Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data

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Abstract. Resistance models provide a key foundation for landscape connectivity analyses and are widely used to delineate wildlife corridors. Currently, there is no general consensus regarding the most effective empirical methods to parameterize resistance models, but habitat data (species’ presence data and related habitat suitability models) and genetic data are the most widely used and advocated approaches. However, the practical consequences of applying one or the other approach have not been well studied. To address this knowledge gap, we performed a comparative study on the implications of using habitat suitability versus genetic data for determining effective landscape distances (a proxy inversely related to isolation among patches) based on least-cost and circuit-theoretic approaches, and for identifying potential movement corridors. For our comparison, we used data for the Cantabrian brown bear in Spain, an endangered population for which connectivity has been identified as a major conservation concern. Our results show that for brown bears, habitat models tend to overestimate resistance to movement through non-optimal areas, whereas genetic data yield higher estimates of effective distances within habitat areas. Therefore, our results suggest that (1) dispersal might be generally less constrained by landscape conditions than habitat utilization in home ranges, and that (2) dispersing animals might be more flexible in their movement behavior than residents are in their habitat resource utilization behavior, with records for residents dominating species occurrence data and subsequent habitat models. The assessed approaches provided dissimilar connectivity models with notable differences in patterns of predicted corridors across the study area, mainly due to differences in predicted connections between subpopulations. Our results highlight that the functional differences in habitat vs. genetic data, as well as the assumptions and potential limitations of different analytical approaches that use these data, need to be considered more carefully in connectivity modeling and subsequent corridor delineation.

Key words: circuit theory; connectivity; dispersal; habitat suitability; landscape genetics; least-cost paths; resistance.

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INTRODUCTION

The establishment and conservation of corridors has been widely suggested as a key means to facilitate movement between wildlife habitat patches and to preserve and enhance landscape and population connectivity (Simberloff et al. 1992). The classical concept of corridors as narrow strips of habitat that facilitate movements of organisms between habitat patches (Rosenberg et al. 1997) has been recently broadened. Rather than experiencing landscapes as categorical mosaics (habitat vs. non-habitat), it is more likely that organisms experience the landscape matrix as a gradient of differential permeability (Cushman et al. 2010). This generalization mainstreams the concept of resistance to movement and suggests reconceptualization of connectivity problems to address how species movement is affected by landscape features across a range of spatial scales. Formally, landscape resistance represents an integration of multiple behavioral and physiological factors such as aversion, energy expenditure, or mortality risk when moving through a particular environment (Zeller et al. 2012). In a practical sense, landscape resistance is a spatial layer that reflects step-wise costs of moving through each cell in a raster map for least cost path analyses (Singleton et al. 2002) or the relative probability of moving across the cell for circuit theory-based analyses (McRae et al. 2008).

Since modeling landscape resistance is increasingly used as the basis to predict population connectivity and therefore is a crucial step in identifying movement corridors, resistance modeling has received much attention from corridor designers (Beier et al. 2008, Spear et al. 2010, Zeller et al. 2012). However, despite the existence of multiple and varied approaches, there is no consensus on how to best parameterize resistance surfaces (Zeller et al. 2012). Parameterizing resistances involves identifying and combining the important resistant factors (e.g., land cover, transport infrastructure, etc.) that affect the species’ movement in an optimal way to realistically estimate the cost of movement through any location in the landscape. Resistance values have usually been determined by assigning resistance scored on an arbitrary scale (Beier et al. 2008, Pereira et al. 2011) on the basis of expert opinion itself or in combination with literature review (Larkin et al. 2004, Kautz et al. 2006). However, such approaches have frequently been shown to perform poorly (Beier et al. 2008, Shirk et al. 2010). To address these limitations, some authors have suggested that habitat suitability models predicting species occurrence on the basis of empirical data may provide a better estimation of resistance (Ferreras 2001, Chetkiewicz et al. 2006, O’Brien et al. 2006, Beier et al. 2008). This approach essentially implies that animal movements are influenced by the same environmental factors as habitat selection (e.g., Chetkiewicz et al. 2006, Wasserman et al. 2010, Zeller et al. 2012). More recently, the field of landscape genetics has shown great potential to provide more rigorous methods to parameterize resistance models by inferring the influences of landscape on realized population connectivity (Spear et al. 2005, Cushman et al. 2006, Storfer et al. 2007, Balkenhol et al. 2009). Individual-based analysis comparing pairwise genetic distances to pairwise effective distances under multiple landscape resistance hypothesis are a powerful tool for supporting conservation efforts (Cushman et al. 2006, 2013a, Epps et al. 2007, Segelbacher et al. 2010).

Understanding how different approaches can affect the analyses that aim to identify conservation corridors is a critical issue given the large conservation implications and investments that are potentially derived from such analyses. In this paper we addressed this issue by comparing predicted movement corridors and effective distances (derived from least cost analysis and circuit theory) across alternative resistance surface scenarios based on different parameterization methodologies: habitat modeling and landscape genetics. We also assessed how two different variable integration approaches (additive and multiplicative) affected the predictions and implications of landscape genetic models of resistance.

Our aim was to gain insights into the differences and similarities between the results obtained using the different approaches, their potential limitations, and consequent management implications. We considered brown bear (Ursus arctos) in the Cantrabrian Range (NW Spain) as the focal species. Brown bear is a long-lived omnivorous mammal with a solitary social structure and promiscuous mating system.
Males and females have intra and inter-sexually overlapping home ranges (Dahle and Swenson 2003) and dispersal primarily occurs by males, while females typically are philopatric (Swenson et al. 1998). Brown bear is highly dependent on large landscapes with low human-footprint and large extents of forest cover (Clevenger et al. 1997, Apps et al. 2004, Mateo-Sánchez et al. 2014a). The brown bear population in the Cantabrian Range 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). We considered this population highly suited for this analysis for the following reasons. (1) In the Cantabrian Range, brown bears occur in two small, apparently isolated and endangered subpopulations, with about 220 individuals in total (Pérez et al. 2014). Connectivity has been identified as a major conservation concern for this species, with potentially large implications for actual planning and conservation measures in the study area (Ballesteros and Palomero 2012). (2) Brown bears and other large mammals are of particular interest for connectivity networks because these species operate at broad scales and occur at low densities, which imply that their populations are more likely to be affected by the loss of connectivity (Beier et al. 2008). (3) Large amounts of habitat and genetic data are available for the species and recent research has focused on landscape resistance and connectivity for this species (Pérez et al. 2009, 2010, Mateo-Sánchez et al. 2014a, b) which provides a unique opportunity for the comparative analyses needed to effectively tackle the aforementioned objectives.

MATERIALS AND METHODS

Study area

The study was carried out in the Cantabrian Range (northwestern Spain). This area is within a larger transnational initiative covering protected areas from the Cantabrian Range to the Western Alps (SW Europe), in which previous studies on connectivity and the barrier effect of roads for forest mammals have focused (Gurrutxaga et al. 2011, Jongman et al. 2011). The region is 49,472 km² in extent and contains the whole known range of the native populations of the brown bear in Spain, its peripheral areas and the belt area between the two subpopulations. As shown in Fig. 1, both subpopulations occupy a similar area of about 2,500 km² each and are separated by about 50 km of unoccupied range.

Landscape resistance parameterization

Landscape resistance was parameterized under three different scenarios based on different methodological approaches (habitat scenario, genetic-multiplicative scenario, and genetic-additive scenario), as described next. All resistance maps were produced with a spatial resolution of 100 m.

Habitat suitability as a proxy for resistance to movement. — A plausible way to empirically estimate relationships between connectivity and environmental conditions is to assume that habitat quality has a direct (inverse) relationship with resistance to movement (e.g., Pullinger and Johnson 2010, Kuemmerle et al. 2011, Mateo-Sánchez et al. 2014b). We used this approach in our first parameterization scenario (habitat scenario), in which we created a resistance surface where resistance to movement was obtained through an inverse function of habitat suitability. We used a multiscale suitability habitat model developed by Mateo-Sánchez et al. (2014a) to predict brown bear occurrence in the study area. After transformation every pixel represented the unit cost of crossing each location, so that the lowest resistance value represented the cost of moving through the highest quality habitat. Landscape variables included in the model were landscape composition (percentage of landscape covered by forest), forest canopy cover and density of buildings (Mateo-Sánchez et al. 2014a, b).

Landscape genetics to infer resistance to movement. — We used individual-based landscape genetics approaches to produce resistance models under two different scenarios (Mateo-Sánchez et al., in press). Specifically, we used genetic samples of brown bears genotyped at 17 polymorphic microsatellite loci to quantify genetic structure and measured the genetic distance among samples as the proportion of shared alleles (Bowcock et al. 1994). The relationship between the genetic structure observed within the bear population and likely drivers of landscape resistance was systematically evaluated through

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reciprocal causal modeling (Cushman et al. 2006, 2013) and the multi-model optimization approach developed by Shirk et al. (2010). The resulting resistance models included variables of landscape composition (percentage of landscape cover by mixed forest and agricultural lands), landscape configuration (cohesion of mixed forest and shrubland) and canopy cover.

One of the key questions in resistance parameterization relates to the method for combining the effects of individual landscape variables into a multivariate resistance surface (Beier et al. 2008). Hence, we explored two different ways for combining individual landscape variables: through multiplication (genetic-multiplicative scenario) and through addition (genetic-additive scenario).

**Corridor identification and effective distance estimation**

We used an individual-based approach to predict expected movement corridors. We considered as sources and destinations for the corridor mapping a set of 173 empirical brown bear locations distributed across the species range for which we also counted with genetic data, which allowed meaningful comparisons between results of the different approaches (habitat vs. genetic).

We applied two different approaches: (A) least cost path modeling, using the UNICOR software (Landguth et al. 2012), in which the movement of individuals is assumed to follow the optimal (least costly) pathway between locations and (B) circuit theory, using CIRCUITSCAPE (v3.5.8; McRae and Beier 2007, McRae et al. 2008), in which multiple available pathways (including suboptimal ones) can be followed by the individuals and contribute to estimated connectivity among locations. These two approaches were used to (1) produce corridors expected to concentrate brown bear movements in the study area (least cost path density and current density map for approaches A and B, respectively; further details on our analyses can be found in Appendix A), and to (2) calculate the accumulated cost of movement between source and destination areas, corresponding to the so called...
effective distances in least cost path modeling and to effective resistances (or resistance distance) in circuit-based modeling (hereafter both referred to as effective distances). Higher effective distances among locations are assumed to correspond to a higher degree or likelihood of isolation among habitat areas or locations. Effective distances were calculated between (a) the western subpopulation core area and eastern subpopulation core area, (b) the western subpopulation peripheral area and eastern subpopulation peripheral area (i.e., the edge of each core population area that is closest to the other subpopulation edge) and (c) end to end within each subpopulation area (i.e., travel through the whole occupancy area) (Fig. 2). We focused on these positions due to their strategic significance in terms of connectivity between and within the two subpopulations (see also Table 1). These linkages (corridors) and effective distances were produced for each of the three landscape resistance scenarios described above. Since we aimed to compare the effective distances produced by the three resistance scenarios, each with different ranges of variation in the resistance values, we first normalized effective distances by dividing the effective distance in each scenario by the mean resistance value of all the 173 pixels with bear locations in the corresponding resistance surface.

We therefore produced and compared six sets of corridors and effective distance/resistance values, corresponding to the two analytical approaches (least cost paths and circuitscape) and the three resistance surface scenarios (Table 2).

RESULTS

Corridor comparison

The predicted movement corridor network among individuals showed substantial differences across the three resistance scenarios and two

Table 1. Definition of analyzed effective distances.

<table>
<thead>
<tr>
<th>Name</th>
<th>Definition</th>
<th>Meaning</th>
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</thead>
<tbody>
<tr>
<td>a: between subpopulation centers</td>
<td>Movement between two individuals located in the core of the west subpopulation and the core of the east subpopulation.</td>
<td>Connectivity between subpopulations, assuming most dispersers move from core to core.</td>
</tr>
<tr>
<td>b: between subpopulation edges</td>
<td>Movement between two individuals located in the peripheral area of the west subpopulation and the peripheral area of east subpopulation (border of each area closest to the other subpopulations). Peripheral areas correspond with the limit of both subpopulations occupancy area.</td>
<td>Connectivity between subpopulations, assuming that most dispersers will first try to stay within established ranges and eventually move outside currently occupied areas through the more hostile matrix to relocate into another range.</td>
</tr>
<tr>
<td>c: within subpopulations</td>
<td>Movement through the whole occupancy area (for each subpopulation).</td>
<td>Connectivity within populations.</td>
</tr>
</tbody>
</table>

Fig. 2. Locations for effective distance and effective resistance calculations. We calculated effective distances and resistances between (a) the cores of the ranges of the two subpopulations, (b) the periphery of the two ranges, and (c) within the two ranges. See also Table 1.
analytical approaches (Figs. 3 and 4). Important-
ly, major functional links did not match among 
scenarios or methods (least cost path vs circuit 
theory). In the case of linkages defined through 
cumulative density of least cost paths on a 
resistance map derived from habitat suitability, 
connections between subpopulations followed 
two main routes that converged in the peripheral 
area of the East subpopulation (Fig. 3a). In 
contrast, for the resistance scenarios based on 
genetic data and least cost path analysis, connec-
tions showed more extensive networks consisting 
in one major route complemented by several 
secondary routes that converge with the princi-
pal route when using multiplicative genetic 
resistance (Fig. 3b). In the additive genetic 
resistance scenario analyzed with least cost 
paths, three parallel and interconnected routes 
coalesce in both subpopulations (Fig. 3c). When 
analyzing connections designated through circuit 
theory, potential connections identified through 
current maps also differed across the assessed 
resistance scenarios. A higher concentration of 
current in narrower and more clearly defined 
areas is found in the habitat based resistance 
scenario (Fig. 4a). When resistance was based on 
genetic data, more and wider permeable areas 
were detected (Fig. 4b, c), with movements less 
concentrated in thin strips of land. Results also 
show that within-subpopulation connectivity 
network pattern was relatively similar for all 
the scenarios in both approaches.

**Effective distances comparison**

There were strong correlations between effec-
tive distances across the three resistance scenar-
ios assessed when all pairs of locations where 
simultaneously considered: Pearson’s correlation 
coefficient $r > 0.96$ in all the cases for effective 
least cost distances and $r > 0.82$ in all the cases 
for effective resistances based on circuit theory. 
However, effective distances between strategic 
locations showed considerably different values 
among scenarios (Fig. 5). Effective distances 
between two individuals located within different 
centers of the two subpopulations were 7–9% 
lower for genetic scenarios (multiplicative and 
additive) than for the habitat scenario. More 
importantly, when two individuals were located 
in the proximate peripheral areas (edges) of both 
subpopulations, effective distance was much 
higher for the habitat scenario than for genetic 
scenarios (47% and 79% higher for the genetic-
multiplicative and genetic-additive scenarios, 
respectively). When comparing the multiplicative 
and additive genetic scenarios, the normalized 
effective distances were more similar than when 
comparing the habitat and genetic scenarios, but 
the additive genetic scenario showed the lowest 
effective distances between individuals. In con-
trast, effective distance between two individuals 
located in the same core in both subpopulations 
was 40–30% lower when calculated across 
resistance based on habitat suitability than when 
computed for resistance scenarios based on 
genetic data. Effective distances within cores 
were relatively similar in the two genetic 
scenarios, but the multiplicative approach 
showed higher values.

Effective distances (effective resistances) calcu-
lated through circuit theory followed the same 
general pattern as least-cost effective distances 
when considering movements between popula-
tion edges and movements within populations 
(Fig. 5b). In these cases, effective resistances in 
the genetic-multiplicative and genetic-additive 
scenarios were again considerably lower than for 
the habitat-based resistance scenario (37% and 
51%, respectively). Oppositely, effective resistanc-
es between the centers of both subpopulations

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Table 2. Sets of methods being compared for delineating corridors and estimating effective distances. These methods are based on three different approaches for parameterizing resistance models, and two different approaches for delineating corridors and estimating effective distances based on these models.

<table>
<thead>
<tr>
<th>Corridor delineation approach</th>
<th>Resistance parameterization</th>
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<tbody>
<tr>
<td></td>
<td>Habitat scenario</td>
</tr>
<tr>
<td>Least-cost path density</td>
<td>Corridor option 1 (Fig. 3a)</td>
</tr>
<tr>
<td>Circuit theory</td>
<td>Corridor option 4 (Fig. 4a)</td>
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Fig. 3. Corridors defined by using least-cost paths for the three resistance scenarios: (a) Habitat suitability-based scenario, (b) genetic-multiplicative scenario, and (c) genetic-additive scenario.
Fig. 4. Current maps defined by circuit theory for resistance scenarios: (a) Habitat suitability-based scenario, (b) genetic-multiplicative scenario, and (c) additive genetic-based scenario.
were 18% higher in the multiplicative genetic based model than in the habitat-based model. However, the additive genetic model and the habitat-based model led to very similar resistances. Remarkably, effective resistance between centers of both populations was lower than effective resistance between population edges for the habitat model (Fig. 5b).

DISCUSSION

Most current methods to predict population connectivity and to identify areas important for animal movements rely on landscape resistance surfaces (Spear et al. 2010). However, the methods and assumptions used to create these surfaces are critical for their effectiveness in guiding conservation decisions. Therefore, it is important to explore the effects that different analytical approaches have on predicted population connectivity and identified corridor routes. Here, we compared resistance surface parameterization and resulting connectivity models created by two different analytical approaches for quantifying resistances and two commonly used methods to predict likely movement paths from these resistances. Our findings showed that alternative approaches substantially affected the assessment of effective distances and largely changed the delineation of potential corridors across the study area.

Implications of multiplicative vs. additive combination of factors

The way in which factors are combined in a resistance model has important implications for resulting connectivity models. Our additive resistance surface showed denser connectivity networks and lower effective distances/resistances than the multiplicative surface. This suggests that multiplicative resistance models are more restrictive in identifying permeable areas for movement and hence indicate lower connectivity. This is because areas predicted to be highly permeable in a multiplicative model correspond to those raster cells where all the factors involved in the models have low resistance values. Thus, in a multiplicative model, even a single factor with high resistance in an area can decrease predicted landscape permeability in that area. In contrast, an additive combination of factors allows compensation among factors and can lead to less restrictive connectivity predictions.

Comparison of least cost-path and circuit theory predictions

Least-cost path analysis and circuit theory are based on different assumptions to model con-
nectivity (Spear et al. 2010). While least-cost analyses assume animals follow a single and optimal pathway, circuit theory assumes random walks so that movement is influenced by all possible pathways. Therefore, results from both methods provide different and complementary insights about brown bear movement. For both approaches, effective distances between subpopulation centers (the individual has to cross part of the habitat area and the matrix in-between subpopulation ranges) differed from effective distances between subpopulation edges (the individual only crosses the matrix between habitat areas). However, and surprisingly, we found that circuit-theoretic effective resistance between subpopulation edges was actually higher than the effective resistance between population centers in the habitat-based resistance scenario (Fig. 5b). To have a lower effective resistance between the centers of the habitat areas than between the less distant edges of those areas is rather difficult to interpret ecologically, because bears moving away from the edges first have to reach the edges before crossing the matrix to reach the other subpopulation. This result might point out to a potential limitation of circuit theory (or of the implementation of it) to assess landscape connectivity. We ensured that our finding was not an artifact arising from some idiosyncratic and unnoticed characteristic of our particular brown bear spatial data by creating a simple and purposefully controlled example depicting a resistance pattern similar to the one of the habitat-based scenario (i.e., similar extent, resolution and arrangement). This controlled example confirmed our results from the real bear data set, i.e., effective resistances were smaller between the cores than between the edges (further details can be found in Appendix A and Appendix B: Fig. B1). This finding advocates for further research to fully clarify this issue from an analytical point of view and, if possible, to provide guidelines for avoiding potentially unintended results in the application of circuit theory for connectivity analyses.

Habitat models may overestimate resistance to movement through non-optimal areas

Corridors between subpopulations predicted from habitat suitability-based resistance did not match the locations or intensity of corridors identified through genetic-based resistances. In addition, effective distances between subpopulations were substantially higher when habitat suitability was used as a surrogate for landscape resistance. These findings suggest that resistance surfaces based on habitat models may tend to overestimate landscape resistance in areas with low habitat suitability. In our analysis, this effect was dramatic when effective distance was calculated between peripheral areas of both subpopulations and individuals had to cross mostly unsuitable areas. In contrast, effective distances between individuals located within subpopulations were lowest when resistance surfaces were based on habitat suitability. Thus, congruent with results from Wasserman et al. (2010), we found that habitat suitability can predict a greater resistance to poor habitat than is suggested by genetic data. In other words, the fact that the species does not occur (permanently) in a particular habitat does not imply that it cannot move when needed (e.g., dispersal) through this area. In this sense, landscape genetics models integrate the movement of many individuals over time and thus lead to a more synoptic measure of landscape resistance (Zeller et al. 2012, Cushman et al. 2013a). This suggests that there is not necessarily a correspondence between habitat use patterns and dispersal movements. Conditions providing suitable habitat for permanent establishment and local resource may often be different than the conditions facilitating dispersal movements (Cushman et al. 2013a, Peterman et al. 2014). Since suitability models are based on occurrence data that usually represent locations within home ranges, habitat suitability models may not adequately reflect how environments affect animals during movements outside of their usual home ranges, such as dispersal or mating excursions (Cushman et al. 2013a). For our study species, results suggest that dispersing bears are more flexible in their movement behavior and less constrained by landscape conditions than suggested from their occurrence in typical bear habitats. While our analyses have only been conducted for a single species, we believe that the results may be similar for many other organisms as well, particularly for species that are highly mobile and not strictly confined to a specific type of habitat.
Genetic data estimate higher resistance to movement through suitable habitat areas

For within-population movements, the genetically-derived resistance surfaces predicted larger effective distances among individuals than the habitat suitability-based resistance surface. This is likely due to the fact that resistance models derived from landscape genetic analyses are based on comparison of genetic distances and effective distances. Such landscape genetic approaches may lead to resistance surfaces that overestimate effective distances in areas that are highly suitable (and eventually well connected to each other) when factors other than resistance to movement govern spatial-genetic structure; for instance, even when two sampled individuals are separated by a very short distance (or even located in the same raster cell), they will show some genetic differentiation, which may translate in such genetic resistance models exacerbating the effective distance estimates at short ranges to explain such genetic structure. Spatial-genetic structure within populations is likely less dependent on the resistance of the landscape matrix (Fahrig 2007), but more strongly influenced by many other biological and ecological factors acting locally, including sex-specific space-use behavior, local population density, survival, or reproductive success (Pflüger and Balkenhol 2014). Another issue related to genetic data is that in long-lived species there may be a temporal disconnection between genetic structure and the current landscape; i.e., there may be legacy effects of previous landscapes (James et al. 2007, Spear et al. 2010) that could lead to misestimate current connectivity. However, Landguth et al. (2010) showed that the legacy of past landscape features is not a particularly important problem in species with relatively large dispersal abilities. Hence, landscape legacies are unlikely to affect our conclusions about brown bear dispersal and gene flow.

The importance of inter-population movements for predicting connectivity

Movements outside of typical habitat are less frequent than within-habitat movements, but they are also critical for genetic exchange and range expansion (Nathan et al. 2003, Chetkiewicz et al. 2006). Previous research has shown that a variable but generally low number of migrants per generation can lead to a sufficient amount of gene flow between populations (e.g., Mills and Allendorf 1996, Vucetich and Waite 2000). Therefore, facilitating sufficient levels of inter-population movements should be a priority in connectivity strategies. Importantly, it is precisely in this kind of movements where, according to our results, resistance estimates and connectivity models varied most strongly between the analytical approaches we compared. Within the two subpopulations, effective distances and resistances were always low, and predicted movement paths were very consistent among the different analytical approaches. However, estimated distances and predicted movement paths differed substantially among the different approaches for connectivity between the two subpopulations. Thus, analytical choices for parameterizing and utilizing resistance surfaces will be most important when trying to predict inter-population movements, when individuals move out of established ranges and cross the unsuitable landscape matrix. Importantly, this is also the kind of analysis most relevant for corridor design, as the goal is usually the (re-) connection of different subpopulations located across a landscape or the support of species range shifts in response to climate change, rather than the facilitation of within-population movements.

Conclusions for connectivity analysis based on habitat suitability

Based on our study, it seems reasonable to question the assumption that habitat suitability models can accurately capture landscape resistance to movement for corridor design. Location data used to produce habitat suitability models tend to be dominated by habitat use (i.e., shelter, foraging) and thus by frequent routine movements within established home ranges. However, genetic structure may be strongly determined by mating movements and rare dispersal events. These types of movements are unlikely to be well-captured by occurrence data and may be therefore poorly represented in resistance models derived from such data. Thus, as already suggested by Beier et al. (2008) and Zeller et al. (2012), genetic-based studies are likely to be more useful to understand connectivity of populations. However, if genetic data are not available or when recent landscape changes are not yet
reflected in genetic data, parameterization based on habitat models, direct movement data (e.g., telemetry) or even expert opinion may be still required (Spear et al. 2010). Indeed, resistance surfaces should ideally be assessed though analyses of multiple data sources. For example, a resistance surface that is supported by independent analysis of movement and genetic data (e.g., Cushman and Lewis 2010) is much more likely to be robust than one developed from a single empirical data set. For example, recent research in telemetry data analysis provides methods that help to distinguish habitat use from dispersal locations (e.g., Dickson et al. 2005, Squires et al. 2013, Zeller et al. 2014). Compared to occurrence-based habitat models, these novel approaches could provide resistance models that more reliably reflect actual species movement across complex landscapes.

**Implications for conservation**

Connectivity models should accurately predict inter-population movement and gene flow, and enable researchers to reliably identify the most likely movement routes among subpopulations. As shown in this study, connectivity models and the corridors suggested by them depend strongly on the analytical methods used for creating and utilizing underlying resistance surfaces. Several published studies have suggested ways for finding optimal resistance values (e.g., Kuroe et al. 2011, Shirk et al. 2010, Graves et al. 2014), and these studies have certainly improved resistance-based connectivity modeling. However, the effects of different conceptual approaches underlying resistance models (habitat suitability vs. resistance to inter-population movement) or the analytical choices made during their creation and analysis (additive vs. multiplicative models, least-cost vs. circuit-theory) appear to be at least as important as the numerical optimization of resistance values. Indeed, our results suggest that these other aspects substantially impact the outcome of resistance-based connectivity predictions, which could be a challenge for applying resistance-based connectivity models in practical conservation. If different approaches predict vastly dissimilar areas to be important for conservation efforts (e.g., optimal locations for corridors or road-crossing structures), it will be rather difficult to objectively choose and justify a single ‘best’ management action.

For now, we advocate the use of genetically-derived resistance surfaces over the use of occurrence data, but agree with Zeller et al. (2012) that more comparative research is needed to fill current knowledge gaps related to landscape resistance and connectivity modeling. Indeed, we argue that research identifying the advantages and limitations of various conceptual and analytical approaches, such as those here reported, is urgently needed for assessing how meaningful and useful different resistance-based connectivity models actually are for practical conservation planning. We hope that our study has highlighted some of these future research needs and that it will motivate others to further investigate this important topic.

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**LITERATURE CITED**


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Mateo-Sánchez, M., S. Cushman, and S. Saura. 2014b.


SUPPLEMENTAL MATERIAL

APPENDIX A

DETAILS ON CORRIDOR IDENTIFICATION ANALYSES

Least cost path density modeling

UNICOR (UNIversal CORridor and network simulation model, Landguth et al. 2010) identifies the shortest path between every specified species location on a landscape to every other specified species location. The combination of all the movement paths produces a least cost path density map that represents the pattern of the most probable movement paths for brown bear in the study area (e.g., Cushman et al. 2013a; Mateo-Sánchez et al. 2014b). To identify putative corridors, we computed the focal density of the factorial least cost path network with a moving window of 1-km radius with a GIS (Mateo-Sánchez et al. 2014b). UNICOR also calculated effective (least cost) distance between all combinations of sources and destinations.

Circuit theory modeling

Circuitscape (McRae et al. 2008) uses circuit theory to model landscapes as conductance surfaces and predict important connections among locations. Based on the assumption of a random walk, all plausible paths between each two locations are integrated creating a current map. Analogously to the factorial least cost path density map described above, the combination of every pairwise current map allows the identify corridors with higher current flow.

This software also computes pairwise effective resistance between all combinations of locations (here brown bear occurrences). In this study we used a four-neighbor case for the calculations.

APPENDIX B

DETAILS ON THE EXAMPLE OF CIRCUITSCAPE ESTIMATES OF EFFECTIVE RESISTANCES

The simulated example consists of two habitat areas with low resistance to movement that are separated by a high resistance matrix. We computed circuit-based effective resistances between two points located in the center of both habitat areas and two points located on their closest edges (Fig. B1). Results showed that centre to centre effective resistance was lower than edge to edge (see Fig. B1), confirming our findings from the brown bear data set. This suggests that there might be a previously unreported issue related to some conceptual aspects of circuit theory or its application to model landscape connectivity, or issues related to details of the implementation of the calculations in Circuitscape.
Fig. B1. Simulated landscape for illustrating the results of the effective resistances through circuit theory as implemented in Circuitscape. The landscape consists of two habitat areas with low resistance to movement (resistance score 10) that are separated by a portion of landscape matrix with a high resistance (resistance score 100). Effective resistance was calculated (1) between two points located in the center of both habitat areas (shown in magenta in the figure), resulting in 137.1 and 57.5 Ohms, respectively, for a four- and eight-neighbors case and (2) between two points located in the habitat area edges (border of one habitat area closest to the other habitat area, shown in blue in the figure), resulting in 162.3 and 69.84 Ohms, respectively, for a four- and eight-neighbors case.