Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis

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Abstract

Measures of genetic structure among individuals or populations collected at different spatial locations across a landscape are commonly used as surrogate measures of functional (i.e. demographic or genetic) connectivity. In order to understand how landscape characteristics influence functional connectivity, resistance surfaces are typically created in a raster GIS environment. These resistance surfaces represent hypothesized relationships between landscape features and gene flow, and are based on underlying biological functions such as relative abundance or movement probabilities in different land cover types. The biggest challenge for calculating resistance surfaces is assignment of resistance values to different landscape features. Here, we first identify study objectives that are consistent with the use of resistance surfaces and critically review the various approaches that have been used to parameterize resistance surfaces and select optimal models in landscape genetics. We then discuss the biological assumptions and considerations that influence analyses using resistance surfaces, such as the relationship between gene flow and dispersal, how habitat suitability may influence animal movement, and how resistance surfaces can be translated into estimates of functional landscape connectivity. Finally, we outline novel approaches for creating optimal resistance surfaces using either simulation or computational methods, as well as alternatives to resistance surfaces (e.g. network and buffered paths). These approaches have the potential to improve landscape genetic analyses, but they also create new challenges. We conclude that no single way of using resistance surfaces is appropriate for every situation. We suggest that researchers carefully consider objectives, important biological assumptions and available parameterization and validation techniques when planning landscape genetic studies.

Introduction

The distribution and connectivity of natural populations is influenced by many factors, including population demography, behavioural traits, and physiological tolerances. Increasingly, species' distributions are also

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affected by land-use change, and such impacts are likely to be compounded by climate change (Pyke 2004; Ewers & Didham 2006). As a result, habitat for different species may be lost, fragmented, or degraded due to the combined effects of natural and anthropogenic disturbances, creating a mosaic of habitats of varying qualities. Characteristics of species' habitat patches and the intervening landscape 'matrix' can either facilitate or impede movement of organisms between locales or

populations. Because landscapes are spatially heterogeneous and temporally dynamic, it is therefore important to understand how landscape features affect animal species' abilities to move in order to meet requirements for daily foraging, migration, dispersal, or other movement-dependent processes (Taylor *et al.* 1993; With *et al.* 1997; Crooks & Sanjayan 2006).

Understanding how landscape features affect spatial genetic structure is a major goal of landscape genetics (Manel *et al.* 2003; Storfer *et al.* 2007). Instead of simply estimating isolation by Euclidean distance, many landscape genetic studies seek to calculate an effective distance between individuals or populations (Vignieri 2005). The effective distance is a measure of separation between sampling sites or individuals that incorporates the effects of differing permeabilities across the matrix. It is generally assumed to represent functional connectivity, or the ability of organisms or genes to move between landscape elements (Taylor *et al.* 1993; With *et al.* 1997).

Measures of spatial genetic structure among individuals or populations are commonly used as surrogate measures of functional connectivity (Boulet *et al.* 2007). In order to understand how landscape characteristics influence functional connectivity, resistance surfaces are typically calculated in a raster GIS environment. We define here resistance surfaces as spatial layers that assign a value to each landscape or environmental feature that represents the degree to which that feature impedes or facilitates connectivity for an organism of interest. Thus, resistance surfaces can be thought of as hypothesized relationships between landscape variables and movement (O'Brien *et al.* 2006) or gene flow (Wang *et al.* 2008), and are based on underlying biological functions such as relative abundance or movement probabilities in different land cover types. The biggest challenge for modelling resistance surfaces is the assignment of resistance values to different landscape features, as the actual effects of different cover types or gradients on movement, survival, abundance, and reproduction are generally unknown.

In this paper, we review the varied objectives, assumptions and methods involved in developing resistance surfaces. We focus on landscape genetic applications, but many of the issues we highlight will be relevant to management applications such as corridor design as well. Our emphasis is on the use of resistance surfaces for terrestrial animals, as this is the group that most studies have focused on (Storfer *et al.* 2010). However, we do address plant or aquatic studies when appropriate. We first identify several research objectives that resistance surfaces can be used to answer. We then describe common methods for parameterizing resistance surfaces and address a number of factors that need to

be explicitly considered before developing a resistance surface. Finally, we list potential future directions as well as provide guidelines to aid researchers wishing to use resistance surfaces. Underlying this synthesis is the idea that there is no single best approach for using resistance surfaces. Moreover, and despite the deceptive ease of creating resistance surfaces, there are many decisions and pitfalls involved (Beier *et al.* 2008); studies need to account for a number of confounding variables and uncertainties to have confidence in their analytical results.

Types of research objectives

One of the advantages (and challenges) of developing resistance surfaces is that they provide a flexible framework to represent the landscape of interest; that is, they can be used to test many different hypotheses and address a number of different research questions. We believe that resistance surfaces are particularly well-suited for four different research and management objectives: (1) identifying landscape features that influence genetic connectivity, (2) determining what ecological processes influence genetic connectivity, (3) designing movement corridors or reserves, and (4) predicting impacts of future environmental change on connectivity for species. We are not suggesting that resistance surfaces have already been used to address each of these objectives, and acknowledge that current landscape genetic studies largely focus on the first objective. Nevertheless, the remaining three objectives are future directions that could greatly benefit from the use of resistance surfaces.

The most common and general objective is to identify landscape or environmental features that facilitate or constrain genetic connectivity (Storfer *et al.* 2007; Holderegger & Wagner 2008). For this, researchers develop resistance surfaces that represent the feature(s) of interest, and the strength of the relationship of effective distance measured across the resistance surface is correlated with some measure of genetic differentiation to infer the importance of each feature or suites of features to genetic structure (Wang *et al.* 2008). Such resistance surfaces are primarily based on structural connectivity (i.e. connectivity based only on landscape features), without a priori biological information. For example, Fig. 1 represents several potential resistance surfaces that could be used to determine the relative importance of variables structuring gene flow. Note that measures of resistance can be quantified using either univariate or multivariate surfaces, with the assumption that a strong correlation with a multivariate surface suggests multiple variables are important. Overall, the first objective is probably best used to test a number of
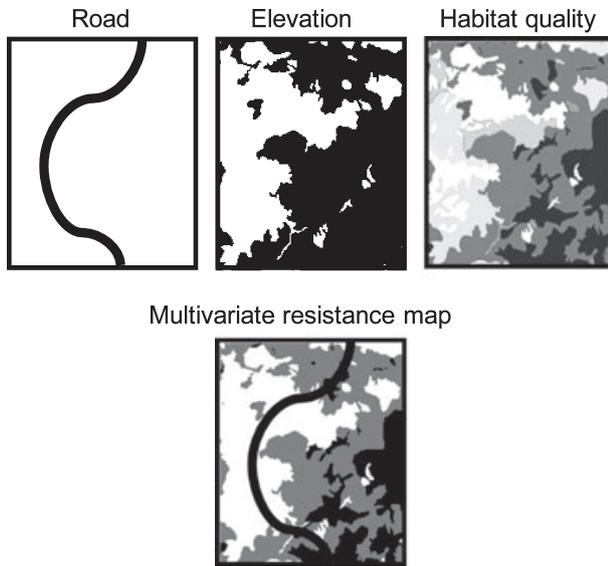
Fig. 1 Cumulative resistance map of the resistance values of different landscape features. Lighter shades have less resistance values (i.e. ease of movements between occupied sites) and darker colours have higher resistance values.

Fig. 2 Hypothetical examples of how least-cost paths may vary with resistance values from surfaces based on only landscape features (structural resistance) to values based on expert knowledge, of species behaviour and learning to functional resistance bases on genetic data. Light grey: good habitat; White hospitable habitat; Black: inhospitable habitat (patch and solid line); Black dashed line: least-cost path based on the different resistance values; Black solid line: least-cost path that correlates best with gene flow.

variables in lesser-known systems to guide future research on that system, and we suggest that this objective is a necessary first step to the remaining objectives we identify.

A second objective is identifying what ecological processes (e.g. dispersal, habitat selection, abundance, survival, or fecundity) most influence spatial genetic structure. This objective naturally follows the identification of important landscape features, and requires the further step of identifying how the significant variables are related to ecological processes. While certainly challenging, this could be accomplished by creating and evaluating different resistance surfaces that each represent a different process (e.g. one surface representing habitat selection, another representing estimated survival rates across the landscapes). These resistance surfaces would clearly need to address *functional* connectivity and require some previous knowledge of the species' biology (Fig. 2). Ideally, such surfaces would be based on independent additional data, for example from telemetry or mark–recapture (see below).

The use of resistance surfaces for identifying movement corridors or planning reserves differs from the previous two objectives in that contemporary movement and habitat use are the variables of interest, and specific mapping of suitable areas is the ultimate goal (Beier *et al.* 2008). This requires a good understanding of underlying ecological processes, so that this objective can be seen as an extension of the previous one. Resistance surfaces provide an excellent tool to model corridors or reserves, but the methods and assumptions
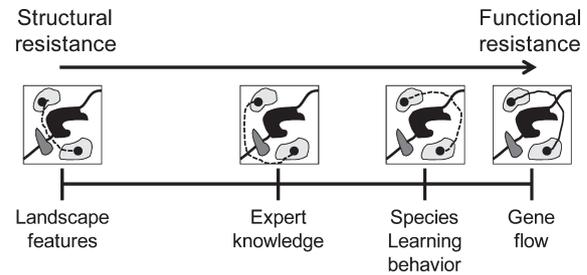
used to create and validate such a resistance surface are critical to its effectiveness, and such issues are a large part of the discussion in the next section. This objective is also one of the most direct ways in which resistance surfaces can inform applied resources management and conservation decisions.

Finally, resistance surfaces may be applied to predict how future landscapes might influence genetic connectivity or movement within and among populations. This may ultimately be the most important, yet most difficult, of the listed objectives given the challenges that rapid land-use and climate change pose for understanding and conserving ecological and evolutionary processes (Moritz 1999; Parmesan 2006; Knowles & Alvarado-Serrano 2010; Sork *et al.* 2010). It will certainly require creating and testing resistance surfaces across the range of predicted environmental changes and will rely heavily on under-utilized methods such as simulations (see Epperson *et al.* 2010). Other than grappling with considerable uncertainty about the future environment (Beier & Brost in press), this line of research will face similar challenges to those listed for identifying important ecological processes or corridor development.

Review and comparison of currently used methods for resistance surface parameterization

Addressing any of the above objectives in a satisfactory manner is not a trivial matter, and errors in developing and parameterizing resistance surfaces could lead to misleading conclusions. To overcome these challenges, current studies are using three different approaches for resistance surface parameterization: field data, expert opinion and model optimization. In this section, we

evaluate the advantages and disadvantages of these three approaches and provide empirical examples of their use. Although we do not focus on analytical methods used once resistance surfaces are created, many of the references in this section provide examples of different tools and methods used for analysis.

Non-genetic field data

Intuitively, the use of independent data (e.g. point counts, mark–recapture studies, radio telemetry, GPS loggers, track or fecal surveys) for parameterizing resistance surfaces should be preferred relative to more subjective methods. Yet of a sample of 32 studies that have created resistance surfaces (Table S1, Supporting Information), only eight have used some type of non-genetic field data to independently inform resistance assignment. There are two probable reasons for the rarity of this approach. The first is that it can be quite difficult to obtain field data for many organisms, particularly those that are small, elusive or rare. In fact, a major motivation for many landscape genetic studies is that direct estimates of dispersal and habitat use are so difficult to obtain (Spear *et al.* 2005; Boulet *et al.* 2007).

The second, and more important, reason is that it is uncertain how relevant many field measures are for observed genetic structures. The studies that have incorporated field data have used three different approaches: presence-absence data (Laiola & Tella 2006; Wang *et al.* 2008), radio-telemetry, GPS, or satellite tracking (O'Brien *et al.* 2006; Driezen *et al.* 2007; Epps *et al.* 2007; Chietkiewicz & Boyce 2009) and experimental movement studies (Michels *et al.* 2001; Stevens *et al.* 2004, 2006a). Habitat suitability models require presence or presence-absence data (Boyce 2006; Pearce & Boyce 2006) and the habitat suitability values generated for each pixel across the landscape can then be converted directly into resistances (i.e. if model values ranged from 0 to 100, the resistance could be calculated based on 100 minus the suitability value). However, biases in locations of study areas and differing levels of detectability in different landscape types can make this approach problematic (O'Brien *et al.* 2006). For example, habitat suitability models for organisms that breed in aggregations in discrete patches will most certainly be biased and may ignore critical features for interpopulation connectivity. Furthermore, such models do not incorporate any information on movement behaviour, and thus do not explicitly model movement or gene flow. Two empirical examples of this approach found significant correlations of the response variable (genetic distance, Wang *et al.* 2008; and call dissimilarity, Laiola & Tella 2006) with a resistance surface based on habitat suitability, but both studies also found evidence for significant isolation by distance, which may have been strongly correlated with habitat suitability.

Data from radio-telemetry, GPS, or satellite tracking devices can also be used to parameterize resistance surfaces because they provide information on actual movement paths, which are ultimately what many researchers using resistance surfaces would like to model. These tools suffer from some of the same limitations as habitat suitability models, but their primary drawback is the intensive effort required, resulting in low sample sizes and limited study area extents. Thus, even if we assume movements based on radio-telemetry locations are representative of successful dispersal leading to gene flow (and this assumption may certainly be violated), the spatial and temporal extent of the tracking study is likely to be inconsistent with the geographic extent of a genetic study. This can lead to problems in areas with high temporal and spatial heterogeneity. How critical such issues are for landscape genetics remains to be determined, as only one genetic study has incorporated telemetry data, and in a very coarse manner. Epps *et al.* (2007) used previous radio-telemetry data to determine least-cost paths based on slope values, but then used an optimization approach to select the best resistance surface. However, two other studies have used radio-telemetry to generate or validate resistance surfaces in a manner that might be useful for landscape genetics. Driezen *et al.* (2007) created several potential least-cost paths for hedgehog (*Erinaceus europaeus*) dispersal based on expert opinion, but used a training set of radio-telemetry points to select the most supported path, which was then tested on a separate group of telemetry points. Chietkiewicz & Boyce (2009) used a different approach, in which they calculated resource selection functions based on radio-telemetry of grizzly bears (*Ursus arctos*) and cougars (*Puma concolor*) to create an occurrence probability surface that was translated into a least-cost path for corridor selection. Either paper provides a method that allows for the use of radio-telemetry in informing landscape genetic studies, but assumptions and limitations of such studies (i.e. low sample sizes, uncertainty that detected movements lead to successful reproduction) must be carefully considered (O'Brien *et al.* 2006).

A final method of incorporating field data is through experimental studies of movement behaviour, i.e. the tracking of animals as they navigate artificially constructed or manipulated landscapes. The most thorough example of this approach was by Stevens *et al.* (2006b), who used two previous experimental studies of habitat type resistance (Stevens *et al.* 2004) and habitat border permeability (Stevens *et al.* 2006a) to create least-cost paths for natterjack toads (*Epidalea calamita*). Habitat resistance was assessed using experimental arenas

mimicking sand, forest, cement, grass and field, and the response variable was the effective speed at which toadlets crossed each surface. Habitat border permeability was tested with the same habitat types using a track that presented the option of two surface types, with the response variable being the percentage of toads that crossed into that cover type. Interestingly, resistance based on effective speed had no correlation with genetic distance, whereas permeability did have a significant correlation. Thus, studies focused on habitat selection may be more appropriate than studies focusing on speed of movement. While experimental studies afford control of numerous confounding variables and a focus on resistance variables of interest, we caution that behaviour in artificial landscapes may not always yield reliable inferences about behaviour under natural conditions. As with telemetry studies, handling animals for experimental studies can impose significant costs, risks, and regulatory hurdles. This, along with the cost and difficulty associated with constructing artificial landscapes that match the scale of the species' movements, will typically restrict the use of artificial landscapes to smaller, relatively abundant organisms.

Expert opinion

Not surprisingly, given the issues associated with collection and use of field data, expert opinion is the most common form of assigning costs to resistance surfaces (Murray *et al.* 2009). This approach is particularly inviting for researchers who have much experience with a particular study system, or for species that have been well studied. Furthermore, when resistance surfaces created with expert opinion are tested based on genetic data, surfaces provide opportunities to test assumptions about species' biology based on independent data (Fig. 2). Of course, the major problem is that expert opinion can easily be inaccurate, and generally gives little insight into assigning specific resistances. Clevenger *et al.* (2002) used a transparent decision making process based on expert opinion and literature review to develop weightings for landscape variables used to predict black bear (*Ursus americanus*) road crossings. They found that a literature review model compared especially well with an empirical model based on radiotelemetry. However, in most studies, it is unclear what rationale is used for choosing the specific weight representing a variable. In many cases, especially with categorical variables (i.e. land cover), the researcher hypothesizes arbitrary costs based on the perceived relative costs among variables (e.g. Chardon *et al.* 2003; Broquet *et al.* 2006). In the case of continuous variables, the researcher generally assumes a linear relationship with genetic distance (e.g. Coulon *et al.* 2004; Spear

et al. 2005). However, such a linear relationship should not necessarily be assumed, as critical thresholds can exist (With & Crist 1995), and non-linear relationships sometimes are a better fit for the data (Cushman *et al.* 2006; Balkenhol 2009). We suggest that researchers who use expert opinion to parameterize models use some type of established decision making procedure (such as used by Clevenger *et al.* 2002) and take advantage of published studies for the population or species of interest. However, the appropriateness of expert opinion models is likely to vary substantially from study to study, dependent on both the experience of the investigator and the amount of research conducted on the organism of interest.

Model optimization

Optimization approaches are primarily used to select among candidate models of landscape resistances. In the context of landscape genetic studies, we define optimization broadly as any approach in which multiple resistance surfaces attempting to account for the same landscape feature(s) are statistically compared to determine which surface has the greatest fit with genetic data (e.g. Cushman *et al.* 2006). Typically, an investigator chooses a range of potential resistances associated with each feature, and tests each of the potential resistances (or combination of resistances for multi-variable surfaces) against each other. Thus, while optimization is most certainly a preferred method compared to testing one possible model, its success is still highly dependent on the range of values chosen by the researcher and therefore subject to the same errors inherent in any expert opinion approach.

An optimization approach is also dependent on the choice of model selection technique. For example, the optimal model may be chosen based on Mantel or correlation coefficients (Epps *et al.* 2007), r^2 (Perez-Espona *et al.* 2008; Lee-Yaw *et al.* 2009), probability values (Cushman *et al.* 2006) or AIC (Spear *et al.* 2005). It is not the intent of this paper to provide a statistical evaluation or assessment of which model selection techniques are most appropriate. Using multiple model selection techniques to determine if the same model is chosen with all techniques may be one way to increase confidence in biological inferences, but problems arise if different techniques do not give consistent results. Furthermore, the choice of an optimal model does not necessarily imply that it is a good model for describing population connectivity or genetic structure, as all candidate models could be poor descriptors, or spurious correlations could lead to incorrect conclusions. We return to this issue when discussing future directions for the use of resistance surfaces.

Important considerations and challenges for use of resistance surfaces

It should be clear from the diversity of questions that different objectives are based on a number of assumptions regarding how the landscape features influence genetic connectivity or movement. Resistance surfaces are simply models, and thus certain assumptions or compromises are necessary. However, there are a number of issues that we feel may strongly influence conclusions from studies that use resistance surfaces and need to be considered in resistance surface development. Note that we do not consider this an exhaustive list of challenges; as one example, we do not discuss errors inherent in spatial data layers used for resistance surfaces, but such errors may be quite important.

Gene flow and movement are not synonymous

Bohonak (1999) and Whitlock & McCauley (1999) have demonstrated that gene flow and direct movement (such as dispersal) are generally correlated, but cannot exactly predict each other. Thus, landscape genetic studies can be quite useful to understand movement of individuals, as long as the differences are recognized and carefully considered in interpretation of the study results. Herein, we focus on the consequences of the discrepancy between gene flow and movement for developing resistance surfaces for different study objectives. We are mostly concerned with the consequences of using genetic data as a response variable to predict actual movement, and using movement data as the basis for creating resistance surfaces to explain genetic connectivity.

Direct observations of movement or dispersal and indirect measures of gene flow often differ for several reasons (e.g. Wilson *et al.* 2004; Fedy *et al.* 2008), and the degree of incongruence between ecological and genetic measures of population structure can have consequences for development of resistance surfaces used in landscape genetic studies. First, gene flow refers to the transfer of genes from one spatial location to another (i.e. an individual dispersing from one area to breed in the area to which it has dispersed, or genes moving from one population to another, via intermediate populations, over multiple generations). Direct observations (e.g. based on telemetry or mark–recapture), however, can only document the physical presence of an individual in more than one location at two or more time periods. Such individual movements may have very little to do with dispersal or gene flow, and therefore using resistance values based on those movements may be misleading. For example, a study of Columbia spotted frogs (*Rana luteiventris*) detected

movements to ponds that were used for summer or overwintering habitat, but not for breeding (Pilliod *et al.* 2002). Therefore, resistance surfaces based on movement data in summer or fall would not capture the relevant movements for gene flow. However, resistance surfaces based solely on genetic data would be insufficient for reserve design because they would likely not detect the ponds necessary for overwintering. Further, inferences from direct observations are only germane to those areas where observations were made. Gene flow can occur over a much broader area, for example from unsampled populations characterized by unsampled landscape features (Kinlan & Gaines 2003). Thus, it may be inappropriate to use direct movement data to parameterize resistance surfaces for questions of genetic connectivity, or to use genetic distance to predict areas of movement.

Secondly, there is a disconnect in temporal scale between measures of gene flow compared to direct movement. This topic is explored more extensively elsewhere (Anderson *et al.* 2010), but we briefly discuss some of the scale issues that are relevant to resistance surfaces. Direct observations chronicle the extent of movements only over a period of observation but do not describe, nor are they likely predictive of, historical levels of dispersal (e.g. other seasons, other years). Estimates of gene flow reflect both episodic (Cain *et al.* 2000; Gibbs *et al.* 2000; Williams *et al.* 2003; Roe *et al.* 2009) and long distance dispersal events (Kinlan & Gaines 2003) because they represent the long term average of effective dispersal from all contributing areas. Physical landscape features are also typically characterized using recent GIS data, and are thus static in time. There may be legacy effects of previous landscape conditions (Harding *et al.* 1998; James *et al.* 2007) or effects related to past extinction and recolonization events (Wade & McCauley 1988; Hess 1996). Further, the relative rates of temporal change are not likely to be constant for all landscape features (e.g. forest succession vs. forest harvest). Consequently, observable genetic structure is always the result of both contemporary and historical factors. Studies attempting to understand landscape influences on genetic connectivity have attempted to address this issue through the use of spatial data from multiple temporal points (Keyghobadi *et al.* 2005; Vandergast *et al.* 2007; Spear & Storfer 2008). Contemporary spatial layers are ideal for studies investigating contemporary movement, but may require that the genetic data are used differently, such as identifying first-generation migrants with assignment tests (Wang *et al.* 2009).

Thirdly, gene flow depends on survival and reproduction following immigration into a new area. Reproductive isolation can be caused by natural selection

against migrants (Nosil *et al.* 2005). Additionally, there is strong selection for adults to breed at times and in locations that are conducive to the survival of offspring. Successful reproduction depends on offspring fitness which is in part based on local adaptation. Rates of gene flow are also affected by introgression and potentially by outbreeding depression (Edmands 2007), as evidenced by reduced survival of offspring (e.g. Nosil *et al.* 2005). Studies that attempt to identify the ecological processes that influence genetic connectivity should therefore attempt to sort out the different possibilities, for example by estimating parameters of fitness, in- or outbreeding for the sampling localities. Future studies that integrate characteristics of source and destination locales and a cost of dispersal (or arrival) due to selection could contribute to new developments in quantifying landscape resistance. Adaptive divergence may reduce rates of gene flow because individuals dispersing between divergent habitats are maladapted (Crispo *et al.* 2006). In other words, there are other costs that can be incurred that could be quantified or modelled that deal with other factors than the landscape matrix between sites which cannot be included by using landscape features as surrogate for them (Fahrig 2007). Gravity models that model both site and pairwise variables (Murphy *et al.*, 2010) may be quite useful to address these issues.

Lastly, an underappreciated distinction between movement and gene flow is that areas that are not connected by direct movements at all may still experience high rates of gene flow. Genes can move over multiple generations, often connecting spatial locations separated by distances greater than an individual can move within a lifetime (Bohonak 1999). Moreover, estimates of gene flow are often made using pairwise F_{ST} or $\hat{M}$ (Slatkin 1993) calculations based on empirical data. Here, $\hat{M}$ is the effective number of migrants, rather than the actual number, and is influenced not only by multigenerational movement, but also by overall effective population sizes. Indeed, two populations could never exchange genes (even over multiple generations) but still have high effective migration. Consider three populations, where a central population exports large numbers of migrants to two peripheral populations, each of which export no migrants. The peripheral populations would have low pairwise F_{ST} and high $\hat{M}$ values, without ever exchanging migrants or genes. Thus, landscape characteristics may modify gene flow between pairs of populations directly by affecting movements between them, or indirectly by affecting the spatial arrangement of, and movement rates among, intervening populations (McRae 2006; Dyer *et al.* 2010). This distinction is probably not important for studies which have the goal of explaining overall genetic structure, presuming all relevant populations are sampled. However, the indirect connectivity of populations has very clear and important implications for using genetic data in corridor design.

Does gene flow or movement through a landscape indicate high quality?

Another challenge to development of predictive measures of resistance is that dispersal is frequently condition-dependent (Ronce *et al.* 2001) and phenotype-dependent (Clobert *et al.* 2009; Gibbs *et al.* 2009). Thus, the decision to disperse depends on resource availability (e.g. food, access to mates, etc.) and population density as well as inter-individual variation in physiological, morphological and behavioural traits that may differ from population to population. Often habitats that are perceived to be of poor quality, are fragmented, or otherwise assumed to be of high resistance to gene flow have been found to be highly connected genetically. In plants, under certain circumstances fragmentation can increase gene flow (Young *et al.* 1996) and can counter the effects of anthropogenically-mediated disturbance (White *et al.* 2002). Animals may select poor habitats (Battin 2004), disperse through poor habitats if the movement occurs within a single generation (Haddad & Tewksbury 2005), or may have evolved traits correlated with increased dispersal that might persist despite landscape change. Conversely, habitats with high suitability or resource selection indices as determined based on high population abundance or high occupancy rates may be poorly predictive of dispersal because individuals may be less inclined to leave good habitat, but may leave (and disperse through) poor habitat more readily (Winker *et al.* 1995). As an example, Fig. 3 shows a landscape comprised of a heterogeneous mosaic of habitats of varying quality. Population abundance is high in the white patches, but there is little movement because all of the species' resource needs are met. Contrast this with the unsuitable patches, from which there is much movement into suboptimal habitat. Resistance surfaces based on actual movement might characterize these suboptimal habitats as high quality habitat. This scenario is somewhat hypothetical and simplified, but might be especially relevant for highly mobile organisms (such as large mammals) that are more likely to be opportunistically sampled or tracked moving through fringe habitats, even if they do not successfully reproduce there. Finally, the ability of landscape features to predict gene flow will often vary on a population-by-population basis because of differences in both species-specific ecology and evolutionary histories of populations occurring across different landscapes. Development of feature weights, resistance
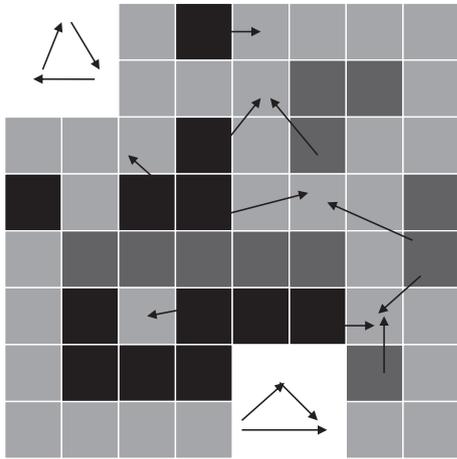
Fig. 3 Example of how habitat suitability might not be highly predictive of movements or gene flow. White patches indicate optimal habitat and darker patches indicate progressively less suitable habitat. Arrows represent movement either within a patch (triangular arrows) or movement from one path to another. In this case, the majority of movement is into patches of only intermediate suitability.

estimates for features, and decisions about the width of paths (corridors, strips, grids) should consider behaviour and vagility differences that may be species- and population-specific, particularly as it perceives the grain of features in the landscape matrix (Baguette & Van Dyck 2007; Beier *et al.* 2008; Kadoya 2009; Beier *et al.* 2009; Fig. 2).

Genetic data might reflect only a portion of movements

Resistance measures should consider that many species exhibit ontogenetic changes in resource requirements (e.g. Dunning *et al.* 1992; Pope *et al.* 2000). Dispersal occurs at certain stages with higher probability than others (e.g. at the time of sexual maturity) and resistance estimates can be focused on these life stages accordingly. However, there may be costs incurred at other stages that affect probabilities of dispersal and success (i.e. the outcome of the dispersal process—survival and reproduction upon arrival at a new location). In addition, dispersal in many vertebrates is sex-biased (e.g. Scribner *et al.* 2001) and the ability of landscape features to predict gene flow may differ for males and females (Coulon *et al.* 2004). Further, males and females in many vertebrates are often spatially segregated for much of the year. Occupancy of particular habitats is an evolutionary response to differences in reproductive strategies (reviewed in Main 2008). Females typically occupy (and disperse through) habitats that are conducive to offspring survival. Males occupy habitats that maximize access to quality forage in preparation of

reproductive activities. Dispersal in plants is complicated by the fact that factors underlying rates and direction of movements of pollen must be reconciled with processes contributing to movements of fertilized zygotes (Epperson 2007). Gene flow is often mediated not by the permeability of landscape matrices on the organism in question but by physical processes such as wind (Munoz *et al.* 2004) and water flow (Knight 1985).

The underlying model of how resistance affects movement or gene flow is important

Different models of connectivity that take resistance surfaces as inputs use different assumptions and algorithms to translate resistance values into measures of inter-population or inter-locale connectivity. Least-cost path models assume that movement or gene flow rates will be directly related to the total cumulative resistance or 'cost' (sum of per-pixel resistance values) along a single, optimal path between locales (Adriaensen *et al.* 2003; Fig. 4). On the other hand, circuit theory-based models incorporate all possible pathways across landscapes, and their parameters and predictions can be expressed in terms of random walk probabilities (McRae 2006; McRae *et al.* 2008; Fig. 4). These two models represent opposite ends of a spectrum, at one end assuming that individuals have the knowledge necessary to choose an optimal path (regardless of width) between populations. The other assumes that all pathways to some degree influence movement rates or gene
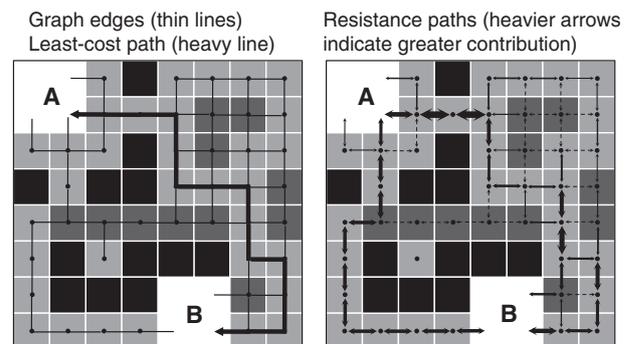

Fig. 4 Resistance values, graph edges, and least-cost and circuit solutions for connectivity between two habitat patches, A and B. Per-cell resistance increases with darker colours. Both least-cost and circuit theory algorithms construct a graph that connects cells. Typically, graph edge weights are inversely proportional to average cost or resistance of cells being connected. Left-hand panel shows graph and least-cost path (this example shows only four-neighbour connections for simplicity). Right-hand panel shows pathways for effective resistance calculations based on circuit theory. Heavier arrows indicate higher contribution/importance of pathways.

flow. Neither is likely to be wholly correct; the optimal pathway may not be at all obvious to a disperser, but some individuals may exchange information (Clobert *et al.* 2009) or use exploratory movements (Bruggeman *et al.* 2009) to make more informed and focused movements. However, both approaches likely provide meaningful and complementary indices of connectivity. Least-cost-path distances may be more informative at local scales (Anderson *et al.*, 2010), where animals may have substantial knowledge of the landscape and least-cost paths are also conducive to creating biologically plausible networks among individuals or sampling sites (Rayfield *et al.* 2010). Circuit theoretic models may be particularly useful for incorporating effects of gene flow over multiple generations, where multiple pathways and dimensionality of habitat are particularly important. Both may be useful for identifying corridors or connective areas for conservation (McRae *et al.* 2008). A third approach emphasized by Beier *et al.* (2008, 2009) is to use resistance surfaces to produce corridor polygons of various widths. This is less useful if the goal is to identify landscape variables important to connectivity (as it is difficult to give specific variable values to polygon data) but is very relevant to corridor design. Understanding the differences between these and other models will be important in parameterizing, implementing, and interpreting resistance surfaces.

Modelling resistance as univariate or multivariate surfaces

Even if all of the above factors are accounted for, one of the most difficult aspects of using resistance variables is the decision to create surfaces using univariate or multivariate parameterizations, and if multivariate, how to weight the variables in relation to one another (Fig. 1). A number of studies have used univariate surfaces to investigate landscape influences on genetic connectivity (Michels *et al.* 2001; Spear *et al.* 2005; Vignieri 2005; Epps *et al.* 2007). The advantage of this approach is that the surfaces are relatively easy to parameterize, although choosing specific cost values is still problematic. Of course, the major disadvantage is that using a univariate surface assumes that only one variable influences connectivity, and this is not generally the case. Spear *et al.* (2005) attempted to account for this by measuring values of multiple variables along a least-cost path based on a univariate cost surface, but the values of other variables are dependent on the placement on the path, which is based on only one variable. Thus, univariate surfaces are probably only appropriate in a comparative framework with a study goal of identifying one or few landscape variables that have the greatest influence on genetic connectivity. It clearly would not

be appropriate for corridor design or attempting to predict future genetic connectivity. An additional consideration for univariate surfaces is that if the variable is correlated with another variable that is actually responsible for the genetic pattern, then misleading conclusions can result. For example, in Fig. 1, the road appears to be correlated with high elevations. A study that only created an elevation layer might find a significant negative impact of high elevations that may actually only be due to the presence of the road.

Multivariate surfaces certainly have the advantage of being more biologically realistic, but also become much more complex to develop. The main problem is that it is often unclear how the feature resistances should be weighted relative to one another. This problem can partially be addressed through model selection of competing scenarios, but another important aspect is identifying how sensitive the resulting least-cost, circuit theory or corridor analysis is to different multivariate resistance surfaces. Rayfield *et al.* (2010) and Beier *et al.* (2009) present recent analyses dealing with this particular issue. Not surprisingly, both analyses found that different relative resistance values would lead to different locations of least-cost paths or corridors on the landscape. Rayfield *et al.* (2010) suggested using several least-cost paths to delineate a 'probable movement zone' and Beier *et al.* (2009) found that alternative proposed corridors tended to be similar in resistance values. Such studies help validate the use of multivariate resistance surfaces, assuming uncertainty analyses are conducted.

Emerging and future approaches

Simulations

One way to further strengthen resistance surface analyses is through landscape-genetic simulations (Epperson *et al.*, 2010). For example, simulations can help to determine whether developed resistance models could indeed have led to spatial genetic patterns observed in empirical data (Cushman & Landguth 2010). A good fit between simulated and observed genetic structures does not necessarily mean that the underlying resistance surface is correct or ecologically meaningful, but the more analyses that support a resistance model, the more confident researchers can be about conclusions drawn. It is also possible to ask under what circumstances observed patterns have most likely evolved, for example by altering simulation parameters (i.e. movement processes; birth and mortality rates; mutation) and comparing results obtained from different simulation runs with the empirical data. Thus, simulation-based cross-validation of resistance surfaces can lead to

refined or additional ecological inferences about landscape–genetic relationships. However, such cross-validations still require the development of resistance surfaces, and therefore provide a complement rather than an alternative to resistance modelling.

Network or transect-based approaches

Network or transect-based approaches do not require resistance surfaces, as landscape configuration or composition are quantified along straight lines (Reh & Seitz 1990; Holzhauer *et al.* 2006; Murphy *et al.* 2010), or within polygons (e.g. lines buffered by a certain width) connecting all sample locations (Lindsay *et al.* 2008; Pavlacky *et al.* 2009; Emaresi *et al.* in press). Network connections can also be used to develop measures of genetic differentiation that may be more appropriate than more traditional genetic distance measures such as F_{ST} (Dyer *et al.* 2010). Landscape–genetic relationships can then be evaluated by statistically relating measures of genetic connectivity (i.e. genetic distances, migration rates, number of exchanged migrants) to landscape data measured along or within transects. For example, Emaresi *et al.* (in press) used an information-theoretic approach to assess how the density of various landscape features within corridors influenced genetic structure in Alpine newts (*Mesotriton alpestris*). They found that the amount of forest between newt populations positively influenced gene flow, while urban areas and orchards acted as dispersal barriers. Similarly, Goldberg & Waits (2010) used a network of straight-line connections to compare landscape influences on gene flow in Columbia spotted frogs (*Rana luteiventris*) and long-toed salamanders (*Ambystoma macrodactylum*), and found different responses to landscape features in each species.

These transect-based methods have the potential to lead to unbiased estimates of landscape connectivity, because they correctly use the empirical (i.e. genetic) data as the dependent variable and then infer landscape influences on functional connectivity based on these empirical data (Goodwin 2003). This is different from most current landscape genetic studies, which generally define landscape connectivity a priori (e.g. by developing resistance surfaces) and then test whether the empirical data support the assumptions reflected in these surfaces.

Transect-based methods can also help to aid in resistance modelling. For example, Hirzel (2001) introduced the 'Frictionnator' approach, in which the frequency distribution of landscape features is measured within transects among all sampling locations. Then, these frequencies are used to model genetic distances (or any other measure of connectivity). Resulting model coefficients (e.g. from multiple regression) measure the influence or weight of each landscape feature on observed genetic distances. These weights can then be used to create a resistance surface, for example using the following conversion:

$$F_{x,y} = \sum_{i=1}^{p} O_{x,y,i} e^{wi}$$

where $F_{x,y}$ is the resistance of a cell with centre coordinates x,y; p is the number of predictors (i.e. landscape features used in the model); $O_{x,y,i}$ is 1 if the ith landscape feature is present in that cell, and 0 otherwise; and w is the regression weight for that predictor. The resulting resistance surface can be used to calculate effective distances among sampling units, which can again be validated against the genetic distances. Other ways to weigh and combine the different landscape factors exist (see Beier *et al.* 2008). To our knowledge, this approach has not yet been applied to an empirical data set, and its performance in a landscape genetic context has yet to be evaluated. Indeed, while transect-based approaches have certain advantages over resistance surface analyses, they also lead to new challenges. For example, results obtained from corridor-based analyses can depend on the width of the corridor (e.g. Emaresi *et al.* in press). Thus, multiple corridor widths should be used in such analyses, and the different widths need to be well justified from the perspective of the study species. Furthermore, when actual movement paths diverge strongly from straight-line paths, transect-based approaches may include little information about the landscape that is actually experienced by dispersing individuals.

Cross-validation machine learning approaches (Genetic algorithms)

Future research in the area of resistance surface estimation may profitably explore ways in which genetic data and resampling methods may serve to evaluate least cost estimates. Using a combination of training and testing datasets, different networks can be built, each represented by different combinations of variables and weights resulting from a search of multi-feature space. In such a manner, spatial genetic patterns could be analyzed via machine learning approaches, leading to models that explain landscape influences on genetic variation. For example, genetic algorithms (GAs; Holland 1975; Goldberg 1989) allow researchers to find solutions within a set of features based on user-defined optimality criteria (e.g. amount of variance accounted for in analyses of landscape and genetic variables).

Iterative, computational approaches

Another interesting future research avenue could be the development of an iterative approach in which the 'best' resistance surface is developed based on the genetic data. In such an approach, a relatively simple resistance surface (e.g. based on a neutral landscape) could first be used to calculate effective distances among sampling locations. The correlation between these effective distances and the empirical genetic data could be assessed, and the process would then be repeated a very large number of times with different numbers and spatial distributions of resistance classes, ranges of resistance values, cell resolutions, etc. Effective distances and their correlation with the genetic data would be calculated each time, and the surface that leads to the highest correlations is accepted as the 'best' underlying resistance model. In the end, a spatial regression could model the cell values in the final (i.e. 'best') resistance model as a function of the landscape data in these cells. This approach would be computationally intensive, because of the large number of possible resistance values, spatial configurations, and effective distances that would have to be calculated each time a surface is changed. However, modern machine learning techniques such as simulated annealing or genetic algorithms have successfully been used for similar purposes (Possingham *et al.* 2000; Guinand *et al.* 2002; Olden *et al.* 2008). Additionally, it is possible to restrict such an iterative approach to only a subset of the data, for example by focusing on levels of genetic connectivity that are different from random expectations. For example, (Wang *et al.* 2009) compared 24 843 different resistance models for the California tiger salamander (*Ambystoma californiense*). Wang *et al.* (2009) were able to test such a large number of models because they limited the resistance calculations to only those four populations for which migration rates obtained in BayesAss+ (Wilson & Rannalla 2003) were significantly different from those obtained with uninformative data.

Synthesis and guidance for the use of resistance surfaces

There is no one approach for developing and implementing resistance surfaces that will be optimal or scientifically justifiable under all circumstances. Decisions regarding how to create and use resistance surfaces will be dependent on study objectives, biological and analytical assumptions, and methods used to assign resistances. In Box 1, we summarize considerations for developing resistance surfaces described throughout the paper. Even though each individual study will have different goals and needs, Box 1 can best be envisioned as a decision tree for landscape genetic researchers. Since

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Box 1 Four steps to guide researchers interested in using resistance models for landscape genetics. For each step, a list of important considerations and options is provided. Decisions for each step should be well-justified, and depend on decisions made in the previous step.

Step 1. Define objectives (*What are the exact goals of the study?*)

- Determining which landscape features influence genetic connectivity
- Determining which ecological processes (e.g. dispersal, habitat selection, survival) influence genetic connectivity
- Designing movement corridors or land banks/ reserves for conservation
- Predicting the (genetic) response of species to environmental and anthropogenically-mediated change

Step 2. Identify assumptions (*Which ecological & biological aspects are particularly relevant for addressing the study objectives?*)

- Are movements predictive of gene flow?
- Does occupancy of high quality habitat predict good habitat to move through?
- What type of movement?
- Are movements seasonal or do movements vary as a function of sex or age?
- What analytical methods will be used?
- Are univariate or multivariate models more appropriate?

Step 3. Parameterize models (*How can researchers best incorporate relevant ecological & biological features?*)

- Expert opinion
- Field data (e.g. telemetry, mark-recapture)
- Habitat models (e.g. distribution or suitability models)

Step 4. Validate models (*How can researchers ensure that created resistance models are predictive of genetic connectivity?*)

- Statistical model optimization
- Simulation-based cross-validation
- Statistical cross-validation
- Cross-validation with independent, empirical data

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many of the steps outlined in Box 1 will be dependent on the study objective, we return to each of the four study objectives we identified at the beginning of this

paper, and briefly describe the aspects of Box 1 that will most often be relevant to that objective.

Determining what landscape features influence genetic connectivity

As identifying specific areas where organisms are moving is rarely a specific goal under this objective, indirect measures of movement based on genetic distance are generally suitable for analyses. If direct movement data are instead used to parameterize resistance surfaces, then these data must be carefully evaluated to ensure that movements are likely to lead to gene flow. For species that have previously been studied, expert opinion combined with some type of optimization or iterative approach may be a good way to develop resistance surfaces. The use of univariate surfaces may be appropriate if there is a dominant environmental factor expected to structure populations. This objective is also potentially well-suited to modelling using either least-cost paths or circuit theory, as long as the rationale for either is well justified.

Determining what ecological processes influences genetic connectivity

Identifying the ecological processes that most influence spatial genetic structure requires careful attention to many of the topics listed in step 2 of Box 1. For example, if a researcher is interested in whether juvenile dispersal is the primary vector for gene flow, then resistance surfaces should be parameterized from direct movement data, and the movement data must represent juveniles moving to places where genetic exchange might occur. This requires directed study designs and likely preliminary pilot studies to gather basic life history information. For this reason, unless the study involves a well-known species, expert opinion models are unlikely to provide much insight into this objective. Simulations may be a fruitful way to validate models of ecological process, as simulations could be designed that constrained gene flow to the process being modelled and then compared with the empirical data.

Designing corridors or reserves for conservation

Corridor or reserve design requires actual delineation of connectivity areas on the landscape and must address questions regarding the relationship between movement and gene flow, how habitat suitability translates to movement and what types of movement ultimately connect spatial localities. Both direct estimates of movements and gene flow are important parameters: the goals are to protect habitat that individuals can survive in, but also to ensure genetic connectivity for long-term viability (Crooks & Sanjayan 2006). Resistance surfaces based on habitat models, direct movement and expert opinion may all be appropriate here, and comparisons among surfaces developed with each of the three models may lead to the most robust conclusions. Finally, cross-validation with independent empirical data would be ideal given the importance to effective conservation.

Predicting genetic responses to future environmental change

Using landscape genetic models to predict genetic responses to future landscapes is a research direction that has yet to be addressed in a published study. This objective would need to follow a study addressing one of the previous objectives to first understand what currently structures gene flow. For instance, an optimization approach could be used to identify resistance values for a current landscape. Next, predicted landscape layers based on land-use change (Pocewicz et al. 2008) or future climate scenarios can be converted to resistance surfaces using the same weighting scheme as for the current landscape. Least-cost path methodology or circuit theory could then be used to predict future areas of high (or low) gene flow. The development of realistic landscape genetic simulations (e.g. Landguth & Cushman 2010) is also key to attaining this objective and will be a critical element in validating these models. However, given the relatively simplistic development and use of resistance surfaces in most published studies thus far, there remains more work to be done before resistance surfaces are likely to be highly informative for such 'genetic forecasting'.

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Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 List of some representative publications that have used resistance surfaces to illustrate different parameterization

methods. Not all studies used resistance surfaces in conjunction with genetic data, but created resistance surfaces that potentially could be useful for landscape genetic studies. For studies that used expert opinion, we noted whether resistance values were arbitrarily given categorical values or were continuous

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