


# Expert-based versus habitat-suitability models to develop resistance surfaces in landscape genetics

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**Abstract** Landscape genetics aims to investigate functional connectivity among wild populations by evaluating the impact of landscape features on gene flow. Genetic distances among populations or individuals are generally better explained by least-cost path (LCP) distances derived from resistance surfaces than by simple Euclidean distances. Resistance surfaces reflect the cost for an organism to move through particular landscape elements. However, determining the effects of landscape types on movements is challenging. Because of a general lack of empirical data on movements, resistance surfaces mostly rely on expert knowledge. Habitat-suitability models potentially provide a more objective method to estimate resistance surfaces than expert opinions, but they have rarely been applied in landscape genetics so far. We compared LCP distances based on expert knowledge with LCP distances derived from habitat-suitability models to evaluate their performance in

landscape genetics. We related all LCP distances to genetic distances in linear mixed effect models on an empirical data set of wolves (*Canis lupus*) from Italy. All LCP distances showed highly significant ( $P \leq 0.0001$ ) standardized  $\beta$  coefficients and  $R^2$  values, but LCPs from habitat-suitability models generally showed higher values than those resulting from expert knowledge. Moreover, all LCP distances better explained genetic distances than Euclidean distances, irrespective of the approaches used. Considering our results, we encourage researchers in landscape genetics to use resistance surfaces based on habitat suitability which performed better than expert-based LCPs in explaining patterns of gene flow and functional connectivity.

**Keywords** *Canis lupus* · Expert knowledge · Least-cost path distances · Linear mixed effect models · Species distribution models

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## Introduction

A main issue of landscape genetics is to identify the relationships among landscape features and the genetic structure of natural populations (Segelbacher et al. 2010), providing evidence of functional connectivity across landscapes through gene flow (Manel et al. 2003; Holderegger et al. 2007; Holderegger and Wagner 2008; Balkenhol et al. 2009). The ability of animals to move among habitat patches is fundamental for the viability of spatially structured populations. In landscape genetics, movement paths connecting populations or individuals are usually identified through resistance surfaces. Resistance surfaces are grid maps representing the resistance to move through the landscape features of each cell. From resistance surfaces, distances along least-cost paths (LCP; Cushman 2006;

Cushman and Lewis 2010; Shirk et al. 2010; Sawyer et al. 2011; Galpern et al. 2012; Parks et al. 2013) are then determined and related to genetic distances among populations or individuals. In the case, landscape features have significant effects on movement, and LCP distances are supposed to better correlate with genetic distances than simple Euclidian distances (Holderegger and Wagner 2008). However, empirical knowledge of the factors facilitating or hindering movements of individuals (and thus genes) across landscapes is often limited (Graf et al. 2007).

When creating resistance surfaces, different resistance values are assigned to specific landscape features. Defining the resistance of landscape features to movement is challenging (Spear et al. 2010; Zeller et al. 2012), and the best way for assigning resistance values to different landscape attributes is still debated (Zeller et al. 2012). For instance, one could use direct observations, radio tracking, or GPS rendering to obtain empirical data on the use of landscape features by target species (Spear et al. 2010). Nevertheless, due to the limited availability or often complete lack of empirical data on movement, resistance surfaces are typically based on expert opinions only (Spear et al. 2010; Zeller et al. 2012). However, resistance surfaces derived from expert opinions can be error prone; because they rely on the potentially biased experience of the experts, the knowledge of the study area can be scarce and the information on the general ecology of the studied species often limited in published literature (Spear et al. 2010; Shirk et al. 2010; Zeller et al. 2012; Balkenhol et al. 2014; Stevenson-Holt et al. 2014).

A method avoiding expert opinions to develop resistance surfaces is provided by several types of habitat-suitability models (HSMs; also known as species distribution models; Guisan et al. 2013). HSMs interpolate locations of species occurrence with environmental variables and show high accuracy in predicting species distributions (Rebelo and Jones 2010). Models of habitat suitability can be directly used to assign resistance values to particular landscape features by assigning a resistance value of “1-habitat suitability” to each grid cell of the resistance surface (Wang et al. 2008; Pullinger and Johnson 2010; Spear et al. 2010). To date, HSMs are widely applied in ecological research, e.g., to design protected areas (Johnson et al. 2004), assess the risk of colonization of invasive species (Beaumont et al. 2009), evaluate the impact of climate change on biodiversity (Hof et al. 2012), or identify the environmental variables affecting species occurrence (Franklin 2013). Surprisingly, HSMs have been rarely used in landscape genetics to develop resistance surfaces (Laiola and Tella 2006; Wang et al. 2008, 2013; Huck et al. 2010; Brown and Knowles 2012; Duckett et al. 2013; Mateo-Sánchez et al. 2014; Milanese et al. 2016). The limited application of HSMs in landscape genetics is possibly due to the hypothesis that HSMs

may correctly identify the home range or the reproductive habitat of a species, but not the landscape elements that are used during movement or dispersal (Spear et al. 2010; Keller and Holderegger 2013). However, in addition, the resistance to movement across landscapes is reflected by the distribution of suitable habitats and resources (e.g., food and/or prey availability; Van Dyck and Baguette 2005; Baguette and Van Dyck 2007). Thus, HSMs could be objective tools to develop resistance surfaces and LCPs in landscape genetics (Laiola and Tella 2006; Wang et al. 2008, 2013; Huck et al. 2010; Pullinger and Johnson 2010; Brown and Knowles 2012; Duckett et al. 2013).

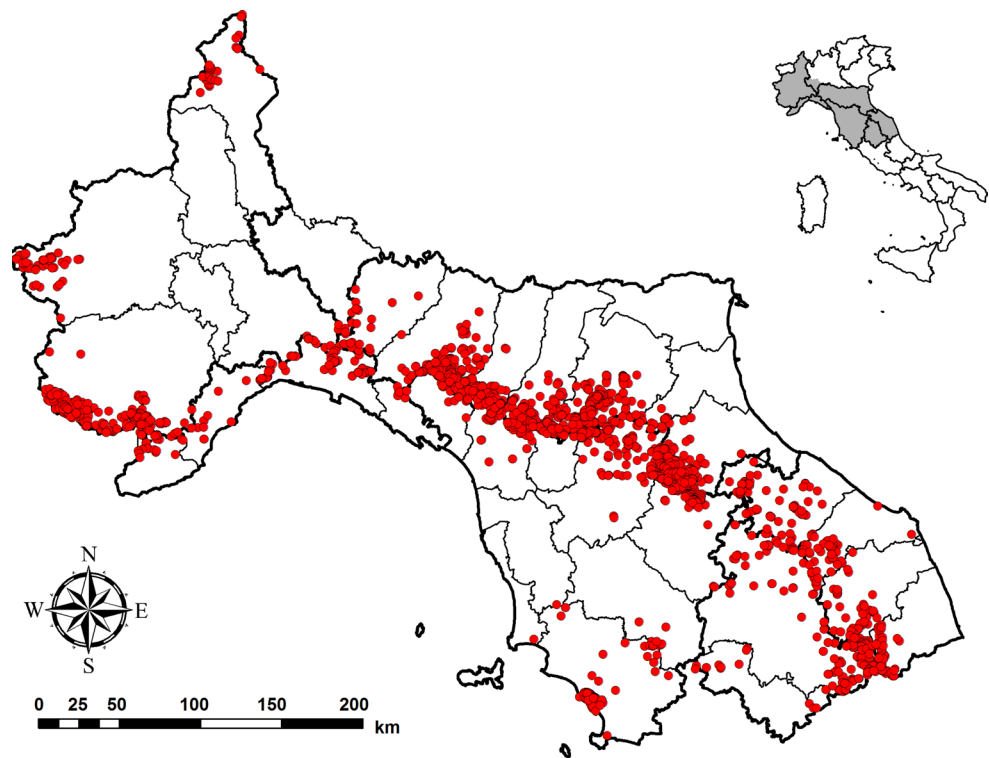
To our knowledge, a comparison of expert-based and HSMs-derived LCPs has not been performed on any empirical data set in landscape genetics so far, except for the study by Mateo-Sánchez et al. (2015), which applied only one HSM. Since different HSMs could lead to different resistance surfaces (Milanesi et al. 2016), the aim of our study was to compare the performance of several expert-based LCPs with that of HSM-derived LCPs in explaining individual genetic distances. Taking also into account Euclidean distances (Van Strien et al. 2012; Etherington and Holland 2013), we carried out linear mixed effect models (Selkoe et al. 2010; Van Strien et al. 2012) between a matrix of pairwise genetic distances and matrices of LCP distances derived by 13 expert-based and 9 widely used HSMs. Our empirical data set consisted of individual wolf (*Canis lupus*) genotypes collected in the northern part of Italy (Fabbri et al. 2007; Caniglia et al. 2014; Milanese et al. 2016). Specifically, unlike Milanese et al. (2016), which tested whether different HSMs may result in different landscape genetic inferences, in the present study, we compared LCP distances based on expert knowledge with those derived from HSMs to evaluate their performance in landscape genetics.

## Materials and methods

### Study area

We sampled a wolf population distributed across an area of 97,044 km<sup>2</sup>, extending from the Central Apennines to the western-central Alps in Italy (6°62′–13°91′E; 46°46′–42°39′N; Fig. 1). Due to a wide altitudinal range (from 0 to 4634 m a.s.l.), a strong environmental gradient (from temperate to alpine ecosystems), and diverse human land uses, the study area shows a variety of habitat types. Forests, meadows, pastures, rocky areas, and glaciers characterize the mountainous sector. In the lower mountains and hills, the traditional rural ecosystems have mostly been abandoned and are evolving towards semi-natural shrub-lands and deciduous, mixed, or evergreen forests. Cultivated

**Fig. 1** Study area and wolf locations (*red dots*) within Italy (*upper-right corner*). *Black lines* indicate regional borders, *grey lines* indicate provincial borders (*color figure online*)



fields and urban areas are located in the main valleys, the plains, and along the Mediterranean coast.

### Genetic data set

From 2000 to 2011, wolves in the study area were monitored based on non-invasive sampling and molecular identifications. Trained personnel collected 9317 putative wolf samples (mainly feces, but also blood or muscular tissues from carcasses) along randomly chosen trails and country roads across the whole study area (Caniglia et al. 2012, 2014). Sampling locations were recorded with a GPS in the UTM WGS84 32 N coordinate system, and samples were stored at  $-20^{\circ}\text{C}$  in ten volumes of 95 % ethanol or Tris/SDS buffer (Caniglia et al. 2012).

DNA was extracted using the MULTIPROBE IIEX robotic liquid handling system (Perkin Elmer) and the QIAGEN stool and tissue extraction kit (Qiagen). DNA extracts were amplified by polymerase chain reaction (PCR) then genotyped according to the methods described in Caniglia et al. (2014), at: (1) a 350 bp sequence of the mtDNA control region, containing diagnostic mutations for the identification of the Italian wolf haplotype W14; (2) four Y-linked microsatellites (Y-STRs MS34A, MS34B, MSY41A, and MS41B) used to describe paternal haplotypes in males, previously molecularly sexed by a PCR–RFLP assay of the zinc finger protein genes ZFX/Y; and (3) 12 unlinked, neutral, and autosomal microsatellite loci

(CPH2, CPH4, CPH5, CPH8, CPH12, C09.250, C20.253, FH2004, FH2079, FH2088, FH2096, and FH2137) to reconstruct genetic profiles. All microsatellites were analyzed by a multiple-tube procedure to account for genotyping errors. Taxon assignment (i.e., wolf, dog, or wolf  $\times$  dog hybrids) identified a total of 3815 wolf samples, belonging to 923 individual wolves. In addition, 93 dogs and 118 wolf  $\times$  dog hybrids were identified and discarded from further analyses.

We then computed a genetic distance matrix based on microsatellite data (ranging between 0, low, 1, and high distances) between all pairs of 923 wolf genotypes using GENALEX 6.41 (Peakall and Smouse 2006) as 1 proportion of shared alleles (Hartzlitt et al. 2004). We used the proportion of shared alleles because of its wide and successful application in individual-based landscape genetics analyses (Waits and Storer 2016).

### Landscape features

To develop resistance surfaces, we selected ten landscape features (Table 1) potentially relevant for both wolf distribution and movement (Rodríguez-Freire and Crecente-Maseda 2008; Huck et al. 2010, 2011; Carroll et al. 2012; Llana et al. 2012; Kaartinen et al. 2015). We derived data on land cover types from the CORINE Land Cover level IV (European Environment Agency 2006; Table 1): coniferous forests, deciduous forests, mixed woods, shrub lands,

**Table 1** Landscape features and relative resistance values assigned to develop true and extrapolated expert-based (tEBMs and sEBMs, respectively) resistance surfaces to wolf movement

Landscape element	Coniferous forests (%)	Mixed woods (%)	Shrub-lands (%)	Cultivated fields <sup>a</sup> (%)	Deciduous forests (%)	Meadows (%)	Altitude (m a.s.l.)	Human settlements (%)	Distance from human settlements (m)	Human population density (n/km <sup>2</sup> )
tEBM 1	50	50	75	–	50	50	50	1	100	10
tEBM 2	90	95	50	–	50	25	25	1	75	5
tEBM 3	50	50	25	–	75	10	95	50	25	1
tEBM 4	25	25	10	–	1	10	5	100	1	100
sEBM 1	95	5	50	–	1	10	25	100	90	75
sEBM 2	100	10	75	–	5	25	50	1	95	90
sEBM 3	1	25	90	–	10	50	75	5	100	95
sEBM 4	5	50	95	–	25	75	90	10	1	100
sEBM 5	10	75	100	–	50	90	95	25	5	1
sEBM 6	25	90	1	–	75	95	100	50	10	5
sEBM 7	50	95	5	–	90	100	1	75	25	10
sEBM 8	75	100	10	–	95	1	5	90	50	25
sEBM 9	90	1	25	–	100	5	10	95	75	50
VIF	1.09	1.07	1.12	>3	1.64	1.38	2.39	1.33	1.95	1.65

<sup>a</sup> Landscape features with a variance inflation factor (VIF) higher than three were removed from further analyses due to multicollinearity with other features. The same landscape features were used as predictor variables in habitat-suitability models (HSMs)

meadows, and cultivated fields. We further considered the presence of and distance to anthropogenic elements, human settlements (i.e., urban areas and villages also derived from the CORINE Land Cover level IV; roads and railways from OpenStreetMap; <http://www.openstreetmap.org>), and human density (<http://dati.istat.it>; Table 1). Altitude was taken from a digital elevation model of Italy (<http://www.sinanet.isprambiente.it>; Table 1). To avoid that multicollinearity among predictors negatively affected landscape genetic analyses (Prunier et al. 2015), we calculated the variance inflation factor (VIF). As suggested by Zuur et al. (2010), we removed the predictor variable “cultivated fields”, because it showed a VIF value higher than three (i.e., highly related with other predictor variables; Table 1). To verify that grid size did not significantly affect landscape genetic analysis (Cushman 2006; Wasserman et al. 2010; Keller et al. 2013; Mateo-Sánchez et al. 2013), we considered three grid sizes of 500, 1000, and 2000 m. All variables were re-sampled to these grid cell sizes in ARC-GIS 10 (ESRI, Redlands, California).

### Resistance surfaces and least coast paths

We used three different types of resistance surfaces:

1. To develop resistance surfaces derived from expert-based models, the four authors with extensive knowledge of the Italian wolf biology were asked to act as experts to provide values of resistance. After discussing the chosen landscape features above and the meaning of resistance values (1 indicating favourable and 100 non-favourable landscape features for wolf movement), each expert independently assigned a resistance value to each landscape feature. These were the landscape resistance values that we used in four “true” expert-based models (tEBMs; Table 1).
2. From the existing literature, it is evident that there is no agreement on which landscape elements particularly favour wolf movement and dispersal. For instance, wolves are considered habitat generalists (Fechter and Storch 2014) and show successful dispersal and movement also across human-dominated areas (Ciucci et al. 2009; Andersen et al. 2015). It is thus not easy to deduce appropriate resistance values for wolf movement from the literature. Thus, in a second set of models, we simply randomly varied the resistance values of the chosen landscape features, from 1 to 100 to generate another set of nine simulated expert-based models (sEBMs) that reproduce different hypotheses on how landscape features affect wolf movement (Table 1).
3. Among the many HSMs currently available, we choose nine widely applied methods: (1) generalized linear models (GLM; McCullagh and Nelder 1989), a

binary logistic model relating species occurrences and pseudo-absences with predictor variables; (2) boosted regression trees (BRT; Friedman 2001), which fit a wide number of models and combine their predictions to provide a robust estimate of species occurrence; (3) generalized additive models (GAM; Hastie and Tibshirani 1990) that use smoothing functions derived from predictors to estimate conventional parametric components of linear predictors; (4) artificial neural networks (ANN; Ripley 2007), which model unobserved variables derived by a linear combinations of predictors; (5) multiple adaptive regression splines (MARS; Friedman 1991) that model unobserved variables derived by non-linear combinations of predictors; (6) random forests (RF; Breiman 2001), which combine regression tree predictors with a random vector sampled independently; (7) maximum entropy (MAXENT; Phillips et al. 2006), which computes functions to find the best approximation between the density distributions of predictors at locations, where the species was recorded and those of the entire study area; (8) factorial decomposition of Mahalanobis distances (MADIFA; Calenge et al. 2008), a factorial method that associates eigenvalues derived from uncorrelated axes to calculate scores of habitat suitability; and (9) flexible discriminant analysis (FDA; Hastie et al. 1994), derived from linear discriminant analysis, which uses a classification method based on mixture models.

HSMs included the same landscape features, as described in Table 1, and all wolf locations (including locations or recurrent wolf genotypes) were used to classify all cells as either “used”, if at least one wolf genotype was sampled within the cell or “available” otherwise.

Moreover, we calculated a measure of sampling effort through Gaussian kernel density analysis (Elith et al. 2010; Fourcade et al. 2014) based on all sampling locations (including wolves, dogs, and wolf  $\times$  dog hybrids; Milanese et al. 2016). Sampling effort (ranging from 0 to 1) was higher in mountainous and hilly areas of the Central Apennines and the western-central Alps than in lowlands and along the Mediterranean coast, resulting in a cline of per-cell values from the mountainous part of the study area to the coast (Milanese et al. 2016). Per-cell values of the resulting sampling effort map were used as weights in MADIFA, as grid bias in MAXENT and as case weights in all other HSMs.

Spatial autocorrelation among wolf locations was investigated with 10,000 permutations and Moran’s I (Dormann et al. 2007). Considering that there was spatial autocorrelation among wolf locations up to a distance of 1550 m, we developed HSMs with only 987 non-autocorrelated samples. Residual spatial autocorrelation (as 1-predicted



HSMs) was also investigated with Moran's  $I$  with 10,000 permutations (De Marco et al. 2008). HSMs  $k$ -fold cross validations were carried out using a random subsample of 50 % of all wolf locations to calibrate models and the remnant 50 % to validate them (Boyce et al. 2002), through the evaluation of the area under the curve (AUC; Ko et al. 2011) and Boyce's index (BI; Boyce et al. 2002; Table S1). To create resistance surfaces, we calculated the resistance value per grid cell as one-habitat suitability (Wang et al. 2008; Pullinger and Johnson 2010; Spear et al. 2010).

For both the EBM and the HSMs, we determined the distance along LCPs between all pairs of locations ( $n = 923$ ), where individual wolves had first been sampled. We also determined the Euclidian distance among all these pairs of wolf locations.

### Landscape genetic analysis

We used linear mixed effect models (with 10,000 permutations), recently applied and strongly promoted in landscape genetics (Selkoe et al. 2010; Van Strien et al. 2012; Bolliger et al. 2014), to investigate the relationship between genetic distances and LCP distances. Linear mixed effect models combine fixed and random effects in linear models. In our case, LCP distances (from both EBM and HSMs) and Euclidian distances were considered as fixed effects. Genetic distances among individuals were the response variable. As pairwise distance estimates do not provide independent data, a Toeplitz covariance matrix was taken into account as a random effect (Selkoe et al. 2010).  $R^2$ - and standardized  $\beta$  values were used as a measure of the relationship between response and predictor variables (Van Strien et al. 2012). We also verified whether resolution (i.e., 500, 1000, and 2000 m; see above) affected the relationship between genetic and LCP distances. All statistical analyses were carried out in R (R Core Team 2013).

## Results

HSMs evaluation showed high values of all statistical validation tests and thus high predictive accuracy (especially for AUC in RF and for BI in MAXENT, BRT, FDA, and GAM; Table S1). Moreover, spatial autocorrelation among the residuals of all nine applied HSMs was not significant.

Considering the resulting LCPs (Figs. 2, 3, 4), inter-individual genetic distances were significantly explained by all EBM and HSM-derived LCP distances in linear mixed effect models ( $P \leq 0.0001$  in all cases; Table 2). In addition, all standardized  $\beta$  values of all LCP distances were higher than those of Euclidean distances, showing that LCP distances, and therefore, landscape features had a larger effect on genetic distances among pairs of wolves than

geographic distances alone. This also held true for all three grid cell sizes considered (Table 2).

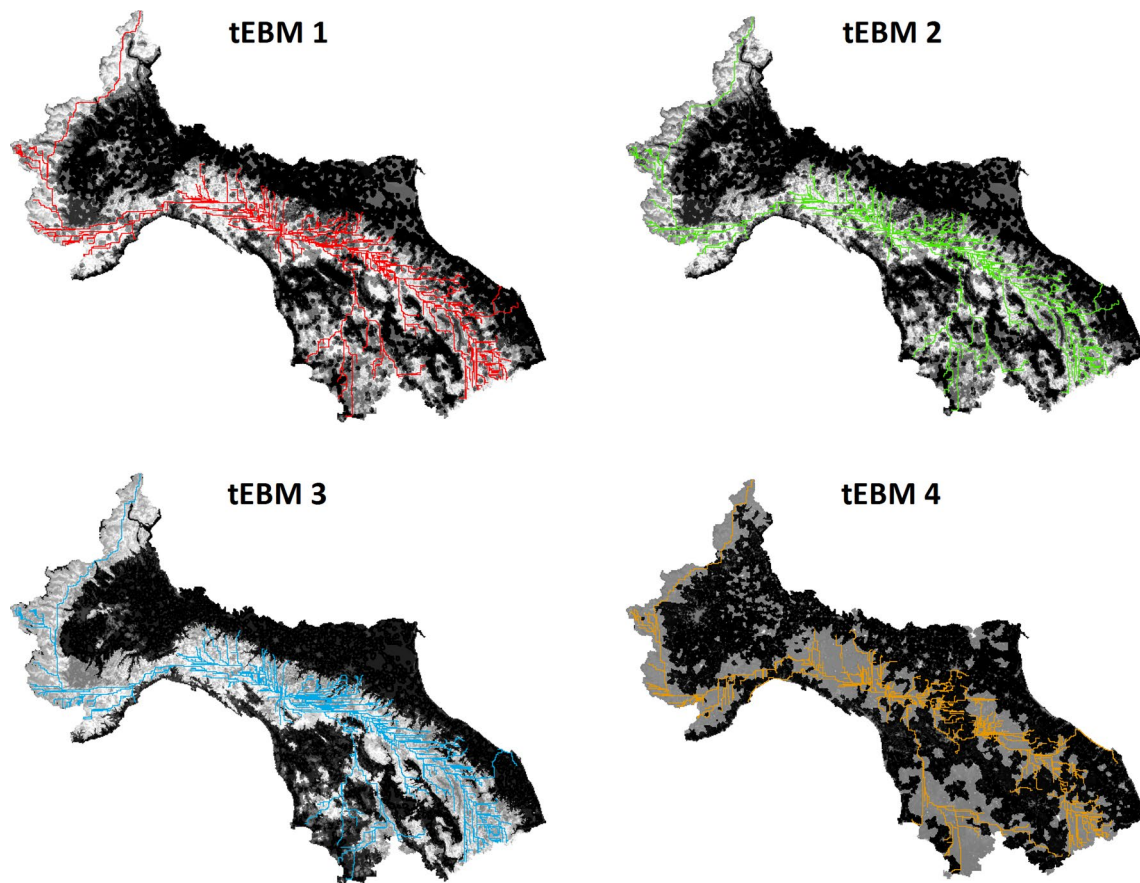
The standardized  $\beta$  values of LCP distances highlighted marked differences among the LCPs based on EBM and those based on HSMs. In particular, at a grid cell size of 1000 m, LCP distances from MADIFA showed the highest  $\beta$  coefficient (0.943) followed by those from GLM (0.773) and ANN (0.604; Table 2). All other HSMs showed higher  $\beta$  values than those of EBM, except for tEBM 4 (0.526), sEBM 1 (0.526), sEBM 9 (0.484), sEBM 8 (0.465), and sEBM 7 (0.442; Table 2). We found similar results at the 500 m grid cell size. Again, LCP distances derived from MADIFA showed the highest  $\beta$  coefficient (0.774) followed by LCP distances from GLM (0.742) and GAM (0.573; Table 2). sEBM 7 showed a  $\beta$  value (0.521) higher than those of the other HSMs and all other EBM (Table 2). In addition, at the 2000 m grid cell size, LCP distances derived from MADIFA showed the highest  $\beta$  coefficient (0.915) followed by LCP distances of GLM (0.727), ANN (0.644), GAM (0.557), and BRT (0.551; Table 2). Similar to the 1000 m grid cell size, tEBM 4, sEBM 9, sEBM 1, sEBM 8, and sEBM 7 showed  $\beta$  values (0.551, 0.497, 0.495, 0.485 and 0.465, respectively) higher than those of the other HSMs and EBM. Standardized  $\beta$  values of LCPs were generally lower at the 500 m than at the 1000 and 2000 m grid cell size.

All LCPs showed very high and similar  $R^2$  values (ranging from 0.805 to 0.808) at the 1000 m grid cell size (Table 2).  $R^2$  values of all LCPs at the 500 m grid cell size (0.828–0.832) were similar but somewhat larger than those at the 1000 m grid cell size. Those at the 2000 m grid cell size were markedly smaller, but still high (0.746–0.753; Table 2).

There was no congruent pattern between sEBMs and tEBMs: some tEBMs showed very low  $\beta$  values, lower than the  $\beta$  coefficients of some sEBMs, but sEBM 4 generally showed the highest  $\beta$  values across the three grid cell sizes.

## Discussion

Resistance surfaces are mostly based on expert opinions (Lee-Yaw et al. 2009; Murray et al. 2009; Cushman and Lewis 2010; Shirk et al. 2010; Zeller et al. 2012), but the application of HSMs to derive resistance surfaces in landscape genetics has recently increased (e.g., Wang et al. 2008, 2013; Brown and Knowles 2012; Duckett et al. 2013; Mateo-Sánchez et al. 2014). In this study, we compared LCPs estimated from resistance values derived from several EBM to LCPs resulting from some currently used HSMs in a landscape genetic framework. Our results demonstrated that HSMs-derived LCP distances might outperform those based on EBM and that the former could thus



**Fig. 2** Resistance surfaces (*dark grey shading indicates higher resistance and light grey shading lower resistance, respectively*) and corresponding least-cost paths (*colored lines*) among 923 individual wolf

locations (1000 m grid cell size) for resistance surfaces based on four true expert-based models (tEBMs). For abbreviations, see “[Materials and methods](#)” section (color figure online)

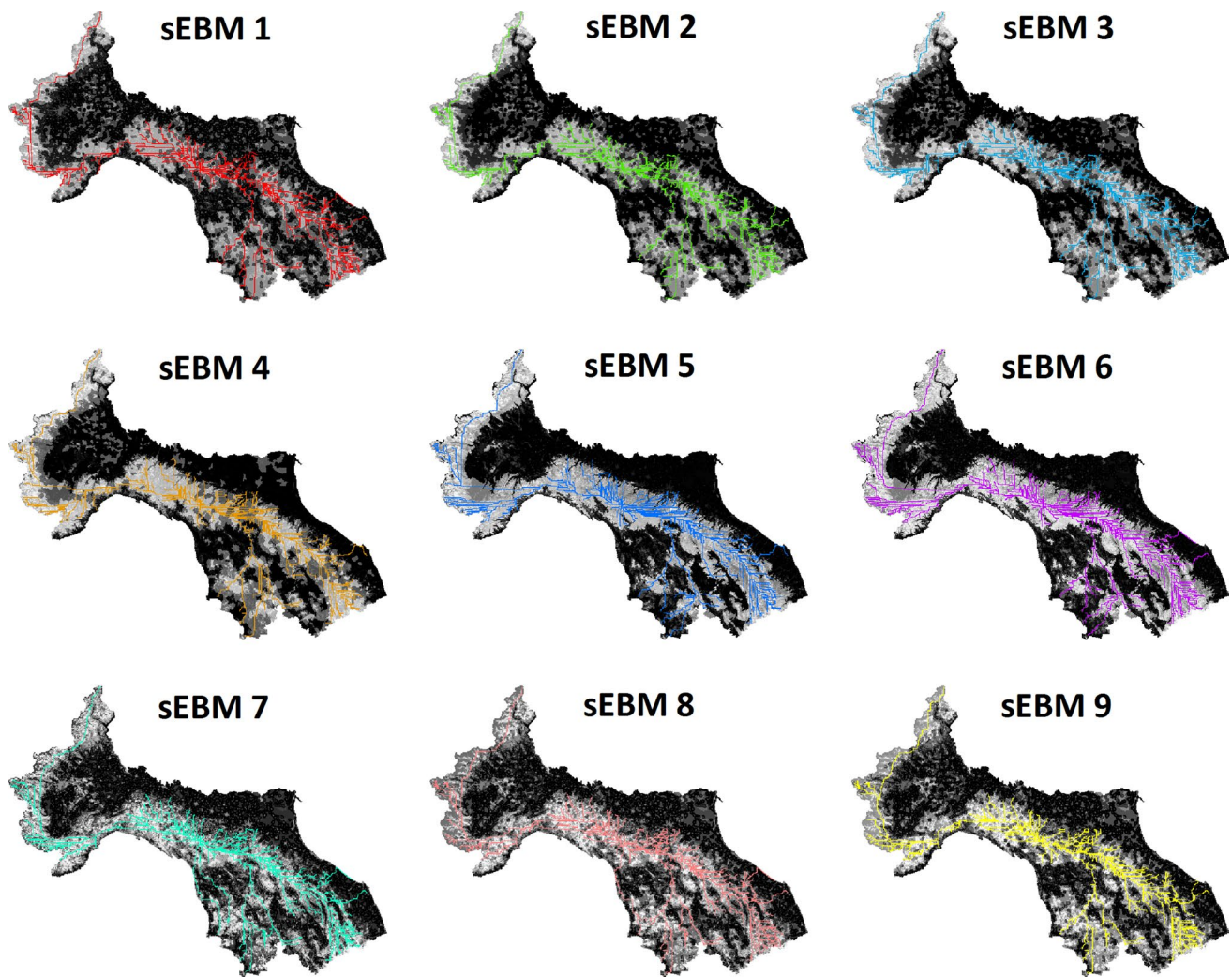
represent a more objective tool to define resistance values in landscape genetic analyses.

### Resistance surfaces derived from expert-based and habitat-suitability models

To enable a direct comparison of the performance of EBMs versus HSMs-derived resistance surfaces in landscape genetics, we used the same set of landscape features as predictor variables in all models. In contrast to recently applied factorial methods, which lead to the use of different variables even when starting from the same set of landscape features (Mateo-Sánchez et al. 2015), our resistance maps were always based on the same set of predictor variables, in both EBMs and HSMs. Actually, factorial approaches are based on a selection procedure for the variables best fitting to genetic distances in a multivariable context (Mateo-Sánchez et al. 2015). In contrast, our EBMs and HSMs entailed the use of variables from the same starting set. Differences among our resistance maps derived from EBMs and HSMs were due to the application of

different resistance values to the same landscape features in the former and different model assumptions, complexities, and algorithms in the latter (Elith et al. 2005; Tsoar et al. 2007). Accordingly, this also held true for LCPs estimated from the respective resistance surfaces. Thus, our approach allowed for a direct comparison of the performance of EBMs and HSHs in landscape genetics.

However, both EBMs and HSMs present some caveats. The main problem when using EBMs is that the resistance values assigned to specific landscape features are (largely) subjective (Spear et al. 2010; Zeller et al. 2012). They might be more or less accurate, but there is no way to directly evaluate them. Experts may over- or underestimate the effect of certain landscape features on movement (Clevenger et al. 2002; Stevenson-Holt et al. 2014). The appropriateness of EBMs also varies depending on the experience of the expert and the general knowledge of the target species ecology (Clevenger et al. 2002; Seoane et al. 2005; Clark et al. 2008; Lee-Yaw et al. 2009; Murray et al. 2009; Spear et al. 2005, 2010; Cushman 2006; Shirk et al. 2010; Zeller et al. 2012; Balkenhol et al. 2014; Stevenson-Holt



**Fig. 3** Resistance surfaces (*dark grey shading* indicates higher resistance and *light grey shading* lower resistance, respectively) and corresponding least-cost paths (*colored lines*) among 923 individual

wolf locations (1000 m grid cell size) for resistance surfaces based on nine simulated expert-based models (sEBMs). For abbreviations, see “[Materials and methods](#)” section (color figure online)

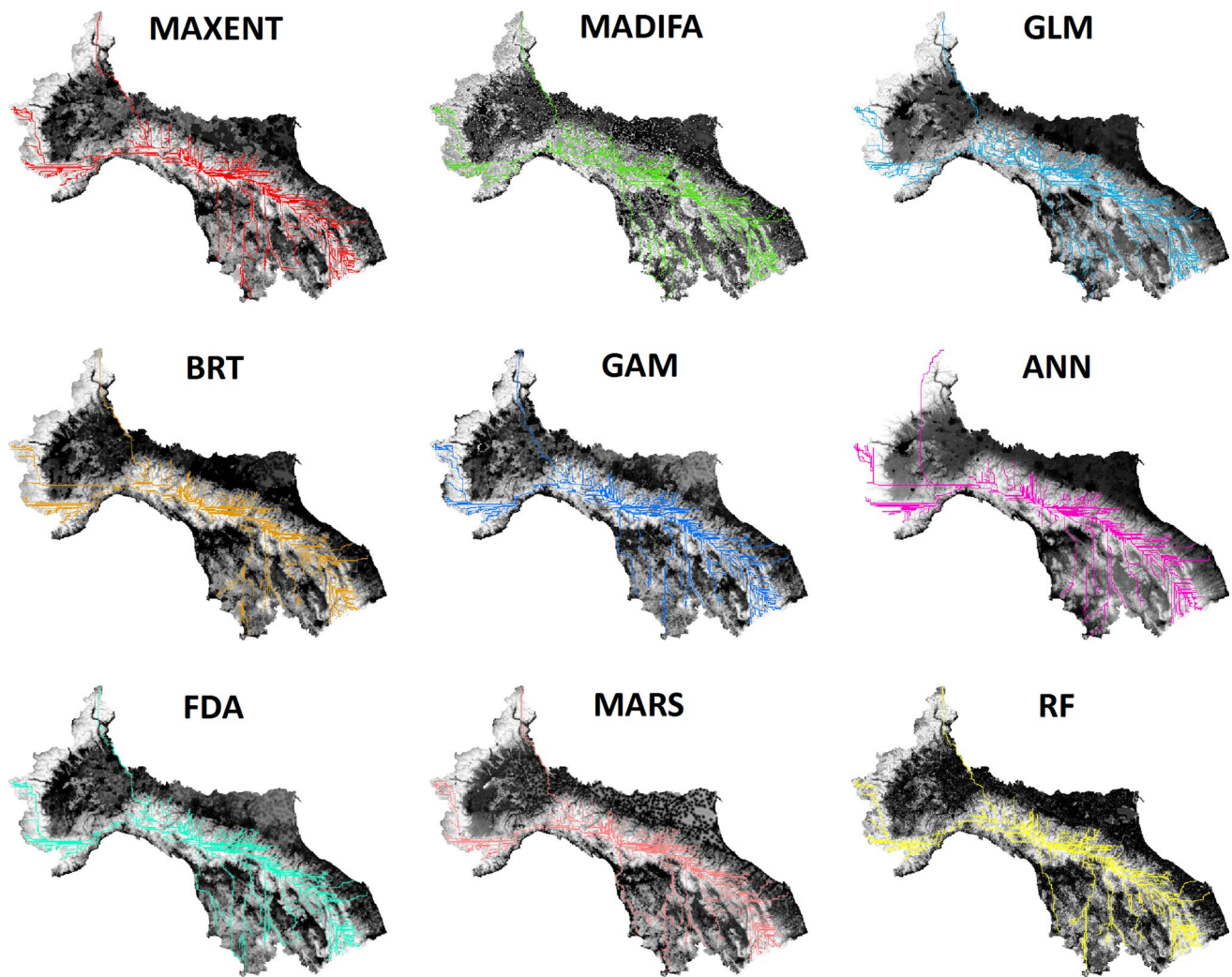
et al. 2014). This uncertainty is the reason why in EBMs researchers tend to use several hypotheses on landscape resistance based on different combinations of resistance values assigned to different landscape features.

Although the use of expert opinions to parameterize LCPs is subjective, many studies successfully applied this approach to parameterize models in landscape genetics (Cushman and Lewis 2010; Shirk et al. 2010). Clevenger et al. (2002) found that expert opinion compared well with an empirical model based on radio telemetry data for black bears (*Ursus americanus*) in Canada. Moreover, the use of expert opinions may be appropriate in cases, where there is a shortage of empirical data on the species distribution (Stevenson-Holt et al. 2014).

On the other hand, the main problems when using HSMs to derive LCP distances are that they are correlative

approaches, and thus, they may mainly represent the reproductive habitat of species or the home ranges of individuals, but not necessarily the landscape elements affecting movement and dispersal (Spear et al. 2010; Keller and Holderegger 2013). However, the resistance or the relative cost of a landscape feature to movement and dispersal is also reflected by the spatial distribution of suitable areas and the resource availability for a species (Van Dyck and Baguette 2005; Baguette and Van Dyck 2007). If so, HSMs may be more objective tools to derive resistance maps in landscape genetics (Wang et al. 2008; Milanese et al. 2016). HSMs need thorough data on species distribution (many sampling locations of a study species in as many diverse habitat types as possible), deep data exploration to avoid biased estimation due to multicollinearity among predictor variables, which could cause spurious





**Fig. 4** Resistance surfaces (*dark grey shading* indicates higher resistance and *light grey shading* lower resistance, respectively) and corresponding least-cost paths (*colored lines*) among 923 individual wolf

locations (1000 m grid cell size) for resistance surfaces based on nine habitat-suitability models (HSMs). For abbreviations, see “[Materials and methods](#)” section (color figure online)

correlations in landscape genetics (Prunier et al. 2015), and analysis of spatial autocorrelation among species occurrences or sampling locations (Dormann et al. 2007; Zuur et al. 2010). Moreover, different modelling techniques use different approaches regarding adjustment to data (Guisan and Zimmermann 2000). While the use of presence-only models, such as MADIFA and MAXENT, is particularly useful when absence data are not available (Segurado and Araujo 2004), such as in our case, also presence–absence models can be applied with presence-only data through selection of pseudo-absences (Phillips et al. 2006; Warren and Seifert 2011; Barbet-Massin et al. 2012). Actually, pseudo-absences equally weighted to presences can yield the most reliable distribution models (Barbet-Massin et al. 2012). For this reason, we used a sampling effort map to equally weight pseudo-absences to presences in this study.

In addition, Milanesi et al. (2016) showed that LCPs based on different HSMs may result in different landscape genetic results, even when applied to the same genetic data set.

We found rather similar results on landscape effects on movements at different grid sizes of the resistance surfaces: while standardized  $\beta$  values of LCP distances were generally lower at the 500 m than at the 2000 m grid size, they were rather similar at the 1000 and 2000 m grid sizes. We thus concluded that grid size did not qualitatively affect our results. However, analyzing different grid sizes is strongly suggested, because the use of different sizes during the construction of LCPs can influence landscape genetic results (Galpern et al. 2012). Moreover, organisms experience landscape heterogeneity at different sizes and thus using a too fine or a too coarse spatial grid may lead to inaccurate resistance surfaces (Anderson et al. 2010).

**Table 2** Results of landscape genetic analysis using linear mixed effect models

Model	500 m			1000 m			2000 m		
	LCP $\beta$	Eu $\beta$	$R^2$	LCP $\beta$	Eu $\beta$	$R^2$	LCP $\beta$	Eu $\beta$	$R^2$
MAXENT	0.425*	0.313*	0.832	0.487*	0.369*	0.805	0.431*	0.301*	0.753
MADIFA	0.774*	0.661*	0.831	0.943*	0.829*	0.807	0.915*	0.869*	0.751
GLM	0.742*	0.629*	0.831	0.773*	0.659*	0.807	0.727*	0.595*	0.752
BRT	0.425*	0.313*	0.831	0.507*	0.394*	0.807	0.551*	0.419*	0.753
GAM	0.573*	0.459*	0.831	0.518*	0.406*	0.807	0.557*	0.427*	0.752
ANN	0.501*	0.388*	0.831	0.604*	0.495*	0.806	0.644*	0.514*	0.752
FDA	0.461*	0.348*	0.831	0.525*	0.413*	0.807	0.487*	0.356*	0.751
MARS	0.481*	0.368*	0.831	0.483*	0.351*	0.806	0.471*	0.338*	0.752
RF	0.348*	0.237*	0.830	0.331*	0.221*	0.807	0.409*	0.277*	0.746
tEBM 1	0.189*	0.101*	0.823	0.111*	0.083*	0.807	0.167*	0.131*	0.749
tEBM 2	0.212*	0.105*	0.831	0.211*	0.108*	0.808	0.178*	0.145*	0.752
tEBM 3	0.177*	0.107*	0.828	0.303*	0.206*	0.807	0.335*	0.232*	0.751
tEBM 4	0.329*	0.259*	0.831	0.526*	0.472*	0.806	0.551*	0.404*	0.751
sEBM 1	0.335*	0.119*	0.832	0.526*	0.469*	0.806	0.495*	0.365*	0.753
sEBM 2	0.235*	0.104*	0.832	0.027*	0.018	0.808	0.082*	0.005	0.753
sEBM 3	0.197*	0.105*	0.832	0.062*	0.056*	0.808	0.136*	0.009	0.753
sEBM 4	0.226*	0.108*	0.831	0.116*	0.001	0.808	0.147*	0.011	0.753
sEBM 5	0.207*	0.109*	0.832	0.246*	0.132*	0.807	0.231*	0.097*	0.753
sEBM 6	0.174*	0.105*	0.831	0.110*	0.001	0.808	0.229*	0.096*	0.752
sEBM 7	0.521*	0.138*	0.828	0.442*	0.326*	0.807	0.465*	0.332*	0.752
sEBM 8	0.256*	0.113*	0.828	0.465*	0.351*	0.807	0.485*	0.352*	0.752
sEBM 9	0.141*	0.103*	0.831	0.484*	0.369*	0.807	0.497*	0.366*	0.752

Standardized  $\beta$ - and  $R^2$  values for least-cost path (LCP) distances based on nine habitat-suitability models, four true expert models (tEBM), and nine simulated expert-based models (sEBMs) as well as Euclidean (Eu) distances are shown for three different grid cell sizes. For abbreviations, see “Materials and methods” section

\*  $P \leq 0.0001$

However, our results are in contrast to those obtained by other authors (Wilmer et al. 2008; Anderson et al. 2010; Cushman and Landguth 2010; Mullen et al. 2010; Galpern et al. 2012), where significant differences in landscape genetics analyses were detected at different spatial scales. We consider such differences to be mainly due to different species characteristics, but this also implies that landscape geneticists should carefully evaluate the effects of different spatial scale, because grid size of landscape feature information will affect the ability to identify relevant landscape features affecting movement and gene flow in landscape analysis (Balkenhol et al. 2009; Cushman and Landguth 2010; Galpern et al. 2012).

### Expert-based versus habitat-suitability models in landscape genetics

The linear mixed effect models we applied showed that LCP distances derived from both EBMs and HSMs had similar  $R^2$  values and thus explained genetic distances to a similar and rather high degree in linear effects models

at all the three considered grid cell sizes (500, 1000, and 2000 m). The  $R^2$  values of LCP distances presented in this study on wolves in Italy were similar to those of Van Strien et al. (2012) on the southern damselfly (*Coenagrion mercuriale*) in Switzerland and those of Selkoe et al. (2010) on three rocky reef predators, namely, kelp bass (*Paralabrax clathratus*), Kelle's whelk (*Kelletia kelletii*), and California spiny lobster (*Panulirus interruptus*). In our study, both EBM and HSM-derived LCP distances better explained genetic distances than Euclidean distances in all cases and irrespective of the particular approach applied. This means that landscape features always showed a stronger effect on gene flow than geographical distance alone. This result is in agreement with many other landscape genetic studies, e.g., Shirk et al. (2010), who considered EBM-LCPs on black bears in Idaho, and Wang et al. (2008), who derived LCPs from HSMs on the spiny rat (*Niviventer coning*) in Taiwan.

All  $\beta$  coefficients of EBM and HSM-derived LCPs were highly significant ( $P \leq 0.0001$ ). In particular, the  $\beta$  coefficients of LCPs from HSMs showed a good performance, in agreement with other studies (Laiola and Tella 2006, Wang

et al. 2008, 2013; Huck et al. 2010; Brown and Knowles 2012; Duckett et al. 2013; Milanese et al. 2016). The values of  $\beta$  coefficients that we found were similar to those of Murray et al. (2009) on the logrunner (*Orthonyx temminckii*) in Australia and those of Selkoe et al. (2010).

Nevertheless, our main result was that standardized  $\beta$  coefficients were markedly different between LCP distances derived from EBMs and HSMs (Table 2). In fact, in most of the cases, there was a lower correlation between genetic distances and LCP distances derived from EBMs (true or simulated) than between genetic distances and LCP distances from HSMs. One would have interpreted these  $\beta$  values as either strong or weak landscape effects on gene flow depending on the particular approach used. Therefore, in our study, HSMs better reflected how the landscape features affect wolves during movement and dispersal. Specifically, at the grid cell size of 1000 m, LCP distances from two HSMs (MADIFA and GLM) showed very high  $\beta$  coefficients of 0.943–0.773, respectively. Only the  $\beta$  coefficients of LCP distances of five out of 13 EBMs, namely, tEBM 4, sEBM 1, sEBM 9, sEBM 8, and sEBM 7, were higher than those of some HSMs, and most HSMs  $\beta$  coefficients were clearly higher than those of EBMs. With small variation, these differences were similar at the 500 and 2000 m grid cell sizes. These results suggest that LCP distances derived by more objective HSMs, such as MADIFA and GLM, can better explain genetic distances among pairs of wolf individuals than LCP distances derived from more subjective EBMs. Regarding EBMs, it was particularly surprising that three out of four true expert models (tEBMs) performed in no way better than the simulated ones (sEBMs). When applying EBMs in landscape genetic analysis, it might thus be relevant to also include some random or dummy EBMs to evaluate the performance of true EBMs against them.

Our main results are apparently in contrast with the previous published literature (Stevenson-Holt et al. 2014; Mateo-Sánchez et al. 2015). Both the latter studies concluded that HSMs potentially do not capture relevant landscape information with respect to movement and dispersal and that EBMs are better in explaining patterns of connectivity. However, they compared EBMs to a single HSM, namely MAXENT. Thus, these studies did not consider that different HSMs can lead to different resistance surfaces and, therefore, LCP distances (Milanese et al. 2016). Moreover, Stevenson-Holt et al. (2014) performed a comparison of EBM and HSM-derived LCPs in landscape ecology, without validating them against genetic distances among sample locations. In contrast, our results show that HSMs can be successfully used to derive resistance maps, but we strongly suggest the application of more than a single HSM to estimate LCP distances in landscape ecology and landscape genetics, to avoid potential limits of particular HSMs.

## Conclusions

In landscape genetics, resistance models are mainly derived from optimization procedures based on expert opinions and rarely based on habitat-suitability models derived from species occurrence data. We showed that HSMs, widely used in ecological and biodiversity conservation researches (Elith et al. 2010) could represent a better tool than EBMs to parameterize landscape genetic models and to identify those landscape patterns that either hinder or foster movement and dispersal across landscapes. Thus, we encourage researchers to use and further test the application of accurately developed and validated HSMs in landscape genetics. However, our results also showed that LCPs derived from expert knowledge were appropriate and are certainly valid methods to derive resistance maps when species occurrence data are missing—though in our case, they were less effective in explaining genetic distances than LCPs from HSMs. In conclusion, we recommend to (1) develop and compare EBMs and HSMs to further test which approach best suits the patterns of gene flow of a study species and (2) apply more than a single HSM in landscape genetic analyses to avoid HSMs with assumptions, algorithms or complexities that do not fit to the particular case under study. When species distribution information is available, HSMs may well provide a valid and objective tool to explain patterns of gene flow and functional connectivity.

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**Author contribution statement** PM maintained the data set, carried out GIS, population genetic, and landscape genetic analyses, and wrote the manuscript; RH designed analyses and shared in the writing of the manuscript; RC, EF, and MG produced the Italian canid data base, shared ideas to realize this paper, and revised the manuscript; ER produced the Italian canid data base, designed analyses, shared ideas to realize this paper, and revised the manuscript.

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