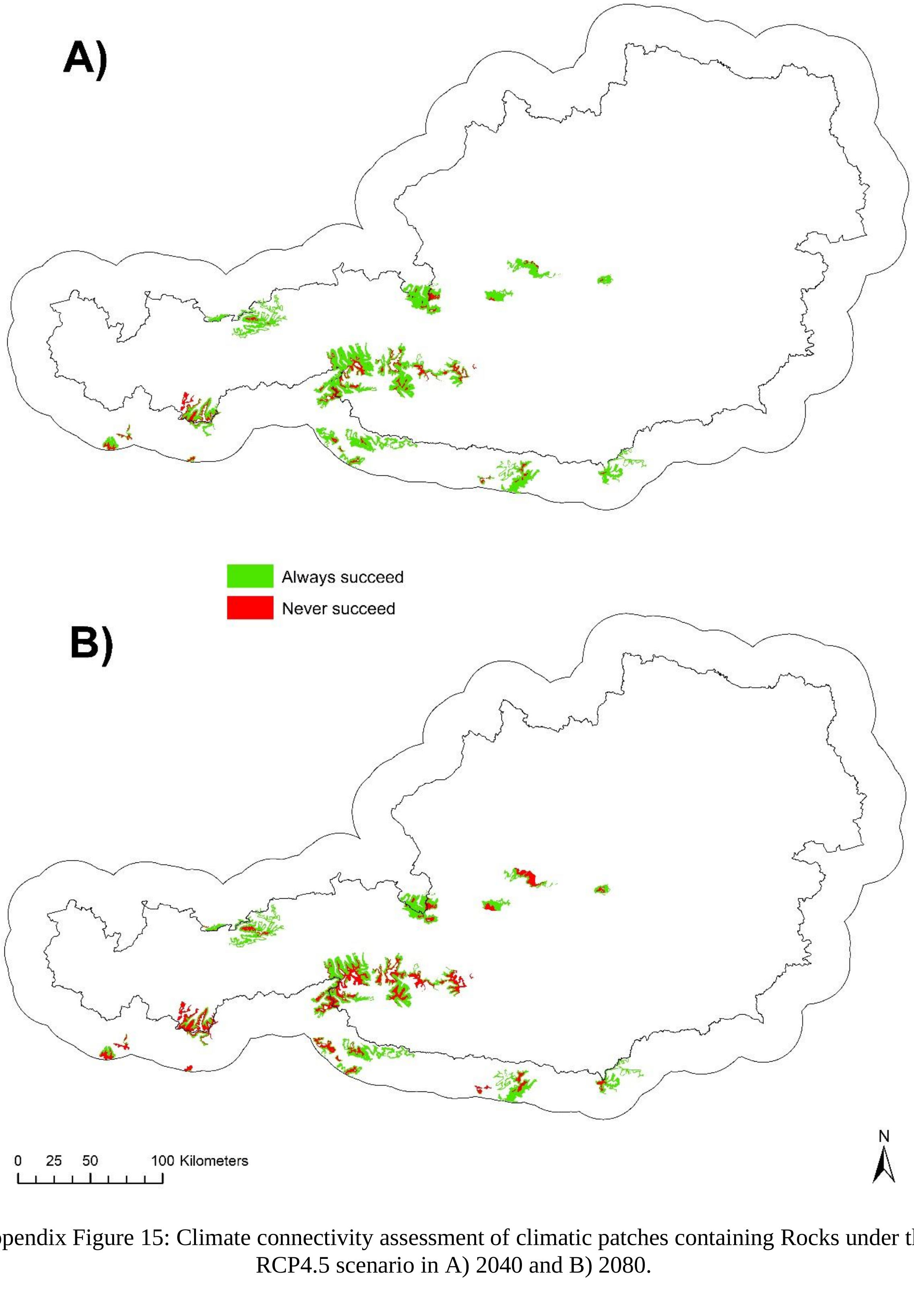
Appendix Figure 12: Percentage area and density curves of climatic patches with Wetlands that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



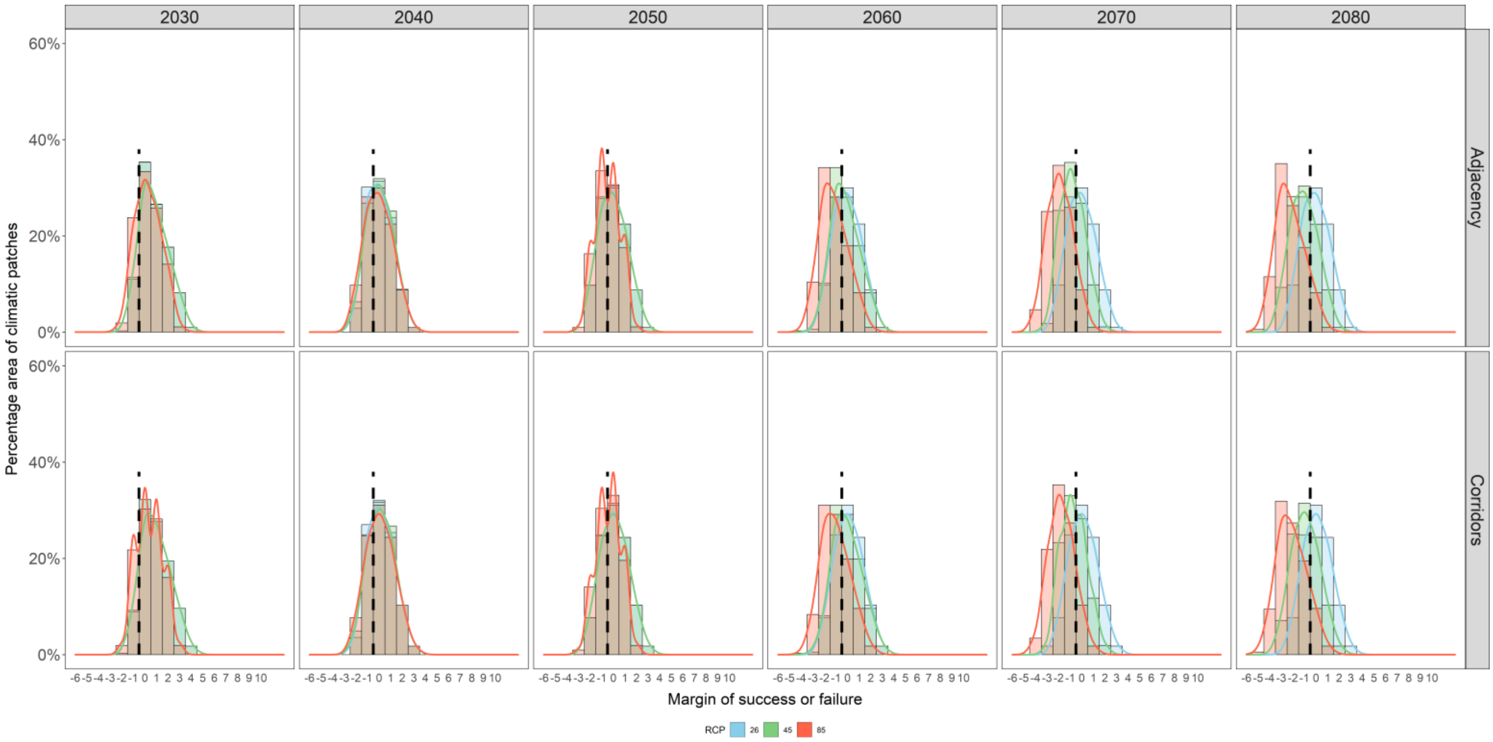
Appendix Figure 13: Corridors improving the climate connectivity of Wetlands in 2080 under the RCP4.5 scenario, ranked by their efficiency.



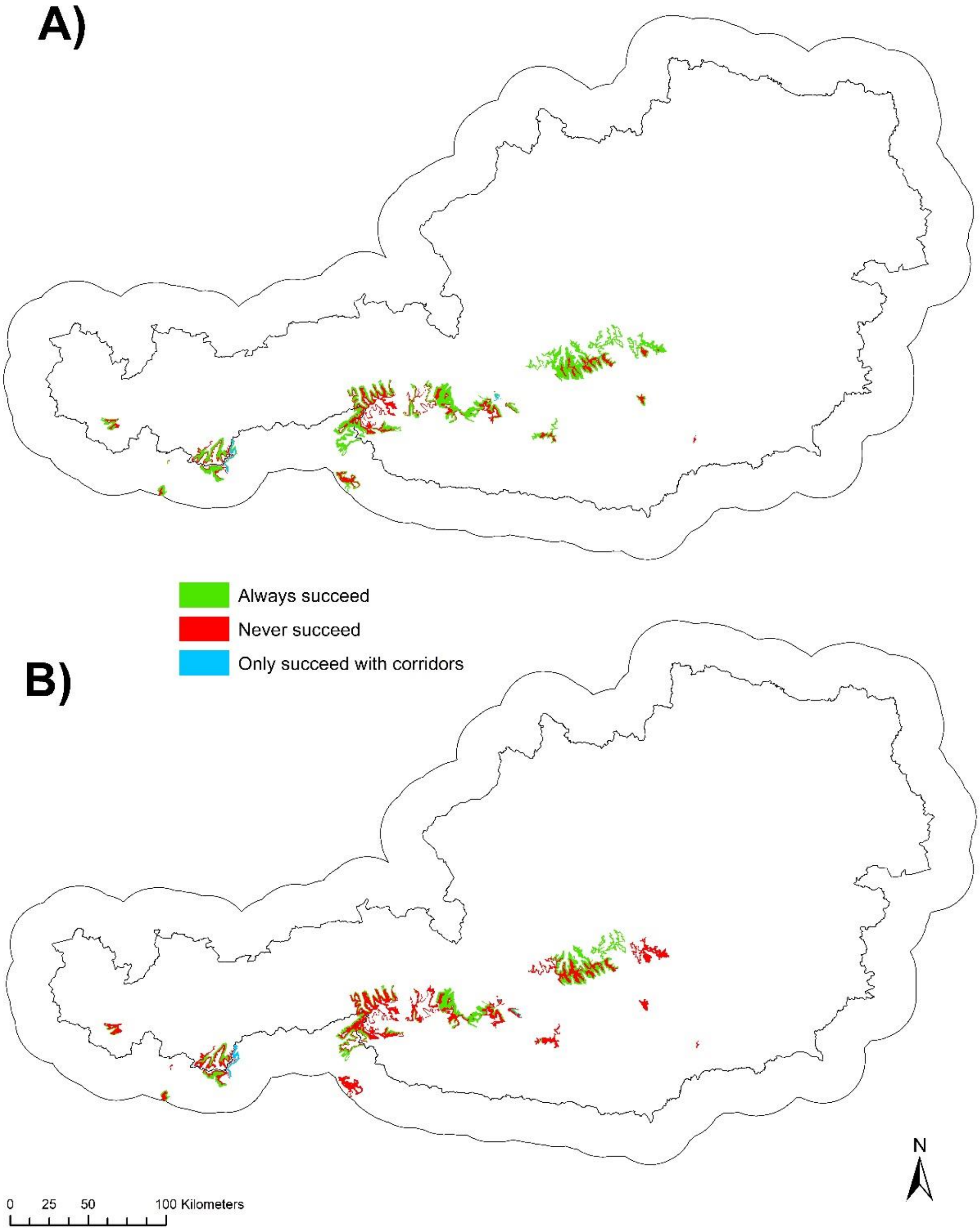
Appendix Figure 14: Percentage area and density curves of climatic patches with Rocks that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



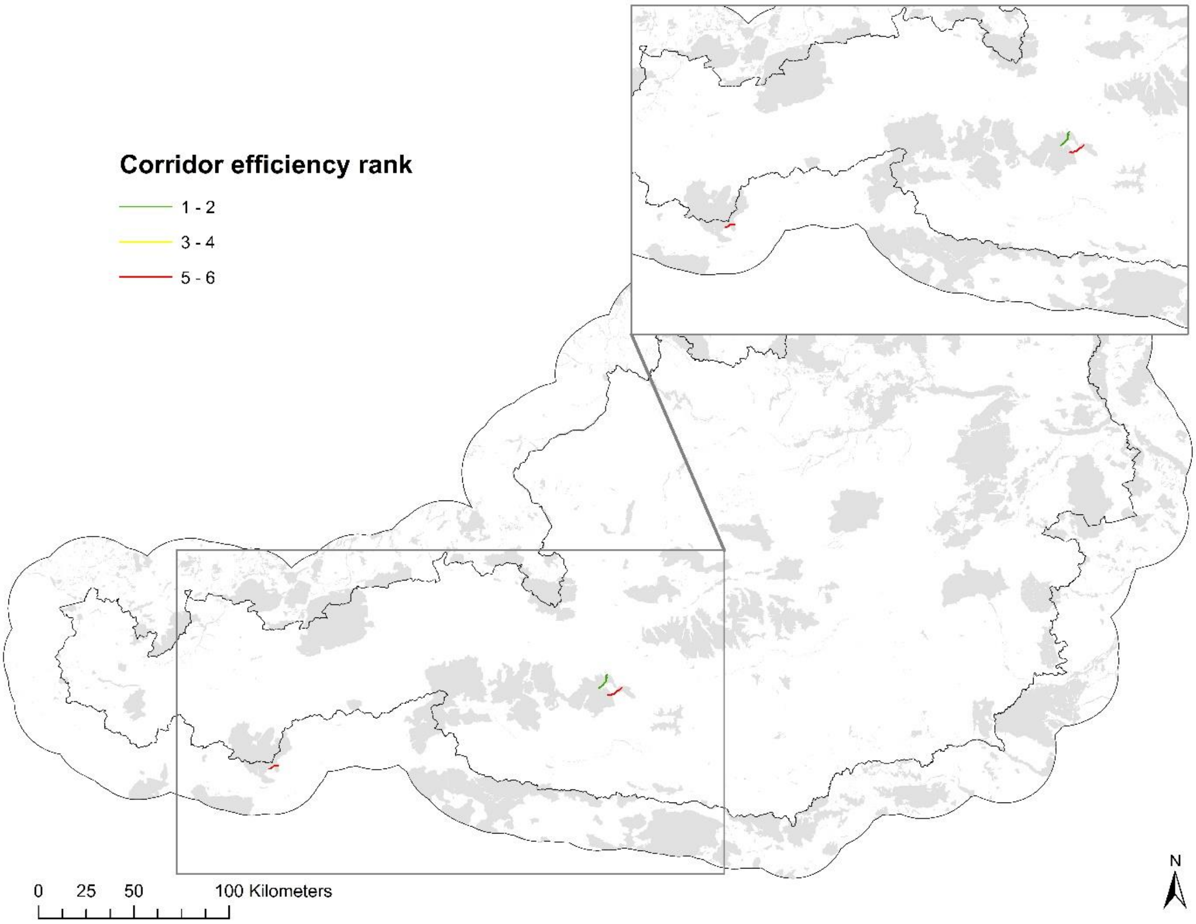
Appendix Figure 15: Climate connectivity assessment of climatic patches containing Rocks under the RCP4.5 scenario in A) 2040 and B) 2080.



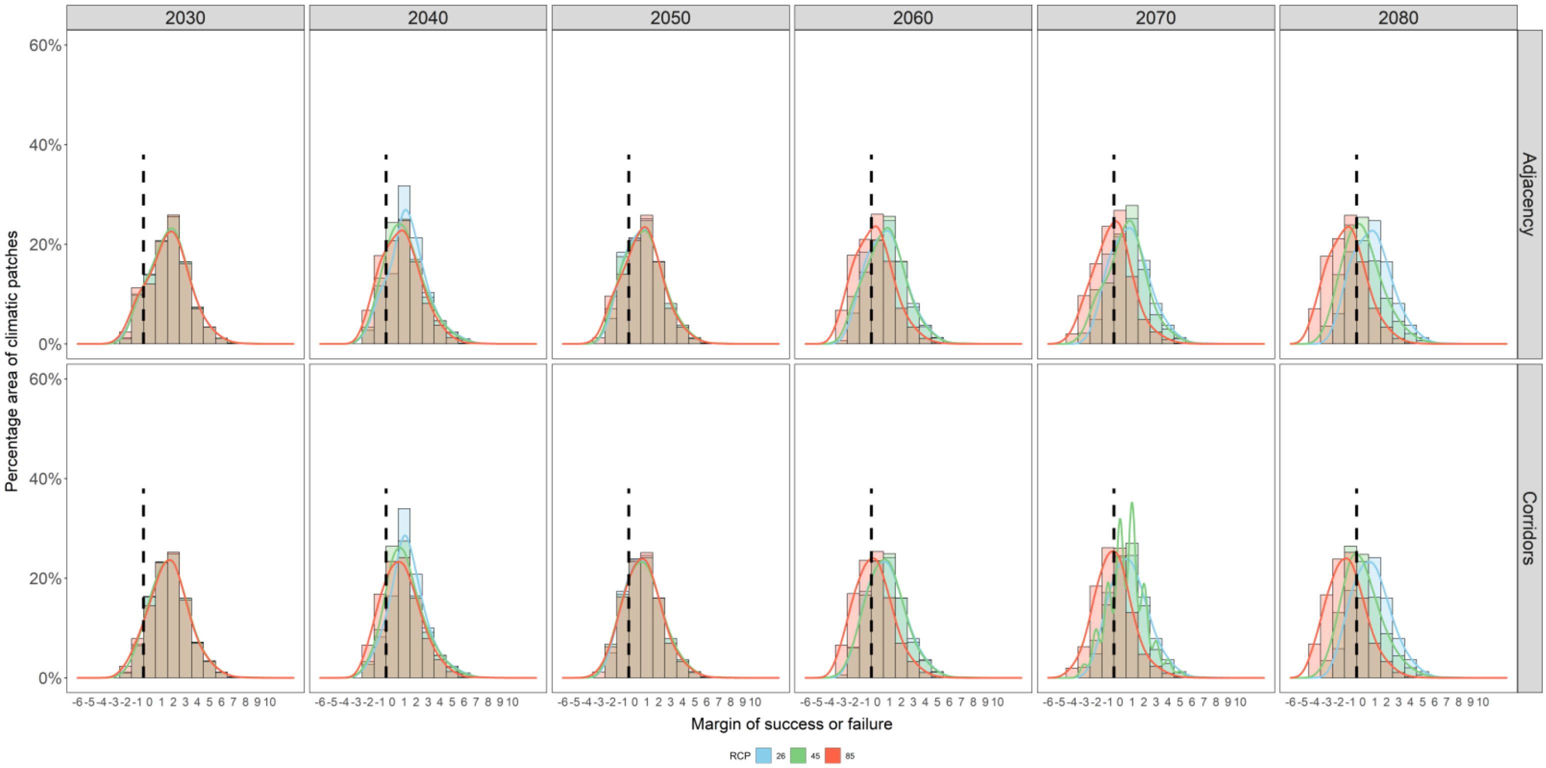
Appendix Figure 11: Percentage area and density curves of climatic patches with Alpine Grasslands that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



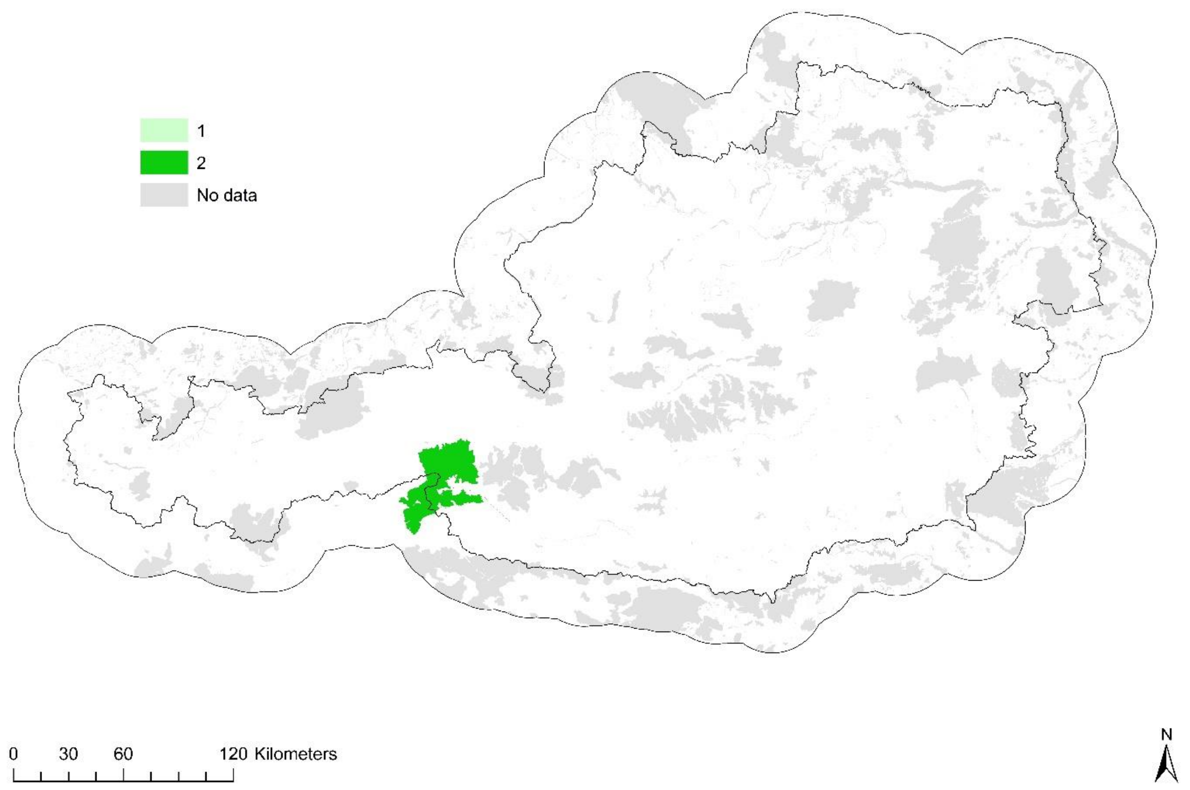
Appendix Figure 17: Climate connectivity assessment of climatic patches containing Alpine Grasslands under the RCP4.5 scenario in A) 2040 and B) 2080.



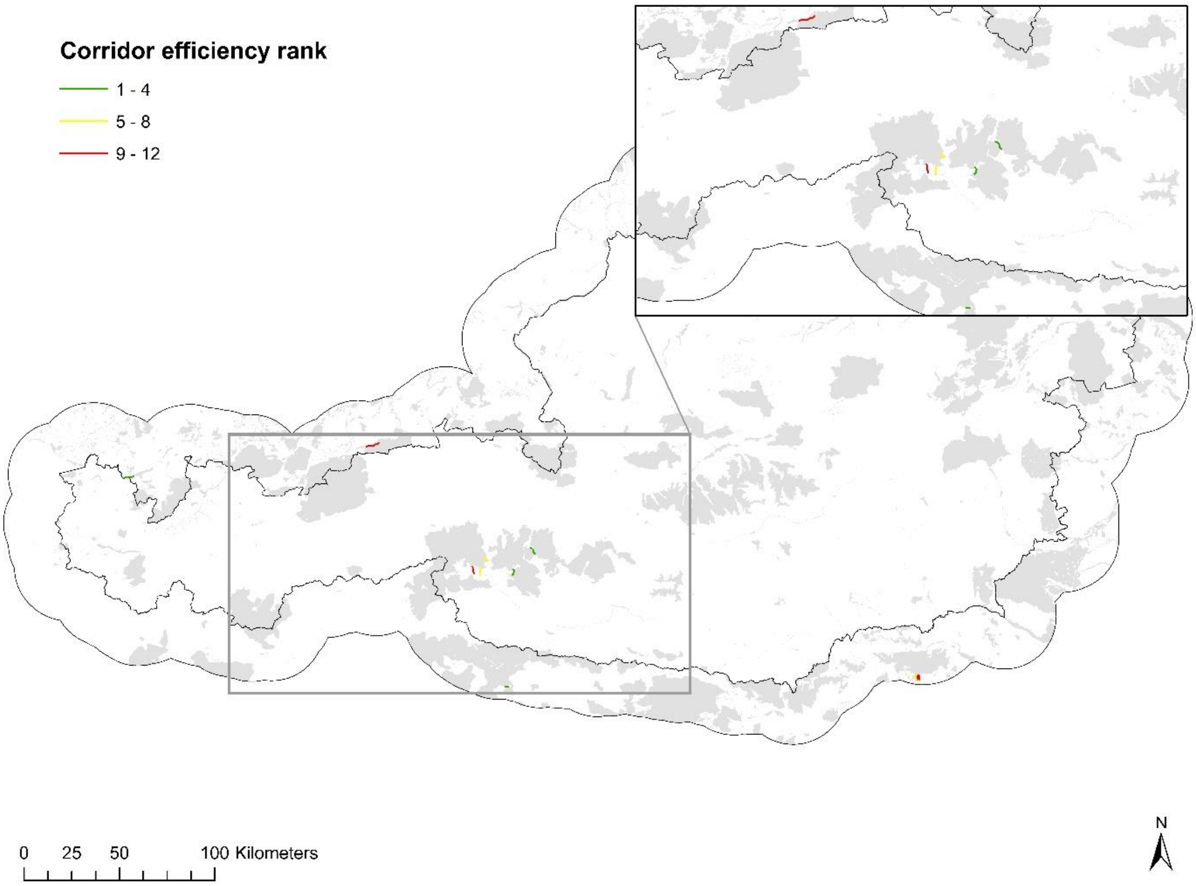
Appendix Figure 18: Corridors improving the climate connectivity of Alpine Grasslands in 2080 under the RCP4.5 scenario, ranked by their efficiency.



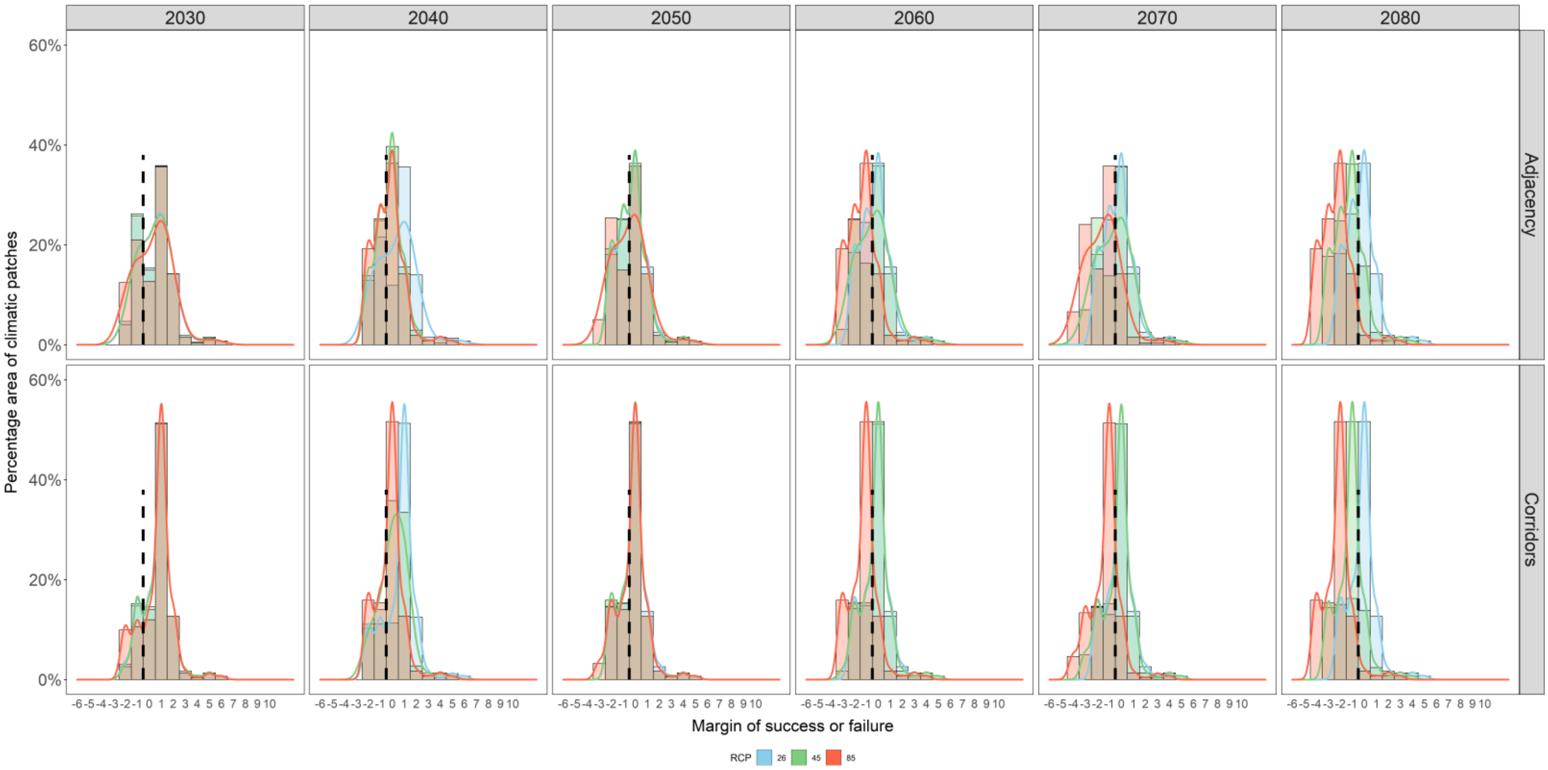
Appendix Figure 19: Percentage area and density curves of climatic patches with Extensive Grasslands that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



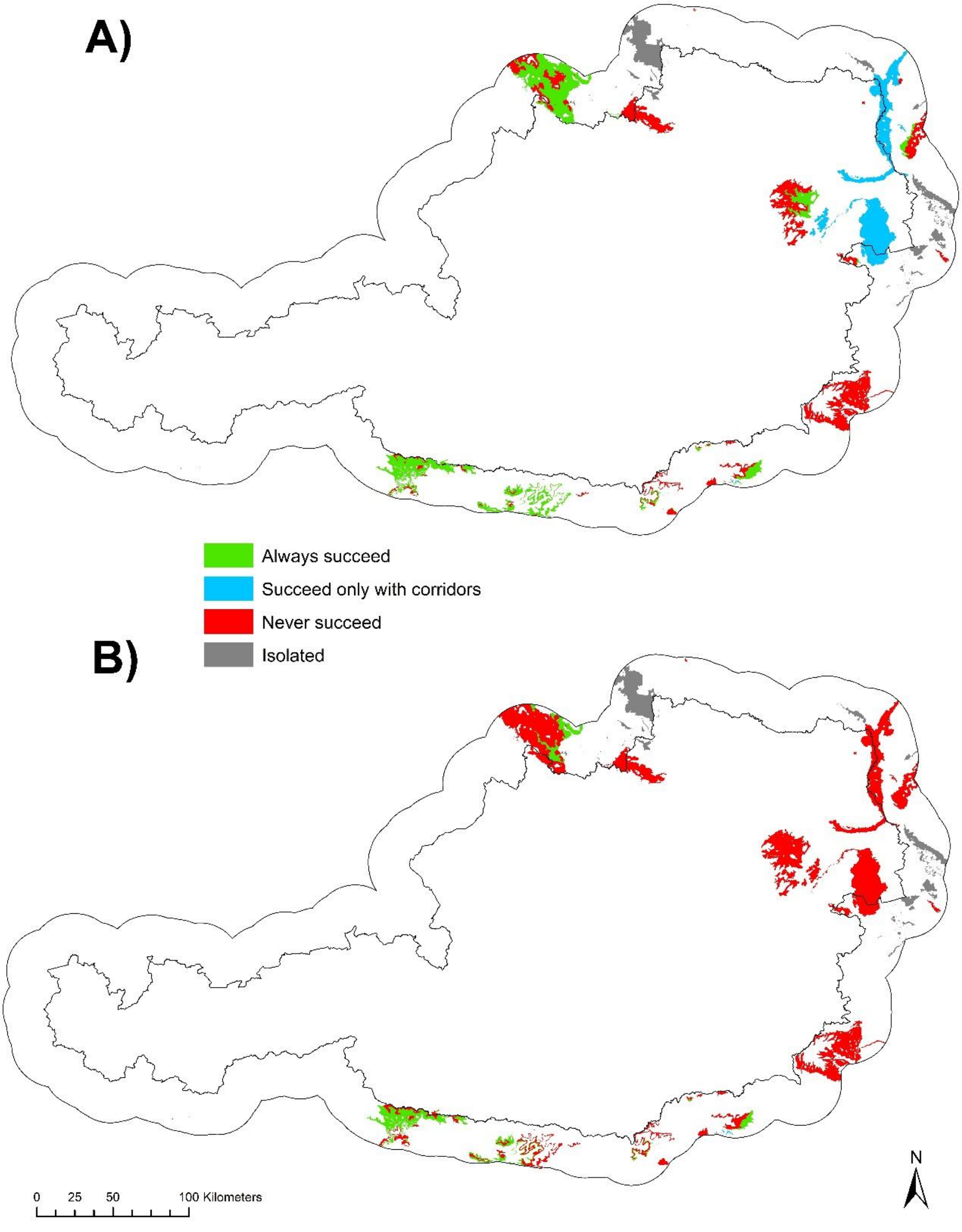
Appendix Figure 20: Absolute gain, due to corridors, in endemic species of Extensive Grasslands achieving climate connectivity under the RCP4.5 climate scenario for the year 2040.



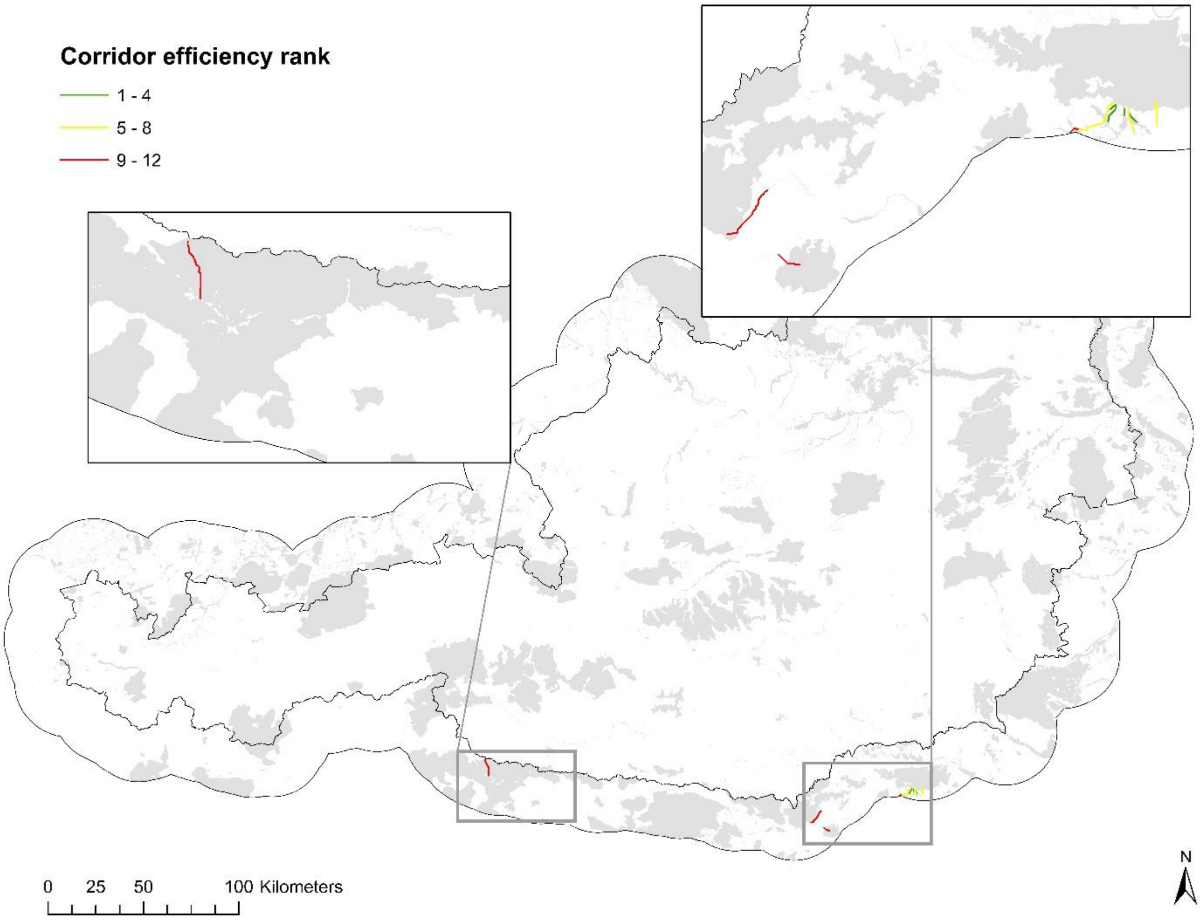
Appendix Figure 21: Corridors improving the climate connectivity of Extensive Grasslands in 2080 under the RCP4.5 scenario, ranked by their efficiency.



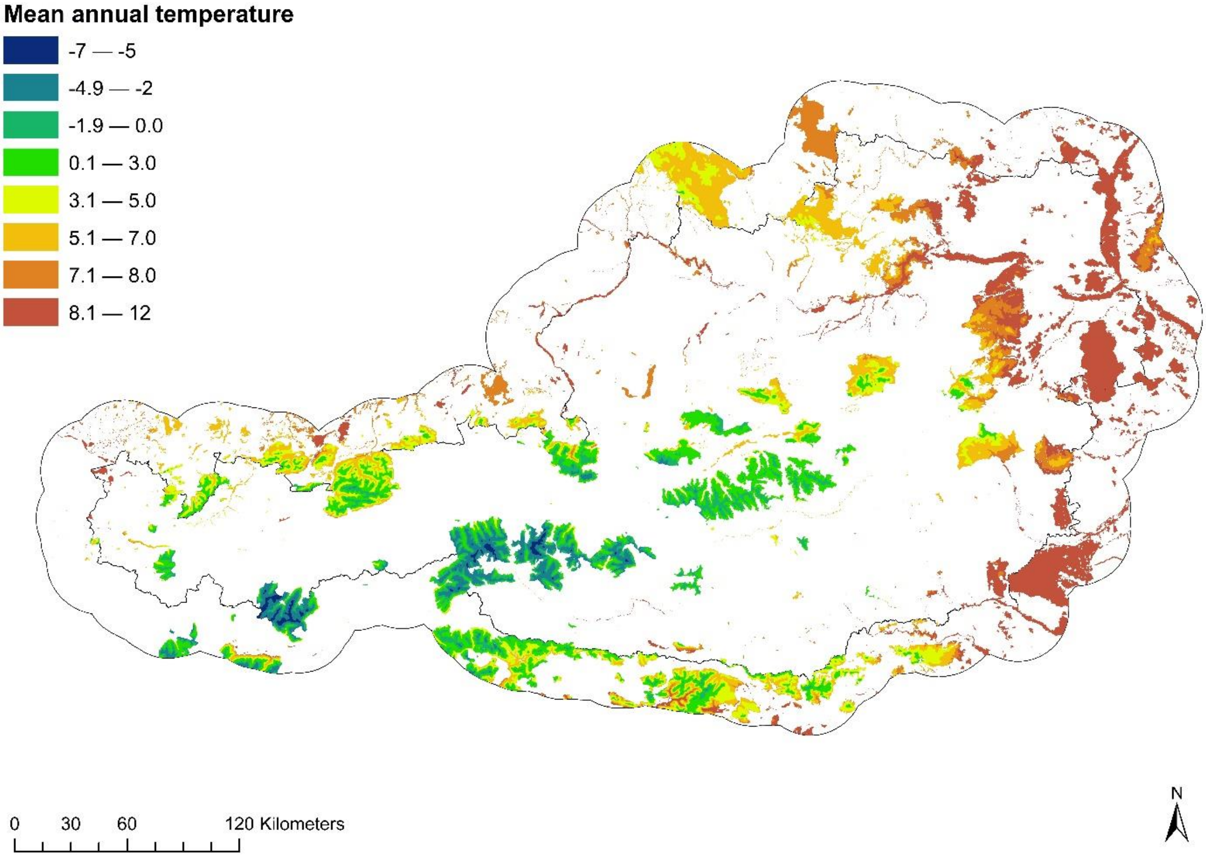
Appendix Figure 22: Percentage area and density curves of climatic patches with Dry Grasslands that reach a certain margin of success or failure at achieving climate connectivity. Top graphs represent the margin under adjacency only, and lower ones when corridors are added. Dashed lines separate success and failure.



Appendix Figure 23: Climate connectivity assessment of climatic patches containing Dry Grasslands under the RCP4.5 scenario in A) 2040 and B) 2080.



Appendix Figure 24: Corridors improving the climate connectivity of Dry Grasslands in 2080 under the RCP4.5 scenario, ranked by their efficiency.



Appendix Figure 25: Partitioning of protected areas into 7350 patches with equal temperature (climatic patches). Patches were actually distinguished in steps of 1°C mean annual temperature, but merged here to broader temperature ranges for reasons of presentation.