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Connecting endangered brown bear subpopulations in the Cantabrian Range (north-western Spain)

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Abstract

The viability of many species depends on functional connectivity of their populations through dispersal across broad landscapes. This is particularly the case for the endangered brown bear in north-western Spain, with a total population of about 200 individuals in two subpopulations that are separated by a wide gap with low permeability. Our goal in this paper is to use state-of-the-art connectivity modeling approaches to provide detailed and quantitative guidance for conservation planning efforts aimed at improving landscape permeability for brown bears in Spain, with a particular focus on alleviating the barrier effect of transportation infrastructure. We predicted a regional connectivity network for brown bear by combining a multiscale habitat suitability model with factorial least-cost path density analysis. We found that the current composition and configuration of the landscape considerably constrain brown bear movements, creating a narrow bottleneck that limits flow of individuals between the two subpopulations. We identified key locations along the predicted corridors where efforts to increase road and railway permeability should be prioritized. The results provide a foundation for the development of spatially optimal management strategies to enhance connectivity within and between the subpopulations and to mitigate the impact of potential barriers to movement.

Introduction

Habitat connectivity plays a crucial role in enabling dispersal and gene flow within and among populations (e.g. Hanski, 1998; Flather & Bevers, 2002; Crooks & Sanjayan, 2006; Cushman, 2006; Cushman *et al*., 2013; Saura, Bodin & Fortin, 2014) and thus is considered a key consideration in evaluating regional viability of animal populations. Despite the clear importance of habitat connectivity for population persistence, the best ways to mitigate population isolation remains an object of intense debate (Crooks & Sanjayan, 2006; Awade, Boscolo & Metzger, 2012), and specific factors mediating connectivity are largely unknown for most species (With, Gardner & Turner, 1997; Bowne & Bowers, 2004; Cushman, 2006). One commonly proposed approach to conserve population connectivity involves the creation and protection of movement corridors (Haas, 1995; Beier & Noss, 1998; Crooks & Sanjayan, 2006; Cushman, McKelvey & Schwartz, 2009). However, the 'classic' concept of a corridor as a narrow strip of habitat that facilitates movements of organisms between habitat patches (Simberloff *et al*., 1992; Rosenberg, Noon & Meslow, 1997) is a point of controversy, given limited evidence of their effectiveness and issues related to scale and delineation that may lead to inappropriate characterization of connections and ecological flows between habitat patches (Cushman *et al*., 2009). Instead of experiencing landscapes as categorical mosaics (habitat/not habitat), it is more likely that organisms experience their surroundings as gradients of differential habitat quality (McGarigal & Cushman, 2005; Cushman, 2006; Cushman *et al*., 2010*a*), and adopting this perspective can profoundly change the conservation planning guidelines at the landscape scale.

Several approaches are available to evaluate connectivity across complex landscapes, including least-cost path modeling (Adriaensen *et al*., 2003; Cushman *et al*., 2009, 2010*a*; Cushman, Chase & Griffin, 2010*b*), circuit theory (McRae & Beier, 2007; McRae *et al*., 2008), other forms of network analysis (Urban *et al*., 2009; Saura *et al*., 2014), resistant kernel modeling (Compton *et al*., 2007; Cushman *et al*., 2010*b*), agent-based movement (Palmer, Coulon & Travis, 2011), gene flow simulations (Landguth & Cushman, 2010), statistical modeling (Cushman *et al*., 2006; Compton *et al*., 2007; Spear *et al*., 2010) or empirically derived understandings from detailed movement data (Sawyer *et al*., 2009; Cushman *et al*., 2011). Most past applications of these methods have focused on delineating movement corridors among small collections of habitat patches at relatively fine spatial and have not accurately accounted for the distribution and density of dispersing organisms across the landscape. To provide meaningful guidance to regional conservation efforts, it is often essential to expand the scope of analysis to shift from local, patch-level definition of habitat connectivity to a broader gradient perspective on landscape structure to assess performance of populations across complex landscapes (Berger, Cain & Berger, 2006).

One framework that is useful to accomplish this expansion in scope is to evaluate landscape connectivity among all the individuals of a population across the entire occupied range and across multiple landscape resistance scenarios (e.g. Cushman *et al*., 2006). Synoptic least-cost movement analysis on species-specific landscape resistance map is a helpful approach to comprehensively analyze the effects of landscape structure on animal movement. Resistance represents an integration of several behavioral and physiological factors such as aversion, energy expenditure or mortality risk when moving through a particular environment (Zeller, McGarigal & Whiteley, 2012), and cost is the cumulative resistance incurred in moving from the source to the destination locations (Adriaensen *et al*., 2003). Therefore, by integrating least-cost movement assessment in a spatially extensive scope of analysis (i.e. across all occupied locations within a population), the strength of corridors and locations of movement barriers can be rigorously evaluated (Cushman *et al*., 2009, 2013).

Many published studies analyzing least-cost corridor models have made several simplifying assumptions that may lead to unrealistic characterization of organism behavior. First, very often movement parameters, such as the resistance to movement presented by different landscape features, have been estimated through expert opinion due to lack of detailed information on animal movement (Zeller *et al*., 2012), which is not desirable (Seoane, Bustamante & Díaz-Delgado, 2005). To overcome this limitation, some authors proposed that resistance to movement could be estimated as an inverse function of a habitat suitability model (e.g. Ferreras, 2001; Chetkiewicz, St. Clair & Boyce, 2006; O'Brien *et al*., 2006; Beier, Majka & Spencer, 2008). Second, assuming that individuals will actually follow the single least-cost paths connecting locations is simplistic and unrealistic in many cases (Fahrig, 2007), and approaches to predict wider permeable routes through the habitat matrix have been proposed (Theobald, 2006; Beier *et al*., 2008). Thus, it is beneficial to consider either multiple low-cost paths, or to smooth output paths using a probability density function such as Gaussian kernel (Cushman *et al*., 2009, 2013; Pinto & Keitt, 2009; Landguth *et al*., 2012), which relax the assumption of optimum use of single least-cost paths.

In this study, we used a new methodology that combines multiscale habitat suitability modeling with factorial least-cost path density analysis based on empirical point occurrence data for the brown bear *Ursus arctos* L. in the Cantabrian Range (north-western Spain). We adopt a broadscale, synoptic framework that calculates movement corridors among all occupied locations within the range of the brown bear to provide an evaluation of the population-wide connectivity network in the study area. The brown bear is a long-lived omnivorous mammal with a solitary social structure and promiscuous mating system (Nores & Naves, 1993; Schwartz, Miller & Haroldson, 2003). Males have larger home ranges than females, and both males and females have intra- and intersexually overlapping home ranges (Dahle & Swenson, 2003). Dispersal in brown bear populations has been reported to be sex biased, with highly philopatric females establishing their breeding home ranges in or adjacent to their natal areas and males dispersing long distances from their mothers' home range (Blanchard & Knight, 1991; McLellan & Hovey, 2001; Palomero *et al*., 2007). Recent multiscale habitat modeling has revealed that the preferred habitat of brown bear in Spain consists of large landscapes with low human footprint and large extents of forest cover (Mateo-Sánchez, Cushman & Saura, 2013).

The brown bear population in the Cantabrian Range (north-west Spain) has suffered a dramatic decline in the last several centuries as a result of human persecution and progressive loss and fragmentation of its habitat (Naves *et al*., 2003). Currently, the Cantabrian brown bear occurs in two small and endangered subpopulations (Palomero *et al*., 2007) with limited gene flow between them, with potentially deleterious effects on viability (Pérez *et al*., 2009). The isolation of these two subpopulations is considered to be a result of the distribution of suitable habitat being separated by intensively modified intermediate landscapes and transportation infrastructure, which has created potential barriers to dispersal between the two subpopulations (Nores & Naves, 1993; Wiegand *et al*., 1998). Brown bears have been protected in Spain for over three decades. Much of the known range of the species is included within protected areas such as European Nature 2000 Network, natural parks and recovery plans of each of the regional institutions involved in its management. Although recent studies revealed that both subpopulations are growing, loss of genetic diversity due to small population size and demographic stochasticity has hampered the recovery of the species and continues to threaten its viability (García-Garitagoitia, Rey & Doadrio, 2007). Hence, the importance of maintaining large blocks of protected core areas within a connected network is the cornerstone of European, national and regional brown bear conservation initiatives, and the definition and protection of movement corridors, together with the incorporation of connectivity in landscape planning, have become top priority and a critical issue for conservation efforts (Palomero *et al*., 2007). Furthermore, because large carnivores such as brown bear have large habitat area requirements and occur at low densities, they are often among the first species to be harmed by loss of connectivity. For this reason, they are also considered as appropriate focal species for connectivity design (Servheen, Waller & Sandstrom, 2001; Singleton, Gaines & Lehmkuhl, 2002) and thus can serve as an umbrella for other native species and processes (Beier *et al*., 2008).

In this study, we aimed to apply the aforementioned new methodology to (1) designate movement corridors that are most critical for the maintenance of landscape connectivity for brown bear in north-western Spain; (2) identify potential barriers to movement (transportation infrastructure) that should be prioritized for mitigation; (3) evaluate the results of our analysis to provide practical guidance and recommendations for management and conservation of brown bear habitat and subpopulations in Spain.

Materials and methods

Study area

The study was carried out in north-western Spain (Fig. 1), in the provinces of Lugo, León, Asturias, Cantabria and Palencia. The region is 49 472 km^2 in extent and contains the whole known range of the brown bear *U. arctos* native populations in Spain, and the belt area between the two subpopulations. Both subpopulations occupy a similar area of about 2500 km^2 each, and are separated by about 30 km of unoccupied land (Palomero *et al.*, 2007; Fig. 1). The study region has a complex topography with altitudes ranging from sea level to 2647 m (mean elevation of 800 m). Climate is a humid Atlantic climate with mild temperatures and short summers. According to the Third Spanish National Forest Inventory [Ministerio de Medio Ambiente (MMA), 1997–2007], forests occupy 39%, shrubland 23%, natural grasslands 4% and agricultural lands 33% of the landscape. Portions of the area have low human densities, whereas others have experienced extensive urban and agricultural development connected by a network of local and national roads, highways and railways. This history of development together with the dominant rural economic activity in the region has led to extensive modification of the region's native forest landscapes that, together with the network of transportation infrastructure, potentially hinder brown bear movements.

Landscape resistance surface

Most current methods to predict population connectivity and map areas that are important in facilitating animal movements begin with landscape resistance maps (Spear *et al.*, 2010; Fig. 2). Landscape resistance maps depict the difficulty or resistance for movement through any location in the landscape (defined as a pixel or cell in a raster map) as a function of landscape features of that cell. In its most basic sense, landscape resistance reflects the local movement cost incurred by an animal. More formally, the resistance reflects

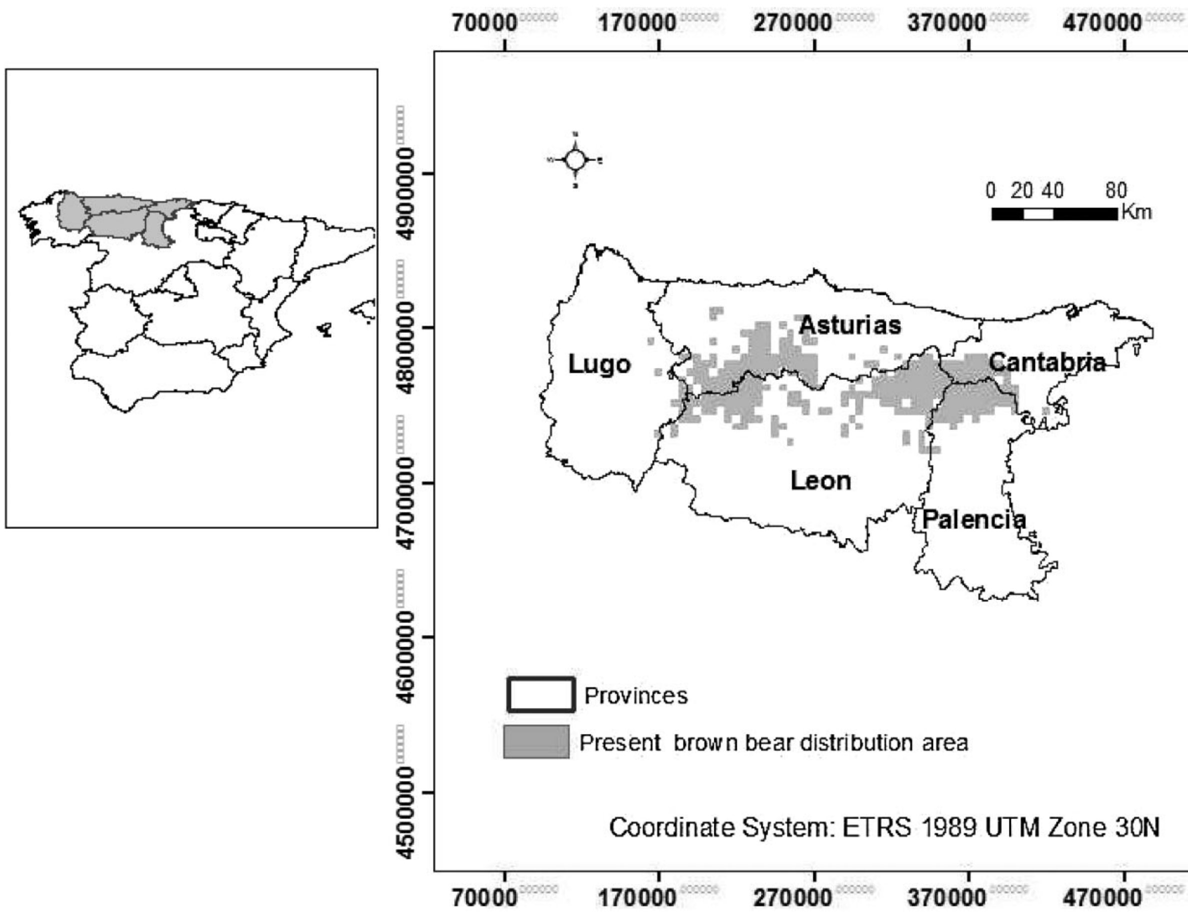

Figure 1 Study area.

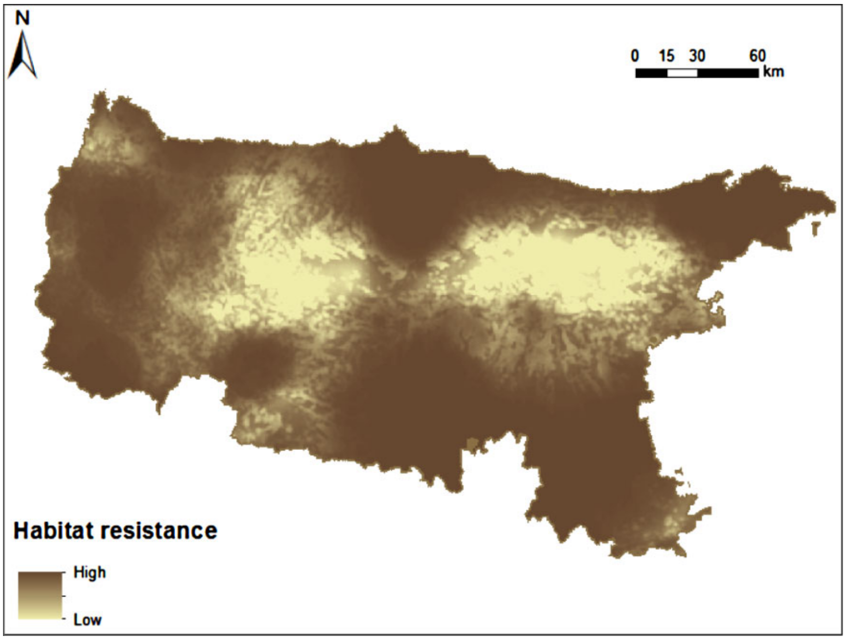

Figure 2 Resistance surface calculated as a transformation of a multiscale habitat suitability model for the brown bear in the study area. Lowest resistance values represent the highest permeability for the movement of species.

the stepwise cost of moving through each cell for least-cost analyses (Singleton *et al*., 2002; Adriaensen *et al*., 2003).

A plausible way to empirically estimate relationships between connectivity and environmental conditions is to assume that habitat quality has a direct relationship with population connectivity (Beier *et al*., 2008). We created a resistance surface in which resistance to movement was inversely related to habitat suitability. We used a multiscale habitat suitability model developed by Mateo-Sánchez *et al*. (2013), who used the maximum entropy algorithm (Maxent; Phillips, Anderson & Schapire, 2006) to predict brown bear occurrence as a function of multiple environmental variables at multiple scales. The data on location of bears used to build the model were a set of 8648 bear locations collected between 2000 and 2011. The habitat variables included in the model were related to landscape composition and configuration as well as human disturbance. This model provided a value representing the relative suitability (*HS*) for species occurrence (Phillips *et al*., 2006) for each pixel throughout the study area, ranging from 0 to 0.79. We derived landscape resistance as an inverse function of habitat suitability (equation 1):

$$\left(\frac{R'}{R'min}\right)^2 \quad (1)$$

where R' is $(1 - HS)$ in a given pixel and $R'min$ is the minimum value of $(1 - HS)$ across all pixels in the study area.

This transformation resulted in resistance values ranging from 1 to 22; every pixel represented the unit cost of crossing each location, with the lowest resistance values given to the highest quality habitat (Fig. 2).

Corridor network among species presence locations

We used a new individual-based approach to predict landscape connectivity among all individuals in a population (Landguth *et al*., 2012). We represented network connectivity as a graph with nodes and edges/links (Diestel, 2005; Landguth *et al*., 2012). Species location (presence) pixels were considered to be the nodes, whereas the links were represented by the potential movements between each pairwise combination of nodes. Point locations were based on the occurrence locality records used for the suitability model described in previous section. The initial set of point locations used for the habitat model was resampled to a 5-km grid to summarize locations and to avoid spatial overlap. This resolution has been used in previous brown bear studies (e.g. Naves *et al*., 2003) and is slightly smaller than the reported seasonal home ranges for this population (Clevenger & Purroy, 1991; Naves *et al*., 2003). After resampling we obtained a total of 308 pixel bear locations that defined the starting and ending points of links in a full population-wide connectivity network. Additionally, we calculated the connectivity network among the pixel locations within the western and eastern subpopulations separately (152 of the 308 total locations corresponded to the east subpopulation, whereas the other 156 locations were in the west).

We used the UNICOR software (Landguth *et al*., 2012) to find the shortest functional movement paths between all pairs of nodes. UNICOR (UNIversal CORRidor and network simulation model) uses a modified Dijkstra's algorithm (Dijkstra, 1959) to solve the single-source shortest path problem between every specified species location on a landscape to every other specified species location. The summation of the full network of movement paths produces a least-cost path density map representing the connectivity network for the brown bear in the study area. Considering the effects and contribution of multiple low-cost paths (Cushman *et al.*, 2009, 2013; Pinto & Keitt, 2009) avoids the simplistic and unrealistic assumption that all individuals follow a single movement path of least resistance (McRae, 2006; Theobald, 2006; Beier *et al.*, 2008). Accordingly, we also computed the focal density of least-cost paths with a moving window of 1-km radius to produce buffered cumulative density of optimal paths to identify movement corridors within and between both subpopulations. The value of these cumulative paths reflects their putative importance as corridors within the connectivity network. We intersected these putative corridors with transportation route maps in the study area (major highways, national roads and railways) to identify potential impediments to brown bear dispersal and prioritize those where mitigation measures could be implemented to reduce the barrier effect.

Results

Connectivity networks

The cumulative density of least-cost paths across the full population extent showed the potential global connections within and between the two subpopulations (Fig. 3). Connections between both subpopulations followed one principal route complemented by a secondary route that converged with the first at the western border of the area currently occupied by the eastern subpopulation. We found that the maximum number of least-cost paths traversing this route was 19 416, about 40% of the theoretical maximum number of paths (47 432) that could be achieved if all the pairwise connections among brown bear locations crossed through a single pixel.

The movement pattern was different for movements within each subpopulation. Specifically, within subpopulations less concentration of least-cost paths was apparent, producing more extensive and dendritic network patterns (Fig. 3b,c) compared with the case where movements among different subpopulations were considered (Fig. 3a). No unique main paths were identified for the movements within subpopulations; higher density of areas with optimal paths was shown (Fig. 3b,c). This more spatially distributed pattern of movement paths within subpopulations suggests less constraints to brown bear movements within the currently occupied areas, in contrast to the bottlenecks for dispersal indicated by few and narrow concentrated routes predicted between the two subpopulations. The eastern subpopulation showed a higher maximum number of least-cost paths per pixel (3021), corresponding to about 26% of the theoretical maximum (11 552) for the locations within this subpopulation, while this number was lower (2073) and corresponded only to about 17% of the theoretical maximum (12 168) for the west subpopulation.

Transportation infrastructure as potential barriers to brown bear movement

Our result identified numerous potential barriers associated with transportation infrastructure along the major predicted movement routes. We identified 25 potentially significant barriers (Fig. 4). Nine of these potential barriers intersected the predicted principal corridors in the provinces of León and Asturias. Ten barriers were associated with national roads, eight with railways and seven with highways. A young male brown bear was killed by a car in 2008 at the location of one of the predicted potential movement barriers (number 13 in Fig. 4) (Fundación Oso Pardo, 2010).

Discussion

Landscape connectivity is a major concern for the conservation of Cantabrian brown bears in north-western Spain, whose long-term viability may depend on establishing functional connections among subpopulations that are currently largely isolated with limited gene flow among them (Pérez *et al.*, 2009). Therefore, it is critical to provide rigorous, empirically based and spatially explicit predictions of potential corridors to guide habitat conservation and restoration to increase permeability of the landscape matrix and mitigate linear barriers to dispersal such as highways. Our findings support the perspective that a combination of methods developed for connectivity and conservation planning can provide large improvements in management recommendations. Specifically, by combining a multiscale habitat suitability model with factorial least-cost path density analysis and the quantification of the potential conflicts between transportation infrastructure and putative corridors, we provide a comprehensive and practical assessment of factors limiting brown bear connectivity in Spain.

Our results show relatively limited connectivity between the two subpopulations, with movements funneled through one major least-cost route. This indicates that landscape resistance is highly constraining dispersal between the two subpopulations, and that connectivity along this single major corridor could be threatened by additional development given the concentration into very few predicted routes. In addition, our results suggest a higher dependence on fewer suitable movement pathways for brown bears within the eastern subpopulation, compared with a higher number of alternative corridors able to facilitate brown bear movements within the western subpopulation. This suggests that the western subpopulation exists in a landscape with a comparatively more uniform high-quality habitat and fewer potential barriers, whereas the more concentrated corridor network in the eastern subpopulation suggests higher habitat fragmentation, which may limit the ability of brown bear to disperse throughout the eastern subpopulation. Limited dispersal ability within the eastern subpopulation may also reduce the probability of dispersal from the eastern to the western subpopulation as movements within the eastern subpopulation already may incur in a comparatively

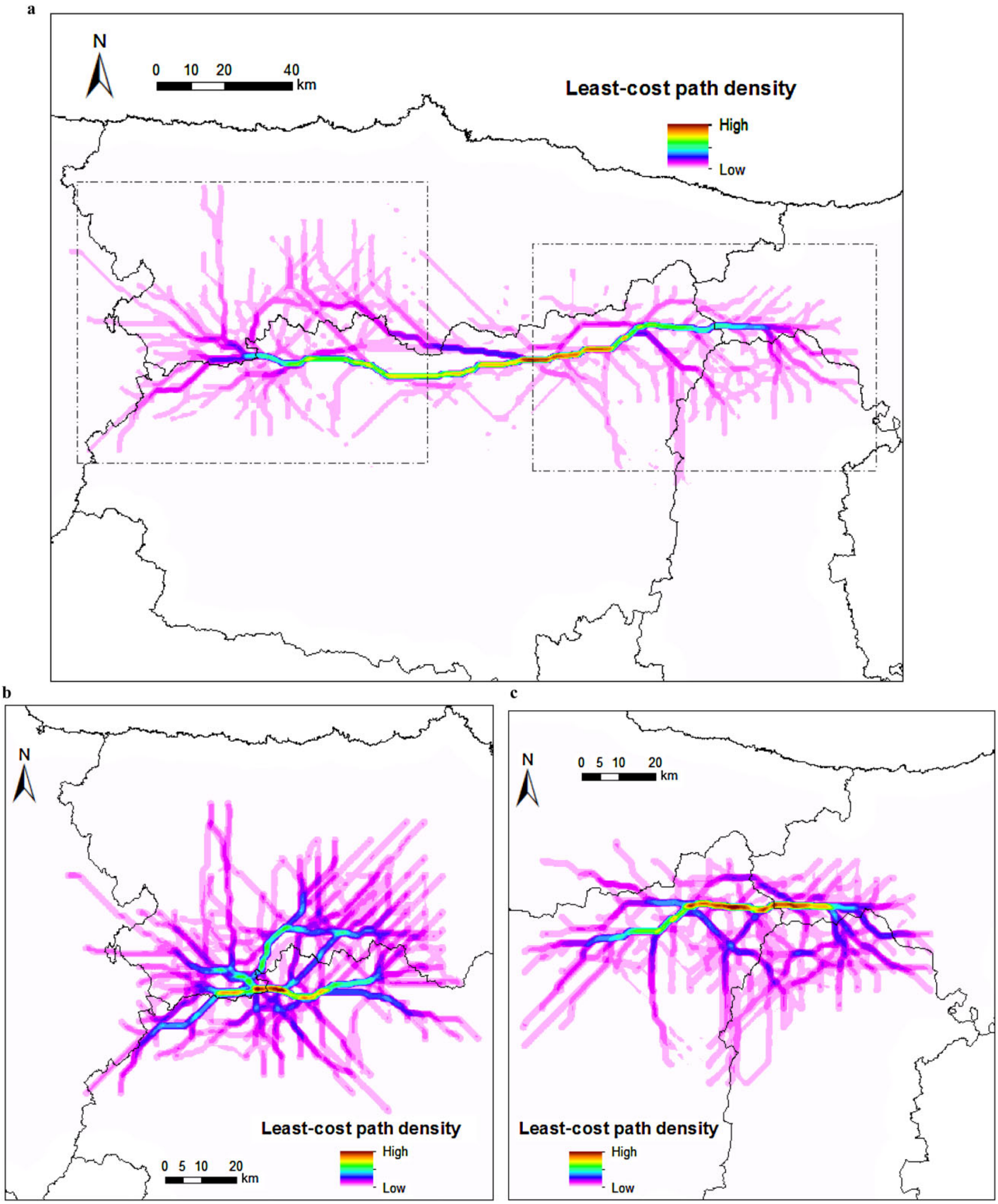

Figure 3 Buffered cumulative density of least-cost paths from every paired combination of source and destination nodes (cells with empirical brown bear occurrence data) (a) across the whole study area. (b) Across the west subpopulation. (c) Across the east subpopulation.

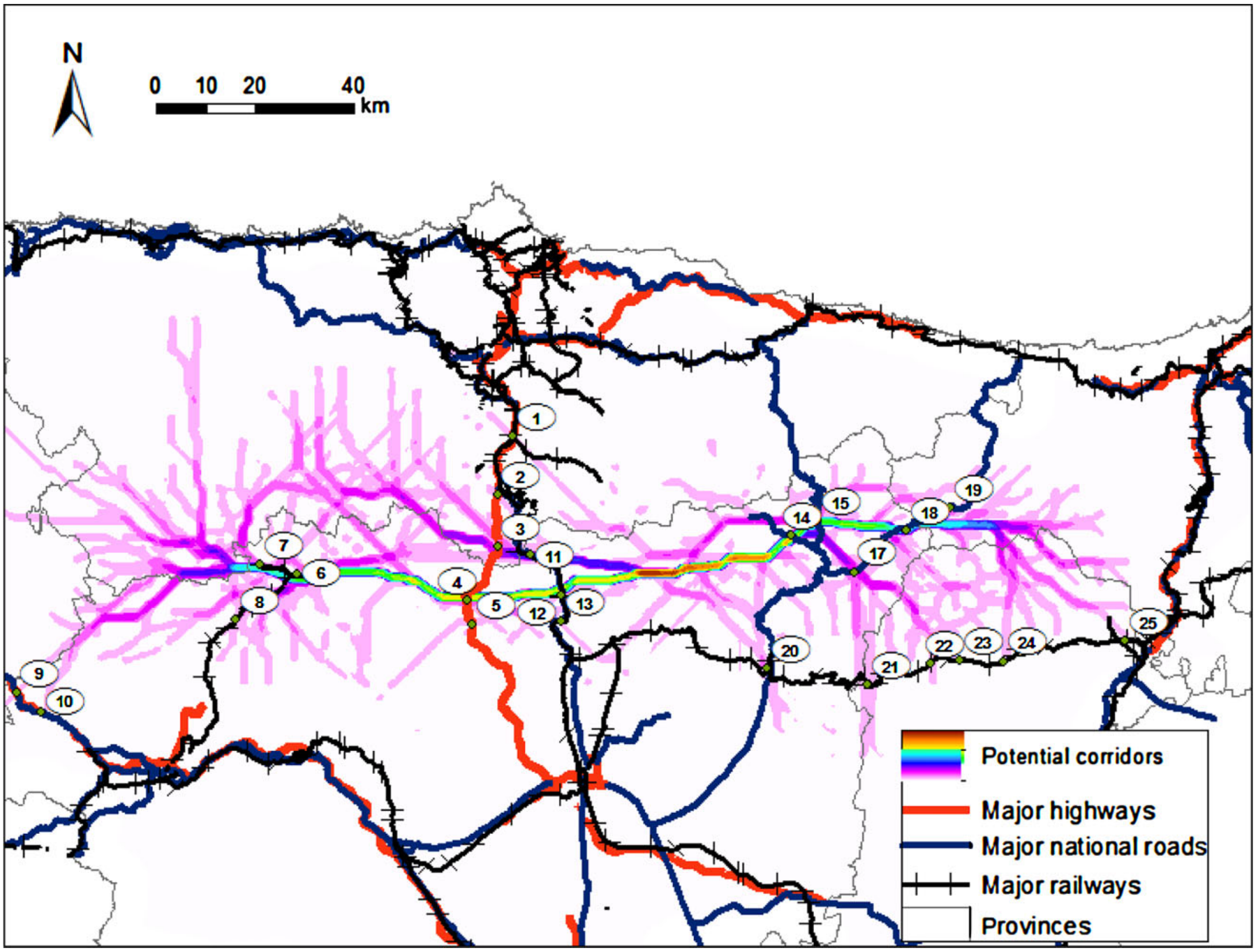

Figure 4 Intersection of predicted corridors for brown bears with major highways, national roads and railways. The numbered locations represent areas that may act as barriers to movement.

higher dispersal cost and the associated energy expenditure and mortality risks, reducing likelihood of long-distance dispersal from the eastern to the western subpopulation. This probability of dispersal bias from the west to the east is further reinforced by the higher population size in the western subpopulation. The larger number of male individuals capable of long dispersal distance movements in the western subpopulation may result in a highly directional dispersal potential in the study area for this species, as suggested by the insights from recent habitat network connectivity models (Saura *et al*., 2014).

Our corridor network analysis suggested relatively well-connected movement networks within the two subpopulations, whereas less frequent, long-distance movements between subpopulations are predicted to be concentrated into narrow corridors among them. This different pattern is critical, given that these long-distance movements between the two subpopulations are likely essential to maintain genetic diversity and to promote the expansion of the species' range. These results suggest that restoration efforts should focus on improving habitat quality and permeability in strategic locations between the two subpopulations to create a more permeable landscape matrix. Our analysis enables prioritization of locations for habitat protection, restoration and barrier mitigation that may have the largest effect in promoting reestablishment of connectivity between the two subpopulations. Management should increase the extent and quality of brown bear habitat by increasing the amount of undisturbed forest, increasing average canopy closure and maintaining a mosaic of interspersed shrubland patches, and minimizing factors found to be strongly avoided at broad scales, such as expanded human settlements in brown bear habitat (Clevenger, Purroy & Campos, 1997; Naves *et al*., 2003; Mateo-Sánchez *et al*., 2013).

Our connectivity modeling approach allows evaluation of the synoptic pattern of potential connectivity across the full extent of the Cantabrian brown bear population. This enables identification of particular locations where habitat conservation or barrier mitigation measures would have the largest net effect in promoting the coalescence of the two populations and establishment of functional connectivity between them. We found that the identified corridors traversed a number of potential movement barriers (Fig. 4; Supporting Information Table S1), highlighting the importance of mitigating movement obstruction caused by transportation infrastructure as a primary consideration for restoring connectivity of the Cantabrian brown bear. To highlight the potential barriers that represent priority locations for measures to increase highway and road permeability, such as overpass and underpass construction, it may be valuable to consider jointly the importance of the barrier in terms of landscape resistance (density of least-cost paths traversing through a particular location) and some key features determining the barrier effect of the infrastructure, such as traffic intensity. Several studies (Alexander, Waters & Paquet, 2005; Clevenger & Wierzchowski, 2006; Riley *et al*., 2006; Koreň *et al*., 2011; Grilo *et al*., 2012) show that traffic intensity and other physical restrictions for animals (e.g. perimeter fences) strongly increase barrier effects. Thus, highways (with at least four lanes and a median strip) will likely present much larger resistance to brown bear movements compared with secondary roads in the study area. Potential barriers 1, 3 and 4 are likely particularly important obstacles to movement between both subpopulations in the main predicted corridor, whereas 2 and 9 are also important movement obstructions in the secondary corridor connecting the two subpopulations (Fig. 4; Supporting Information Table S1). Other potential barriers (e.g. 13 and 14) may represent obstructions for the potential range expansion of the species, rather than for episodic movement of dispersing bears among subpopulations.

The study area is within a larger transnational initiative covering protected areas from the Cantabrian Range to the Western Alps (south-west Europe). This transnational area has been the focus of previous studies of connectivity and road impact for forest mammals to provide conservation guidelines in landscape planning at broad scales (Worboys, Francis & Lockwood, 2010; Gurrutxaga, Rubio & Saura, 2011; Jongman *et al*., 2011). In this context, our study improves knowledge of connectivity for this larger conservation initiative by providing a finer scale analysis with a higher level of spatial and ecological detail for a particular species of high conservation concern. It should be noted that two key intersections between corridors (least-cost paths among protected areas) and highways found by Gurrutxaga *et al*. (2011), in a case for forest mammal species with different dispersal abilities as the generic focal species group, coarsely match with the ones identified in this study. However, our study considerably expanded the analysis of connectivity and more accurately identified a set of about 20 priority locations for reducing the effect of transportation infrastructure on brown bear population fragmentation. Given the importance of brown bears as an indicator and umbrella species, and the key role of the Cantabrian Range as a connecting element at a wider European scale, the more detailed corridors and mitigation priorities here reported should be relevant to more broadly promote the functionality of such transnational protected area networks.

Our approach is unique in that we addressed landscape connectivity among all occupied locations in a population on a resistance map derived from an empirically developed habitat suitability map. Ideally, resistance should be assessed through analyses of movement or gene flow (e.g. Zeller *et al*., 2012; Cushman *et al*., 2013), and habitat use may sometimes be an imperfect surrogate for resistance (e.g. Wasserman *et al*., 2010). Recent advances in landscape genetics enable direct optimization of resistance surfaces based on the relationships between genetic differentiation and landscape cost distance (e.g. Cushman *et al*., 2006; Shirk *et al*., 2010; Wasserman *et al*., 2010), whereas analyses of step or path selection functions enable direct estimation of resistance from global positioning system movement data (e.g. Cushman & Lewis, 2010). In our study area, there is insufficient movement data to use path or step selection functions to predict landscape resistance (e.g. Cushman *et al*., 2010*b*; Cushman *et al*., 2011). However, there has been a large effort to collect molecular genetic data from a large number of individuals across the study area (Pérez *et al*., 2009). Future work should use these genetic data to develop an empirically optimized resistance surface. However, resistance optimization based on landscape genetics does not account for potential recent landscape changes that the habitat model may more sensitively reflect. Thus, the use of habitat models as proxies for landscape resistance will likely remain an important approach for estimating population connectivity across broad landscapes. At the same time, development of a resistance surface supported by landscape genetics and further comparison with the results shown in this study would provide important complementary insights on the connectivity network and patterns of individual movement and gene flow for this species. Additionally, further analysis at the level of individual patches or ownerships could help to identify the most effective locations for new or restored habitat patches acting as connecting elements that complement and reinforce the current ecological network of the species elements (e.g. Saura & Rubio, 2010). Finally, recent generalizations of habitat network connectivity models (Saura *et al*., 2014) could provide additional insights by more explicitly accounting for (1) the effect on connectivity of increasing population sizes; (2) the directionality in movement likelihood resulting from differences in subpopulation sizes; (3) the potential long-term role of suitable habitats in the intermediate landscapes to support reproduction and species range expansion across generations, in addition to the role of just reducing the effective distances or resistances among occupied areas as currently assessed through standard connectivity models based in least-cost paths or circuit theory.

Conclusions

Habitat connectivity is a crucial factor affecting brown bear viability in its fragmented habitat in north-west Spain. The analysis presented here combined the use of several different methods to quantify landscape connectivity for brown bears and allowed us to identify key locations where efforts to increase the permeability of transport infrastructure could provide the largest contribution to enhance population connectivity. The current composition and configuration of the landscape constrain brown bear movements in the study area, leading to bottlenecks in the movement network among the two subpopulations. Our results provide a practical guide to prioritize locations for restoration or mitigation and to develop spatially optimal management strategies to enhance connectivity within and between the subpopulations. We hope that this work will be useful to identify precise locations for habitat conservation, restoration or barrier mitigation actions can be taken to improve habitat connectivity for brown bear in northern Spain.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Description of major potential barriers to brown bear movement along predicted corridors. The information on barriers includes their ID (corresponding to the numbered location of the barrier in Fig. 4), type of road that conflicts with corridors (HW, highway; NR, national road; RW, railway) and their names in the national road classification system (only for roads and highways), the type of corridor it intersects [main (1) or secondary (2) corridor routes], the density of least-cost paths intersecting each location, and the municipality or municipalities and province (AS, Asturias; CA, Cantabria LE, León, LU, Lugo; PA, Palencia).