LIFE
DINALP
BEAR

Population level management and
conservation of brown bears in northern
Dinaric Mountains and the Alps

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Action A3: Analysis of spatial connectivity and preparation of environmental impact assessment guidelines

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Izvleček

Podobno kot pri drugih vrstah velikih zveri se tudi pri rjavemu medvedu njegovo območje razširjenosti in številčnost povečujeta v več delih Evrope, in to ob različnih upravljavskih pristopih. Vendar uspešno širjenje vrste vselej zahteva specifične biološke in varstvene pogoje na individualni in populacijski ravni. V gosto poseljeni Evropi širjenje medveda pogosto spremljajo tudi konflikti s človekom. Za pravočasno napovedovanje in racionalno preprečevanje konfliktnih situacij s človekom in s tem lajšanja procesa odločanja so ključne zanesljive prostorske raziskave. Te nam omogočajo prepoznavanje potencialnih habitatov za medveda in območij/koridorjev, ki so ključna za ohranjanje povezljivosti populacije. V prvi fazi pričujoče raziskave smo zato izvedli večstopenjsko hierarhično prostorsko eksplicitno napovedno modeliranje habitatne ustreznosti prostora (scale integrated RSF), s katerim smo lahko prepoznali glavne omejitvene dejavnike rabe prostora za tri obravnavane medvedje populacije oz demografske enote (Trentino-Švicarske, pred-Alpska in Dinarska) na treh prostorskih nivojih (populacijski nivo, nivo območja aktivnosti in nivo notranje rabe znotraj območij aktivnosti). Izvedli smo tudi analizo povezljivosti prostora med osnovnimi zaplatami habitata in opredelili prispevek vsake zaplate k »vitalnosti« celotne medvedje populacije v raziskovalnem območju. Končno smo z namenom lažjega prepoznavanja potreb po prihodnjih presojah vplivov posegov na okolje (PVO) opredelili še najbolj verjetne prehode med habitatnimi krpami (least-cost paths). Na osnovi napovednih spremenljivk, ki opisujejo rabo tal, reliefne značilnosti in prisotnost človeka (npr. ceste, naselja) smo pripravili modele habitatne ustreznosti prostora za medveda in prepoznali tudi razlike v habitatnem izboru med 3 obravnavanimi populacijami in prostorskimi merili. V vseh treh populacijah so medvedi primarno izbirali gozdnata območja, so pa med populacijami in prostorskimi merili opazne razlike v rabi/pomenu ostalih okoljskih spremenljivk. Zlasti odstopa skupina medvedov v Trentinu, za katere je značilna izbira bolj nedostopnih območij (težji, topografsko bolj razgiban teren). Naš prostorsko eksplicitni model kaže, da je v obravnavanem območju veliko habitata, ki je primeren za medveda, vendar pa je zanj značilna močna fragmentiranost. Največje in najbolj pomembne zaplate habitata za povezljivost populacije se nahajajo na območju trenutne razširjenosti vrste, z najbolj primernim habitatom na območju pred-Alpske in Dinarske populacije. Zadostno povezanost najprimernejših zaplat (ki so dovolj velike, da v njih lahko žive samice – medvedke), bi bilo mogoče vzdrževati preko ohranjanja dovolj povezanih habitatnih krp v koridorjih (step-stones). Za ohranjanje zadostne povezanosti prostora/habitatov, zagotavljanja povezav med deli populacij in populacijami medvedov ter za dolgoročno viabilnost medveda v območju Alp in Dinaridov je ključna poenotena – med državami usklajena - politika odločanja in rabe prostora.

Abstract

As for other large carnivores in Europe, the brown bear shows a trend of recovering under different management scenarios. However, this recovery comes with specific biological and conservation requirements at individual and population levels often followed by conflicts in a highly humanized continent. To foresee conflicts with humans and to facilitate decision-making, spatially-explicit research is required to identify potential habitats and the connectivity of fragmented bear populations. First, we conducted multiscale modeling based on scale-integrated resource selection functions (SRSFs) to identify drivers shaping the space-use of three bear populations/demographic units (“Trentino-Swiss”, “pre-Alps”, and “Dinaric”), and across 3 scales of space (population distribution, home range establishment, and use of individual home range). Secondly, we also conducted an analysis of the connectivity patterns of suitable habitat patches (nodes) to identify the potential importance of each node to contribute to individual mobility, survival, and population connectivity. Lastly, to support further environmental impact assessment analyses, we identified the most plausible least-cost paths connecting different areas of the same large patch with itself and surrounding patches. Using topographic, landcover, and anthropogenic predictors, our analytical approach transcended from scale dependence bias to produce a predictive map on habitat suitability while delivered information on habitat selection trends for each population. Bears mostly selected forest habitats in all the populations; however, habitat selection differed for the other variables among populations and scales, especially in the Trentino area where the species selected the most intricate topography. Predictive maps revealed a broad range of suitable but fragmented patches of bear habitat. The largest and most important patches for connectivity occurred in the current distribution range of the species, with the most suitable habitat lying in the pre-Alpine and Dinaric populations. Connecting viable patches to host female home-ranges is possible through stepping-stone patches of corridors reachable within the estimated dispersal distance of females. Unified transnational decision-making is required for the conservation of stepping-stone patches, facilitate bear mobility, and ultimately connect bear populations.

1. Introduction and aims

Large carnivores have traditionally been perceived as a threat to humans due to socioeconomic, political, and emotional issues that have often resulted in the direct persecution of these species (Miller et al., 2016). After a dramatic historical decrease, large carnivores are currently recovering throughout the human-dominated landscapes of Europe but direct persecution and habitat disappearance continue to jeopardize their existence in remnant populations (Chapron et al., 2014).

The brown bear, an emblematic large carnivore, is recovering in most of the European populations as a result of different management strategies applied on, often, well diverse scenarios of different intensities of human-pressure (Chapron et al., 2014). However, the viability of recovering populations and the well-being of the populations that have best withstood human pressure depend very much on appropriate decision-making in conservation strategies. Consequently, it is important to hone the understanding of the requirements of bears in the current context of population recovery and likely expansion, including the specific spatial needs for the species.

Technical advances on wildlife tracking based on global positional systems (GPS), current computational methods to treat abundant locational data along with the application of mathematical methods suitable for the analysis for these data, allow today to gauge and further with more accuracy the patterns of space use of wildlife species (Cagnacci et al., 2010; Recio et al., 2011). Predictions on the potential habitats suitable for bears and for the connectivity among populations are capable to assist decision-making on conservation plans. Brown bears have been tracked using GPS collars for the last decade in the Alps and the Dinaric Mountains. Thus, rich location datasets on tracked bears are available to combine and to address questions on the space use by the species at broader geographical scales involving different European countries; specifically, Slovenia, Croatia, Austria, Italy, and Switzerland. Three main bear populations or demographic units inhabiting these countries can be considered: the Trentino-Swiss, the eastern pre-Alps, and the Dinaric population. Although the eastern pre-Alps and the Dinaric populations are essentially the same population, the presence of a fenced highway (A1 highway from Trieste to Ljubljana) has been identified as an important barrier for bear movement. This highway is mostly crossed towards the eastern Alps by dispersing males, which ultimately biases the sex ratio there, and presumably also the trends of habitat selection. Moreover, the 3 analysed bear population units were exposed to different management regimes for decades, which possibly resulted in different responses to human disturbance and thus, to different habitat selection patterns. Bears to the south of the highway were traditionally managed as valuable game species (sustainable hunting quotas, protection of females with cubs), while bears to the north of the highway had no protection until the nineties. In the Trento region, bears were exposed to heavy persecution and were nearly extirpated in the nineties; nevertheless, they have been under a full protection since then and many conservation efforts have been set up recently for the conservation of this population. From an ecological and behavioural perspective, bears have adapted to survive in the manifold compositions and configurations of the landscape available in the distribution range of the three central European populations.

To evaluate the need for active management, e.g. corridor maintenance/restoration., it is of high importance to predict the space use of bears in the Alps and the Dinaric Mountains, as well as the potential of natural movement between the existing populations. Ecological and behavioural processes occur at different spatial and temporal scales. In this sense, scientific literature identifies the need to ideally integrate knowledge on species-habitat selection across scales and to elude conclusions based on a single scale (Turner et al., 1989). Therefore, decision-making in management and conservation strategies can benefit from the suitable integration of conclusions from species-habitat analyses at hierarchically nested processes of behavioural selection. Ultimately, these processes shape the selection of available resources by the species from broad to fine spatial scales. In addition, species-habitat analyses commonly produce models using at once all the available data on species presence over different study areas and populations. However, these approaches ignore the specific patterns of selection of each different population that might be the consequence of local and specific characteristics of the environment or the type and availability of resources.

Predictions on the potential areas of habitat suitable for bears from integrated multiscale approaches can also provide the foundation for further analyses able to identify the viability of populations in new areas where the species could be reintroduced or naturally expand in central Europe. In this sense, identifying the connectivity and possible corridors between and within the three Alps and Dinaric populations is of high relevance for 1) decision-making in the conservation of the species, and 2) environmental assessments required for actions that could compromise the movements and expansion of bears within and between populations.

Considering the needs explained above, we targeted three main objectives in this research:

1) Creating a multiscale habitat suitability map for bears in Central Europe accounting for population differences in the patterns of habitat selection.

2) Identifying the functional connectivity properties of each patch of habitat suitable for bears, including the step-paths connecting larger patches capable of hosting bear home ranges in central Europe.

3) Identifying the most plausible least-cost paths in a population that connect different areas within a given large-size patch, and with the surrounding patches.

2. Material and methods

2.2 STUDY AREA

We selected a study area that comprised a total planar surface of 173,479 km^2. This area included the whole Croatia and Slovenia, the central and eastern Italian Alps, the southern face of the Austrian Alps, and the most eastern region of Switzerland (Figure 1).

2.3 DATASET ON BEAR LOCATION DATA

The dataset on GPS bear locations per country varied in the number of animals tracked, sex ratio (Table 1), and fix acquisition rates (from 30 min to 6 hours). We discarded bears considered as conflictive (N = 19) from the total initial dataset (N = 82) to avoid biases in habitat selection caused by any “abnormal” bear behaviour as consequence of habituation to humans. Firstly, we filtered the raw location data by removing the first and last 10 locations of each animal dataset. This initial filtering aimed to avoid location errors that commonly occur after the activation of a collar, locational bias due to erratic animal behaviour after sedation, or before the end of the battery-life. Secondly, we applied another sequential filter to remove unrealistic locations based on plausible bear movements (Bjorneras et al., 2010). For each location, this filter removed unrealistic points sequentially in several steps and using a moving window. The first step removed those points that depicted a distance beyond the median distance estimated from the 10 previous and 10 next points. A second step applied the same previous analysis but applying the mean instead of the median. A third step removed those points shaping an unrealistic spike in the movement path displayed by a bear that would imply an unrealistic sudden fast movement to leave its trajectory and return to it showing an abrupt turning back. For the purpose of the analysis on resource selection functions, we next filtered the location dataset (N = 184,687, μ ± SE = 2931 ± 416) to match a location acquisition rate of 6 hours (N = 40,835, μ ± SE = 648 ± 72). We aimed to increase computational performance to homogenize the different acquisition rates used among bears and to reduce spatio-temporal autocorrelation.

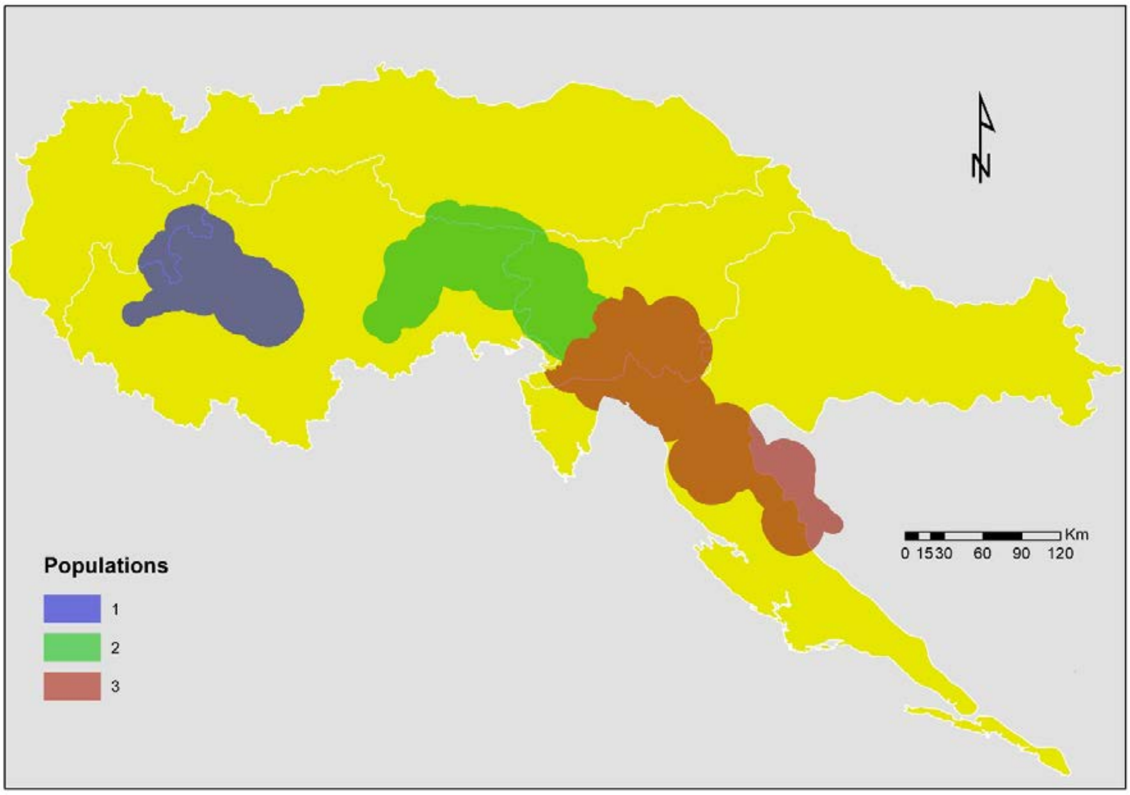

Figure 1.- Population home ranges of the Trentino-Swiss (population 1), pre-Alpine (population 2), and Dinaric population (population 3) delineated from analyses on movement capabilities of bears regarding the maximum distance travelled at each acquisition rate of GPS-locations.

Table 1.- Number of bear individuals per country, population, and sex.

Country and population	Total bears	Total males	Total females
Switzerland (Population 1)	1	1	0
Italy - Trentino (Population 1)	5	1	4
Italy – pre-Alpine (Population 2)	3	3	0
Slovenia – Prealpine (Population 2)	5	4	1
Slovenia – Dinarics (Population 3)	29	13	16
Croatia (Population 3)	20	13	7
TOTAL	63	35	28

2.4 DATASET ON DIGITAL ENVIRONMENTAL DATA

We compiled or calculated a set of topographic, landcover, and anthropogenic variables depicting bear resources from varied digital geographic sources (Table 2). A final set of rasters of 25 × 25 m grid-cell size for each variable was produced to rely on accurate fine-grain estimations of the resources. All the variables were selected attending to previous information on bear habitat selection, expert knowledge, and the importance of these variables for food provision, shelter, and human influence.

2.5 MULTISCALE MODELLING PROCEDURES

We followed a multiscale procedure to model resource selection of bears in the study area. The analysis of the resource selection by a wildlife species refers to modelling the response of the species to use the available resources in a heterogeneous habitat and a specific scale that results from a given sampling design. To enable multiscale analyses, we used scale-integrated resource selection functions (SRSFs) (DeCesare et al., 2012). This method focuses on management-oriented habitat suitability mapping through modelling in a nested fashion the resource selection of a species and synthesizing the results across scales. Our nested steps of three different scales of selection were (as adapted from Meyer and Thuiller 2006):

1. Scale 1 (S1), also known as first-order population level of selection. This scale’s objective was to identify where the distribution range (i.e. population home range) of bears occurs within the study area.

2. Scale 2 (S2), or second-order individual level of selection. The analyses at this scale determined where individual bears selected to establish their home ranges within their population home range.
3. Scale 3 (S3), or third-order individual level of selection. This scale focused on the selection of bear locations within individual home ranges.

2.5.1 Sampling procedures

Scale 1

We first determined the distribution range of each population using the location data obtained from GPS-tracked bears. This analysis identified where the potential boundary of a population distribution range occurs assuming the capability of a bear to ideally reach any given area around a given location and considering its capacity to move at specific distances during a certain time interval. The distance between locations and their associated time interval (i.e. fix acquisition rate) were compiled. We then identified the maximum distance any bear travelled for each time interval. Using ArcGIS 10.5 (Redlands, California), we applied a circular buffer around each point of radius equal to the maximum distance associated to the time interval used to collect that point. The buffers around each location indicated what habitat was potentially available to reach for that bear from any specific location according to the movement capacities of the species, although the animal actually moved towards the next location registered by the GPS-collar. We dissolved all the resulting buffers to obtain a final polygon depicting the outermost line of the feasible area that could have been reached by any of the tracked bears. This method ensured a generous delineation of the population home range to characterize an area of the species presence and absence inside and outside of that range, respectively.

Scale 2

We employed a used/available design. Firstly, we estimated each individual bear home range using the minimum convex polygon (MCP) and assumed this home range depicted the piece of space used by that bear within the entire population home range. Second, to spatially characterize the existing resources inside the MCP home ranges versus the available outside of that range, we drew an equal number of random locations within both individual MCP (used) and population home range (available). For each population, the number of random locations was equal to the mean number of locations collected per individual.

Scale 3

At this scale, we also employed a used/available design. We analyzed where bear locations occurred (used resources) within the individual home range, versus any other random location (also within the home range) depicting available resources where the animal could have been or not but we do not know. We drew the same number of random locations within each individual home range than the number of used locations.

Table 2.- Variables considered for the scale-integrated resource selection functions of bears in the central Europe populations.

Variable type	Variable	Grain (cell-size in metres)	Buffer radius (m)	Scale of selection		
				S1	S2	S3
Topographic	Elevation	25	-	×	×	×
	Roughness[1]	25	1000	×	×	×
	Hillshade	25	-			×
	Slope	25	-			×
	TPI-1000[2]	25	1000		×	
	TPI-100	25	100			×
Natural landcover	Forest1000	25	1000	×	×	
	Forest100	25	100			×
	Scrubs1000	25	1000		×	
	Scrubs100	25	100			×
	Open1000	25	1000		×	
	Open100	25	100			×
Antropogenic	Agriculture1000	25	1000		×	
	Agriculture100	25	100			×
	Road decay (decay function 0-1)	25	-	×	×	×
	Human settlements (decay function 0-1)	25	-	×	×	×

2.5.2 Variables

The types of variables referred to topographic, land cover, and anthropogenic features. All the variables were extracted from 25 × 25 m grid-cell rasters. Certain variables were quantified at 100 and 1000 m radius buffers to assume two different scales of perception of the surrounding environment by bears. Full information on the variables included at each scale and their quantification is resumed in Table 2.

The topographic variables included elevation, topographic roughness (Jenness, 2004), hillshade, slope, and topographic position index (TPI, Jenness, 2007) quantified at 100 and 1000 m radius buffers. The elevation was extracted from a 25 m grid-cell digital elevation model (DEM). Roughness, hillshade, and slope were computed using the extension DEM Surface Tools for ArcGIS (Jenness, 2004) from the DEM raster. The TPI depicts the differences in elevation between a given cell and the cells in the neighbourhood within a given buffer distance. Positive TPI values indicate a trend towards ridgetops and hillstops while negative values tend towards bottoms of valleys and canyons; a value of zero depicts flat or mid-slope areas.

The variables on landcover included the features forest, shrubs, and open areas quantified both at 100 and 1000 m radius. We also quantified cover of agricultural lands within 100 and 1000 m radius; however, we included this variable in the set of anthropogenic variables. This set of anthropogenic variables was completed by the variables distance to roads and distance to human settlements, both expressed as decay functions as computed by Nielsen et al. (2005), and with values of 0 at the feature and 1 at long distances from it.

2.5.3 Modelling procedures

We conducted a combined correlation test ($r < 0.7$) and a variance inflation factor ($VIF < 4$) (Zurr et al., 2010) to select only the variables of low multicollinearity within the models at each scale. For S1, we considered each random location as the sample unit for each population model. Therefore, we applied logistic regressions using generalized linear models (GLM) to model presences (1) and absences (0) of population home range. Conversely, for S2 (population home range selection) and S3 (individual home range selection), we considered each individual as the sampling unit for each population. In this case, we used generalized linear mixed models (GLMM) for each population to model used (1) vs. available (0) locations with individual bears as random factors.

2.5.4 Species habitat mapping

Because S1 responded to a used-unused design, we used resource selection probability functions (RSPF, Manly et al., 2002) for the model of each population at this scale to calculate the probability of bears using each pixel unit mapped. Conversely, because we applied a used-available design for S2 and S3, we used resource selection function (RSF, Boyce and McDonald, 1999), which are proportional to the probability of use in each pixel unit mapped. Each resulting map was rescaled to range between 0 and 1. Subsequently, we integrated the three scales for each population to comply with a scale-integrated resource selection function approach. Therefore, considering that each pixel within the study area has different probabilities of being part of the population home range, of being occupied by a bear home range, and of being used by a bear within its home range, the final map integrating S1, S2, and S3 at each population resulted from multiplying the maps produced at each scale (DeCesare et al., 2012).

To integrate the three population maps as calculated above, we weighted each pixel value across the study area attending to the distance of the pixel to each population home range. Hence, the pixels within the population home range had the value predicted by that population’s SRSF, whereas the pixels outside of the population home ranges were weighted by averaging the inverse distances to each population. Under this approach, the contribution of each population’s map to the average final map depended on the area of the populations and the proximity between them. From a biological perspective, this weighting approach implied that the suitability for each pixel is associated to the bear behaviour observed for that specific population and the resource selection by the species. Conversely, for the areas outside of the population, the value of the pixel is averaged to all of the behaviour in the resource selection observed among the populations but weighted towards the nearest population.

2.5.5 Model/Map validation

We identified the areas of most suitable habitat for bears against those less suitable or fully unsuitable. For this binary output, we calculated the threshold that split the continuous suitability predictions using the maximum sum of sensitivity and specificity. This method has been proven in the literature to produce the best results for models based on presence-only data, as it is the case of used-available designs (Liu et al., 2013). Using the binomial map, we conducted two different analyses to target the objectives 2 and 3 (see below).

2.6 FUNCTIONAL CONNECTIVITY ASSESSMENT

The number of habitat patches classified as suitable over the entire study area was computationally intractable for the analyses to conduct under this objective. Therefore, we selected only those patches of area larger than 75 ha, which represented the minimum area where 99% of the bear locations placed inside of the suitable patches occurred. For computational feasibility, we also resampled the habitat suitability map into a 200 × 200 m grid-cell raster. We calculated the effective distance (i.e. cost distances) between each pair of adjacent habitat patches using Linkage Mapper for ArcGis (McRae & Kavanagh, 2011). This software identifies and maps the least-cost paths between core areas (habitat patches of study) using a map of resistance or friction opposing to animal movement and survival. We considered as resistance raster the inverse of the habitat map previously produced and rescaled into values ranging from 1 to 100 of difficulty to move across the landscape. Values close to 1 depicts the best conditions for animal movement and survival, while the highest resistance values represent the least favorable areas (with 100 as the maximum resistance of a complete full barrier). With this information, Linkage Mapper finds the adjacent core areas to create a network of connections using the Euclidean distance between them. Finally, it calculates cost-weighted distances (i.e. effective distances) and least-cost paths. For computational reasons, we limited the calculations of these distances to those patches separated by less than a Euclidean distance of 4640 m, which corresponded to the maximum distance observed of any female bear out from the suitable area.

We converted the calculated effective distances into the probability of a bear to move between two patches based on their movement capacity within their home ranges (Pardo et al., 2017). Because the movement capacity of female bears is more limited than that of males and because females are more important for the viability of the populations, we focused on the conversion of the effective distances moved by females within their home range as the minimum reference. First, we calculated the mean Euclidean distance of each GPS location to the centroid of each individual MCP home range. Secondly, this distance was converted into an effective distance after multiplying its value by the mean resistance value of the pixels contained in the female's home ranges. As a result, the mean effective distance moved by female bears within their home ranges was 150202 cost units. Thirdly, we obtained the probability of bear movement between two patches using a negative exponential function of the Euclidean distance between nodes multiplied by a decay parameter that accounts for the dispersal distance of the species (Pardo et al., 2017). We made this parameter equal to the previously calculated 150202 cost units that we equated with a probability of dispersal of 0.05. The probability of movement between patches ranged from 0 (no connectivity) to 1 (fully connected, i.e. the distance between patches is 0).

To analyze the connectivity of suitable bear patches, we used a set of indices (see Saura & Pascual-Hortal (2007), and Saura & Rubio (2010) for extended information) calculated in the software Conefor 2.6 (Saura and Torné, 2009):

- **The probability of connectivity index (PC)**: This index considers a number of habitat patches and the connections among them to score a probability that two organisms randomly placed anywhere in the landscape are within patches reachable or interconnected between them. This index is based on the concept of habitat availability of any patch for itself (intrapatch connectivity) and for other connected patches (interpatch connectivity), on the interpatch dispersal probabilities, and on spatial graphs.
- **The absolute variation in connectivity decrease (varPC)**: This index evaluates the absolute loss of connectivity in the landscape when a patch is removed. Therefore, this index is valuable to illustrate the importance of a patch to maintain the connectivity of the entire system. The varPC index can be decomposed in three fractions depicting three indices of importance for patch connectivity: $varPC_{flux}$, $varPC_{intra}$, $varPC_{connector}$,
- **$varPC_{flux}$**: Quantifies how well a patch is connected to others.
- **$varPC_{connector}$,**: Quantifies the contribution of the patch as stepping stone to the interpatch connectivity between other nodes.
- **$varPC_{intra}$**: This index is related to intrapatch connectivity and the availability of habitat offering independently of its position and distance to other patches in the system.
- **Betweenness Centrality metric based on PC (BC(PC))**: Like $varPC_{connector}$, this index also quantifies the contribution of the patch to animal movements among other patches in the landscape, but in this case without removing the patch. Therefore, it

shows the contribution of the patch as stepping stone in the intact landscape instead of after its removal as it quantifies $varPC_{connector}$,.

We produced the maps representing each of the indices above and the identified least-cost paths obtained from the analyses in Linkage Mapper. These paths were classified as the ratio between the cost-weight and least-cost values for each path.

2.7 PLAUSIBLE LEAST-COST PATHS IN POPULATION PATCHES

Animal movement is often a stochastic process that depends not only on external drivers but also on other manifold factors of animal cognition, individual characters and perception differences. However, estimations on plausible paths of movement based on habitat selection outputs are possible using least-cost path analyses as surrogates of the feasibility of the landscape to facilitate individual animal movements. It can be expected that animals move preferably across suitable habitats and avoid those less suitable. Large patches of suitable habitat tend to show intricate shapes so that often movements within patches can be solved along shortcuts crossing less favourable or unfavourable habitats. The identification of these plausible crossing points attending to criteria of species-habitat selection is of relevance to promote habitat improvements in those areas of plausible crossing and to promote infrastructures facilitating animal movement.

We estimated a set of plausible crossing points within and among the largest bear suitable habitat patches overlapping the MCP home ranges of the three study populations. We considered a minimum patch size of 9696 ha because this corresponds to mean amount of suitable habitat contained in the individual MCP home ranges of female bears in the study area. This selection resulted in several patches for population 1 (N = 6, $\mu_{area} \pm SD = 98{,}666 \pm 73{,}150$ ha), population 2 (N = 12, $\mu_{area} \pm SD = 22{,}305 \pm 10{,}690$ ha) and one single large patch for population 3 (area = 810,896 ha). We split the patches at each population using a grid of 22 × 22 km covering a total area of 48,400 ha, which approximated to the mean MCP home range area for all the bears tracked in this research (area = 46,700 ha). The suitable patches were divided into different polygons within each grid-cell and created a point layer in ArcGIS depicting the centroid of each polygon. This sampling fashion arranged the covering of most of the patch areas by a representative node, so that we conducted connectivity analyses in Linkage Mapping to determine the least cost paths connecting each node with the nodes included in the adjacent grid-cells. Using this method, we made a computational estimation of the most plausible paths linking any random point created inside the patch of study. Once identified the paths, we selected those specific sections not overlapping the patches over 75 ha, i.e. connections, and classified each path attending to its itinerary longitude for visualization purposes.

3 Results

3.1 MODELLING RESULTS

The model outputs for each population at the three scales are summarized in tables 2, 3 and 4. The results for each scale-specific model and for each population show that forest cover was the only variable selected in all the populations and scales, i.e. positive selection of increased forest cover. The rest of the variables yielded different selection patterns either among populations, scales, or both. Topographic variables showed that population 1 (Trentino-Swiss population) occurred in areas with a higher elevation and roughness than those where the population was absent (Table 3).

Conversely, this trend was the opposite for populations 2 and 3 (Table 3). Although the placement of home range followed different trends in relation to the elevation in S2, the use of space per individual home range was associated with areas of higher elevation and rougher terrains for all the populations (Table 4). Overall, the S1 models captured the topography and landscape composition of the well different characteristics of these variables in the areas where each population occurs. This was also the case for the placement of home ranges within the population home range S2. Models at S3 revealed more specific information about the variables directly selected by bears (through the use of GPS locations) within their individual home ranges for each population (Table 5). At this scale, the topographic variables indicated that bears mostly selected high and rough areas within their home ranges, although the trends of selection for the variables slope, hillshade and topographic position indices were unequal among populations. In terms of natural landcover variables, forest and shrubs were positively selected by bears of the three populations while the open areas were avoided. Anthropogenic variables showed bears selected to move far from roads and human settlements, although for the latter variable, this occurred only in populations 2 and 3. In population 1, bears showed a positive selection towards human settlements and agricultural areas.

Table 3.- Results from scale 1 (population home range) models for the three bear populations

	Population 1		Population 2		Population 3	
	β	SE	β	SE	β	SE
Intercept	-3.67	0.07	-2.86	0.05	-2.22	0.04
Elevation	0.69	0.07	-0.44	0.04	-0.84	0.06
$(\text{Elevation})^2$	0.24	0.03	-0.22	0.03	-3.16	0.08
Roughness	1.07	0.06	0.74	0.04	-1.59	0.06
$(\text{Roughness})^2$	-0.21	0.02	-0.10	0.01	0.13	0.02
Forest1000	0.54	0.04	0.34	0.03	0.55	0.03
$(\text{Forest1000})^2$	-0.21	0.04	0.01	0.03	-0.20	0.03
Agriculture1000	0.25	0.07	-0.38	0.04	-0.40	0.03
$(\text{Agriculture1000})^2$	-0.27	0.06	0.30	0.03	0.42	0.03
Settlements	-0.15	0.03	-0.16	0.02	0.01	0.02
$(\text{Settlements})^2$	0.11	0.03	-0.05	0.02	0.55	0.02

Table 4.- Results from scale 2 (individual home range placement within the population home range) models for the three bear populations.

	Population 1		Population 2		Population 3	
	β	SE	β	SE	β	SE
Intercept	-0.002	0.035	-0.0002	0.021	-0.001	0.007
Elevation	-	-	-0.351	0.018	0.197	0.005
Roughness	0.087	0.017	-0.153	0.013	-0.066	0.004
TPI-1000	0.091	0.016	0.094	0.011	-0.061	0.004
Forest1000	0.231	0.019	0.349	0.0151	0.189	0.005
Scrubs1000	0.021	0.019	0.154	0.014	-0.103	0.004
Open1000	-	-	0.173	0.015	-0.035	0.004
Agriculture1000	0.212	0.023	-	-	-	-
Road decay	-0.115	0.020	0.046	0.011	-0.131	0.004
Settlements	-0.103	0.020	0.070	0.012	-0.008	0.005

Table 5.- Results from scale 3 (selection within individual home range) models for the three bear populations.

	Population 1		Population 2		Population 3	
	β	SE	β	SE	β	SE
Intercept	0.06	0.07	-0.12	0.03	-0.04	0.03
Elevation	0.24	0.06	0.56	0.03	0.23	0.01
Roughness	0.82	0.05	0.04	0.03	0.06	0.01
Slope	0.13	0.04	-0.03	0.03	0.10	0.01
Hillshade	0.35	0.03	0.12	0.02	-0.03	0.01
TPI-100	0.04	0.03	-0.01	0.02	0.03	0.01
Forest100	0.79	0.06	0.74	0.04	0.48	0.01
Scrubs100	0.38	0.06	0.16	0.04	0.18	0.01
Open100	-	-	-0.16	0.03	-0.02	0.01
Agriculture100	0.35	0.05	-	-	-	-
Road decay	0.02	0.04	0.29	0.03	0.10	0.01
Settlements	-0.30	0.04	0.30	0.03	0.25	0.01

The scale-integrated habitat suitability map based on the probability of space used by bears calculated from the models reported above is shown in Figure 2. The validation of the map accuracy revealed that the scale-integrated RSFs performed with a good prediction capacity ($\bar{r}$ = 0.90) according to Baldwin et al. (2009) classification.

The thresholds calculated from the maximum sum of sensitivity and specificity were 0.015, 0.087, and 0.068 for population 1, 2, and 3, respectively. The binomial resulting map from applying these thresholds for each suitability pixel value within their respective home range and their distance-weighted value outside these ranges is shown in Figure 3, and a sub-classification of this binomial map in Figure 4.

3.1 CONNECTIVITY AND CORRIDOR ANALYSES

The maps of the results of each of the indices evaluated for the connectivity and corridor analysis in the Central European brown bear populations are shown in figures 5, 6, 7, and 8.

The maps showing the results on the most plausible least-cost paths for intra and interpatch connectivity are shown in figures 10, 11, and 12, 13.

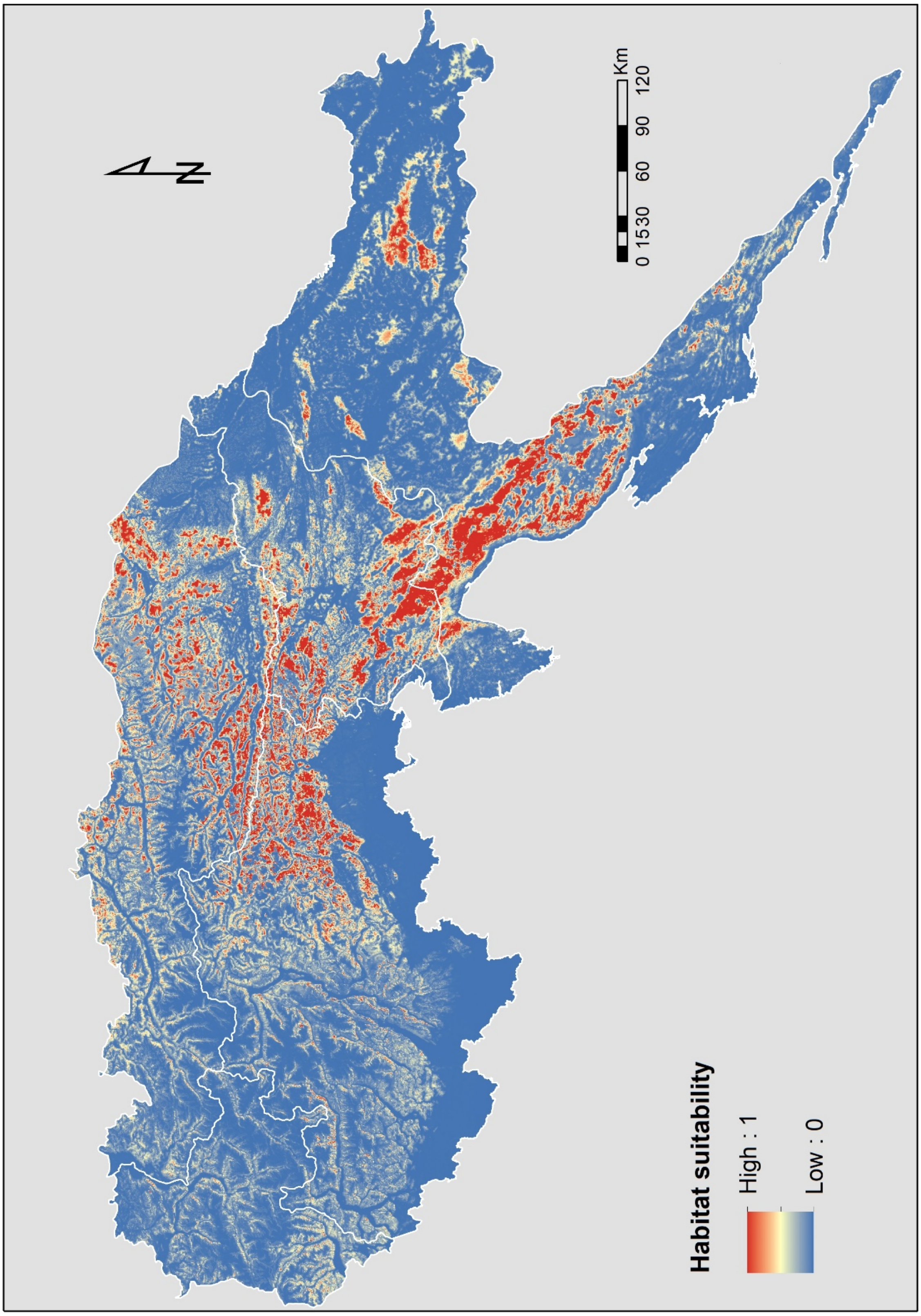

Figure 2.- Brown bear habitat suitability map based on the probability of use calculated from scale-integrated resource selection functions (RSFs).

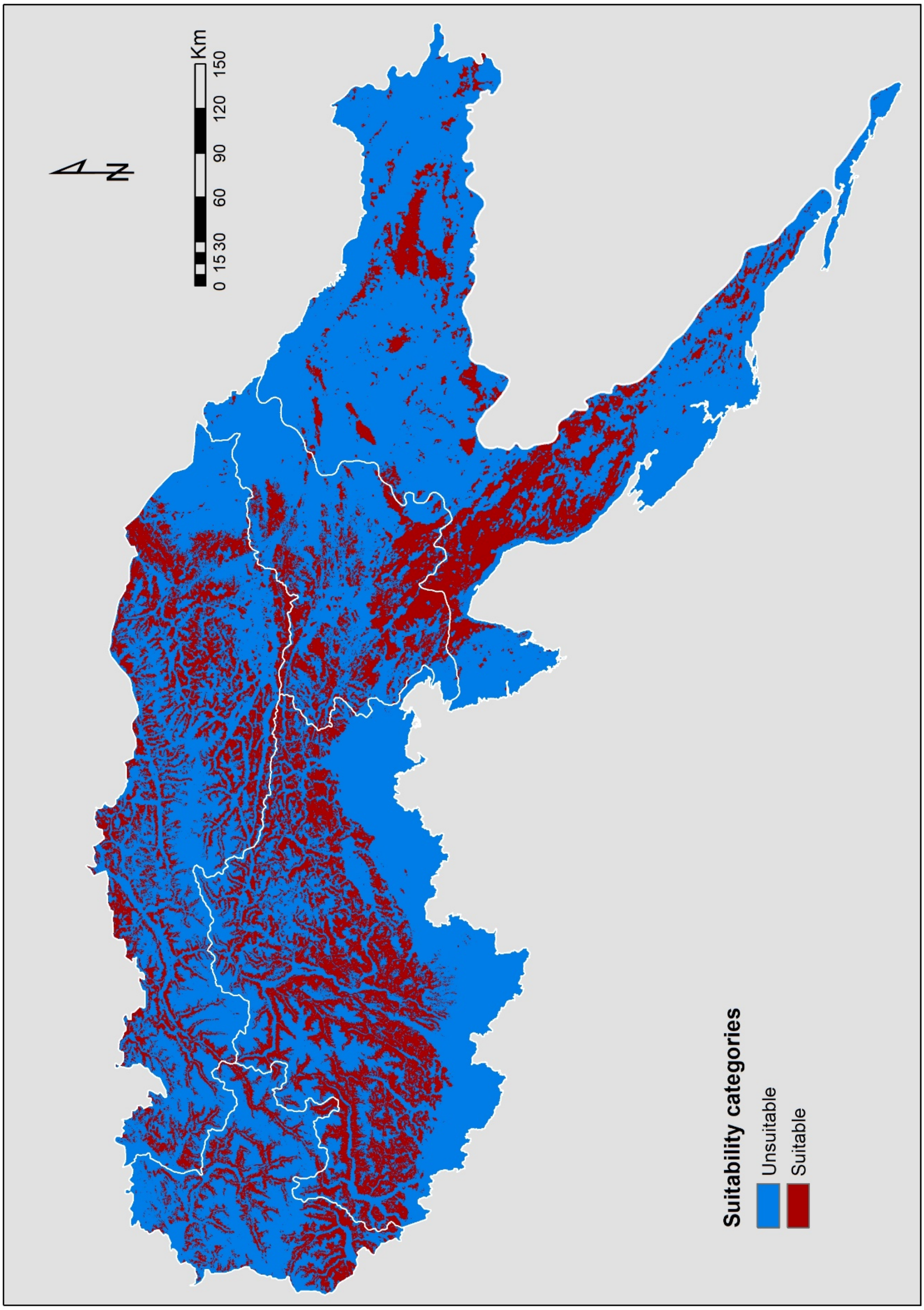

Figure 3.- Categorical map depicting suitable and unsuitable categories.

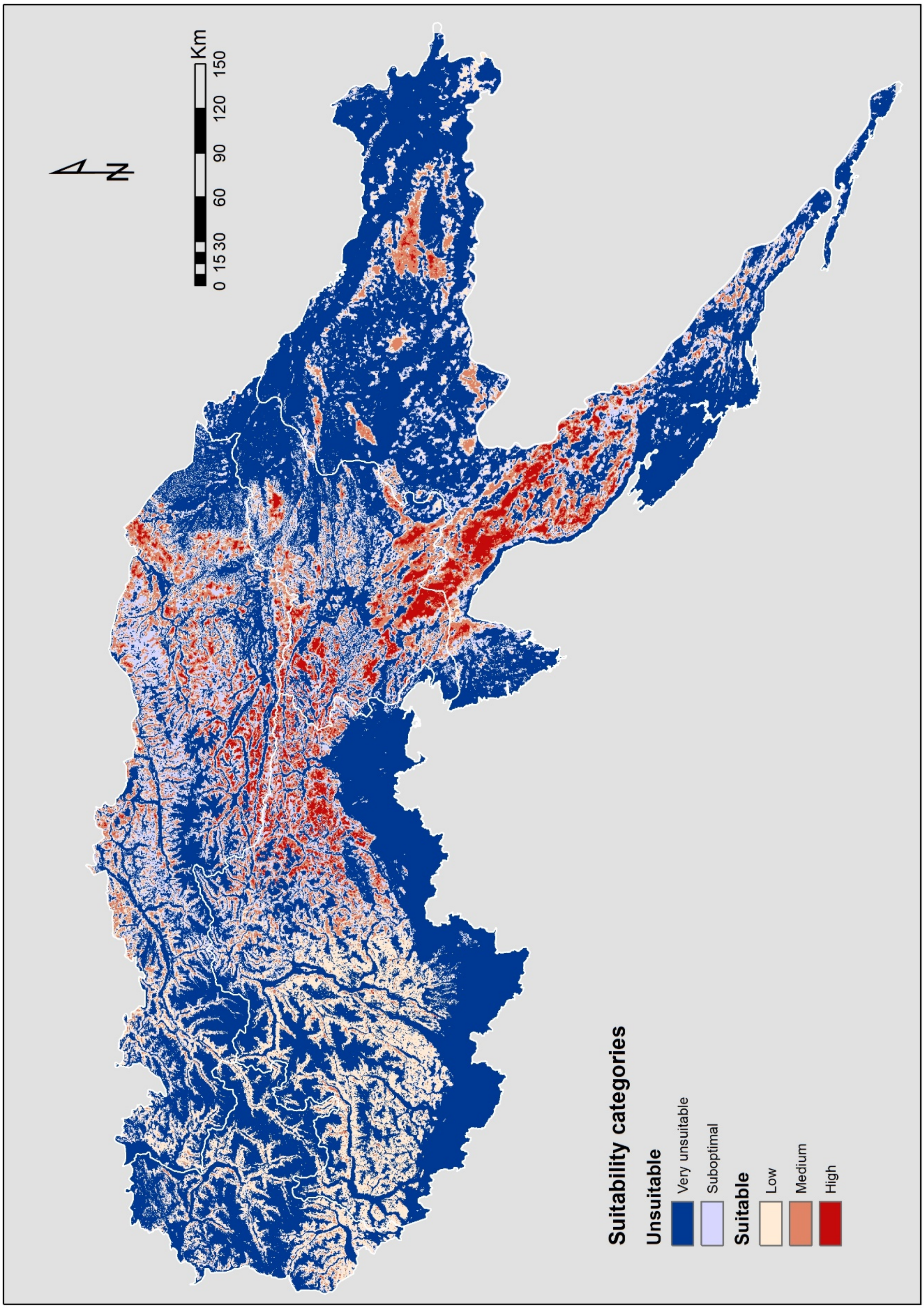

Figure 4.- Categorical map classified from the continuous habitat suitability map. The classification was conducted for each suitable and unsuitable area using natural breaks.

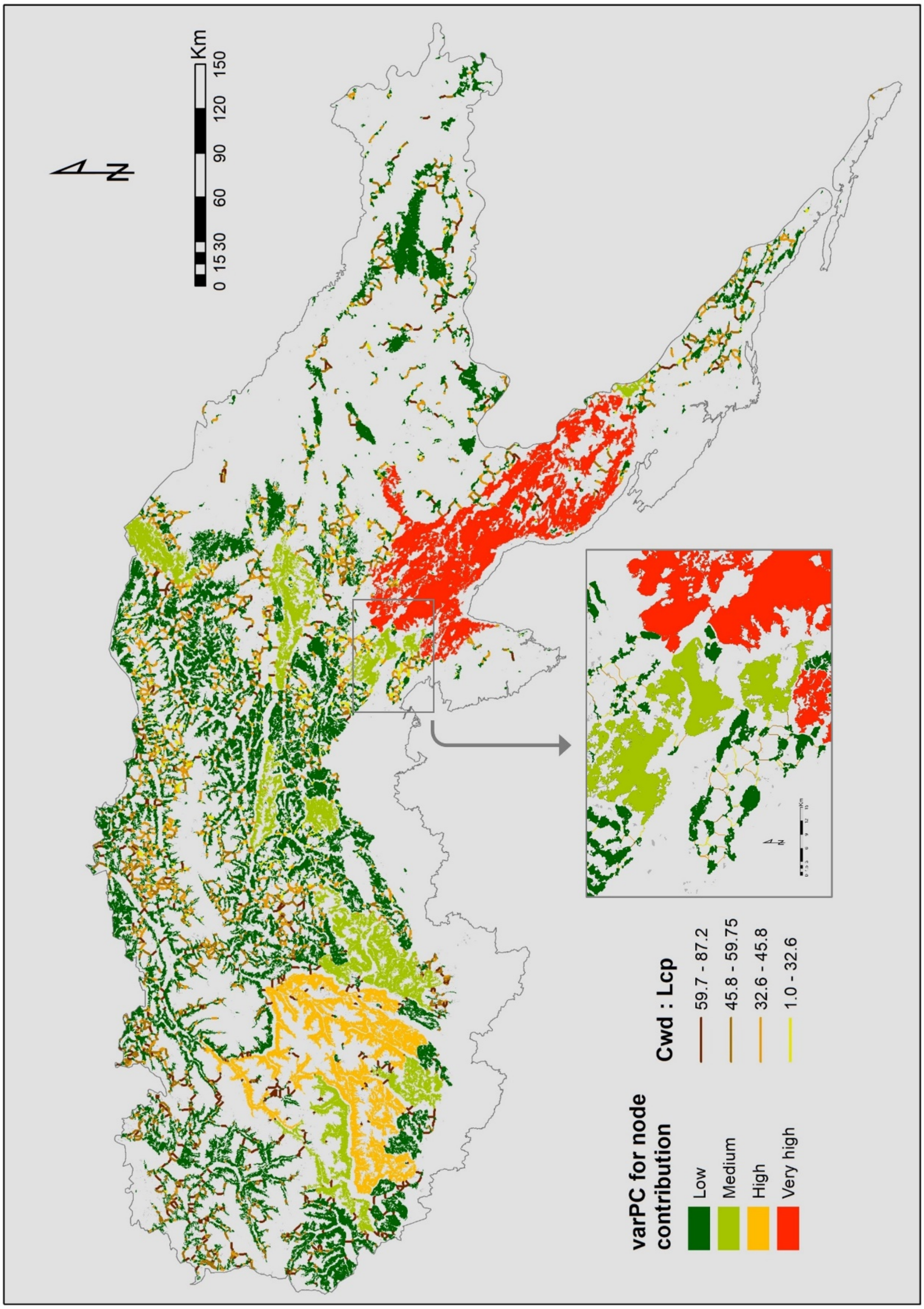

Figure 5.- Absolute variation in the probability of connectivity decrease (varPC) index for each node (habitat patch). The different color in the connecting paths represent the quality of these linkages reported as the ratio of cost-weighted distance (Cwd) to least-cost path (Lcp), wherein the lower values indicate the best quality of paths with lower cost of movement along this patch (yellow?). Conversely, higher values of linkages depict higher cost of movements.

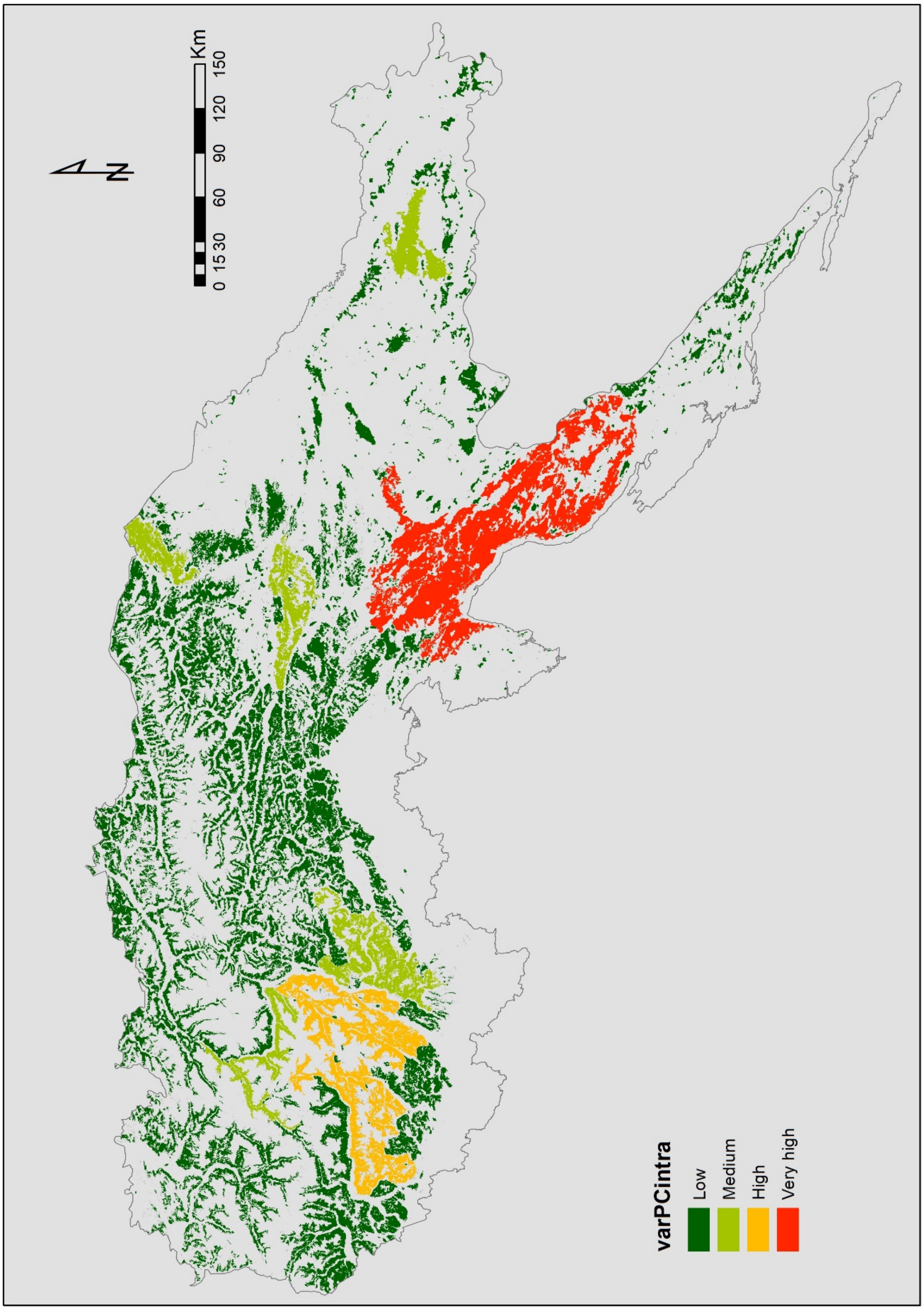

Figure 6.- Fraction of the varPC accounting for intrapatch connectivity among habitat patches or varPCintra, which indicates the availability of habitat offered by the patch independently of its position and the distance to other patches in the system.

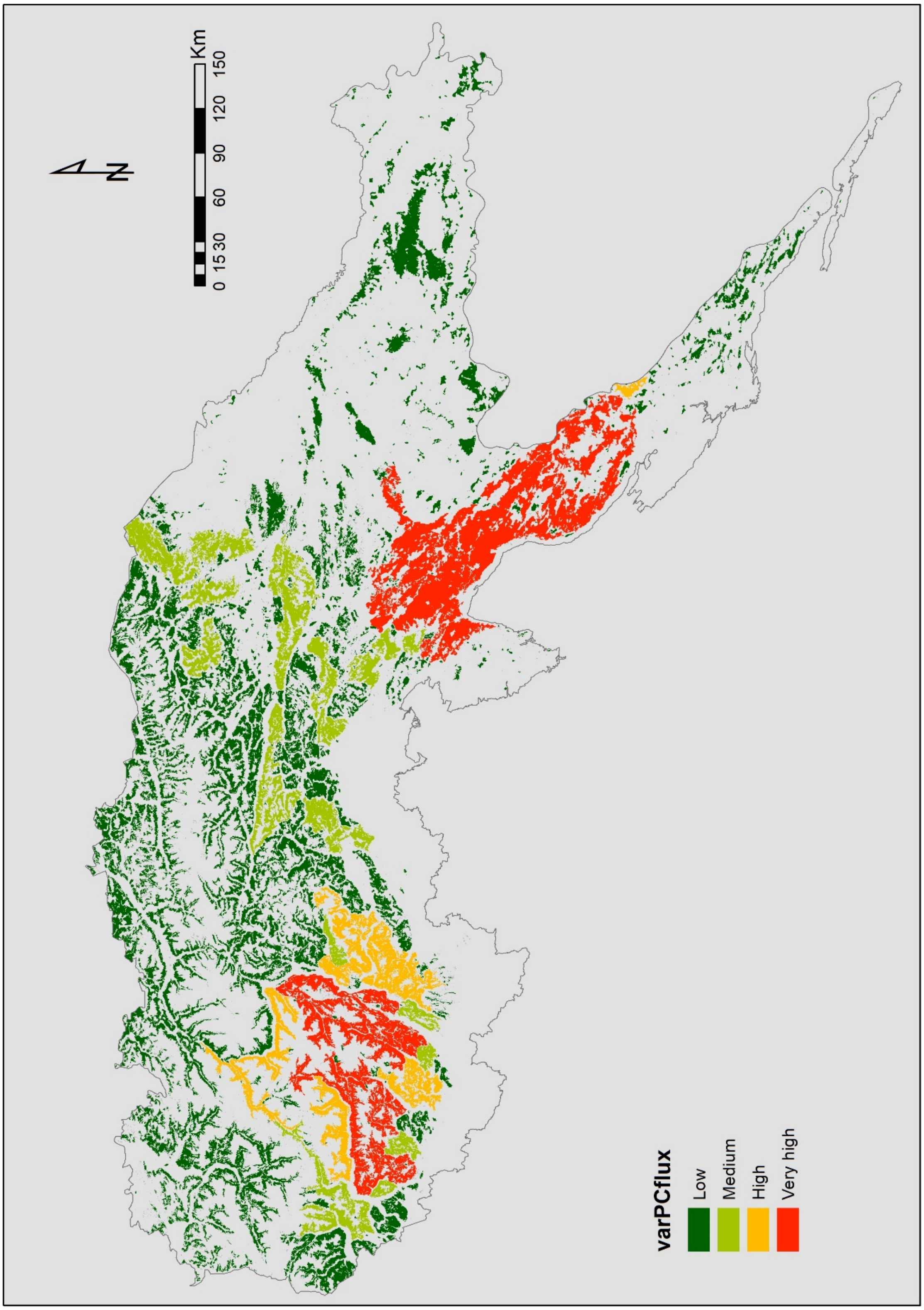

Figure 7.- Fraction of the varPC accounting for flux among habitat patches or varPCflux, which indicates how well a patch is connected to others.

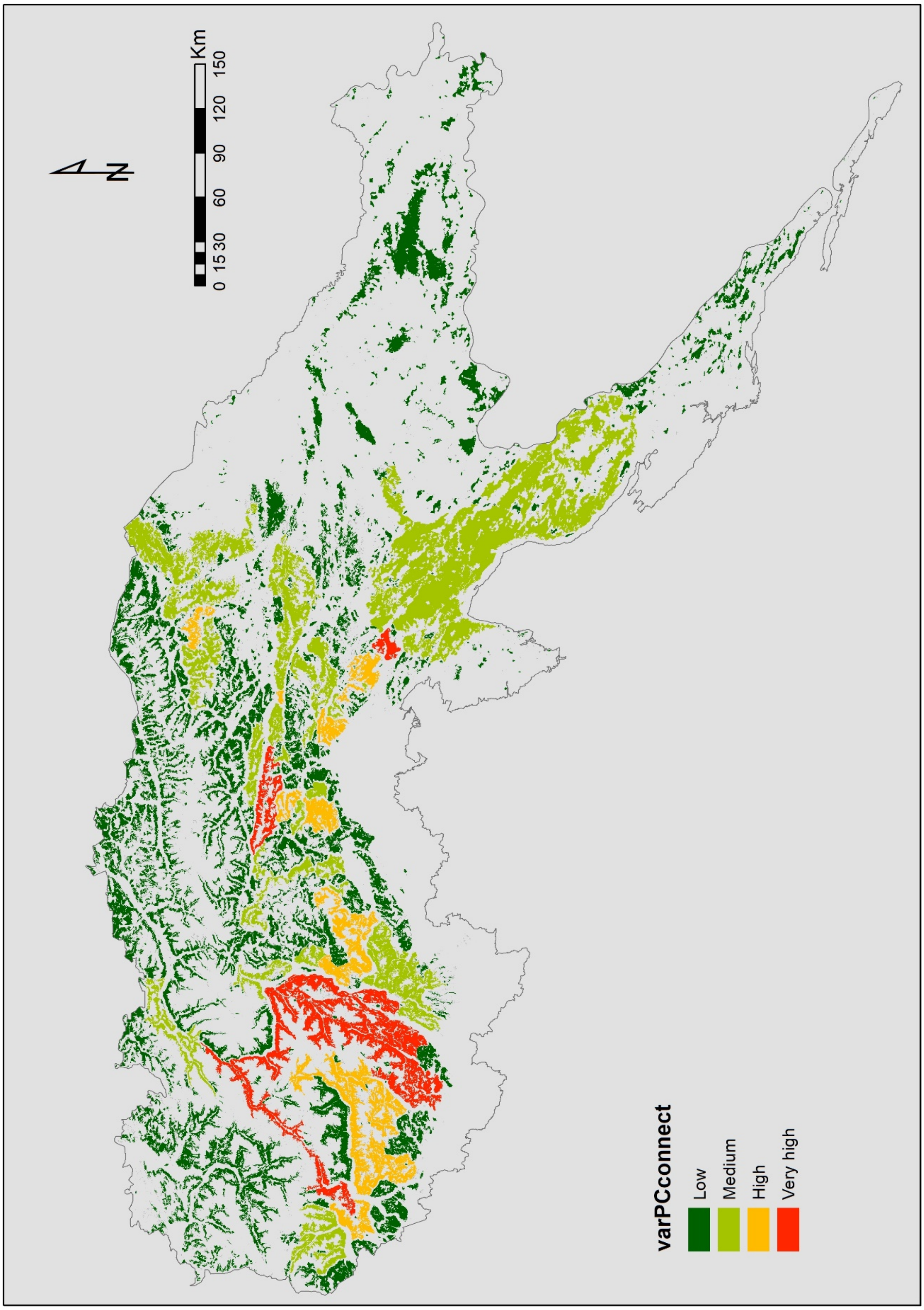

Figure 8.- Fraction of the varPC accounting for interpatch connectivity or varPCconnect, which measures the contribution of the patch as stepping stone to the interpatch connectivity between other nodes.

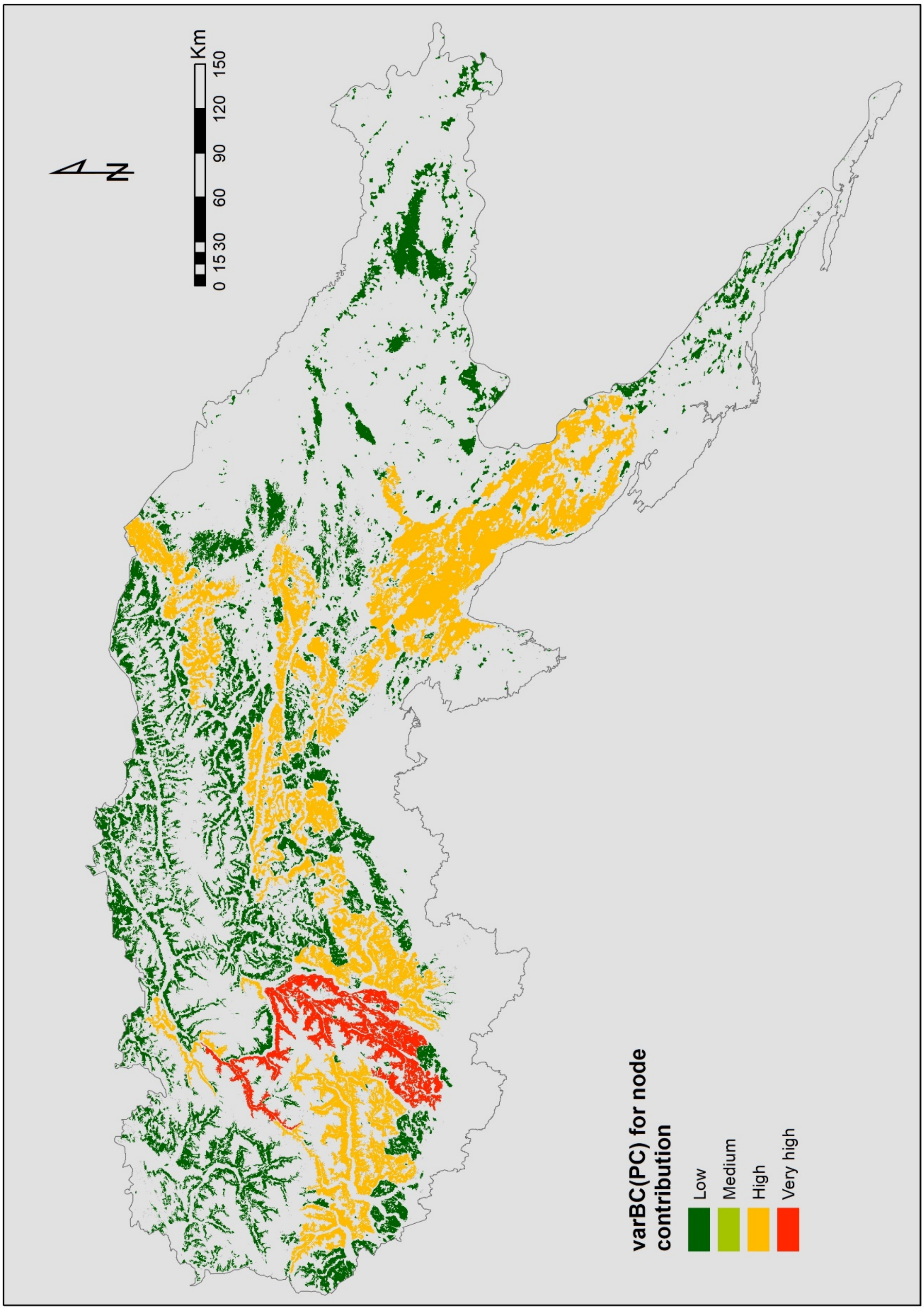

Figure 9.- Absolute variation in the centrality index (varBC(PC)) index for each node (habitat patch), which shows the contribution of the patch as stepping stone in the intact landscape instead of after its removal as it quantifies $varPC_{connector}$.

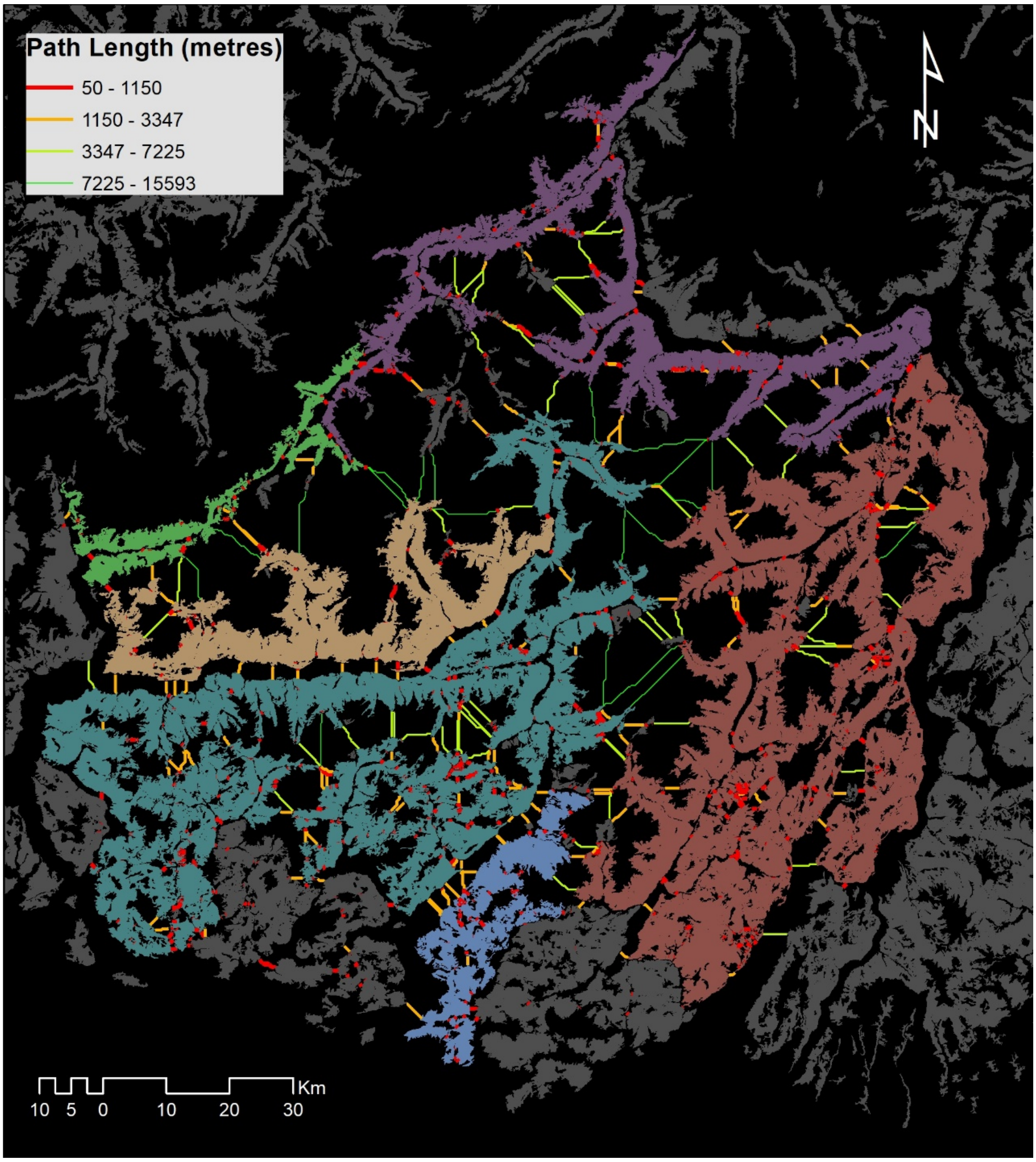

Figure 10.- Most plausible least-cost paths connecting areas between and within patches of population 1 (Trentino-Swiss).

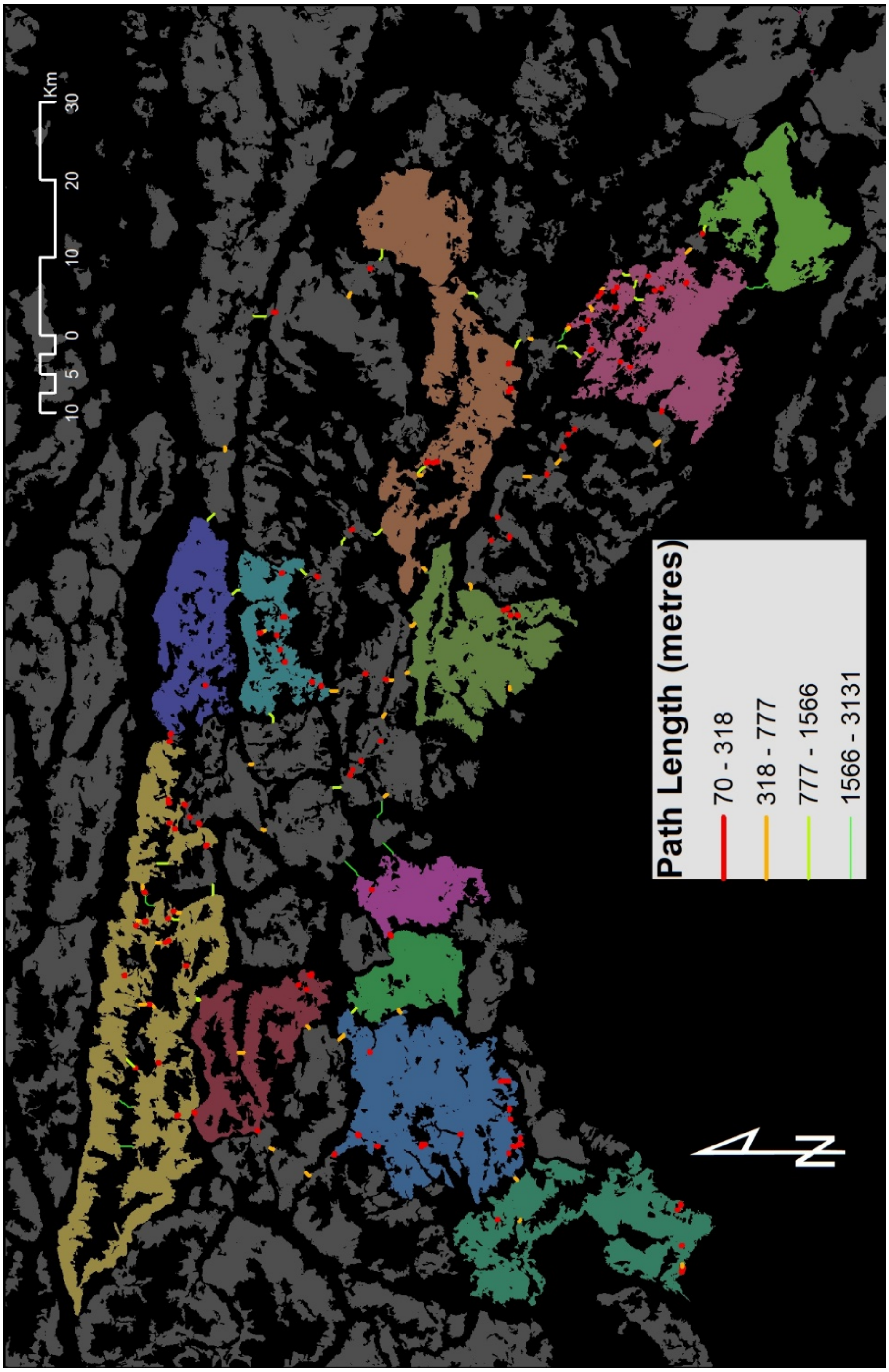

Figure 11.- Most plausible least-cost paths connecting areas between and within patches of population 2 (Pre-Alpine population).

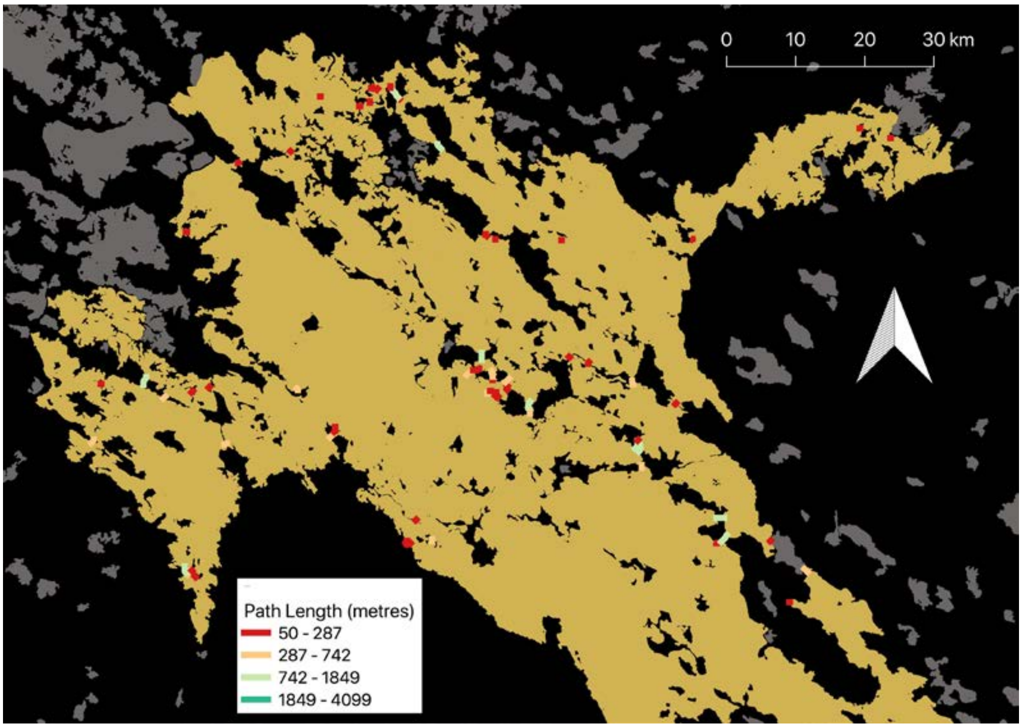

Figure 12.- Most plausible least-cost paths connecting areas between and within the northern patches of population 3 (Dinaric population).

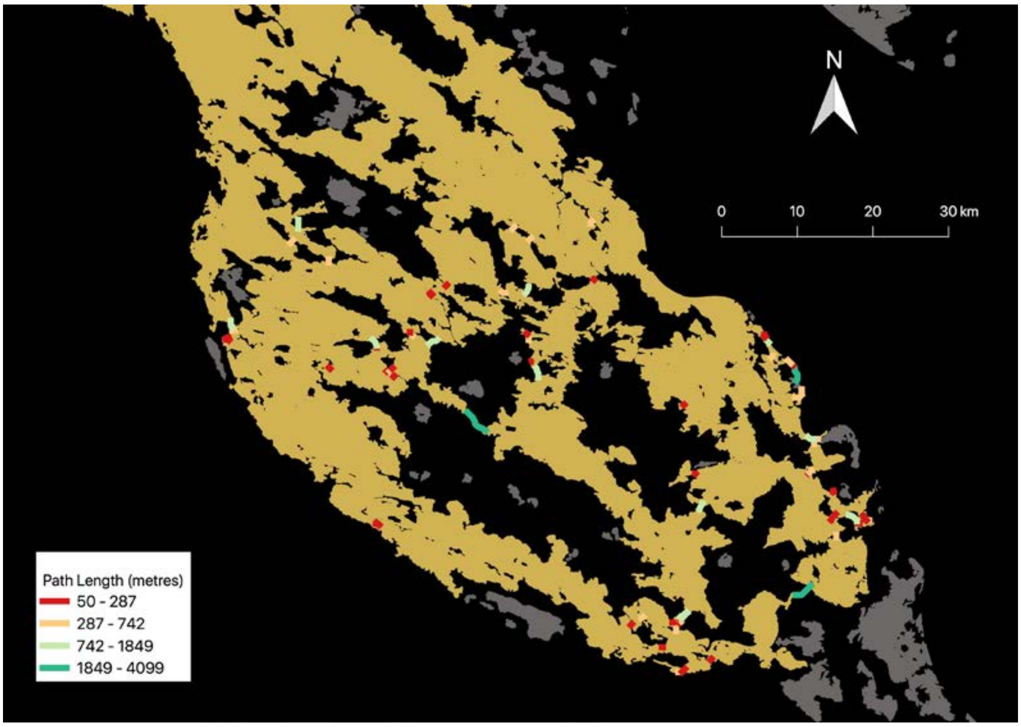

Figure 13.- Most plausible least-cost paths connecting areas between and within the southern patches of population 3 (Dinaric population).

4 Discussion

4.1 Habitat suitability

The scale-integrated RSFs employed in this research is a convenient approach to deal with longstanding discussions on scale selection concerns in habitat selection analyses (see for instance Boyce 2006). Our approach to model each population independently at three different scales and to integrate all the results offered a more localized approximation to habitat selection for each population than the overall inclusion of all the available data into a single transversal model for all of the populations. Under this framework, our scale-integrated models yielded different results on habitat selection behavior for each bear population. The predictions on suitable habitat revealed that population 3 was the one containing the largest and most suitable habitat patches. Population 2 showed a similar pattern but with smaller and more fragmented patches than population 3. Lastly, population 1 had also large patches of suitable habitat (as observed in the binomial map) but of lower suitability than the other populations and with more concentrated and scarce areas of high to very high suitability.

In the Trentino-Swiss area, humans have conducted a historical more intense transformation of the landscape and persecution of large predators than in the other populations. Nevertheless, bears are able to adapt to the “modified” landscape. The models at the 3 scales for population 1 confirm a general positive trend of selection for elevated and rough terrains across all the scales that is more pronounced than for populations 2 and 3. Therefore, bears could be pushed in population 1 to select and occupy more inaccessible areas for humans occurring at higher and rugged terrains. However, the intense human presence in this population might imply that bears are not capable of establishing their home ranges and use the space within their home ranges, thus avoiding human settlements, agricultural areas, or road presence. The model coefficients for the anthropogenic variables in this population and at the different scales suggest this conclusion. We acknowledge that the habitat selection models for population 1 is limited to only 6 animals that could have displayed a very specific individual selection pattern by concentrating most of their activities in rough and elevated areas still close to anthropogenic features. However, the model predictions over the entire population area reveal that this combination of variables is mostly unavailable, which can also explain the very limited availability of high to very high suitable patches.

Populations 2 and 3 showed in general similar patterns of habitat selection. However, the differences between these two populations might be caused by a sex bias towards males due to the fact that most of the bears in population 2, included those tracked, are dispersing males from population 3. Also, some differences in S1 and S2 for these populations might most likely be caused by certain differences in landscape composition and configuration, with population 2 being an interface among the landscapes of population 1 and 3. Overall, the high abundance of forest in these populations makes this variable the most important and valuable resource for bear population viability and growth. Consequently, it is required the conservation of large forest patches and to promote connectivity among these patches.

3.1 Connectivity and corridors

The two different indices quantifying the contribution of each patch to the connectivity and movement of all the suitable bear patches in the study area, i.e. varPC and varBC(PC), revealed the importance of the largest patches where current bear populations occur in the study area. This importance was especially relevant for the patches in populations 1 and 3, which scored high and very high values of these indices. There is potential for connecting the three populations, although population 2 contains smaller and more abundant fragmented patches than the other populations. However, population 2 contains habitat patches of importance for the hypothetical flux and connection between population 1 and 3 (see varPCconnect and varPCflux indices, respectively).

In terms of potential patches, there are some large suitable patches of connectivity importance for the survival and movement of bears in Austria under a hypothetical scenario of bear colonization of this region. These patches are surrounded by other smaller ones that could act as stepping-stones connecting mainly with population 2.

Overall, the connectivity analyses at the study area level supported the need to preserve suitable and well connected large patches of mostly forest habitat. This priority does not diminish the importance of preserving smaller patches capable of acting as stepping-stones for connecting patches of current or potential suitability and connectivity importance.

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