



Potential habitat connectivity of European bison (*Bison bonasus*) in the Carpathians

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ABSTRACT

Habitat connectivity is important for the survival of species that occupy habitat patches too small to sustain an isolated population. A prominent example of such a species is the European bison (*Bison bonasus*), occurring only in small, isolated herds, and whose survival will depend on establishing larger, well-connected populations. Our goal here was to assess habitat connectivity of European bison in the Carpathians. We used an existing bison habitat suitability map and data on dispersal barriers to derive cost surfaces, representing the ability of bison to move across the landscape, and to delineate potential connections (as least-cost paths) between currently occupied and potential habitat patches. Graph theory tools were then employed to evaluate the connectivity of all potential habitat patches and their relative importance in the network. Our analysis showed that existing bison herds in Ukraine are isolated. However, we identified several groups of well-connected habitat patches in the Carpathians which could host a large population of European bison. Our analysis also located important dispersal corridors connecting existing herds, and several promising locations for future reintroductions (especially in the Eastern Carpathians) that should have a high priority for conservation efforts. In general, our approach indicates the most important elements within a landscape mosaic for providing and maintaining the overall connectivity of different habitat networks and thus offers a robust and powerful tool for conservation planning.

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1. Introduction

The terrestrial biosphere has shifted from a primarily wild to a primarily anthropogenic state during recent centuries, mainly due to the expansion and intensification of land use (MA, 2005). Land cover transformation and fragmentation have profound consequences for species' habitats and populations, and are the main causes of the current biodiversity crisis (CBD, 2010). In today's increasingly human-dominated landscapes, many species only survive if there is connectivity between spatially separated, local populations (Fischer and Lindenmayer, 2007). Moreover, the relationship between habitat fragmentation and extinction risk is highly non-linear, and characterized by tipping points (Fahrig, 2003) and lagged effects (Rogers et al., 2009; Jackson and Sax, 2010). Conservation planners thus need to preserve resilient habitat networks and this requires identifying habitat patches

and corridors that are crucial for maintaining or establishing connectivity for fragmented populations.

Large carnivores and herbivores are particularly difficult to protect in human-dominated landscapes, because they require large, undisturbed habitats, are often in conflict with people or land use, and frequently poached for either meat or trophies (Woodruffe, 2000; Gordon and Loison, 2009). These species also play an important role in ecosystem functioning, and their loss may trigger ecological meltdown (Terborgh et al., 2001; Pringle et al., 2007). Moreover, they are important targets for conservation because managing for their survival as "umbrella species" may benefit many other creatures (Sergio et al., 2006; Branton and Richardson, 2011).

The European bison (*Bison bonasus*) is a typical example of a threatened species (Pucek, 2004). By the early 20th century, only two isolated herds had survived several centuries of severe habitat fragmentation and overexploitation (Pucek, 2004; Krasińska and Krasiński, 2007; Kuemmerle et al., 2012). The last wild bison was poached in 1927, and only 54 animals survived in captivity (Pucek, 2004). Thanks to a rapidly initiated systematic breeding and

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reintroduction program the species was saved from extinction and there are now about 4200 European bison, 2600 of them in the wild (European Bison Pedigree Book, 2009). However, despite this population increases, European bison are far from safe. The species suffers from low genetic diversity, almost all current herds are small (<100 animals), isolated, and locally threatened by poaching (Pucek, 2004; Daleszczyk and Bunevich, 2009; Parnikoza et al., 2009). Long term survival of the species will depend on linking isolated local populations into a large, well-connected population, through natural or assisted transfers of animals (Perzanowski et al., 2004; Krasíńska and Krasíński, 2007; Kuemmerle et al., 2011a).

The Carpathians, European largest and least disturbed mountain range with favorable conditions for European bison (Perzanowski and Kozak, 2000; Krasíńska and Krasíński, 2007), are among the few places where such a large, connected population could be established (Kuemmerle et al., 2011a,b). In the 1960s and 1970s European bison were reintroduced in the Carpathians. However, conservation success will depend on substantially enlarging existing herds (Pucek, 2004; Krasíńska and Krasíński, 2007; Kuemmerle et al., 2011b), and ensuring connectivity among them through the identification of both areas suitable for reintroductions, and range extensions, and habitat patches that are crucial for connecting existing bison herds (e.g. Parnikoza et al., 2009; Kuemmerle et al., 2011a,b).

In general, landscape connectivity is defined as the degree to which the landscape facilitates or impedes dispersal among habitat patches (Taylor et al., 1993) and can be assessed from either a structural or a functional point of view. Structural connectivity is related to landscape pattern (e.g., size, shape and configuration of habitat patches, existence of corridors and permeability of landscape matrix; Metzger and Décamps, 1997; Tischendorf and Fahrig, 2000; Uezu et al., 2005). In contrast, functional connectivity refers to ecological responses of organisms to individual landscape elements (e.g. patches) and the ability of individuals to move in non-habitat areas (Tischendorf and Fahrig, 2000; Moilanen and Hanski, 2001; Uezu et al., 2005).

Different methods have been proposed to evaluate connectivity (e.g. see review Kindlmann and Burel, 2008), most common are least-cost path analysis (e.g. Tischendorf and Fahrig, 2000; Adriaensen et al., 2003; Rabinowitz and Zeller, 2010), graph theory (see reviews Dale and Fortin, 2010 or Galpern et al., 2011), spatially explicit population models (Wiegand et al., 2005; Minor and Urban, 2007), or morphological analysis (Vogt et al., 2009). However each of these methods has shortcomings, and none of them by itself can provide guidance as to where to focus conservation actions to maintain or improve connectivity. Therefore, it is imperative to integrate existing methods for a more accurate determination of connectivity that can guide conservation efforts (Tischendorf and Fahrig, 2000; Fischer and Lindenmayer, 2007; Kindlmann and Burel, 2008; Atwood et al., 2011).

Combining least-cost path analysis with graph theoretic techniques, i.e., defining the edges of a graph using least-cost routes, allows for incorporation of spatial information about habitat patches and the surrounding matrix into analytic tools and measures of graph theory (Galpern et al., 2011), and therefore is increasingly being used for species-level conservation management, e.g., to preserve or restore habitat connectivity (e.g. Bunn et al., 2000; O'Brien et al., 2006; Fall et al., 2007; Saura and Pascual-Hortal, 2007a). Even though this is a promising approach, Rayfield et al. (2009) drew attention to the challenges that arise when deriving the permeability matrix values (i.e., cost values) that reflect the ecological costs associated with individuals moving through a landscape. They found that the locations of least-cost paths were sensitive to the relative cost values assigned, and to the spatial configuration of habitat patches. Therefore, conducting the least-cost path anal-

ysis on an actual habitat analysis, e.g. by using a habitat suitability model together with spatial data on dispersal barriers to yield a cost surface of species dispersal, provides more ecological realism. Such a modeling framework can be successfully used to preserve species of particular conservation concern or to identify priority areas for restoring habitat connectivity (Kusak et al., 2009).

The goal of our study was to assess potential habitat connectivity of European bison in the Carpathians using a coherent approach which combines three groups of methods: habitat suitability modeling, least-cost path analysis, and graph theory. Our specific objectives were:

- (1) to translate the habitat suitability model and spatial data on dispersal barriers into a cost surface of bison dispersal;
- (2) to assess European bison habitat connectivity across the Carpathians based on location of current herds; and
- (3) to assess the importance of all potential habitat patches for overall bison habitat connectivity in order to identify sites for bison reintroduction that are optimal to improve overall population connectivity.

2. Methods

2.1. Study area

The Carpathians are Europe's largest mountain range, stretching in an arc across Austria, Slovakia, the Czech Republic, Hungary, Poland, Ukraine, Romania, and Serbia (Fig. 1). Elevation ranges from around 100 to 2655 m a.s.l. Climate is moderately cool and humid. Forests cover approximately 50% of the region (up to 90% between 1000 and 1500 m a.s.l.; Kozak et al., 2008). The region is critically important for biodiversity conservation in Europe, hosting vast semi-natural old-growth forests, many endemic species, Europe's largest wolf and brown bear populations (UNEP, 2007), and some of the largest free-ranging populations of the European bison (Perzanowski and Kozak, 2000).

2.2. The Carpathian bison population

The whole Carpathian bison population (belonging to the Lowland-Caucasian-line) has low genetic diversity (only 12 founders), potentially resulting in low reproduction rates and disease resistance (Olech and Perzanowski, 2002; Pucek, 2004; Perzanowski and Olech, 2007). Currently, around 350 European bison live in the Carpathians in five free-ranging herds (Fig. 1; herd here refers to a panmictic subpopulation of European bison): two in the Polish Bieszczady Mountains (together 304 animals; Perzanowski, 2011), one in northeastern Slovakia (Poloniny National Park: 9 animals; European Bison Pedigree Book, 2009), and two in Ukraine (Skole-Majdanska District: 6 animals; Bukovyna Mountains: 28 animals; Smagol et al., 2010). A sixth herd was established in 2006 in Vana-tori Neamt Nature Park in Romania (PDM, 2011). At the time of writing, this herd with 24 animals remained in an enclosure, but release is foreseen for 2012 (information provided by park specialist Razvan Deju). These bison herds are in most cases isolated from each other though (Fig. 1) and the effective population size of even the largest herd is too small to ensure long-term demographic and genetic stability (Perzanowski et al., 2004; Pucek, 2004; Perzanowski and Olech, 2007).

Studies examining European bison dispersal are scarce, and mostly focused on the Lowland bison line at Białowieża Forest (e.g. Pucek, 2004; Krasíńska and Krasíński, 2007). However habitat conditions are very different in the Carpathians, where seasonal bison movements from high elevations in late spring/summer to lower valleys in winter are observed (Krasíńska and Krasíński, 2007). Radio-telemetry observations of individual animals in the



Fig. 1. Study area with total and partial barriers for bison movements and ranges of existing bison herds (black polygons with numbers) in the Carpathian Mountains.

Bieszczady Mountains showed that the maximum distance of their seasonal movements was 18.5 km for a female bison and 22.9 km for a bison bull, but some bulls dispersed considerably further (>50 km; Krasieńska and Krasieński, 2007; Perzanowski et al., in press).

2.3. Habitat maps and landscape use by bison

We used herd range maps of the five free-ranging Carpathian bison herds (we excluded the semi free-ranging herd in Romania, for which at the time of our study herd range map was not yet available) and a European bison habitat suitability index (HSI) map from our previous work (Kuemmerle et al., 2010). Range maps

for Polish herds were based on radio-telemetry data and GPS-locations of bison presence. For the Slovak and Ukrainian herds, range maps were provided by local bison experts based on topographic maps (Kuemmerle et al., 2010). The HSI map was derived at a spatial resolution of 100 m using maximum entropy modeling (Phillips et al., 2006) and land cover variables (forest fragmentation, land cover, and distance to forest), measures of human disturbance (distance to roads and distance to settlements), and topographic variables (aspect and slope) as predictor variables (Kuemmerle et al., 2010).

As barriers for bison movements we included highways and main roads, major rivers (Stream Order Index, SOI > 3), lakes and settlements (Kuemmerle et al., 2011a; Fig. 1). We used the digital

road network from the ESRI Data and Maps Kit 2008 (level 0, level 1 and level 2), and geospatial data on rivers and lakes from Pan-European River and Catchment Database (version 2.1, <http://ccm.jrc.ec.europa.eu>). Settlements were derived from the CORINE 2000 land cover map (CLC2000, 100-m resolution, www.eea.europa.eu/data-and-maps) and digital topographic maps for Ukraine (1:200,000).

We generalized range of each herd, obtained from radio-telemetry data and field observations, with more than one area of bison occurrence to one polygon (habitat patch) using the Minimum Convex Polygons function (MCP) to receive more generalized information for the connectivity modeling.

We defined potential habitat patches, i.e. high-quality bison habitat that could host potential bison herds, as patches with HSI > 0.6 (equivalent to the median of the HSI distribution within existing bison herd ranges; Kuemmerle et al., 2010) that were larger than 200 km². This area threshold has been proposed by Pucek (2004) as the minimum necessary to sustain a population of 50–60 animals. Indeed, investigations in the Bieszczady Mountains in the Carpathians showed that the total range of the bison herd there varies between 200 and 400 km² depending on a year and season (Perzanowski et al., 2008).

2.4. Least-cost modeling

Least-cost analysis allows to incorporate effects of the matrix between habitat patches on an organism's dispersal (Knaapen et al., 1992; Verbeylen et al., 2003). Based on a cost surface (i.e. raster layer, which indicates the travel cost through each grid cell) and a source patch layer, a raster with the accumulative travel cost for each grid cell is created. This accumulative cost raster indicates the cost distance from every grid cell in the landscape to a source patch. By combining accumulative cost surfaces for two or more source patches, least-cost paths between them can be identified (Adriaensen et al., 2003). In our study, we derived the base cost surface CS0 defining the landscape facilitating/hindering effects on the bison movement process, by inverting and linearly scaling the original HSI values from 1 (no matrix resistance) to 11 (highest matrix resistance).

In the study region, potential barriers for bison movement are widespread (Fig. 1). Following Kuemmerle et al. (2010), we grouped them into two categories: total barriers (highways, i.e. level 0 roads; settlements; lakes; rivers with a stream order index >4) and partial barriers (major roads, i.e., level 1 and 2 roads; rivers with SOI = 4). To test if the delineation of least-cost paths was sensitive to different costs assigned to partial barriers, we constructed four additional cost surfaces with partial barrier costs of 100 (CS100), 200 (CS200), 500 (CS500) and 1000 (CS1000), respectively. In all those cost surfaces, the cost assigned to grid cells that included a total barrier was 100,000 (to ensure that constructed least-cost paths will not cross them unless no other possibility of movement exists) and cost of all non-barrier areas was as in our base cost raster CS0. Thus, our different cost surfaces vary in the values of grid cells that included a partial barrier (e.g., a value of 100 for such grid cells for CS100), but were identical for all other grid cells (background and total barriers).

We calculated all cost surfaces using 500 × 500 m² grid cells, because cost surface analyses were not computationally efficient at the original 100-m resolution of the HSI map. Furthermore, there were only negligible differences between these two resolutions when analyzing population viability (Kuemmerle et al., 2011a). On the basis of our cost surfaces, we delineated least-cost paths (i.e. potential connections) between home ranges of existing bison herds, as well as between potential bison habitat patches. The least-cost paths were constructed only between a given habitat patch and its nearest neighbors, assuming that paths between

more distant patches will pass through habitat patches being between them.

For each least-cost path we calculated an effective distance as a sum of its grid cells dimensions (vertical/horizontal or diagonal) multiplied by their respective cost values. Total effective distances of paths were thus comparable to Euclidean distances in areas with no matrix resistance, while paths crossing total barriers resulted in high effective distances. We tested the statistical significance of the observed differences among the effective distances resulting from the various cost surfaces using Wilcoxon rank sum tests, to exclude cost surfaces leading to statistically similar results from further analysis.

2.5. Connectivity assessment

To assess the relative importance of each least-cost path for the overall connectivity of the European bison habitat network in the Carpathians, we used effective distances to calculate inter-patch cost-dispersal probabilities p_{ij} (e.g. Urban and Keitt, 2001; Saura and Pascual-Hortal, 2007a) defined as:

$$p_{ij} = e^{-kd_{ij}}; \quad (1)$$

where k is a cost distance-decay coefficient and d_{ij} is an effective distance between patches i and j .

Because European bison dispersal in the Carpathians is not well examined, we decided to consider five k values (0.070, 0.046, 0.035, 0.028, 0.023) reflecting mean dispersal distances varying from 10 to 30 km (referring to dispersal distances obtained from radio-telemetry observations), using a 5 km interval, to understand how k values influence overall connectivity. We investigated the resulting habitat networks (with different cost dispersal probabilities) using graph techniques, by considering habitat patches as graph nodes and least-cost paths linking habitat patches as graph edges. Later, we compared the number of graph components (that is connected sub-graphs in terms of inter-patch cost-dispersal probabilities) and their distribution within each habitat network, indicating the most important nodes with respect to network connectedness.

To evaluate the importance of habitat patches for landscape connectivity and thus to identify optimal sites for future bison reintroductions, we used Conefor Sensinode 2.2 software (CS22; Saura and Torné, 2009; Saura and Pascual-Hortal, 2007b), which performs node removal operations to assess the importance of each individual node (Urban and Keitt, 2001). Node importance D is computed as the percentage of change in a connectivity index when a given node is removed from the graph (Saura and Torné, 2009).

As connectivity index to compute node importance we used probability of connectivity index (PC ; Saura and Pascual-Hortal, 2007a, 2007b), defined as:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^{\max}}{A_L^2}; \quad (2)$$

where a_i and a_j are the areas of nodes i and j , p_{ij}^{\max} is the maximum product cost-dispersal probability of all possible edges between nodes i and j (including single-step paths) and A_L is the total area of the study region. PC values affect the relative importance $D(PC)_k$ of each individual node k (Saura and Torné, 2009) as follows:

$$D(PC)_k = 100 \cdot \frac{PC - PC_k}{PC}; \quad (3)$$

where PC is the probability of connectivity index computed for all nodes, and PC_k is computed after node k is removed from the graph. Therefore the importance of each node is influenced by its size as

well as the inter-patch cost-dispersal probabilities of connections between nodes.

3. Results

3.1. Connectivity of currently occupied bison habitat patches

Five potential connections (i.e., least-cost paths) occurred between the ranges of the current bison herds (Fig. 2) for each of our cost surfaces. The least-cost paths and cost dispersal probabilities assigned to them were the same for all four cost surfaces that included barriers and differed essentially only for connection 3 in the CS0 cost surface. Only connections between ranges of bison herds located in the Polish Bieszczady Mountains and Slovak Bukovské Mountains had high cost dispersal probabilities, meaning that no total barrier separates them and dispersal between them is possible. On the other hand, cost dispersal probabilities of connections between ranges of the Eastern Bieszczady herd and the Ukrainian Skole herd were close to zero and thus practically inhibiting bison dispersal (Fig. 3A and B), even though these herds were relatively close to each other in terms of their Euclidean distances.

3.2. Distribution and connectivity of potential bison habitat patches

Based on the habitat suitability map, we identified 25 potential bison habitat patches with a mean area of 452 km². The largest had an area of 1586 km² and was located in the Ukrainian Carpathians. Potential bison habitat patches and home ranges of existing bison

herds were partially overlapped in the cross-border region of Poland, Ukraine and Slovakia.

We found 36 connections between patches for the cost surfaces CS100, CS200 and CS500, 35 connections for the cost surface CS1000, and 38 connections for the cost surface CS0 (Fig. 4). We defined corresponding connections for two given cost surfaces as connections, which link the same patches, but could differ in shape and length.

Probability distributions of effective distances of corresponding connections for each pair of habitat networks did not differ significantly ($\alpha = 0.05$) among the four cost surfaces that included barriers (Table 1). Although they differed significantly ($\alpha = 0.05$) from the probability distribution of effective distances of corresponding connections for cost surface without barriers (CS0; Table 1). We therefore analyzed in detail only the habitat networks derived from the cost surfaces CS100 and CS0 (Fig. 4).

Almost half of connections in the habitat network based on the CS100 cost surface were blocked by at least one total barrier, thus fully inhibiting dispersal along these connections. Effective distances of corresponding connections based on the CS0 cost surface were shorter or equal to those based on the CS100. Only a few connections had cost dispersal probabilities higher than 0.5 (from 5 to 7 connections for the CS100 map and from 5 to 8 for the CS0 map depending on k value), and all of them had short Euclidean distances. The differences in cost dispersal probabilities of connections between the networks based on CS100 and CS0 cost surfaces increased with decreasing k value, with the maximum difference (0.4) occurring for $k = 0.028$ corresponding to a dispersal distance of 30 km (Fig. 3C and D). Because connections with very low cost dispersal probabilities effectively inhibit bison dispersal, we modified the original habitat networks and removed all connections with cost dispersal probabilities < 0.1 (this value was selected based on the cost dispersal probabilities distribution) to delineate graph components. Depending on k value, there were from 7 to 13 connections with cost dispersal probabilities < 0.1 for CS100 model and from 8 to 18 for CS0 model.

The habitat networks based on CS100 and CS0 cost surfaces constituted disconnected graphs. The number of graph components depended on both the cost surface and the k value (lower k values resulted in fewer components). For habitat network based on CS100 cost surface, the number of graph components ranged from 13 (for $k = 0.028$) to 18 (for $k = 0.070$) and the largest component consisted of five nodes (patches). Lower numbers resulted for the network based on CS0 cost surface: from 9 (for $k = 0.028$) to 17 components (for $k = 0.070$) and the largest component consisted of 8 nodes (Fig. 4). In all cases that we analyzed, large graph components were located in the Eastern Carpathians. In the Western Carpathians most components consisted of single nodes (Fig. 4).

3.3. The importance of potential habitat patches for connectivity

The spatial pattern of potential habitat patches important for the connectivity was similar for both habitat networks (based on CS100 and CS0 cost surfaces) at all dispersal distances (Fig. 4). Habitat patches located in the Ukrainian Eastern Carpathians (in the Gorgany and Czornohora Mountains) were most important in terms of overall connectivity. These well-connected, large patches of suitable habitat (with a total area of more than 2000 km²), are located between patches occupied by existing herds, and thus could foster a continuous habitat network from the Polish Eastern Carpathians to the Romanian Eastern Carpathians. However, none of the contemporary Ukrainian bison herds were located inside the habitat patches that were important in terms of connectivity. Other important habitat patches for establishing connectivity among bison populations in the Carpathians appeared to be the patches located in the Maramures and Rodna Mountains (the

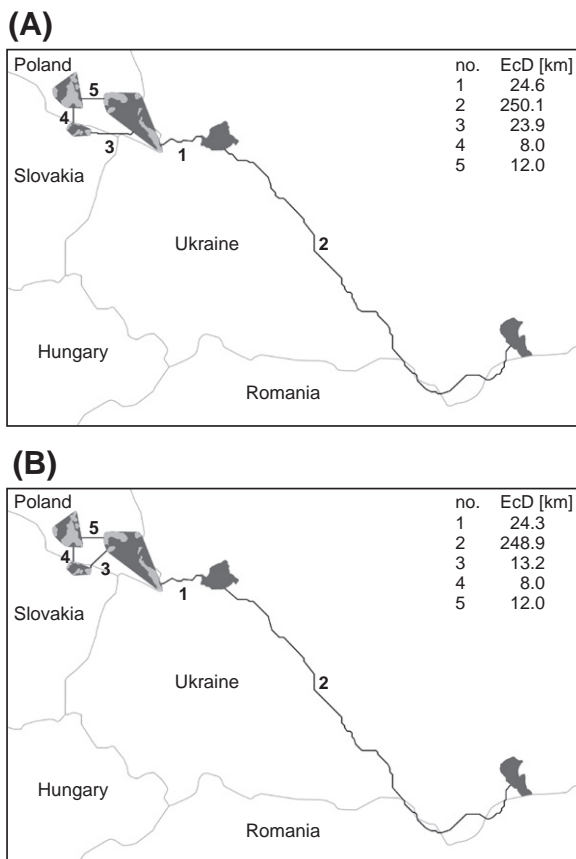


Fig. 2. Ranges of existing bison herds in the Carpathian Mountains (light gray – minimum convex polygons, dark gray – expert-based bison herd range delineation) and potential connections: (A) based on CS100, CS200, CS500 and CS1000, (B) based on CS0; and their Euclidean distances (EcD).

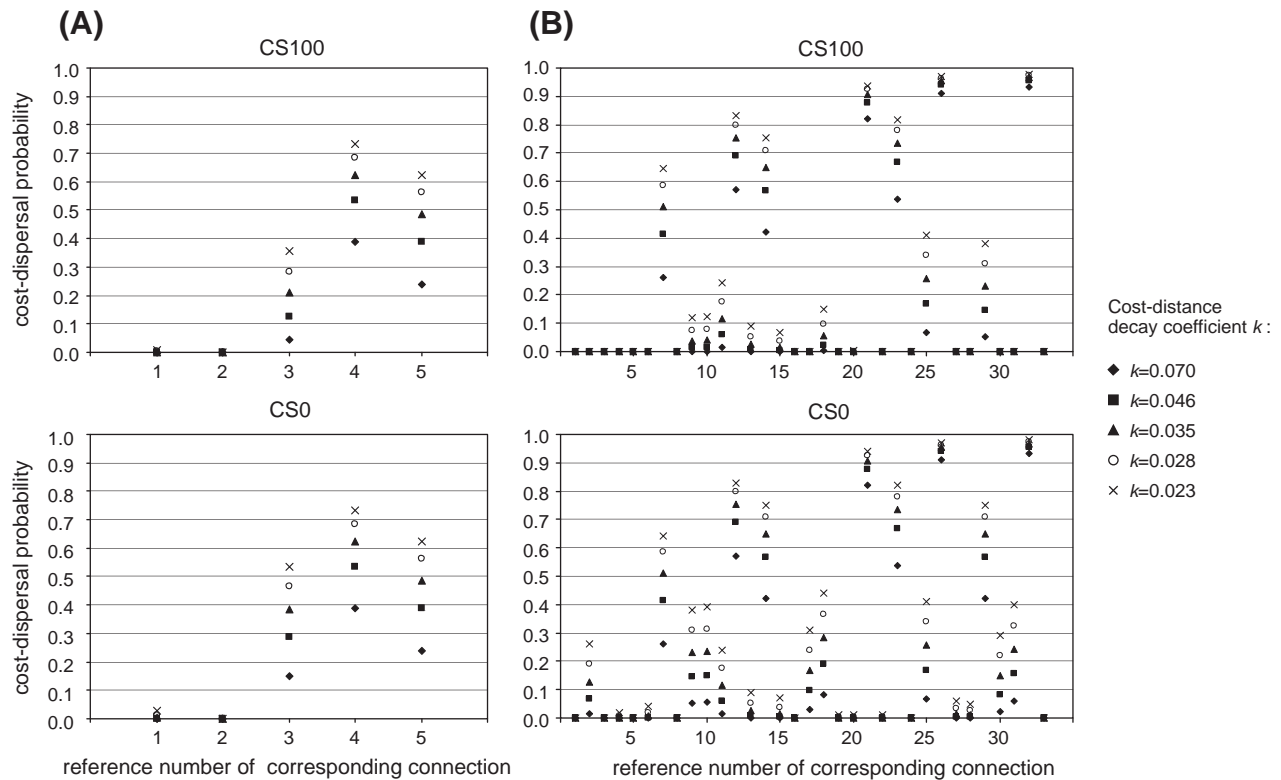


Fig. 3. Cost dispersal probabilities calculated for each corresponding connection delineated between ranges of existing bison herds (A); and between potential bison habitat patches (B).

Romanian Eastern Carpathians), in the Fagaras Mountains (the Romanian Southern Carpathians; all currently uninhabited), and the patches along Polish–Slovak border in the Bieszczady and Bukovske Mountains, inhabited by three bison herds.

4. Discussion

A main goal for the conservation of European bison is to create large and well-connected populations that are demographically safe in the long-term (Pucek, 2004; Krasińska and Krasiński, 2007). The Carpathian Mountains offer favorable conditions for bison with ample suitable habitat and relatively low human pressure, and are potentially among the best places to create such a large, connected population (Pucek, 2004; Kuemmerle et al., 2010, 2011a). However, current bison herds in the Carpathians only occupy a small portion of the available high-quality habitat (almost 11,300 km² if taking into account potential habitat patches delineated in this study) and are partly isolated from each other (Fig. 1). Therefore the determination of potential connections between habitat patches is important to ensure genetic exchange between populations and the effectiveness of reintroductions.

4.1. Modeling of habitat connectivity

Graph theory provides a compromise between estimations of functional connectivity, which require detailed data about species movements and simple estimations of structural connectivity, which often lack biological realism (e.g. Urban and Keitt, 2001; Calabrese and Fagan, 2004; Pascual-Hortal and Saura, 2006). However, graph theory alone does not provide the information necessary for conservation planning, and specifically how to prioritize conservation action, because it does not identify potential connections among habitat patches (e.g. Galpern et al., 2011). Here, we

overcame these limitations by integrating methods from graph theory with habitat suitability modeling and least-cost path analysis to identify potential connections between bison habitat patches, and to assess the importance of each connection.

We based least-cost paths on cost surfaces, which were obtained on inputs from a habitat suitability model and spatial data on barriers to movement. Habitat suitability maps depict the spatial distribution of species (Hirzel et al., 2006), but not necessarily the distribution of habitat suitable for a species' dispersal, which could be problematic for species where the factors governing suitable habitat to reproduce differ substantially from those characterizing dispersal habitat. In the case of European bison though, these factors are similar.

Besides habitat preferences, data on the dispersal abilities of a given species are needed for accurate connectivity analyses. However, for many rare species, such as European bison, reliable dispersal data are not available because dispersal is density dependent and current bison densities are below carrying capacity (Kuemmerle et al., 2011a). This is why we conducted a sensitivity analysis and tested the effect of different dispersal distances. Our results showed that different dispersal distances had substantial effects on our connectivity estimates, and this suggests that conservationists should take this range of results into consideration when prioritizing sites for actions.

4.2. Management recommendations

We here assessed the connectivity of the Carpathian bison population on two levels: (1) between ranges of existing bison herds and (2) between potential bison habitat patches. Among existing bison herd ranges we identified three groups of habitat patches as being well-connected in terms of probability of movement between them: ranges located close to the Polish–Slovak border

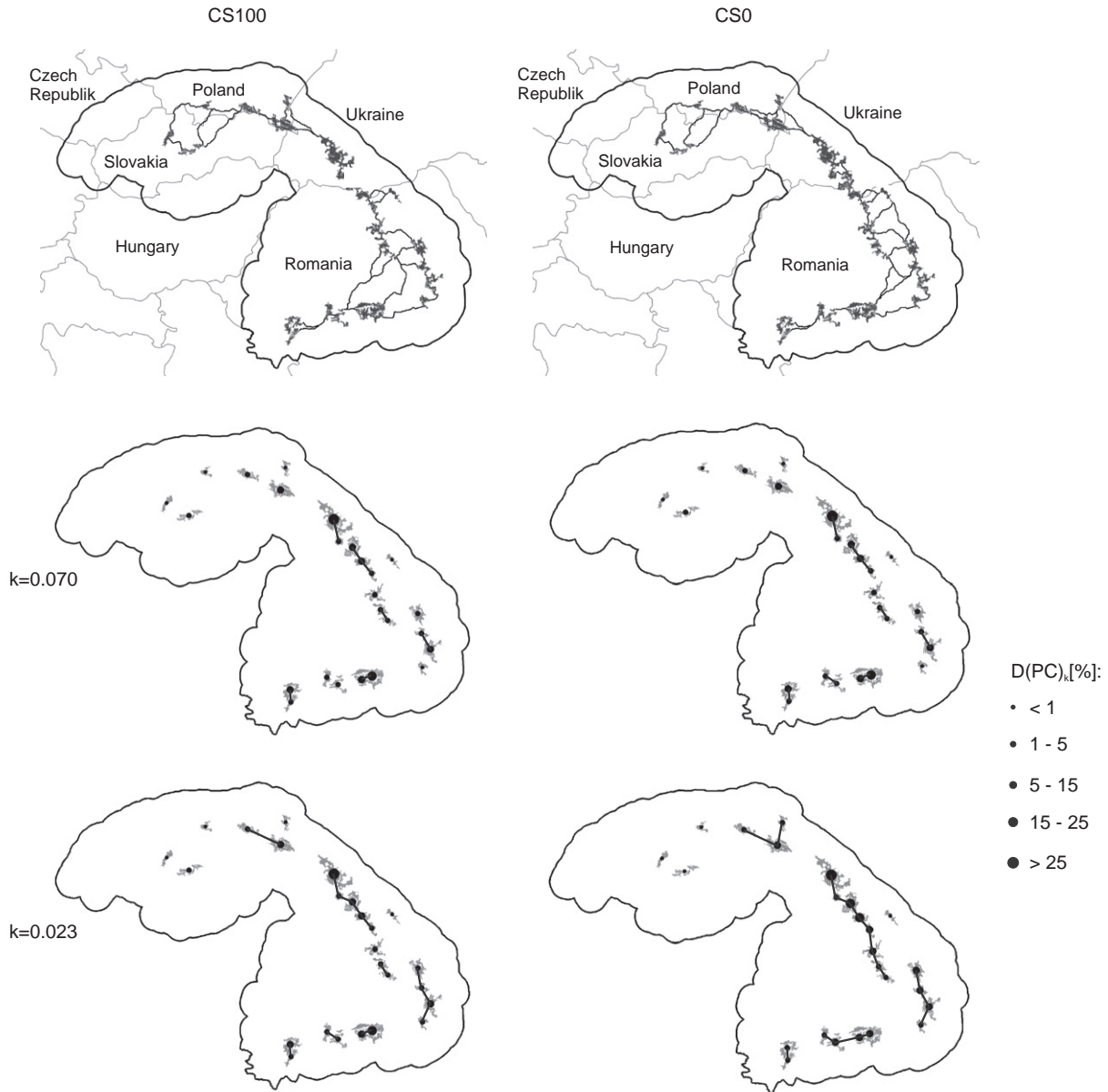


Fig. 4. Connections between potential bison habitat patches together with graph components and the importance of individual habitat patches for connectivity based on the probability of connectivity index (PC) for cost surfaces CS0 and CS100 and two representative k values.

Table 1

Resulting p -values of Wilcoxon rank sum tests with continuity correction conducted for the distributions of effective distances of corresponding connections for each pair of cost surfaces (*for $p < 0.05$ for which the null hypothesis about equality of the probability distributions of the effective distances of corresponding connections was rejected).

| | CS100 | CS200 | CS500 | CS1000 |
|--------|----------------------------------|----------------------------------|----------------------------------|-----------------------------------|
| CS200 | 0.944 (35 ^a) | – | – | – |
| CS500 | 0.778 (35 ^a) | 0.685 (36 ^a) | – | – |
| CS1000 | 0.664 (35 ^a) | 0.485 (35 ^a) | 0.651 (35 ^a) | – |
| CS0 | 0.018 (33 ^a)* | 0.008 (33 ^a)* | 0.002 (33 ^a)* | 0.0008 (33 ^a)* |

^a Number of corresponding connections for each pair of cost surfaces.

(two in the Bieszczady Mountains and one in the Bukovske Mountains), range of the Skole herd and range of the Bukovynska herd. Bison herd ranges in the Bieszczady and Bukovske Mountains were particularly likely to be functionally connected, which is confirmed by field observations (e.g., bison sightings), since bison movements

were noted between the Western Bieszczady herd (animals living in Komańcza and Cisna forest districts) and the Slovakian herd in the Poloniny National Park (Perzanowski et al., 2006). Bison have also migrated from Poland to the Slovakia in that part of the Carpathian range even before the introduction of the Slovak herd (Pčola, 1999). However for animals moving between Polish and Slovakian herds, especially during winter, high elevation is substantial obstacle. There are no records indicating bison presence at 1000 m a.s.l., and only few records at 800 m. A weak connection exists between the Eastern Bieszczady herd and the Ukrainian Skole herd, despite the close proximity of these herds. Although, bison from the Eastern Bieszczady herd frequently cross the border with Ukraine, mostly along the upper run of the San river (Perzanowski et al., 2004), they rarely reach the Skole herd. Low-quality habitat between these herds (a region characterized by high human population density and widespread farmland), as well as poaching, are likely explanations for this. The connection between ranges of two Ukrainian herds (located far from each other Skole and

Bukovynska herds) had very low cost-dispersal probabilities, indicating that those herds are functionally isolated. Again, this is confirmed by field observations: so far there have been no reports of any exchanges of individuals between these herds (Parnikoza et al., 2009).

Our analyses identified several connectivity hotspots within potential habitat patches network, where future reintroductions, would contribute substantially to linking existing herds (Fig. 4). The most important, currently uninhabited, potential habitat patches occurred in the Gorgany and Czornohora Mountains (the Ukrainian Eastern Carpathians), the Fogaras Mountains (the Romanian Southern Carpathians) and the Maramures and Rodna Mountains (the Romanian Eastern Carpathians). These results confirm an earlier, expert-based assessment highlighting the conservation value of areas located in the Ukrainian Carpathians (Parnikoza and Kaliuzhna, 2009).

In terms of improving the connectivity of European bison population in the Carpathians our work results in several recommendations. First, it would be important to enhance linkages among existing herds in the cross-border region of Poland, Ukraine and Slovakia to expand the area occupied by bison. This could include, for example, providing a permanent connection between ecological corridors established recently in Ukrainian Carpathians and Polish protected areas or/and introduction of infrastructure facilitating crossing of main road separating both subpopulations located in the Bieszczady Mountains (road no. 893 on the section Cisna – Lesko), and European route E50 separating two Ukrainian herds. Second, much of this transboundary region is covered by the East Carpathian Biosphere Reserve, but the effectiveness of this reserve differs among countries. Ensuring that the protected area serves as a refuge for bison in all three countries is crucial for establishing a large bison population.

Third, area currently occupied by bison should be enlarged. Several international agreements (e.g., the Carpathian Convention, Nature 2000 within the EU) as well as recent land use changes with farmland having been abandoned in the wake of the collapse of socialism, especially in Ukraine (Baumann et al., 2011), are creating a window of opportunity to extend bison ranges and improve the quality of dispersal corridors. Potential habitat patches in Ukraine and Romania, identified in this study as connectivity hotspots, should be thoroughly investigated as potential sites for reintroductions, especially since reintroductions of bison in Romania's north are already underway. Such assessments should address fine-scale habitat quality (e.g., forage availability) and potential conflicts with land use, e.g. forestry or settlements (considering recent ownership changes). Attention should also be paid to adequately legal protection of herds, and anti-poaching activities, since poaching is currently the main threat to bison in Ukraine (Parnikoza et al., 2009; Kuemmerle et al., 2011a). Financial support as well as educational activities to change people's attitude towards this species will be crucial to address these problems (Parnikoza et al., 2009). Considering the small number of bison and the already low genetic variability, future reintroductions will only be successful once these problems have been addressed.

In addition with other actions, e.g. periodical supplementation of wild herds with individuals of known pedigree (especially young bulls able to replace former reproducers; Olech and Perzanowski, 2004), these steps could lead to creation of the first large and well-connected bison population over an area of about 200–300 km.

5. Conclusions

Our analysis showed that a potentially well-connected, large network of habitat patches suitable for European bison exists in

the Carpathians (especially in the Eastern Carpathians) that could support a large bison population. We identified important connections between existing herds, and several candidate habitat patches for potential reintroductions where on-sites feasibility studies should be carried out (e.g., in the Gorgany and Czornohora Mountains in Ukraine, and in the Fogaras Mountains in Romania). Both enhancing dispersal corridors and establishing new herds would substantially increase the overall connectivity of the Carpathian bison population. Our connectivity analysis combined the advantages of graph theory with those of habitat suitability modeling and least-cost path analysis, and allowed us to assess the quality of the habitat network as a whole as well as the importance of individual habitat patches. Together they offer powerful tools for conservation planning, helping to indicate the most important elements within landscape mosaic for providing and maintaining connectivity.

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