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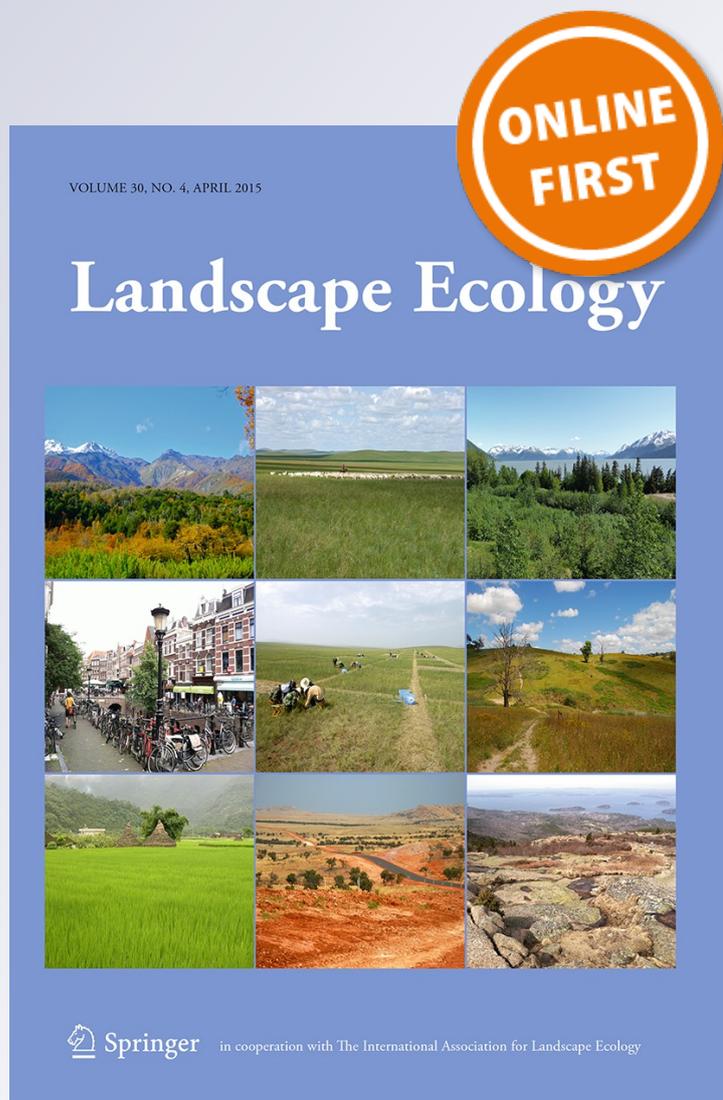
María C. Mateo-Sánchez, Niko Balkenhol, Samuel Cushman, Trinidad Pérez, Ana Domínguez & Santiago Saura

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A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow?

María C. Mateo-Sánchez · Niko Balkenhol · Samuel Cushman · Trinidad Pérez · Ana Domínguez · Santiago Saura

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Abstract

Context Most current methods to assess connectivity begin with landscape resistance maps. The prevailing resistance models are commonly based on expert opinion and, more recently, on a direct transformation of habitat suitability. However, habitat associations are not necessarily accurate indicators of dispersal, and thus may fail as a surrogate of resistance to movement. Genetic data can provide valuable insights in this respect.

Objectives We aim at directly comparing the utility of habitat suitability models for estimating landscape resistance versus other approaches based on actual connectivity data.

Methods We develop a framework to compare landscape resistance models based on (1) a genetic-based multi model optimization and (2) a direct conversion of habitat suitability into landscape resistance. We applied this framework to the endangered brown bear in the Cantabrian Range (NW Spain).

Results We found that the genetic-based optimization produced a resistance model that was more related to species movement than were models produced by direct conversion of habitat suitability. Certain land cover types and transport infrastructures were restrictive factors for species occurrence, but did not appear to impede the brown bear movements that determined observed genetic structure.

Conclusions In this study case, habitat suitability is not synonymous with permeability for dispersal, and does not seem to provide the best way to estimate actual landscape resistance. We highlight the general utility of this comparative approach to provide a comprehensive and practical assessment of factors involved in species movements, with the final aim of improving the initiatives to enhance landscape connectivity in conservation planning.

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M. C. Mateo-Sánchez (✉) · S. Saura
E.T.S.I Montes, Forestal y del Medio Natural, Technical University of Madrid, Ciudad Universitaria s/n,
28040 Madrid, Spain
e-mail: mc.mateo@upm.es

N. Balkenhol
Department of Forest Zoology and Forest Conservation,
University of Goettingen, Buesgenweg 3,
37077 Goettingen, Germany

S. Cushman
Rocky Mountain Research Station, U.S Forest Service,
Southwest Forest Science Complex, 2500 South Pine
Knoll Drive, Flagstaff, AZ 86001, USA

T. Pérez · A. Domínguez
Department of Biología Funcional, University of Oviedo,
Avda. Julián Clavería 6, 33006 Oviedo, Spain

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Introduction

The ability of populations to exchange individuals and genes across landscapes is often critical for their long term viability (Crooks and Sanjayan 2006). Yet despite the clear importance of connectivity for population persistence, the specific factors mediating connectivity are largely unknown for many species (Bowne and Bowers 2004; Cushman et al. 2006). Consequently, developing methods for assessing movement of individuals and genes through heterogeneous landscapes remains an active research topic in landscape ecology and conservation biology (Zeller et al. 2012; Cushman et al. 2013a). Reliably determining the effects of landscape structure on movement is challenging, and is usually based on inferred maps of resistance to movement (Zeller et al. 2012). In its most basic sense, landscape resistance reflects the local cost of movement experienced by an organism, and integrates several behavioral and physiological factors such as aversion, energy expenditure, or mortality risk associated with moving through a particular environment (Zeller et al. 2012). These effects are often represented for analysis as raster resistance maps (surfaces), in which data values correspond to the step-wise cost of moving through each cell (Adriaensen et al. 2003). Since resistance surfaces are frequently used to predict population connectivity and identify most likely movement paths for corridor design and conservation, the estimation of cost values used in these resistance surfaces has recently received much attention (Beier et al. 2008; Spear et al. 2010; Zeller et al. 2012). Multiple and varied approaches to parameterize resistance surfaces exist (Zeller et al. 2012), and the best way for assigning resistance values to different landscape attributes remains a subject of ongoing debate.

Due to a lack of detailed information on animal movement, many of the studies using resistance surfaces to identify optimal routes for conservation corridors rely on expert opinion for resistance parameterization. Since expert opinion may not accurately reflect landscape effects on actual movement (Seoane et al. 2005; Shirk et al. 2010; Zeller et al. 2012), some authors proposed that resistance to movement could be estimated directly from habitat suitability (e.g. Chetkiewicz et al. 2006; Ó'Brien et al. 2006; Beier et al. 2008; Mateo-Sánchez et al. 2014b). In this approach, resistance estimates are inversely

related to the probability that a species will be present at a certain location as function of landscape characteristics found at or around that location (e.g., habitat suitability values). This approach relies on the assumption that animal movement and habitat selection are based on the same preferences (Beier et al. 2008; Shirk et al. 2010; Zeller et al. 2012). However, habitat associations are not necessarily accurate indicators of dispersal (Chetkiewicz et al. 2006; Beier et al. 2008). Several papers have highlighted that habitat suitability and landscape permeability are not necessarily synonymous (e.g., Spear et al. 2010; Zeller et al. 2012). Indeed, multiple papers found that habitat suitability was a poor predictor of realized levels of movement and gene flow (e.g. Horskins et al. 2006; Wasserman et al. 2010; 2010; Reding et al. 2013; Shirk et al. Peterman et al. 2014). However, to date there have been few empirical studies that directly compare the utility of habitat suitability models for estimating landscape resistance versus other approaches that are based on actual connectivity data.

Genetic data provide a powerful means to infer landscape effects on functional connectivity, because gene flow only occurs when movement is successful and subsequently leads to actual reproduction (Manel et al. 2003; Storfer et al. 2007; Holderegger and Wagner 2008). Thus, landscape genetics approaches have great potential to provide more rigorous methods to parameterize resistance surfaces (Spear et al. 2005; Cushman et al. 2006; Storfer et al. 2007; Balkenhol et al. 2009; Shirk et al. 2010; Wasserman et al. 2010). Indeed, recent work has refined and extended landscape genetics approaches by providing optimization and model selection frameworks that improve the reliability of landscape genetic inferences (Shirk et al. 2010, 2012; Wasserman et al. 2010, Cushman et al. 2013b, Castillo et al. 2014).

Here we optimized resistance surfaces using landscape genetics and habitat suitability models, and compared their abilities to explain observed genetic differentiation. We used the brown bear (*Ursus arctos*) in northwestern Spain as a model species due to availability of extensive and high-quality data sources (species presence records and genetic samples) and because of the importance of population connectivity for the conservation of this endangered species in Spain. Our approach involved three steps. First, we combined multifactorial model-selection (Shirk et al. 2010) with reciprocal causal modeling (Cushman et al. 2013b) to

identify landscape factors influencing genetic structure of brown bears. Second, we then compared these optimized resistance models with resistance models directly developed from empirically derived habitat suitability values. Third, we coupled the empirical comparative approach with simulations of species movement and genetic processes to evaluate the robustness of the selected resistance model. Importantly, our analyses highlight that resistance models relying on habitat suitability values derived from species occurrences may not efficiently capture landscape effects on successful movement and gene flow.

Materials and methods

Study area and species

The study was carried out in the Cantabrian Range (northwestern Spain) where brown bears occur in two small and endangered subpopulations (Palomero et al. 2007) with limited gene flow between them (Perez et al. 2009, 2010), (Fig. 1). The study area has an extent of 49,472 km² and contains the entire range of the brown bear in Spain, its peripheral areas and the gap between the two subpopulations. Both subpopulations occupy a similar area of about 2500 km² each, and are separated by about 50 km of unoccupied range

(Palomero et al. 2007). Further details on the study area can be found in Mateo Sánchez et al. (2014a).

The isolation between the two subpopulations is usually attributed to increasing human pressure and to the loss of suitable habitat (Wiegand et al. 1998; Naves et al. 2003). Though recent studies revealed that both populations are growing (Pérez et al. 2014), the extent of suitable habitat is limited (Mateo Sánchez et al. 2014a), which likely will hinder future recovery (Palomero et al. 2007). Given these limitations, maintaining and enhancing connectivity between the subpopulations has become a top priority and critical concern for brown bear conservation efforts.

Genetic data and structure

We used a database of 465 samples (hair and scat) that resulted in 173 genotypes (for genotyping details see Pérez et al. 2009). The data included 17 polymorphic loci (Appendix A1) and showed no evidence of allelic drop out, null alleles, stuttering, or Hardy–Weinberg disequilibrium within subpopulations. The genotyped individuals were allocated to the two subpopulations using genetic assignment tests (see Pérez et al. 2009). A total of 148 of the genotyped individuals were assigned to the western subpopulation, which represents about 75 % of the estimated population size of approximately 200 individuals in this subpopulation

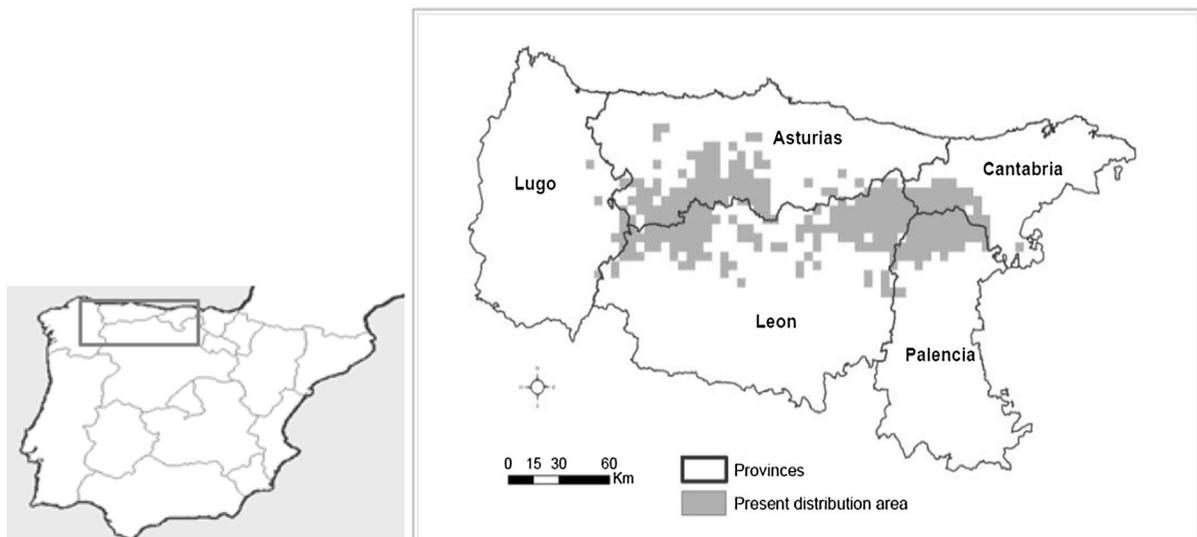


Fig. 1 Study area

(Pérez et al. 2014). Nineteen individuals were assigned to the eastern subpopulation, close to the estimated total size of this subpopulation (Pérez et al. 2014). Furthermore, two migrant individuals (from the West) and four admixed individuals were also found in the eastern subpopulation.

To quantify genetic structure, we calculated genetic distance among individuals by computing the proportion of shared alleles (POSA; Bowcock et al. 1994) in Microsatellite Analyser (MSA, Dieringer and Schlötterer 2003). To ensure that our results are reliable and not dependent on the genetic distance measure, we also calculated two other individual-based genetic distances (see Appendix A1).

General analytical approach to infer landscape resistance to gene flow

We used an individual-based, multi-model landscape genetic approach to infer landscape resistance to gene flow. We built a set of hypotheses, each representing different relationships between landscape features and genetic differentiation. For each of these hypothetical resistance models, we used circuit theory (McRae and Beier 2007) to calculate effective distances among individuals (also called effective resistances or resistance distances in circuit theory terminology). Our approach is based on comparing genetic structure among individuals with effective distance between them in a multi-model competitive framework, which allowed us to identify the landscape resistance model that best explains genetic structure (e.g. Cushman et al. 2006). In addition, we compared the results of two analytical approaches for parameterizing resistance surfaces: (1) a factorial multi-model approach to identify the combination of environmental factors to be included in the genetic-based model (Fig. 2a) and (2) a direct conversion of habitat suitability into landscape resistance for a set of available brown bear habitat suitability models (Fig. 2b).

In the factorial multi-model approach based on genetic data, we considered a set of environmental variables related to land cover, terrain and human disturbance (see next section) as potential factors influencing gene flow (resistors) in our study species (Fig. 2a(1); Table 1) to construct dispersal suitability (DS) models, using different functions (see modeling section) that translate raw resistor variable values into DS values ranging from 0 (low suitability for

dispersal) to 1 (high suitability for dispersal; Fig. 2a(2)). Dispersal suitability models were then systematically translated into multiple alternative landscape resistance models through three different mathematical functions and three different ranges of maximum resistance values (Fig. 2a(3), see resistance models section). The resulting set of candidate resistance models were first evaluated in a univariate optimization framework to select the best resistance value for each variable (Fig. 2a (4)). We then optimized resistance models again in a multivariate context (e.g. Shirk et al. 2010). For this, variables were integrated through two types of algebraic operations: addition and multiplication (Fig. 2a (5)) to select the multivariate model that best fitted brown bear genetic structure.

Concurrently, for approach 2, we used a set of 14 habitat suitability models developed under different ecological hypotheses for this species and study area. The starting set of ecological variables was the same for approach 1 and 2 (i.e. to build the resistance models under the factorial multimodal approach based on genetic data and to build habitat suitability models as the basis for estimating resistance). The habitat models (Mateo Sánchez et al. 2014a) (Fig. 2b(1)) were used to model landscape resistances by directly transforming the habitat suitability values (ranging from 0 to 1) of each model into DS values (Fig. 2b(2)), and then building landscape resistance models using the same mathematical functions and the same three different ranges of maximum resistance values as in approach 1 (Fig. 2b(3)). Resulting resistance surfaces were then optimized to select the habitat-based model that best explained genetic structure of brown bears in the study area (Fig. 2b(4)).

The best resistance models found for each of the two approaches (factorial multimodal approach and habitat suitability) were then compared in their ability to explain genetic structure. Although genetic data were used to optimize and select the best model in both approaches (1 and 2), the habitat models (approach 2) were constructed based on species presence (occurrence) data, while the models in approach 1 were constructed based on a landscape genetics approach. Thus, comparing how well the two approaches explain actual genetic structure allows us to evaluate whether habitat suitability models are effective in capturing landscape effects on functional population connectivity (i.e. movement leading to gene flow).

Fig. 2 General analytical approach flowchart

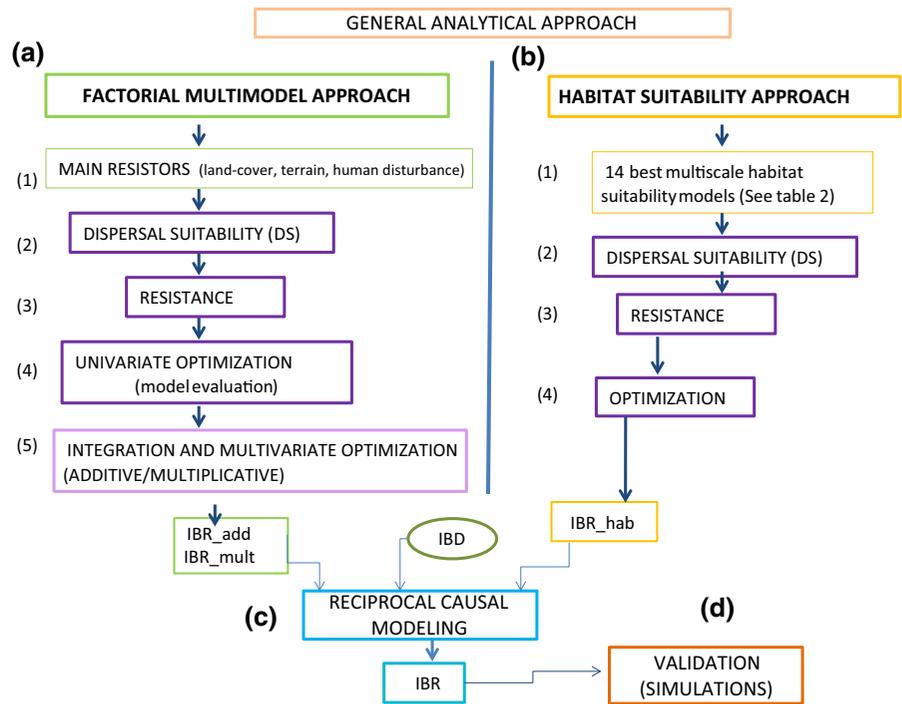


Table 1 Independent variables considered for analyzing landscape resistance to gene flow

Type	Variable	Description
Land-cover (CL)	PLAND (CF DF MF SH AG)	Percentage of landscape occupied by the land cover class
Land- cover(LL)	CC	Forest canopy cover
Land- cover (CL)	COH (CF DF MF SH AG)	Cohesion of the land cover class
Land- cover (CL)	AI (CF DF MF)	Aggregation Index for the land cover class
Land- cover (LL)	CWED	Contrast weighted edge effect
Land- cover (LL)	ED	Land cover types edge density
Land- cover (LL)	PD	Land covers patch density
Terrain	Slope	Slope
Terrain	Elevation	Elevation
Antropic	INFR_DEN	Density o f transport infrastructures
Antropic	HW_DIST	Distance to highways
Antropic	BD	Building density

For the land cover metrics (LL) and (CL) differentiate between landscape level and class level metrics respectively. Class level metrics were calculated for some of the following land covers

CF native conifer forest, DF native deciduous forest, MF mixed forest, SH shrubland, AG agricultural land

In addition, we also evaluated a null model of Isolation by Distance (IBD), where all the cells in the resistance surface have a value equal to 1 (Fig. 2c). Once all the models were assessed, the best supported model was validated through simulations of species movement and genetic processes (Fig. 2d) to evaluate robustness of our inferences.

Environmental variables and dispersal suitability used as inputs for the genetic-based resistance surfaces

Environmental variables (Table 1) were grouped in three categories considered to be major factors affecting gene flow for brown bear in Spain: land

cover, terrain and human disturbance (Table 1). These variables were selected on the basis of previous literature describing brown bear ecology and habitat requirements (e.g. Clevenger et al. 1992, 1997; Naves and Palomero 1993; Naves et al. 2003; Palomero et al. 2007; Mateo Sánchez et al. 2014a). The cell size was 100 m for all the raster variable maps and models in this study. Each variable was measured at the scale at which this species better responds to the landscape in the study area (see Mateo Sánchez et al. 2014a). All environmental variables were converted into dispersal suitability (DS) values normalized between 0 and 1.

Land-cover variables

We derived land cover types from information provided by the Spanish Forest Map at a scale 1:50,000, developed in coordination with the Third Spanish National Forest Inventory. We used FRAG-STATS 3.4 (McGarigal et al. 2002) to calculate a set of metrics quantifying different aspects of landscape structure at two different levels: landscape level and class level (Table 1). The class level metrics were: percentage of landscape (PLAND) and patch cohesion (COH) of conifer, deciduous and mixed forest, shrubland and agricultural lands and aggregation index (AI) for the three forest classes. Landscape level indices were contrast weight edge density (CWED), patch density (PD) and edge density (ED). In addition to these variables, we also evaluated canopy closure for all forest types, so that a total of 17 variables were evaluated for land cover. The raw index values obtained for each variable were translated into dispersal suitability (DS) values normalized between 0 and 1 by using the formula:

$$V_N = \frac{V_i - V_{\min}}{V_{\max} - V_{\min}} \quad (1)$$

where V_i is the value of the variable in a particular pixel, and V_{\min} and V_{\max} are respectively the minimum and maximum values of that variable in the study area. For all variables $DS = V_N$ except for the percentage of agricultural lands, for which DS was calculated as $1 - V_N$ because a lower value is associated with higher suitability for brown bear movement. This resulted in a total of 17 DS models related to land-cover to be evaluated.

Terrain

Two different variables related to the terrain were introduced in the assessment: elevation and slope. Variables were obtained from the 25 meter digital elevation model by the Spanish Geographical National Institute (CNIG). Dispersal suitability (DS) was derived from elevation (Eq. 2) by reclassifying elevation data according to a Gaussian function (e.g. Cushman et al. 2006; Shirk et al. 2010), following the formula:

$$DS(elev) = e^{-\frac{(elev - Eopt)^2}{2Esd}} \quad (2)$$

Where $Eopt$ is the optimal elevation for the species, which was assigned a value of 1300 m according to specific studies for the brown bears in the study area (see Palomero et al. 2007) and Esd represents the standard deviation around the optimal elevation. We selected two values for standard deviation: 500 and 1500 m, therefore obtaining two dispersal habitat suitability functions.

For slope, DS was calculated from slope (in percent) derived from the digital elevation model. Slope values across the study area were normalized (see Eq. 1). DS was calculated as $1 - V_N$ rather than as V_N because a higher value is associated with less suitability for brown bear movement (Palomero et al. 2007). Therefore, a total of three DS models related to terrain (two for elevation and one for slope) were evaluated.

Anthropogenic disturbance

Indicators of human pressure were derived from highways, conventional roads, railways and building vector layers at a 1:25,000 scale developed by CNIG. We considered three different variables related to anthropogenic disturbance: (1) density of linear transport infrastructure (highways, conventional roads and railways), (2) density of buildings and (3) distance to highways. Both densities were measured at a broad scale of 32 km which was previously shown as the best scale to measure human disturbance for this species (Mateo Sánchez et al. 2014a). Dispersal suitability (DS) for linear transport infrastructure and building densities were calculated as $1 - V_N$, (see Eq. 1), while for the distance to highways DS was made equal

to V_N . Therefore, three DS models related to resistance due to human disturbance were evaluated.

Habitat suitability models and dispersal suitability as input for the resistance surfaces

For the habitat based models dispersal suitability was derived from multi-scale habitat suitability modelling for the brown bear in the study area that used the maximum entropy method [Mateo Sánchez et al. 2014a; Fig. 2b(1)]. Mateo Sánchez et al. (2014a) produced 14 different suitability models under different hypotheses of ecological factors governing brown bear habitat relationships. These hypotheses correspond to the cases where brown bear occurrence is primarily a function of: (A) landscape composition; (B) landscape configuration, (C) landscape edge contrast, describing the edge effects between different land cover types and (D) human disturbance, as well as all the plausible combinations among these factors (Table 2). The DS values for each habitat suitability model were calculated by normalizing the suitability values as Eq. 1 producing 14 different DS models related to habitat suitability [Fig. 2b(2)].

Resistance models

Each of the dispersal suitability models (both for the habitat and genetic approaches) was translated into landscape resistance through three different mathematical functions and also for three different ranges of maximum resistance values [Fig. 2a (3) and 2b (3)].

We first used the values in the different DS models directly to define landscape resistances. For this, we used a linear transformation between these suitability values and resistance as used by Singleton et al. (2002):

$$R = CS \times (100 - 100 \times DS) \tag{3}$$

where R is the resistance assigned to a specific cell, CS is the cell size in meters (here 100 m) and DS is the dispersal suitability associated to each variable.

In addition to this linear translation, we also defined two exponential conversions, which account for possible non-linear relationships and threshold effects:

$$R = CS \times 100^{(1-DS)} \tag{4}$$

$$R = CS \times (100 - 100^{DS}). \tag{5}$$

Table 2 Organizational best habitat suitability models according to Mateo Sánchez et al. (2014a)

Habitat model	Mantel r	AUC
A	0.546	0.851
B	0.619	0.843
D	0.500	0.842
AB	0.552	0.851
AC	0.510	0.844
AD	0.574	0.862
ABC	0.621	0.837
ACD	0.578	0.861
ABD	0.581	0.862
ABCD	0.585	0.858
BC	0.590	0.836
BD	0.565	0.846
BCD	0.531	0.843
DC	0.576	0.836

The models were formulated by four ecological factors (A: landscape composition, B: landscape configuration, C: contrast, D: anthropogenic disturbance) and all combinations among them (AB, AC, AD, ABC, ABD, ABCD, BC, BD, BCD, DC). The optimized mantel correlation and their ability to predict brown bear occurrence (AUC) are shown. The AUC (area under the curve) is an index commonly used to evaluate species occurrence models. The index ranges from 0.5 for models that are no better than random to 1.0 for models that predict the presence/absence of a species perfectly

The upper exponential conversion (Eq. 4) and lower exponential conversion (Eq. 5) assumes that bears respond rather non linearly (e.g. convex or concave increase in resistance as dispersal suitability changes). A similar approach has previously been used by Dudaniec et al. (2013).

We scaled the resistance values to account for different values of maximum resistances (R_{max}). (A) R_{max} is 10,000 when DS is 0 as described above (Eqs. 3, 4, 5); (B) $R_{max} = 100$, corresponding to DS equal 0 for models computing the square root of the original models and (C) $R_{max} = 10$, calculating the square root of models in case B (i.e. 4th root of the original models). Thus, we developed a total of nine models of resistance per dispersal suitability model, comprising the combination of three functional transformations and three maximum resistances (Table 3).

A total of 333 resistance models were examined, including 207 resistance models related to the genetic-based factorial multimodal approach (153 related to land cover; 27 related to terrain; 27 related to human

Table 3 Transformation function to build resistance models

Function/resistance (max)	A ($R_{\max} = 10.000$)	B ($R_{\max} = 100$)	C ($R_{\max} = 10$)
(1) (Linear)	Eq. 3	$\sqrt{\text{Eq. 3}}$	$\sqrt[3]{\text{Eq. 3}}$
(2) (Upper exponential)	Eq. 4	$\sqrt{\text{Eq. 4}}$	$\sqrt[3]{\text{Eq. 4}}$
(3) (Lower exponential)	Eq. 5	$\sqrt{\text{Eq. 5}}$	$\sqrt[3]{\text{Eq. 5}}$

disturbance) and 126 estimated from the habitat suitability models.

Model evaluation

To assess the capability of each model to explain genetic structure, we used Mantel tests (Mantel 1967) in a causal modelling framework (as proposed by Cushman et al. 2006; Cushman and Landguth 2010; Shirk et al. 2010; Cushman et al. 2013b) to calculate the correlation between genetic and landscape distance. We identified the most supported model as the one with highest significant correlation once the effects of the null model (IBD) were partialled out. Particularly, for a specific resistance model to be supported as a hypothesis, (1) the partial Mantel test (Smouse et al. 1986) between resistance and genetic distance would need to be significant, partialling out geographical distance and (2) the partial Mantel test between geographical distance and genetic distance would need to be non significant when partialling out the resistance model. This applies to both the univariate and multivariate optimization described below. Statistical significance was assessed with 9999 permutations and the alpha level considered to evaluate significance was 0.05. Evaluations were performed using the *ecodist* package in R (Goslee and Urban, 2007). For the selection among candidate models, we used an optimization framework suggested by Shirk et al. (2010).

Univariate optimization

We selected the best supported univariate landscape resistance model as the one with highest correlation between genetic and landscape (i.e. effective) distance, provided that partial mantel tests fulfilled the requirements to support the model (see above), otherwise the variable or the model was not retained [Fig. 2a(4), 2b(4); (Shirk et al. 2010)]. In this way, variables that were likely to reduce the fit of the subsequent landscape resistance model were excluded.

Resistance models derived from the habitat suitability models were also optimized via the same criteria. But in this case, since habitat models already account for multiple environmental variables (Mateo Sánchez et al. 2014a), the optimization was carried out taking the variables together.

Multivariate optimization

The univariate optimized models were integrated in a multivariate resistance model by two different procedures (a) by adding and (b) by multiplying the univariate resistance models in order to test the differences of alternative ways of producing multivariate models (Fig. 2a(5)). To account for the potential interaction among variables, we re-evaluated and optimized the function models for one variable while holding the other variables constant (e.g. Shirk et al. 2010). If the optimal univariate model related to a particular variable changed when analyzed in a multivariate context, we held the new optimal univariate model constant and then systematically varied the function models of the next variable. The optimization of variables was carried out in order of variable importance (i.e. magnitude of correlation shown in the univariate optimization).

Reciprocal causal modeling and model validation

Once the most highly supported resistance models (IBR) were identified through the additive and multiplicative multivariate optimization processes, we used reciprocal causal modeling (Fig. 2c) to compare these models to each other, to the best supported resistance model derived from habitat suitability, and to the null model of IBD. To mitigate the risk of Type I errors, we implemented a relative support assessment that appears to reduce inferential errors (Cushman et al. 2013b; Castillo et al. 2014) by using the difference between the support among the four resistance hypotheses (IBR additive, IBR multiplicative, IBR habitat and IBD).

Finally, to ensure that our model does not include errors due to poor descriptors or spurious correlations (Cushman and Landguth 2010; Spear et al. 2010), we validated the final resistance surface using movement and gene flow simulations (Fig. 2d, e.g. Shirk et al. 2012; Castillo et al. 2014). Specifically, we simulated gene flow on the most supported resistance surface and compared the results with the real population genetic pattern, as proposed by Shirk et al. (2012). We used CDpop v 1.2 (Landguth and Cushman 2010), which simulates the influence of landscape resistance on individual-based movement, breeding and dispersal.

The input locations of the initial simulated population were distributed according to their current abundance and density that was defined in concordance with a multiscale habitat suitability model developed for the species and study area (Mateo Sánchez et al. 2014a). A total of 211 individuals were placed and were initially assigned 17 neutral and diploid loci (same number of loci studied for the real population).

We simulated gene flow for 500 non-overlapping sexual generations, due to the fact that previous research has shown that this lag time is adequate for equilibrating the relationship between genetic structure and landscape resistance (e.g. Landguth et al. 2010). CDpop calculated a matrix of pair-wise genetic distance between the 211 simulated individuals based on the proportion of shared alleles at generation 500.

To assess the relationship between genetic distances and isolation by resistance (IBR) and isolation by distance (IBD). We evaluated the correlation between simulated genetic distance and cost distance using partial Mantel tests.

Results

The results presented below are based on the percentage of shared alleles (POSA) genetic distance, but all three genetic distances we used were highly correlated and identified the same optimal final model (see Appendix A1 for details).

Resistance based on landscape genetics

Univariate optimization

The univariate optimization only retained five of the 23 variables, all of them related to land cover resistors.

The supported variables were, in order of importance (i.e. magnitude of correlation): percentage of landscape covered by mixed forest, patch cohesion of mixed forest, patch cohesion of shrubland, percentage of landscape covered by agricultural lands, and canopy closure (Table 4). Non-linear, exponential (lower and upper) transformations were the best models for these variables, except for the case of canopy closure where the best model was transformed by a linear function. The values of maximum resistance shown as optimal were relatively low (maximum resistance of 10 for all the variables but for cohesion of shrubland which peaked at 10,000; see Tables 3, 4).

Multivariate optimization

Several optimal models for the different variables changed when they were integrated in a multivariate context for both optimization processes (additive and multiplicative). In the additive final optimal model, canopy closure and the percentage of landscape covered by mixed forest optimal models differed from the univariate optimization in functional form and maximum resistance (Table 4), while in the multiplicative, the percentage of landscape covered by mixed forest also changed but only in terms of maximum resistance (Table 4).

Resistance based on habitat suitability

The only models of genetic isolation due to habitat quality that exhibited significant correlations with genetic distance were based on landscape composition, configuration and contrast (Table 2). The best resistance model produced based on habitat suitability was obtained from a lower exponential conversion of habitat suitability (type ABC). Importantly, resistance models based on the best habitat model for brown bear based on species occurrence records (Mateo Sánchez et al. 2014a) showed lower correlations and did not retain significance when IBD was partialled out.

Reciprocal causal modelling

All the final models had high Mantel correlations between genetic and landscape distances. The highest values were obtained for models obtained through the multivariate landscape genetic optimization framework: $r = 0.634$ and $r = 0.629$ for multiplicative and

Table 4 Univariate optimized variables

	Variable	Model	POSA	PCA	Ra	Model change in multivariate context
	PLAND MF	2C	0.628*	0.609*	0.570*	ADD (1B); MULT (3C)
	PLAND DF	3C	0.612	0.59	0.55	
	PLAND CF	3B	0.616	0.598	0.56	
	PLAND SH	3C	0.609	0.591	0.554	
	PLAND AG	2C	0.620*	0.604*	0.565*	–
	CC	1C	0.617*	0.6*	0.561*	ADD (2B)
	COH CF	3C	0.615	0.597	0.56	
	COH DF	3C	0.59	0.578	0.54	
	COH MF	2C	0.623*	0.605*	0.576*	–
	COH SH	2A	0.622*	0.603*	0.572*	–
	COH AG	3C	0.615	0.597	0.559	
Mantel R correlations between POSA and effective distance. Asterisk Supported variables after partialling out IBD. The optimal transformation function (model) as well as changes on this optimal transformation when integrated in a multivariate context [additive (ADD) and multiplicative (MULT)] are shown (Not supported variables were not introduced in the multivariate analysis)	AI CF	2C	0.6153	0.598	0.56	
	AI DF	3C	0.6152	0.598	0.56	
	AI MF	3C	0.617	0.599	0.559	
	CWED	3C	0.612	0.595	0.557	
	ED	3C	0.613	0.595	0.559	
	PD	3C	0.61	0.594	0.557	
	BD	2C	0.615	0.595	0.556	
	Slope	2C	0.603	0.587	0.553	
	Elevation	2C	0.612	0.594	0.557	
	INFR_DEN	3C	0.603	0.587	0.55	
	HW_DIST	3C	0.611	0.594	0.558	

additive multivariate models respectively, while $r = 0.621$ for the optimal resistance model derived from habitat suitability. The correlation value for null model IBD was $r = 0.614$ (Table 5) and the correlation for the resistance model based on the habitat model with best predictive performance for bear occurrence was $r = 0.578$ (Table 2). The selection of the best model was based on relative support of the causal modeling. IBR based on multiplicative landscape genetic optimization was supported when compared to the other final models (Table 6). The resistance model based on habitat suitability was not supported when compared to both multiplicative or additive optimized models.

Validation of landscape resistance model

The simulated population characteristics such as observed and Nei's estimated Heterozygosity (H_o and H_e) were similar to the real population. H_o and H_e were 0.39 and 0.47, respectively in the simulated population compared to values of 0.47 and 0.54 in the

real population (Pérez et al. 2009). The correlation with IBR was found to be $r = 0.685$ compared to $r = 0.634$ for the real genetic data. The model was also supported when IBD was partialled out.

Discussion

Insights on landscape resistance to brown bear movement provided by the optimization framework: from deforestation to highways

Among all the variables believed to influence brown bear gene flow, the only variables supported in our analysis were five land cover variables related to landscape composition and configuration. This suggests that landscape structure has important influences on bear movements. In particular, our results suggest that the extent of mixed forest and agricultural lands seems to impact the movement of bears, with mixed forest (most abundant class of forest in the study area) and high canopy cover promoting successful movements,

Table 5 Final models

Final models	Mantel R	Variables	Resist _{min}	Resist _{max}
IBR_add	0.629	Pland MF > COH MF > COH SH > PLANDAG > CC	126.9	10,129.9
IBR_mult	0.634		8564.55	1,243,139.4
IBR_hab	0.621	CC > PLAND MF > CWED > COH MF > AI MF	579	9081
IBD	0.614	Isolation by distance	1	1

The variables included in each model are ordered according to their contribution as well as Mantel R coefficient are shown for each model. See Table 1 for description of variables

Table 6 Results for reciprocal causal modelling

Partial r	Tested models			
	IBR_add_	IBR_mult_	IBR_hab_	IBD_
Models partialled out				
IBR_add		0.094*	-0.0111	-0.06
IBR_mult	0.029		0.043	0.015
IBR_hab	0.129*	0.162*		-0.052
IBD	0.183*	0.194*	0.127*	

The table shows the difference of support between final models when compared among themselves. The values of the columns show the models partial mantel R when the alternative models are partialled out. Asterisk is shown when partial mantel test were significant

and intensively human-modified cover types presenting resistance to movements. Also, the spatial connectedness of mixed forest and shrubland appears to be important in providing permeability and effective linkage areas.

Surprisingly, direct human disturbance did not significantly influence brown bear genetic structure, indicating that humans have affected bear gene flow in the landscapes of northwestern Spain primarily by indirectly altering the composition and configuration of the landscape (increased extent of agricultural lands, decreased extent and increased fragmentation of forest cover). The lack of an apparent effect of transportation infrastructure may be due to several reasons. First, transportation infrastructure may not be a complete barrier to bear movement, due to tunnels, viaducts or other fauna passes, which may allow some dispersal events. Migrants and admixed brown bear individuals have been recently detected (Pérez et al. 2010), which may corroborate this conclusion. Second, there may be a time lag effect, in which the genetic consequences of recent reductions in gene flow due to transport infrastructure may not be apparent in the population. This latter explanation is plausible given that a major highway that could be a

barrier between the two subpopulations has existed for less than 50 years (3–4 bear generations). In a simulation study, Landguth et al. (2010) showed that it may take considerably more generations for landscape genetic structure to emerge following the creation of a landscape barrier. Finally, the highway might be located in an area of extremely high resistance due to other factors (i.e., lack of forest and other forms of human impact), which may make the identification of the independent influence of the highway intractable using current methods.

Optimization of habitat-based and genetic-based resistance surfaces

Relying on a previous study that empirically assessed habitat selection under a range of hypotheses about underlying ecological factors (Mateo Sánchez et al. 2014a), we transformed and optimized habitat models in a similar way as the other factors included in the analysis to enable direct comparison of the performance of habitat versus genetic based models of landscape resistance. However, it is important to note that the genetic and habitat models could not be optimized in exactly the same way since the genetic

analysis is an optimization in a link-based framework using distances and the habitat is an optimization in a node based framework using Maxent for different focal neighborhood extents. As pointed by Wagner and Fortin (2013), the difference between link based distance methods and node based neighborhood methods is fundamental to landscape genetic vs habitat analysis. Additionally, the different methodological approaches lead to the use of different variables, even when starting from the same wide set of environment factors for both models (factorial multimodel vs. habitat model). The factorial multimodel approach is based on the selection of variables and then their integration in a multivariable context (i.e. to build a resistance model from scratch), while the use of the habitat models to derive a resistance surface entails the use of variables (from the same starting set) already selected to depict the species occurrence. These different approaches, as implemented in this study, reflect exactly what is currently being done in empirical and conservation-oriented work: either permeability models are based on habitat suitability models derived from occurrence data, or they are derived from optimization procedures using genetic data.

Habitat suitability as a surrogate of landscape resistance

The relative lack of congruence we found among habitat suitability and landscape resistance is important given that habitat suitability is very frequently used as a surrogate for the ease of movement (Chetkiewicz et al. 2006; Beier et al. 2008; Zeller et al. 2012). An important result of our analysis is that the habitat model which best predicted species occurrence, and which was based on landscape composition and human disturbance, was not statistically supported as an explanation of gene flow. Therefore, the habitat suitability models did not accurately reflect how the landscape affects the animals during the dispersal and migration movements directly related to gene exchange.

Even when the final (optimized) habitat-based resistance model was only slightly outperformed by the resistance derived from the factorial multimodel approach, it is necessary to point that a lot of effort was put in the selection of this habitat-based resistance. We carried out a optimization process of a set of habitat-

based resistance models by evaluating a wide range of alternative habitat selection models representing different ecological hypotheses, while commonly other studies use a much simpler approach to create the resistance surface, normally by using only a direct transformation of the single habitat model with best predictive performance. We here showed that the direct and more usual transformation of the best predictive habitat model (in terms of explaining species occurrence) into resistance presented a poorer performance in explaining genetic variation. Additionally, even when the correlations are high for both optimized models (habitat-based vs factorial multimodel approach), the statistical analysis demonstrated that the factorial multimode approach provided a model which was supported independently of the habitat model, while the habitat model was not supported independently of the landscape genetics model. Therefore, using the reciprocal causal modeling approach suggested by Cushman et al. (2013b) helped us to identify the limitations of habitat suitability models for explaining movement driving gene flow.

The results of this study suggest that estimating landscape resistance starting from optimization and selection of variables separately and then subsequent combination and optimization in a multivariate context performed better than optimizing a set of models derived from habitat suitability models for a species. Though three of the variables included in the most supported resistant model were also included in the final model derived from habitat selection, the remaining variables in the habitat-based model had no statistical support when they were separately analyzed in the optimization framework (CWED and AI of mixed forest), therefore introducing drivers without any influence on gene flow and thus on movement. Therefore, the two used approaches (factorial multimodel approach and habitat suitability model approach) differed considerably in the variables included in the final resistances models, so that conclusions about the factors that influence movement and gene flow in bears in this region would be considerably different depending on the approached used.

The mismatch between habitat suitability and landscape permeability was also noticed by other studies (e.g. Haddad and Tewksbury 2005; Horskins et al. 2006; Wasserman et al. 2010; Reding et al. 2013,

Peterman et al. 2014). This is not surprising given that habitat suitability is related to how well a location supports the occurrence of individuals along their lifespan, while gene flow is mediated primarily by mating movements and dispersal, usually of juvenile animals that may have very different behavior and different knowledge of the landscape than resident adults. However, previous studies have shown that habitat suitability can be used to model dispersal (Laiolo and Tella 2006; Wang et al. 2008; Newby 2011), but further evaluation, such as with reciprocal causal modeling in a multi-model framework, would be required to totally support these habitat-based models. The results of this study encourage considering the effects of different conceptual approaches underlying resistance models. We highlight that more comparative research is needed to fill current knowledge gaps related to landscape resistance.

Optimization of resistance models:
a multiplicative combination of variables better captures synergistic effects of multiple landscape factors on gene flow

The optimization approach adopted here (individual explanatory variables first considered separately and then integrated in a multivariate context) allowed for insights about the main resistors involved in gene flow for this species, about their functional response form and the range of relative resistance values, and about change in model parameters due to interactions among variables. We found that the optimal model correlation with genetic structure was affected by the way variables were combined. The multiplicative model had a slightly better performance than the additive approach, which suggests that (i) the absolute differences in the variables may be of less importance than their percentage changes, and that (ii) the synergistic combination of all of several resistors is important to explain brown bear movements through a particular landscape area. This combination may be better captured by the multiplicative than by the additive approach, since in the latter it may be more likely to obtain relatively high resistance values due to high values of individual resistors, rather than by the simultaneous (multiplicative) contribution of several of them in a given area. This finding may shed light on how landscape resistors should be combined, and which arithmetic operation better reflects

contributions and interactions of variables to the overall models, an issue pointed by Beier et al. (2008).

In addition, simulations provide an extremely valuable addition to the optimization framework by evaluating model performance relative to a controlled process as pointed out by Shirk et al. (2010, 2012), and recently illustrated by Castillo et al. (2014). The simulations we performed based on the optimized resistance model produced a population genetic structure highly similar to that observed in the empirical population. Thus, the selected optimal model likely provided a spatially explicit prediction of landscape resistance that also offers a robust ecological inference of landscape resistors and gene flow.

Mantel test in landscape genetics

The validity of the analytical approaches existing to link observed genetic patterns to landscape characteristics is an active topic in the landscape genetics literature. Mantel testing techniques have been the most widely used approach since the inception of the field. There has been considerable discussion in the literature regarding the validity of the Mantel test (e.g. Guillot and Rousset 2013; Graves et al. 2013). When relying simply on significance values of Mantel and partial Mantel tests, high power but also elevated type-1 error rates have been observed (e.g. Balkenhol et al. 2009; Graves et al. 2013; Cushman et al. 2013b). However, we only used Mantel tests in our model optimizations to (a) identify those resistance surfaces that did not lead to a significant correlation with genetic distances; and (b) to identify the model parameterization that led to highest correlations for each variable. For (a), the high power of Mantel tests means that any model not leading to a significant correlation with genetic data is very likely not important for explaining genetic structure and can therefore be removed from further analysis. For (b), we did not use significances, but instead relied on a comparison of correlation values. Hence, the high type-1 errors of Mantel lists are not an issue here. In addition, most of the putative limitations have been refuted or addressed with changes in how the Mantel test is applied. For example, nonlinearity in the relationship between genetic and cost distances (Graves et al. 2013) often is not an issue when the study area extent is relatively small compared to the

dispersal ability of the species (e.g. Cushman et al. 2006) and when it exists can be readily corrected with appropriate transformations (e.g. Ruiz-González et al. 2014). Furthermore, the supposed bias in the permuted p value obtained for the Mantel test is corrected when using the proper permutation procedure. Importantly, as used in this study, most current applications of the Mantel test in landscape genetics use multivariate optimization coupled with procedures to compare all combinations of models directly based on the magnitude of partial mantel correlations rather than inferential tests of significance, which greatly improves strength of inference and avoids the main issues criticized in the literature (e.g. Shirk et al. 2010, Wasserman et al. 2010, Cushman et al. 2013a, Castillo et al. 2014). The optimization approach using partial Mantel tests in a causal modeling framework has been shown to have high power to correctly identify driving hypotheses and reject highly correlated but incorrect alternative models (e.g. Shirk et al. 2010, 2012, Cushman et al. 2013b, Castillo et al. 2014). Indeed, Shirk et al. (2012) and Castillo et al. (2014) used different simulation approaches to demonstrate that multivariate Mantel optimization coupled with causal modeling produce accurate and valid results. There is a continued interest in developing other approaches that may advance the field (e.g. Selkoe et al. 2010; Van Strien et al. 2012). However, it seems that alternative analytical approaches have yet to be identified that do not suffer from other major limitations have not yet been identified. For example there is much interest in applying AIC based information theoretic model selection to multiple regression on distance matrices. However, recent research has shown that the non-independence among observations in the distance based framework and the inherent very high correlation among explanatory variables in resistance modeling results in serious bias to AIC in a distance-based framework (e.g. Francowics et al. submitted, SA Cushman unpublished data).

Conclusions and implications

Understanding how landscapes influence animal movement is a central focus of contemporary connectivity research, which is often linked to conservation and planning efforts. Therefore, it is critical to provide rigorous landscape resistance models as a foundation

for connectivity assessments. In this study, we presented an analytical process to compare two approaches widely used to produce maps of landscape resistance. We used individual-based genetic data to compare a multi-model optimization approach to a direct conversion of habitat suitability. We showed that habitat suitability is not an accurate surrogate of landscape resistance. Gene flow for brown bears in northwest Spain seems not to be simply driven by habitat suitability. Landscape composition and human disturbance were restrictive factors for the species occurrence, but such factors appear not to be determinant for brown bear movement and gene flow. When they need to do so, some species may easily move through areas that are unlikely to be suitable habitats for foraging, sheltering, resting or breeding. Since individuals spend the great majority of time in these suitable habitat areas, habitat models derived from presence data may be biased towards the landscape conditions that provide permanent, stable habitat for the species. At the same time, habitat models may misestimate the ability of species to traverse low-suitability areas through rare but crucial dispersal events driven by a small number of individuals during very concrete and narrow periods of their lifespan. These movement events, which are likely to be underrepresented in most, if not all, habitat models, can largely contribute to the genetic structure and long-term persistence of populations. Infrequent dispersal events and the actual species movement abilities through rarely occupied areas, are best inferred and quantified through an optimized landscape genetics approach as the one here presented and applied for the brown bears. In summary, our results confirmed that movement and habitat selection may be related to different factors and should be separated when studying resistance in order to avoid potential misinformation of conservative efforts. We consider that further 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 models actually are for practical conservation planning.

Finally, our landscape genetics analysis provides important, quantitative and spatially explicit insights for brown bear conservation and management in the Cantabrian range, given that promoting landscape permeability and connectivity has been widely

acknowledged as a key concern and priority for ensuring the long term persistence of this endangered species. The model here presented provides the basis for reinforcing and establishing further linkages to enhance genetic connectivity among native brown bear subpopulations in Spain.

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