

## *Chapter 8*

# RESISTANCE SURFACE MODELING IN LANDSCAPE GENETICS

*Stephen F. Spear,<sup>1</sup> Samuel A. Cushman,<sup>2</sup> and Brad H. McRae<sup>3</sup>*

<sup>1</sup>*The Orianne Society, USA*

<sup>2</sup>*Forest and Woodlands Ecosystems Program, Rocky Mountain Research Station,  
United States Forest Service, USA*

<sup>3</sup>*The Nature Conservancy, North America Region*

### **8.1 INTRODUCTION**

**Resistance surfaces** are an important component of the landscape genetics toolbox and can be defined as spatial layers that represent the extent to which the conditions at each grid cell constrain movement or gene flow. The basic framework for using resistance surfaces in landscape genetics involves the steps of variable selection, parameterizing values for resistance surfaces, correlating resistance with genetic data, and, in many cases, employing the best supported resistance surfaces in downstream analyses. Important considerations for variable selection include whether the variables are hypothesized to influence genetic connectivity, the appropriate spatial and thematic scale, and the accuracy of spatial data used to create resistance surfaces. Parameterizing resistance surfaces can be done through expert opinion or empirical methods. The ideal method for parameterizing resistance surfaces differs somewhat depending on the study system,

although empirical methods are likely to provide the best outcome if they can be directly related to genetic connectivity. Such empirical methods can be based on tracking data, habitat suitability models, or optimization using genetic data. In addition to the method used to parameterize the surface, the translation of the resistance surface to a connectivity model is a critical step in most analyses, with the most common methods being least-cost paths and circuit theory. Each of these methods is based on different assumptions and thus the most appropriate method should be assessed for each study individually. Resistance surfaces that correlate strongly with genetic measures can then be used for applications such as corridor design, barrier detection, or predictions based on scenarios of future landscape change. We anticipate that resistance surfaces will continue to evolve as technology increases the accuracy and resolution of remotely sensed data, genomic advances present opportunities to investigate applicability of resistance surfaces to questions

of natural selection, and models of future landscape and climate scenarios become more refined. Overall, we expect that resistance surfaces will remain a key tool in landscape genetics and will be especially important for those whose interest in landscape genetics focuses on its potential as a predictive science for the various facets of global change that are occurring.

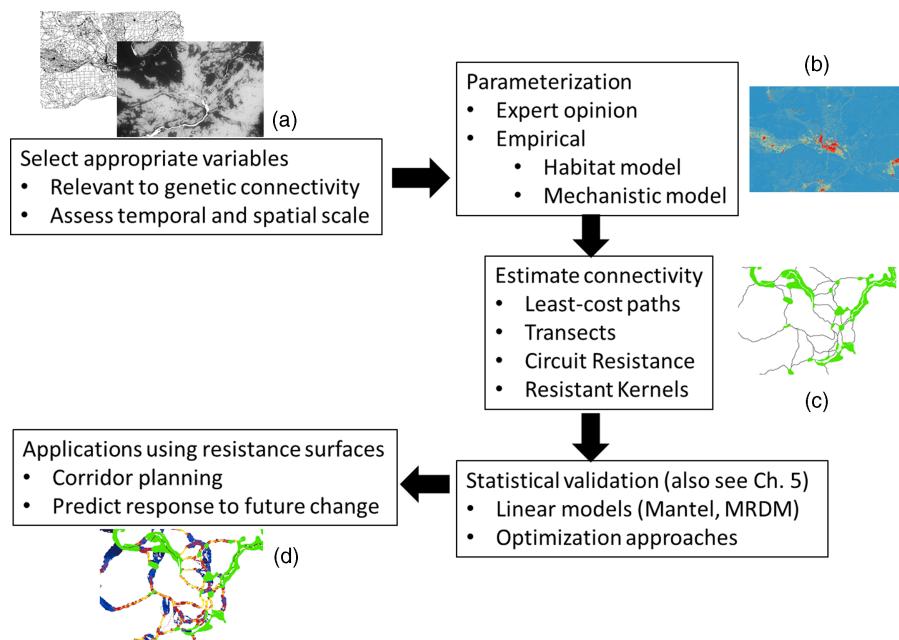
### 8.1.1 What is a resistance surface?

With respect to landscape genetics, a resistance surface is defined as a spatial layer whose values represent the extent to which the conditions at each grid cell constrain movement or gene flow (Spear et al. 2010). Thus, resistance values can represent the willingness of an organism to cross a particular environment, the physiological cost of moving through it, the reduction in survival for the organism, or an integration of all these factors (Zeller et al. 2012). Resistance surfaces can represent a single landscape variable, or several variables can be combined

into a single surface representing multiple variables. The creation of multivariate resistance surfaces, particularly when multiple surfaces need to be created for comparison or hypothesis testing, can be facilitated by the Gnarly Landscape Utilities toolkit (McRae et al. 2013).

### 8.1.2 Using resistance surfaces: a framework

The resistance surface has become a widely used tool in landscape genetics due to its applicability to multiple types of predictive models such as least-cost paths or circuit theory (see below). The underlying simplicity and ease of use of resistance surfaces belie the difficulty of developing, parameterizing (i.e., assigning cost values to landscape variables), and implementing a biologically justified resistance surface (Spear et al. 2010; Zeller et al. 2012). There is a general process involved in any landscape genetic study using resistance surfaces, although the methodology at each step certainly varies (Fig. 8.1). This process occurs in 4–5 steps,



**Fig. 8.1** Framework for incorporating resistance surfaces into landscape genetic studies. The accompanying figures depict a scenario for each step on the same landscape. Inset (A) represents two spatial layers used as input for a resistance surface (in this case, roads and land cover). Inset (B) represents a resistance surface reflecting resistance due to roads and land cover, with lighter colors indicating higher resistance. Inset (C) shows a network of least-cost paths (connecting core areas in gray) for connectivity across the resistance surface. Finally, inset (D) is a network of connectivity corridors based on the least-cost paths, with corridor width and color representing the degree of connectivity expected along the corridor (greater resistance along narrow paths with lighter colors).

beginning with the selection of appropriate landscape or environmental variables that will be used to derive the resistance surface. The second step is to use these variables to parameterize resistance surface(s). Third, the resistance surface is used to develop estimates or hypotheses of connectivity, and then a statistical model is used to test the relationship between the estimate of landscape connectivity and genetic connectivity. Optionally, researchers can then use the resistance surface with the greatest statistical support to conduct additional analyses, such as identifying conservation corridors or predicting genetic structure into the future. This chapter will focus on the various methods that have been used to achieve each of these steps and provide guidance on the benefits and drawbacks of each method depending on study objectives. We then conclude by discussing future directions for the use of resistance surfaces in landscape genetics.

### **8.1.3 Selecting variables for resistance surfaces: initial questions and assumptions**

The most important first question to ask when developing a resistance surface is what factors are likely to create resistance for the species of interest (i.e., landscape definition; Chapter 2). In landscape genetics, researchers use genetic relationships as the dependent variable, so the resistance surface must directly relate to genetic connectivity to be meaningful in a landscape genetic analysis. Resistance surfaces can be applied to a number of different processes such as animal movement or habitat occupancy (Zeller et al. 2012), and these processes may vary in how directly they correlate with genetic structure. As described in Chapter 3, there are many processes and variables that can affect population genetic structure. Estimates of genetic connectivity are influenced by such factors as dispersal (either through active movement of animals or passive dispersal of seed or pollen by wind or animals), population history, population size and spatial distribution, mutation rate, and reproductive mode. A careful consideration of the most important factors influencing genetic structure is needed to inform the best approach to developing resistance surfaces, or whether a resistance surface is even appropriate for the study system. For instance, if dispersal among patches of good habitat is the primary driver for genetic connectivity, then a resistance surface should ideally represent the extent

and configuration of these habitat patches as well as properties of the matrix separating patches that influence movement among the patches. On the other hand, if the system of interest follows source-sink dynamics in which sinks have reduced reproduction relative to sources, then resistance surfaces depicting effects of the landscape structure on movement should be coupled with fitness surfaces that represent habitat quality and enable analysis to couple the separate processes that drive movement and differential mortality in the source-sink system (e.g., Landguth et al. 2012).

### **8.1.4 What factors dictate the utility of variables for resistance surfaces?**

There are several factors that may influence whether the variables used to parameterize a resistance surface can be effectively used in a landscape genetic analysis. These include scale and resolution of landscape variables used, accuracy of remotely-sensed data, and temporal match of resistance surface and genetic data. Each of these should be considered when selecting variables for a landscape genetic study with resistance surfaces.

Scale is an essential consideration in any biological investigation and landscape genetics is no different (Anderson et al. 2010). Resistance surfaces are in many ways defined by the scale of the variables that comprise them (Chapter 2). This is most obvious with respect to the pixel size (the grain) of the resulting resistance surface. As most resistance surfaces are developed from remotely sensed layers, many resistance surfaces typically use the grain of the source GIS layer without transparent consideration of the biological relevance (Sawyer et al. 2011). The defense for this is that remotely sensed layers are often necessary to construct a resistance surface that has an extent large enough to measure differences in gene flow, and a researcher is restricted by the spatial resolution at which the data were collected. However, it is still useful to evaluate whether this is causing misleading results. In an attempt to address this question, Cushman and Landguth (2010a) performed a simulation study in which they examined how landscape genetic correlations (using Mantel tests) might change with different pixel sizes. Interestingly, they found that changing the pixel size did not have a large effect on the landscape genetic associations, at least in the case when the true

scale was a 90 m pixel. Similarly, McRae et al. (2008) found high correlations between effective resistances calculated across a range of pixel sizes in circuit-based analyses. It is important to note that resampling to coarse pixel size through nearest neighbor interpolation can result in total loss of linear features, such as roads and rivers, which may have dominant influences on landscape connectivity. However, this can be addressed by using pixel resampling methods, such as bilinear interpolation, that retain the mean resistance value across the merged pixels and thus do not “lose” the signal of the linear features. An enhancement to this is to coarsen resistance layers based on satellite-derived land cover using average resistances and to coarsen layers based on linear features like roads and rivers using maximum resistances before combining into a multivariate resistance layer. This preserves the integrity of linear features by avoiding the introduction of erroneous weak spots into them that can result from aggregating using average resistances. Furthermore, while Cushman and Landguth (2010a) did not find dramatic differences, they did find that the smallest pixel size tested always had the strongest relationship. The exception to this would be if the data layer being used had a high error rate, in which it may be advisable to use a coarser pixel size than native resolution. In such situations, the Washington Wildlife Habitat Connectivity Working Group (WHCWG) (2012; [www.waconnected.org](http://www.waconnected.org)) found that coarsening grid cell sizes can help to close spurious holes in barriers and remove single-cell patches with low resistance; such features often result from errors in classification of satellite data, and in any case would likely be too small to provide biologically viable movement pathways for many species.

Another scale-related factor for a resistance surface is the thematic resolution at which a pixel is defined (Chapter 2). In other words, is the landscape variable defined discretely, as a series of categorized classes, or as a continuous variable? This is especially relevant for variables whose native resolution is as a continuous variable (e.g., slope, elevation, percent forest cover, etc.) or a detailed category (e.g., lodgepole pine forest), but are represented as simpler categories (medium elevation or forest, respectively). In contrast to pixel size, Cushman and Landguth (2010a) found large influences of thematic resolution on the strength of apparent landscape–genetic relationships. As continuous variables were reclassified into categories, the support for the association dropped significantly. One

can imagine that the same result would occur when categorical variables such as land cover are simplified into fewer classes as well. Of course, there are also situations (such as generalist species) in which fine thematic resolution may not be appropriate. Ultimately, researchers need to consider both the most appropriate spatial and thematic scales relevant to the study system when preparing variables for incorporation into resistance surfaces.

A factor related to remotely sensed data that is rarely accounted for in landscape genetic studies is the accuracy of the map products derived from remote sensing analysis, such as classified land cover maps or continuous estimates of parameters such as canopy closure. This is a somewhat different issue than scale, as one may have a fine-scale, continuous landscape layer that is inaccurate and therefore not useful. Accuracy of data layers is often difficult to evaluate, and most landscape geneticists do not have training in interpreting and classifying remotely sensed data (Zeller et al. 2012). While it would be advantageous for landscape genetic researchers to receive training in these techniques, a reasonable and efficient first step is for studies to examine and report the accuracy assessments of the spatial data used and not use layers that do not meet the level of accuracy required by the researcher. All reliable data layers should have metadata that includes an accuracy assessment. While this information has rarely been reported in the landscape genetic literature, we strongly recommend that future studies include this information in published articles. While landscape genetic researchers often may not be able to fix such inaccuracies, they should be aware of errors in the spatial data they use to evaluate relationships between the genetic structure and landscape features. An important point to remember is that even if there is an accuracy estimate for a layer, different classes in that layer may have different error rates associated with them.

A fourth consideration related to both scale and accuracy is the temporal association of the spatial data with the genetic process being modeled. Most spatial data layers represent snapshots in time and so cannot account for factors of seasonality and environmental change over time unless multiple layers are used. In contrast, genetic data, although generally collected at a specific point in time, are influenced by processes occurring over many generations (see Chapter 3). This mismatch has been recognized by many scientists and several studies have addressed

this issue by using spatial data layers across different time points (Anderson et al. 2010; Spear et al. 2010; see Chapter 12 for specific examples). The general result is that genetic data often have a time lag in which measures of genetic distance correlate more strongly with past landscapes, although it is also common for contemporary landscapes to have significant correlations with genetic data. One study that evaluated the temporal time lag issue in landscape genetics is Landguth et al. (2010), which used an individual-based, spatially explicit simulation model (Landguth & Cushman 2010) to quantify the number of generations for new landscape barrier signatures to become detectable and for old signatures to disappear after barrier removal. They found that the lag time for the signal of a new barrier to become established is short using Mantel's  $r$  (1–15 generations), while  $F_{ST}$  required approximately 200 generations to reach 50% of its equilibrium maximum. In strong contrast, the time scale for loss of signal following the removal of a barrier formerly dividing a population was highly dependent on dispersal distance and ranged from a few generations to several hundred generations. The degree to which a temporal mismatch is important will be most strongly tied to the process that is driving gene flow and how quickly the landscape has changed. For instance, if a species has seasonal reproduction and reproductive events are primarily influenced by vegetation, then spatial data collected during a different season may lead to misleading results, especially in temperate regions (Cushman & Lewis 2010). However, a more common concern is the fact that landscapes change more rapidly than patterns of genetic structure are likely to shift. This possibility can be tested by using multiple temporal resistance surfaces using a model selection approach (Vandergast et al. 2007; Spear & Storfer 2008; Epps et al. 2013), and, if possible, this can be an excellent way to ensure that resistance surfaces based on contemporary landscape data are suitable to use in landscape genetics context.

## 8.2 TECHNIQUES FOR PARAMETERIZING RESISTANCE SURFACES

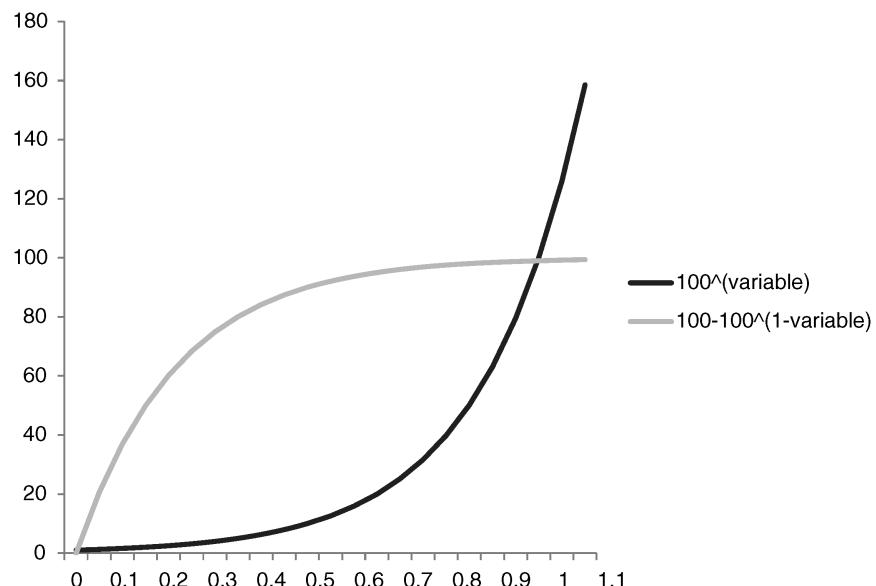
A recent review of resistance surfaces (Zeller et al. 2012) considered that the process of parameterizing resistance surfaces could occur in one or two stages, and classified techniques into one of three categories.

These include a one-stage expert approach, a one-stage empirical approach, and a two-stage empirical approach. The one-stage expert approach is not relevant to landscape genetics, which by definition includes an empirical stage. The two-stage empirical approach may have either an expert or empirical first stage, but then includes a second empirical stage in which alternate models are statistically compared. Below, we discuss the use of both expert opinion and empirical approaches to develop resistance surfaces.

### Expert opinion

Expert parameterization of resistance values is a common method for developing a resistance surface and is often applied to systems with limited biological data or that cover broad spatial extents. Generally, it involves an expert or a group of experts estimating resistance values for the variables of interest. Clearly, this is the most subjective form of resistance surface development, although it does potentially take advantage of widespread expertise that is not represented in empirical data and may be more cost-efficient than gathering empirical data (Murray et al. 2009). The typical process is to develop several resistance surfaces parameterized through expert opinion and then use genetic data to select the best resistance surface based on statistical correlations (see statistical validation section below). This type of approach can involve model selection among resistance surfaces with different variable sets but only one set of resistance values for each variable (Spear et al. 2005, Vignieri 2005, and James et al. 2011 are some examples) or use some type of optimization that identifies which parameter values for each variable has the best correlation, either through a manual or iterative approach (Cushman et al. 2006; Epps et al. 2007; Wang et al. 2009; Shirk et al. 2010; Wasserman et al. 2010; Richardson 2012). Either method is generally used when researchers hypothesize that multiple landscape variables are affecting gene flow but lack non-genetic empirical data, which requires the use of expert opinion.

Studies that do not vary resistance values for each variable typically assume a linear relationship with continuous variables such as canopy cover or slope (Spear et al. 2005; James et al. 2011). Recent work has suggested that non-linear responses could be prevalent in landscape genetics, particularly asymptotic responses at the ends of the distributions (Fig. 8.2; Balkenhol 2009; Koen et al. 2012; Wasserman et al.



**Fig. 8.2** Example of non-linear responses that can be modeled using resistance surfaces, in this case using exponential functions. The dark gray line represents a scenario in which effective resistance remains low until variable values reach high levels and in which resistance becomes very high at the upper extreme of variable values. In contrast, the light gray line represents a scenario in which an organism responds strongly to small increases in variable cost, but that level of resistance plateaus at intermediate to high levels of that variable. These particular exponential transformations are taken from Balkenhol (2009) and Trumbo et al. (2013).

2010; Shirk et al. 2010; Trumbo et al. 2013). If the asymptotic tails intersect with a large portion of the variable range within the study landscape, then modeling resistance based on a linear relationship is unlikely to result in a significant correlation no matter the biological relevance of that variable. Therefore, even if thorough optimization approaches are not used, researchers should at least test some non-linear relationships to better understand how landscape variables will affect genetic structure.

Many variables of interest to landscape geneticists must be represented as categorical variables. Such variables include land cover classes and discrete landscape features (roads, rivers, etc.). The difficulty in using these variables in resistance surfaces is that resistances must be assigned to each variable, usually with much uncertainty as to the “true” value. Therefore, most studies that incorporate categorical variables have developed multiple resistance surfaces that represent different costs for the variable of interest and then use the correlation with genetic distance to select the best resistance value. The techniques to choose the

most appropriate resistance values vary widely. This is because there are an infinite number of cost values that could be given for any variable in a resistance surface. Researchers must therefore determine how extensively to test different variable costs. At the most basic end, a small number of values are chosen for each variable, with the cost value usually differing by a large amount. For example, Spear and Storfer (2010) tested two cost ratios (10:1 and 100:1) for a test of terrestrial versus stream movement in the Rocky Mountain tailed frog (*Ascaphus montanus*). Similarly, Richardson (2012) tested 5–8 different costs per variable that represented at least 1–2 orders of magnitude difference. The strategy behind this approach is to limit the number of alternative models (and possible false positives due to chance because of multiple comparisons) but be able to get a cost that approximates the true resistance of the variable (within an order of magnitude). A limitation of this approach is that the cost values are likely to be too inexact to be able to use the resistance surface for other purposes, such as using the resistance surface to map connectivity corridors or using it as the basis of future

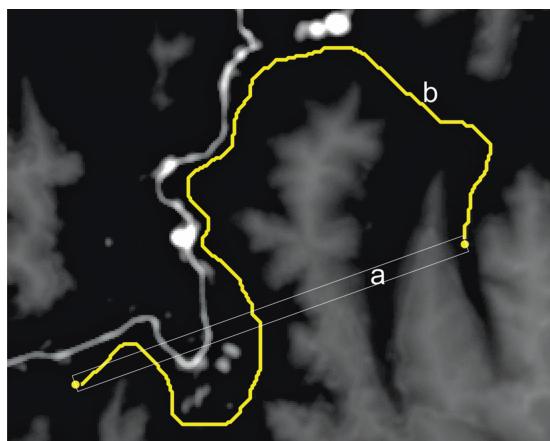
predictions (Rayfield et al. 2010). Instead, a small number of cost values is better suited for studies that wish only to identify variables that have a significant association with genetic structure amongst a large candidate list of potentially important variables.

### Empirical parameterization

Empirical approaches to the parameterization of resistance surfaces can include a variety of methods and are becoming increasingly popular in recent landscape genetic studies (Richards-Zawacki 2009; Shirk et al. 2010; Emaresi et al. 2011; Hagerty et al. 2011; Walpole et al. 2012). A strategy that attempts to use the genetic data to produce a final resistance surface is to measure landscape variables along straight-line transect buffers and use the correlation with genetic data to produce a resistance surface (Fig. 8.3; Braunisch et al. 2010; Murphy et al. 2010; Emaresi et al. 2011). The appeal of this method is that it does not assume any prior relationship with the landscape variables; the researchers must only select what variables are most relevant. It also facilitates the use of both continuous and categorical variables as categorical variables can be easily transformed into a continuous measure, such as proportion of

cover type along a transect. Although the line transect analyses could be conducted without buffers, doing so would implicitly assume that individuals always moved in straight lines between sites, an assumption that would be routinely violated. Instead, calculating the landscape component within a buffer along the transect accounts for multiple movement paths between sites without needing to identify the exact movement routes (Emaresi et al. 2011). Furthermore, Murphy et al. (2010) demonstrated that using different buffer sizes could be informative for understanding the scale at which a landscape process is influencing gene flow. However, straight-line buffers may correlate very poorly with dispersal processes that tend to follow low-cost pathways – for example, a straight line might intersect an insurmountable barrier that could be sidestepped with only a slight detour through a low-cost habitat. Moreover, buffered transects do not account for the spatial configuration of land cover types within them; an impermeable cover type within a buffer may or may not bisect the buffer and disrupt movement. Once landscape variables within a transect are regressed against genetic distances, the results can then be used to build a resistance surface. For example, Braunisch et al. (2010) summed regression coefficients of significant landscape

**Fig. 8.3** Illustration of the differences in assessing connectivity between two points on a resistance surface using transect (a) and least-cost path (b) methods. The resistance surface shown here is that produced by Cushman and Lewis (2010) predicting resistance to black bear movement based on movement pathway analysis. (a) This shows a belt transect between two points on the resistance surface. The transect method would measure the composition of the landscape contained within the belt transect and use that as the independent variable in predictions of genetic differences between the individuals or populations located at the two points. Conversely, (b) shows a least-cost path between the same two points on the resistance surface. The least-cost path method would calculate the lowest accumulative cost on the resistance surface between the two points and use this as the independent variable in analyses predicting genetic differences between the individuals or populations located at those two points. You can see that these methods would produce substantially different predictions of connectivity, with the belt transect indicating that individuals moving between the two points would cross two high ridges and twice cross a major highway, while the least-cost path approach would suggest that individuals would avoid these barriers and instead follow a route through low-cost habitat between the ridges and the highway.



variables to create a resistance surface that was then used to predict corridors for capercaillie (*Tetrao urogallus*). Murphy and Evans (2011) also used the results of the transect analysis in Murphy et al. (2010) to predict landscape connectivity for boreal toads (*Anaxyrus boreas*) in Yellowstone National Park.

There are a number of other empirical approaches for developing resistance surfaces in landscape genetics. An increasingly popular empirical approach is to use some form of a resource selection function (Boyce et al. 2002) or species distribution model (Phillips & Dudik 2008). Essentially, these models aim to describe habitat suitability based on the values of environmental variables. They can be built through a variety of data types. Species distribution models often use presence data only at broad scales to predict distribution (and, by assumption, habitat use), whereas individual radio telemetry observations can be used to build a fine-scale resource selection function. It is easy to see why models of habitat suitability are appealing for researchers interested in using resistance surfaces for landscape genetics: they can be easily represented as raster grids, they are based on objective empirical data, and they are created independently of genetic data (and therefore useful for testing genetic patterns). Some examples include using desert tortoise (*Gopherus agassizii*) observations to build a presence-only habitat model (Hagerty et al. 2011), trapping observations of spiny rats (*Niviventer coninga*) in a presence-only model (Wang et al. 2008), and resource selection functions based on radio telemetry points in mountain goats (*Oreamnos americanus*; Shafer et al. 2012). The disadvantage of using some form of a habitat suitability model is that there is a single best model output and so there are generally not comparable alternative models to test. This can be problematic because it can be difficult to assess whether a correlation is biologically significant without comparative models (Cushman & Landguth 2010b). One exception to this scenario is the investigation of mountain goat resource selection by Shafer et al. (2012). This study actually investigated 10 different resource selection functions (varying by combinations of sex and season) and tested the different models with genetic data (in addition to isolation-by-distance and isolation-by-barrier). This research found that summer habitat selection by both sexes had the highest correlation with genetic distance compared to winter habitat. It should be noted that one may often find poor correlation between habitat selection models and gene flow (e.g., Wasserman et al. 2010). This is because habitat selection and gene flow are governed by different behavioral

processes, typically different life stages, and often act at very different spatial scales. For example, habitat selection generally measures the features that promote occurrence or density of adults in fixed home ranges. Gene flow, on the other hand, is governed by dispersal, which is typically driven by juveniles. Juvenile dispersal behavior and adult territorial behavior are often very different, and individuals may be able to disperse through areas that represent poor habitat. Furthermore, regardless of life stage, landscape features that facilitate dispersal may be very different from features associated with core species habitat. As an example, Wasserman et al. (2010, 2012) showed that modeling connectivity using resistances based on an empirically optimized habitat quality map provided a very poor estimate of genetic resistance.

Experimental animal movement is a further empirical method to develop a resistance surface. This approach literally measures animal movement across different surfaces and uses this to estimate resistance. This method was used by Stevens et al. (2006a, 2006b) with the natterjack toad (*Bufo calamita*) in experimental arenas representing different land types such as roads, agricultural fields, and forests. In two separate studies, they measured both how easy it was to cross a given land type and how willing individuals were to enter a different land cover type. This research demonstrated that these two types of resistance were not always consistent. For example, forest cover was more difficult for toads to move through compared to other types, but was entered preferentially in the selection experiment. Interestingly, bare substrates such as concrete had both low resistance to movement and were selected by the toads. This type of research is quite useful because it provides a more mechanistic rationale behind a resistance surface, but because of the simplified experiment arenas, may not represent the true landscape reality. Add car traffic to roads, and permeability can dramatically decrease because of increased mortality risks. Furthermore, many species are simply too large or vagile to make use of even a simple experimental arena meaningful (but tracking translocated individuals may be occasionally possible and give similar information). As a result, this approach may be most fruitful for small invertebrates or extremely dispersal-limited organisms. Another example in which actual movement rates were incorporated into a resistance surface was conducted with *Daphnia* zooplankton by Michels et al. (2001). The researchers modeled zooplankton genetic connectivity among ponds using different resistance

surfaces representing pond connections, flow rate among ponds, and measures of actual *Daphnia* dispersal. The functional measures of flow rate and dispersal had a stronger correlation with genetic distance than structural connectivity alone.

Another powerful method to empirically estimate resistance surfaces is to use movement pathway data to quantify association of movement path selection with environmental features. Movement pathway data are characterized by multiple sequential locations of the same individuals taken at sufficiently frequent intervals that enable one to treat each sequence as a movement pathway. Pathway data are much preferred over static detection data and relocation data when the focus is estimating resistance to movement of individuals through the landscape (Zeller et al. 2012), as they directly measure the behavioral choices an organism makes in selecting paths in relation to landscape features. There have been quite a few examples of using pathway data to estimate landscape resistance. Dickson and Beier (2007) identified the topographic composition of paths used by tracked cougars; such information could easily be translated into a resistance surface for the area. Cushman et al. (2010a) used pathway data, multivariate scaling, and randomization testing to develop resistance surfaces for elephant movement in Botswana. Similarly, Cushman et al. (2011) used matched case control logistic regression to quantify the effect of landscape fragmentation on landscape resistance to movement of American marten (*Martes americana*). Despite the clear advantages of pathway data, they have only been used in combination with landscape genetic data in two instances. Cushman and Lewis (2010) used matched case control logistic regression to test the resistance hypotheses evaluated using landscape genetics by Cushman et al. (2006) for black bears. They found that movement behavior explained patterns of genetic differentiation and that the same model of landscape resistance was supported both by genetic data and pathway data. In contrast, Reding et al. (2013), using similar methods, found that movement behavior and genetic differentiation of bobcats (*Lynx rufus*) in Iowa were related to different factors. Specifically, movement pathway selection was driven by the pattern of human activity and natural vegetation on the landscape, whereas genetic differentiation appeared to be governed by isolation-by-distance.

Pathway data can further be used to test some of the components of physical resistance that have previously been explored in the experimental arena discussed

above. For instance, organisms may tend to avoid suboptimal habitats when a variety of types are available to move through, but at the same time be able to move quickly through the same suboptimal habitats if high-quality habitat types are not available (Dickson et al. 2005; Kuefler et al. 2010). For instance, agricultural areas might be avoided if adjacent to a natural grassland, but would be much more conducive to movement in a more developed matrix. Therefore, the resistance of such habitats may be highly variable depending on the overall landscape context. Movement rates across different landscapes inferred from pathway data could prove very useful in parameterizing resistance surfaces in such situations.

### **8.3 ESTIMATING CONNECTIVITY FROM RESISTANCE SURFACES**

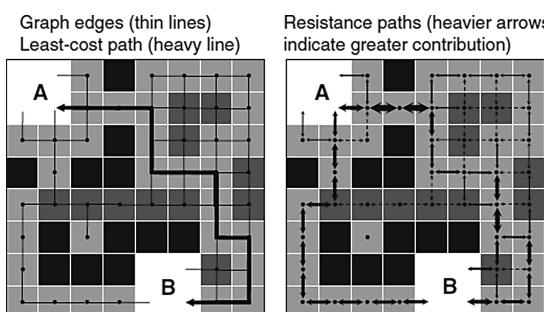
The choice of method to parameterize resistance surfaces is an extremely important consideration, as illustrated in the above sections. However, in landscape genetic studies, the resistance surface cannot be directly compared to genetic data. Genetic data are collected at the level of individuals or discrete sites and therefore genotypes do not form a continuous grid across the resistance surface. While it is possible to convert genetic data into a continuous grid that is directly comparable to a resistance surface (Murphy et al. 2008), it is more likely that both the resistance surface and the genetic data will need to be translated into a pairwise measure to represent genetic connectivity among individuals or sites. There typically have been two approaches to addressing this issue: using the resistance surface to draw least-cost paths (Adriaensen et al. 2003) or representing the resistance surface as nodes of an electrical circuit (McRae 2006). In both cases, the output is a pairwise measure that reflects the overall resistance to gene flow or movement among sites.

The least-cost path has been the most popular technique for studies applying resistance surfaces to landscape genetics (Storfer et al. 2007). The least-cost path approach is fairly intuitive: draw a line between two areas that minimizes the cumulative movement cost moving across the resistance surface (Figs. 8.3 and 8.4). Least-cost paths can be correlated with genetic data in a few different ways. The researcher can measure the Euclidean or topographical length of the least-cost path (Spear et al. 2005), calculate the total resistance cost along each path (Cushman et al. 2006;

Shafer et al. 2012), or simply use the least-cost path as a transect and calculate the value of landscape variables along the path, analogous to the straight-line transect approach discussed above (Spear et al. 2005; van Strien et al. 2012). In addition to the landscape genetic literature, least-cost paths have been commonly used in conservation corridor planning approaches (Singleton et al. 2002; Cushman et al. 2009; Beier et al. 2009; WHCWG 2012) to choose the optimal path to design linkages. However, there are a number of simplifying assumptions that are made with the use of least-cost paths. First, they assume that organisms have enough knowledge of the landscape to follow the ideal path or that the matrix outside the least-cost path is so hostile that it would force the organism to follow the ideal path. In other words, the modeled least-cost path determines movement and genetic structuring, whereas alternative pathways have little to no effect. The limitation of this assumption is addressed with the use of circuit theory (McRae 2006), discussed in the next section. This assumption is most important when using least-cost paths to design corridors, whereas it may be able to be relaxed if researchers are interested in relative differences between paths. However, beyond these assumptions, a common concern with least-cost path methodology is in regards to its sensitivity to differences in resistance surface parameterization and errors in base data. The sensitivity to different relative costs is especially important when the cumulative resistance is used as the independent variable or when the study is attempting to identify specific connectivity corridors that may have different spatial placements with different resistance costs (see examples in Chapter 2). For instance, Rayfield et al. (2010) demonstrated how spatial location of least-cost paths could vary with various relative costs, especially with increasing proportions of inhospitable matrix across the landscape (Chapter 2). Koen et al.

(2012) addressed a similar question of the effect of different relative cost values by examining the influence on both least-cost path length and cumulative least-cost path resistance. The authors found that the cumulative cost of the least-cost path increased linearly with increased relative resistance, but least-cost path length tended to quickly plateau with increasing resistance contrast. While this may provide an argument to use least-cost length as the least-cost measure when resistance parameterization is uncertain, it is probably far better to use an empirical model selection approach to choose the best parameterization scheme when using least-cost paths. In the latter case, cumulative resistance should be used as it will change linearly with resistance and lead to effective model selection (Koen et al. 2012). Least-cost methods can also be particularly sensitive to errors in base data (Beier et al. 2009; McRae et al. 2012).

The second common approach is the use of electrical circuit theory to model resistance across the landscape (McRae 2006). In most applications, landscapes are represented as grids of regularly-spaced nodes connected by resistors. The resistance surface determines the level of resistance among adjacent nodes. Pairwise resistances incorporate all possible pathways connecting patches or locations on the landscape (Fig. 8.4). Circuit theory analysis is typically used in the same fashion as least-cost paths for landscape genetics in that there is a summary pairwise resistance value that is correlated with some measure of genetic distance. In contrast to least-cost paths, circuit analyses incorporate many possible paths into the measure of resistance. This could be especially advantageous in landscapes in which there are several connections of similar total cost between sites such that a least-cost path would only represent a fraction of organismal connectivity. This fact has led many to suggest that circuit analyses are preferable for landscape genetic analyses as compared



**Fig. 8.4** 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 colors. 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.

to least-cost path analyses (McRae & Beier 2007; Lee-Yaw et al. 2009; Munshi-South 2012). Of course, circuit theory has its own set of assumptions. It does not assume complete knowledge of the landscape, but it does assume that organisms are capable of using the entire landscape (although completely unsuitable pixels can be masked out of the analysis). A modification to the circuit theory software to constrain movement to least-cost corridors has recently been implemented (McRae 2012), but this has yet to be evaluated for landscape genetic applications.

Several studies have compared least-cost paths and circuit theory using the same data set. The results from the different studies have not always been consistent, but largely fit within the expectations of each method. For instance, studies that have focused on wide-ranging species with portions of the matrix that are impermeable have often demonstrated a stronger correlation with circuit theory. McRae and Beier (2007) demonstrated that circuit theory modeled range-wide gene flow (i.e., range limits were the only barriers modeled) much better than least-cost paths. Similarly, but on a finer scale, boreal toad (*Anaxyrus boreas*) gene flow was primarily constrained by salt-water barriers and circuit theory described this pattern best (Moore et al. 2011). Furthermore, circuit theory best correlated with genetic distance in a generalist species (the white-footed mouse, *Peromyscus leucopus*) in an urban environment (Munshi-South 2012). On the other hand, gene flow of Cope's giant salamander (*Dicamptodon copei*), a stream-associated amphibian, provides an example of a study with consistently higher correlation with least-cost path models than circuit theory across three different regions (Trumbo et al. 2013). The tendency of this semi-aquatic species to use a linear stream network for dispersal and breeding likely explains this discrepancy. Other studies have found little difference between connectivity estimates using both least-cost paths and circuit resistances (Schwartz et al. 2009; Row et al. 2010). Therefore, while the best analytical method for estimating connectivity from resistance surfaces may be predicted based on the biological characteristics of the study system, more work is needed to demonstrate a consistent result. Ultimately, because different models that use resistance surfaces have different assumptions, no one model is likely to be best in all circumstances. For example, a seldom appreciated assumption of circuit methods that is violated in many landscape genetic applications is that each node (i.e., each grid cell in

raster analyses) is a population. This may be more realistic when predicting broad-scale patterns such as the effects of range size (e.g., McRae & Beier 2007). For finer-scale analyses, it may be that one model (e.g., Euclidean distance, least-cost path distance, or a hybrid of least-cost methods with circuit analyses) may be best at predicting movement between populations or individual locations and another model (e.g., circuit theory or simulation algorithms like those contained in CDPOP; Landguth & Cushman 2010; see also Chapter 6) may be needed to integrate the cumulative effects of gene flow across networks of populations or individuals. The multigenerational nature of genetic connectivity may also influence the appropriateness of least-cost paths or circuit theory approaches. Intuitively, circuit theory may represent multigenerational connectivity better due to the integration of multiple paths, and this has been borne out in simulations of networks of discrete populations with non-overlapping generations exchanging migrants with neighboring populations (McRae 2006). However, a rigorous study of the performance of the two approaches in systems with continuously distributed populations and more complex life history characteristics and dispersal behaviors has not been conducted, and is necessary to provide more concrete guidance on this issue.

#### **8.4 STATISTICAL VALIDATION OF RESISTANCE SURFACES**

The previous sections highlighted the development of resistance surfaces, but direct incorporation of genetic data is the necessary step when resistance surfaces are used for landscape genetic questions. This takes the form of some type of statistical correlation analysis (i.e., Mantel tests, multiple regression on distance matrices, etc.); the details on these techniques are discussed in Chapter 5 and so are not presented here. However, the process by which a researcher determines if a resistance surface is representative of patterns of genetic connectivity goes beyond the statistical correlative method chosen. The simplest type of study is to evaluate whether a specific variable has a significant correlation with gene flow – the researcher only needs to develop a resistance surface for the variable of interest, translate that resistance surface into some measure of connectivity, and then correlate that with a measure of genetic connectivity. For instance, Andrew et al. (2012)

evaluated how genetic divergence in prairie sunflowers (*Helianthus petiolaris*) was explained by a resistance surface representing either bare dune or vegetated dune habitat. The researchers found that a low resistance for bare dunes relative to vegetated dunes had the strongest correlation with genetic distance. In another example, timber rattlesnake (*Crotalus horridus*) gene flow was significantly correlated with basking habitat compared to Euclidean distance (Clark et al. 2008). It is important to note, however, the potentially severe pitfalls associated with seeking correlations between genetic structure and a single variable. Cushman and Landguth (2010b) and Cushman et al. (2013) showed that there are usually high spurious correlations between genetic distance and a very large number of incorrect resistance hypotheses due to the inherent high correlation of cost distances. *A priori* selection of a single landscape resistance model usually yields highly significant support, but would very likely lead to inferential error. Thus, evaluating support for a single landscape resistance model in isolation provides a very weak basis for inference. Reliable inference of the factors driving gene flow instead requires formal evaluation of support among a pool of realistic candidate models involving several variables and several functional responses for each variable (e.g., Cushman et al. 2006; Shirk et al. 2010; Wasserman et al. 2010).

The process to evaluate multiple resistance surfaces can be based on a model selection approach or through an iterative optimization algorithm. The first major attempt at a rigorous model selection framework in landscape genetics was conducted by Cushman et al. (2006). They tested 108 different multivariate resistance surfaces for black bear (*Ursus americanus*) gene flow across northern Idaho. The 108 surfaces represented every combination of four variables (land cover, roads, elevation, slope), each at 3–4 different relative costs. They then determined the combination of resistance values for each variable that had the strongest correlation with genetic differentiation based on Mantel and partial Mantel tests, through a framework described as causal modeling. This study is also instructive of the difficulty of optimizing resistance surfaces. The authors only tested a small number of variables at a small number of potential cost values and yet still had a large number of hypothetical resistance surfaces. Another example that more strongly illustrates this point is a study in which Wang et al. (2009) parameterized cost surfaces for three land cover types (chaparral, grassland, woodland) at every possible combination of values at

cost intervals of 0.1 ranging from 1 to 10 for California tiger salamander (*Ambystoma californiense*) breeding ponds. This created a total of 24,843 resistance surfaces. Interestingly, the authors found that a relatively narrow range of cost values was supported by using genetic estimates of contemporary migration. However, even this extensively optimized resistance surface would incompletely project California tiger salamander gene flow on other landscapes as it only includes three categories of natural land cover. A compromise to this optimization problem has been presented by Shirk et al. (2010). Using mountain goats (*Oreamnos americanus*) as a test case, they presented a framework in which expert opinion was used as a starting point, but then iteratively adjusted the resistance value and tested the correlation with genetic distance until a unimodal peak of correlation support was identified. Each variable was optimized separately and then run through a second set of optimization with all other variables held constant (i.e., a quasi-multivariate optimization). While still computationally intensive, it allows for a larger number of variables to be evaluated and takes advantage of prior knowledge that can be used with expert opinion approaches. However, there has been some recent concern that optimization approaches may not be producing resistance estimates that accurately reflect genetic connectivity. Graves et al. (2013) used a combination of a global optimization procedures based on Mantel correlations (the same metric used by Cushman et al. 2006 and Shirk et al. 2010) and landscape genetic simulations to demonstrate that optimized resistance surfaces rarely produced the true resistance estimates that parameterized the simulations. More recently Shirk et al. (2012) and Castillo et al. (2014) coupled simulation modeling with multivariate optimization using the reciprocal causal modeling method (Cushman et al. 2013) and showed that this method seems to perform quite well in identifying the correct drivers of gene flow and rejecting highly correlated alternative resistance hypotheses. Clearly, statistical optimization approaches may not always guarantee biologically relevant results and further development and testing of statistical analyses for landscape genetic work is of high priority.

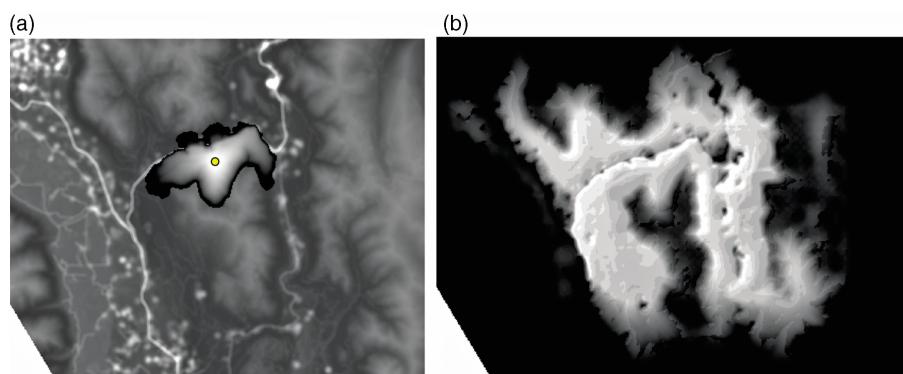
#### **8.4.1 Applications of resistance surfaces in landscape genetics**

The identification of a resistance surface highly correlated with genetic connectivity is often used by

researchers to then address a broader question. Here, we focus on two types of applications that resistance surfaces have great utility for: corridor identification or design and predictive modeling under future conditions. Both of these objectives are of increasing importance to understanding the conservation, ecology, and evolution of species in a changing environment characterized by increased fragmentation due to anthropogenic habitat alteration and global climate change.

Thus far, the resistance surface has served as the “foundation” for connectivity and corridor analyses, and resistance surfaces are by far the most commonly used tool in corridor planning (Clevenger et al. 2002; Epps et al. 2007; Beier et al. 2008, 2009, 2011; Cushman et al. 2009; Wasserman et al. 2012). Of course, the relevance of landscape genetics to this type of conservation planning is strongly dependent on what type of corridors or reserves are being considered. For instance, a migratory bird corridor would be unsuitable for a genetic study because the migrations do not represent a gene flow event. However, most connectivity corridor initiatives are interested in connecting populations through dispersal that does lead to gene flow. Therefore, a resistance surface that has been validated through genetic data is particularly useful, especially considering that most current connectivity efforts rely on expert opinion without

empirical validation (Beier et al. 2008). A genetically validated resistance surface can be used to map corridors based on least-cost paths or current flow, usually incorporating a cutoff value for maximum cost length or resistance value to identify possible corridors (Beier et al. 2011). An emerging methodology that has promise for using resistance surfaces for corridor planning (in addition to other applications) is the resistant kernel approach (Fig. 8.5; Compton et al. 2007; Cushman et al. 2010a, 2012; Cushman & Landguth 2012). This method is a modification of least-cost path principles that addresses some of the criticisms of least-cost paths. The idea behind a resistant kernel is to use a resistance surface to calculate the cumulative least-cost distance to reach each pixel from every source pixel, and then scale this so that it represents a probability of a disperser reaching each pixel. A probability distribution function is used to determine the maximum distance from the source that a pixel can be and still be included in the resistant kernel calculation. Essentially, the resistant kernel approach recognizes that, in addition to the habitat attributes of a pixel, the resistance of the surrounding pixels also affects the likelihood that the focal pixel will promote dispersal or gene flow. Resistant kernels have had extensive use in modeling dispersal synoptically across continuous landscapes (Compton et al. 2007) and mapping corridors and barriers to dispersal (Cushman et al. 2010a,



**Fig. 8.5** Illustration of resistant kernel modeling of connectivity across a resistance surface. The resistance surface is shown in pale gray-scale background in (a). A single-source location is shown in a point in (a). The dispersal kernel from that point is shown as a grey-scale kernel in (a) with white indicating areas with high probability of movement, black indicating areas with low probability of movement, and areas outside the kernel indicating areas that are not reachable from that source point given the dispersal ability of the species. (b) This shows the cumulative resistant kernel surface across the study area, with white areas indicating locations predicted to have high connectivity and high rates of movement of individuals through them and dark areas predicted to have low rates of movement. The structure of the resistant kernel surface can be used to identify corridors, barriers, core areas, and fracture zones of connectivity.

2012; Cushman & Landguth 2012). However, resistant kernels have yet to be used directly with genetic data in the same way as least-cost paths or circuit theory. This is because while it modifies the resistance surface, it still results in a continuous layer of pixel values, which is the same structure as any resistance surface. Researchers could apply a typical least-cost path approach to the resistant kernel surface or possibly even combine least cost and circuit approaches by running current through a resistant kernel surface. The use of resistant kernels has much promise and should correlate with gene flow, but we would recommend tests with combined empirical and simulation data sets to demonstrate their effectiveness in landscape genetic analyses.

Predicting the future genetic structure and connectivity of populations is a key question in understanding population responses to changing or novel landscape conditions. Resistance values for variables in their current state can be extrapolated to predicted future landscape conditions to develop a future resistance surface. Individual-based model (IBM) simulations (see Chapter 6) can then be implemented based on resistance surfaces based on future scenarios. IBMs based on resistance surfaces have produced ecological distances that correlate well with empirical genetic data (Vuilleumier & Fontanillas 2007; Shirk et al. 2012), which suggests that simulations on resistance surfaces can be representative of gene flow. For example, the software CDPOP (Landguth & Cushman 2010) has been used to simulate future scenarios for predicting reduced connectivity and genetic diversity under scenarios of climate change (Wasserman et al. 2012) and forest management (Spear et al. 2010). Other platforms for such simulations exist (see Chapter 6) and may provide even more flexibility for modeling a number of demographic and population parameters, as well as traits under selection, provided sufficient information is available for the species of interest (e.g., HexSim; Schumaker 2012).

#### **8.4.2 Concise considerations for effective uses of resistance surfaces**

Below we provide a short list of considerations that are important for researchers interested in using resistance surfaces for their research. Researchers should attempt to satisfactorily address all these points when designing a landscape genetic study with resistance surfaces,

although they may not be easy to answer for many studies.

- What questions and hypotheses do I want to use a resistance surface to test?
- Are reliable data available for the variables to be used in the resistance surface?
- Is the thematic, spatial, and temporal scale of spatial data appropriate?
- Are appropriate empirical data available to guide choice of resistance values for each modeled variable?
- If empirical data are lacking, what is the strategy to ensure that the expert opinion process is as informative and objective as possible?
- Which model of effective connectivity based on resistance surfaces (least-cost, circuit resistance, etc.) is most suitable given my research questions and characteristics of my study system?

### **8.5 THE FUTURE OF THE RESISTANCE SURFACE IN LANDSCAPE GENETICS**

The resistance surface has clearly been a foundation for landscape genetics to date, but, in a rapidly developing field such as landscape genetics, that alone does not guarantee that it will continue to be an important tool in the field. Below we discuss what we anticipate will be important or necessary directions for research using resistance surfaces in the future.

#### **8.5.1 Advances in remote sensing**

Resistance surfaces used in landscape genetics are currently largely driven by data derived from remote sensing technologies and this is unlikely to change. Remote sensing is using new technologies to substantially increase resolution and accuracy of spatial data layers, and the idea of a resistance surface at a submeter resolution is not outside the realm of possibility. Furthermore, tools such as LIDAR allow for three-dimensional representation and therefore allow modeling of factors such as vegetation height. This could potentially allow for breakthroughs in landscape genetic studies of species that have movement or gene flow over very fine scales, such as many invertebrates or small vertebrates. Of course, extremely fine resolution is of little use for systems in which the organisms exchange genes over broad scales. However, any technology that increases

the accuracy of spatial data or allows for the reliable incorporation of more variables should be beneficial to any study. It should be noted that such advances would improve only the raw material for resistance surfaces – they may do little to improve parameterization and in some cases may lead the process to be more complicated.

### **8.5.2 Development of model selection and optimization methodologies**

The incorporation of approaches to assess multiple alternative models is one of the most important directions that have improved landscape genetic studies (Cushman et al. 2006; Wang et al. 2009; Shirk et al. 2010). However, there is certainly much room for improvement in these model selection procedures. It is still very computationally intensive to test many possibilities for resistance surface parameters and exhaustive optimization can rapidly turn resistance surfaces into little more than a statistical model-fitting exercise divorced from biology. Furthermore, the non-independence inherent in both landscape and genetic data often violate assumptions of the most commonly used metrics of model selection employed in landscape genetics. The Mantel test, which has been commonly used in model selection with resistance surfaces (Cushman et al. 2006; Shirk et al. 2010) has been criticized on multiple fronts as inappropriate for landscape genetics (Legendre & Fortin 2010; Guillot & Rousset 2013), while others have found Mantel tests applied in a strict model comparison framework to have high power to correctly identify the driving process and reject highly correlated alternative models (e.g., Cushman & Landguth 2010b; Shirk et al. 2012; Cushman et al. 2013). Clearly, a widespread consensus has not been reached regarding this issue (see also Chapter 5). Breakthroughs in computational efficiency and statistical methodology will be invaluable in improving model selection. For instance, researchers are currently investigating possible approaches to directly translate genetic data into a parameterized resistance surface (Hand et al. 2014).

An intriguing method for parameterization that combines both mechanistic movement data with telemetry pathway data to create a resistance surface is the idea of an “energy landscape” (Shepard et al. 2013). An energy landscape directly translates the mechanistic cost of movement to the resistance surface and can be calculated by the energetic cost per unit of movement. Therefore, such a surface would be quite intensive to parameterize as it would require movement physiology

studies for the focal species across a range of environments. Energy landscapes in landscape genetics would also assume that the physical ability to move through the landscape is the primary determinant of genetic connectivity, which of course may not be the case. However, if this assumption holds, a correctly parameterized energy landscape provides a highly empirical measure of resistance. Energy landscapes have not been used in a genetic study, but two recent studies have introduced a blueprint for how such a study might unfold. Wall et al. (2006) investigated African elephant (*Loxodonta africana*) movement in relation to slope. The study used estimates of the energy required to climb slopes accounting for body size and determined that climbing 100 vertical meters would require an extra half hour of foraging time, indicating that climbing slopes is costly to a large animal like an elephant. The researchers used radio telemetry to confirm that elephants avoided steep slopes in their movements. In an aquatic environment, McElroy et al. (2012) measured pallid sturgeon (*Scaphirhynchus albus*) movement at various depths and velocities in a large river. Using actual field measurements of velocity across the river and a radio-tracked sturgeon, the study demonstrated that the sturgeon used a least costly path for movement through the river. If key landscape factors affecting energetic relationships can be successfully modeled in a GIS database, then an energetic resistance surface should be a tool for developing a resistance surface for a landscape genetic analysis.

However, perhaps most important is a continued discussion of how parameterization should take place. For instance, what is the role of expert opinion in the advancement of resistance surfaces? It is clear that relying on expert opinion alone is not desirable and may lead to suboptimal models (Spear et al. 2010; Shirk et al. 2010; Zeller et al. 2012). However, a standardized expert opinion procedure may be useful to define the parameter space to be explored during an empirical model selection and thus reduce the chance of an overfit model that does not make biological sense. Regardless, the balance between expert opinion and empirical data will continue to be an important consideration for landscape genetic researchers using resistance surfaces.

### **8.5.3 Resistance surfaces in adaptive landscape genomics**

One of the exciting directions in the field is the incorporation of questions regarding adaptive evolution, due

in part to the advent of next-generation sequencing approaches (Manel et al. 2010a, 2010b; Parisod & Holderegger 2012; Chapter 9) and advanced spatially explicit simulation models (Landguth et al. 2012). This raises the possibility of developing adaptive resistance surfaces. Complex resistance surfaces have not been incorporated into adaptive landscape genetics, although gradients along variables such as elevation (Bonin et al. 2006) or precipitation and temperature (Manel et al. 2012; Yang et al. 2013) have shown an association with adaptive loci. Recently, Landguth et al. (2012), Schumaker (2012), and Rebaudo et al. (2013) have expanded individual-based, landscape genetic simulation modeling to explicitly incorporate selection gradients. Linking landscape effects to key evolutionary processes through individual organism movement and natural selection is essential to provide a foundation for evolutionary landscape genetics. Of particular importance is determining how spatially explicit, individual-based models differ from classic population genetics and evolutionary ecology models based on ideal panmictic populations in an allopatric setting in their predictions of population structure and frequency of fixation of adaptive alleles. The new models can incorporate all factors – mutation, gene flow, genetic drift, and selection – that affect the frequency of an allele in a population. The approach of explicitly coupling gene flow (governed by resistance surfaces) with natural selection (governed by selection surfaces) provides a powerful generalized framework for evaluating interactions between drift, migration, and selection in complex landscapes. The approach essentially formalizes Sewell Wright's adaptive landscape concept (Wright 1931). If selected genotypes can be mapped on an adaptive landscape, and those same genotypes can be associated with landscape variables, then the development of a resistance surface representing fitness might be possible. Of course, none of these prerequisites are particularly easy, as studying adaptive variation in wild populations is still in its relative infancy.

## 8.6 CONCLUSIONS

We have aimed to demonstrate both the process behind resistance surface development as well as to discuss the many advantages and disadvantages associated with the methodology. Resistance surfaces have been extremely important in the development landscape genetics, but there is much room for improvement in

the use of resistance surfaces. In particular, we echo past reviews as to the importance of using empirical data when possible and transparent expert opinion reviews. However, not all empirical data may be relevant to a resistance surface, and in some cases may result in misleading models. Ultimately, the choice of resistance surface parameterization needs to be driven by the larger question that the researcher is asking. We also strongly emphasize the need for effective and appropriate model selection and the comparison of several resistance surfaces and careful consideration of the best method to translate the resistance surface into a form that can be associated with genetic data. Overall, we predict that resistance surfaces will remain a key tool in landscape genetics and will be especially important for those whose interest in landscape genetics focuses on its potential as a predictive science for the various facets of global change that are occurring.

## REFERENCES

- Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003) The application of “least-cost” modeling as a functional landscape model. *Landscape and Urban Planning* **64**, 233–47.
- Anderson, C.D., Epperson, B.K., Fortin, M.J., Holderegger, R., James, P., Rosenberg, M.S., & Spear, S. (2010) Considering spatial and temporal scale in landscape-genetic studies of gene flow. *Molecular Ecology* **19**, 3565–75.
- Andrew, R.L., Ostevik, K.L., Ebert, D.P., & Rieseberg, L.H. (2012) Adaptation with gene flow across the landscape in a dune sunflower. *Molecular Ecology* **21**, 2078–91.
- Balkenhol, N. (2009) Evaluating and improving analytical approaches in landscape genetics through simulations and wildlife case studies. Dissertation, University of Idaho.
- Beier, P., Majka, D.R., & Spencer, W.D. (2008) Forks in the road: choices in procedures for designing wildland linkages. *Conservation Biology* **22**, 836–51.
- Beier, P., Majka, D.R., & Newell, S.L. (2009) Uncertainty analysis of least-cost modeling for designing wildlife linkages. *Ecological Applications* **19**, 2067–77.
- Beier, P., Spencer, W., Baldwin, R.F., & McRae, B.H. (2011) Toward best practices for developing regional connectivity maps. *Conservation Biology* **25**, 879–92.
- Bonin, A., Taberlet, P., Miaud, C., & Pompanon, F. (2006) Explorative genome scan to detect candidate loci for adaptation along a gradient of altitude in the common frog (*Rana temporaria*). *Molecular Biology and Evolution* **23**, 773–83.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modeling* **157**, 281–300.

- Braunisch, V., Segelbacher, G., & Hirzel, A.H. (2010) Modeling functional landscape connectivity from genetic population structure: a new spatially explicit approach. *Molecular Ecology* **19**, 3664–78.
- Castillo, J.A., Epps, C.W., Davis, A.R. & Cushman, S.A. (2014) Landscape effects on gene flow for a climate-sensitive montane species: the case of the American Pika. *Molecular Ecology*, **23**, 843–856.
- Clark, R.W., Brown, W.S., Stechert, R., & Zamudio, K.R. (2008) Integrating individual behaviour and landscape genetics: the population structure of timber rattlesnake hibernacula. *Molecular Ecology* **17**, 719–30.
- Clevenger, A.P., Wierzchowski, J., Chruszcz, B., & Gunson, K. (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology* **16**, 503–14.
- Compton, B.W., McGarigal, K., Cushman, S.A., & Gamble, L.R. (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conservation Biology* **21**, 788–99.
- Cushman, S.A. & Landguth, E.L. (2010a) Scale dependent inference in landscape genetics. *Landscape Ecology* **25**, 967–79.
- Cushman, S.A. & Landguth, E.L. (2010b) Spurious correlations and inference in landscape genetics. *Molecular Ecology* **19**, 3592–602.
- Cushman, S.A. & Landguth, E.L. (2012) Multi-taxa population connectivity in the Northern Rocky Mountains. *Ecological Modeling* **231**, 101–12.
- Cushman, S.A. & Lewis, J.S. (2010) Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology* **25**, 1613–25.
- Cushman, S.A., McKelvey, K.S., Hayden, J., & Schwartz, M.K. (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist* **168**, 486–99.
- Cushman, S.A., McKelvey, K.S., & Schwartz, M.K. (2009) Use of empirically derived source-destination models to map regional conservation corridors. *Conservation Biology* **23**, 368–76.
- Cushman, S.A., Chase, M., and Griffin, C. (2010a) Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In: Cushman, S.A. & Huettmann, F. (eds.), *Spatial Complexity, Informatics and Wildlife Conservation*. Springer, Tokyo, Japan.
- Cushman, S.A., Compton, B.W., & McGarigal, K. (2010b) Habitat fragmentation effects depend on complex interactions between population size and dispersal ability: modeling influences of roads, agriculture and residential development across a range of life-history characteristics. In: Cushman, S.A. and Huettmann, F. (eds.), *Spatial Complexity, Informatics and Wildlife Conservation*. Springer, Tokyo, Japan.
- Cushman, S.A., Raphael, M.G., Ruggiero, L.F., Shirk, A.S., Wasserman, T.N., & O'Doherty, E.C. (2011) Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. *Landscape Ecology* **26**, 1137–49.
- Cushman, S.A., Landguth, E.L., & Flather, C.H. (2012) Evaluating the sufficiency of protected lands for maintaining wildlife population connectivity in the US northern Rocky Mountains. *Diversity and Distributions* **18**, 873–84.
- Cushman, S.A., Wasserman, T.N., Landguth, E.L., & Shirk, A.J. (2013) Re-evaluating causal modeling with Mantel tests in landscape genetics. *Diversity* **5**, 51–72.
- Dickson, B.G. & Beier, P. (2007) Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA. *Journal of Zoology*, **271**, pp. 270–77.
- Dickson, B.G., Jenness, J.S., & Beier, P. (2005) Influence of vegetation, topography and roads on cougar movement in southern California. *Journal of Wildlife Management* **69**, 264–76.
- Emaresi, G., Pellet, J., Dubey, S., Hirzel, A.H., & Fumagalli, L. (2011) Landscape genetics of the Alpine newt (*Mesotriton alpestris*) inferred from a strip-based approach. *Conservation Genetics* **12**, 41–50.
- Epps, C.W., Wehausen, J.D., Bleich, V.C., Torres, S.G., & Brashares, J.S. (2007) Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology* **44**, 714–24.
- Epps, C.W., Wasser, S.K., Keim, J.L., Mutayoba, B.M., & Brashares, J.S. (2013) Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant. *Molecular Ecology* **22**, 1574–88.
- Graves, T.A., Beier, P., & Royle, J.A. (2013) Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. *Molecular Ecology* **22**, 3888–903.
- Guillot, G. & Rousset, F. (2013) Dismantling the Mantel tests. *Methods in Ecology and Evolution* **4**, 336–44.
- Hagerty, B., Nussear, K., Esque, T., & Tracy, C. (2011) Making molehills out of mountains: landscape genetics of the Mojave Desert tortoise. *Landscape Ecology* **26**, 267–80.
- Hand, B.K., Cushman, S.A., Landguth, E.L., & Lucotch, J. (2014) Assessing multi-taxa sensitivity to the human footprint, habitat fragmentation and loss by exploring alternative scenarios of dispersal ability and population size: a simulation approach. *Biodiversity and Conservation* **23**, 2761–79.
- James, P.M.A., Coltman, D.W., Murray, B.W., Hamelin, R.C., & Sperling, F.A.H. (2011) Spatial genetic structure of a symbiotic beetle-fungal system: toward multi-taxa integrated landscape genetics. *PLoS One* **6**, e25359.
- Koen, E.L., Bowman, J., & Walpole, A.A. (2012) The effect of cost surface parameterization on landscape resistance estimates. *Molecular Ecology Resources* **12**, 686–96.
- Kuefler, D., Hudgens, B., Haddad, N.M., Morris, W.F., & Thurgate, N. (2010) The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology* **91**, 944–50.

- Landguth, E.L. & Cushman, S.A. (2010) cdpop: a spatially explicit cost distance population genetics program. *Molecular Ecology Resources* **10**, 156–61.
- Landguth, E.L., Cushman, S.A., Schwartz, M.K., McKelvey, K.S., Murphy, M., & Luikart, G. (2010) Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology* **19**, 4179–91.
- Landguth, E.L., Cushman, S.A., & Johnson, N.A. (2012) Simulating natural selection in landscape genetics. *Molecular Ecology Resources* **12**, 363–8.
- Lee-Yaw, J.A., Davidson, A., McRae, B.H., & Green, D.M. (2009) Do landscape processes predict phylogeographic patterns in the wood frog? *Molecular Ecology* **18**, 1863–74.
- Legendre, P. & Fortin, M.-J. (2010) Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources* **10**, 831–44.
- Manel, S., Joost, S., Epperson, B.K., Holderegger, R., Storfer, A., Rosenberg, M.S., Scribner, K.T., Bonin, A., & Fortin, M.-J. (2010a) Perspectives on the use of landscape genetics to detect genetic adaptive variation in the field. *Molecular Ecology* **19**, 3760–72.
- Manel, S., Poncet, B.N., Legendre, P., Gugerli, F., & Holderegger, R. (2010b) Common factors drive adaptive genetic variation at different spatial scales in *Arabis alpina*. *Molecular Ecology* **19**, 3824–35.
- Manel, S., Gugerli, F., Thuiller, W., Alvarez, N., Legendre, P., Holderegger, R., Geilly, L., & Taberlet, P. (2012) Broad-scale adaptive genetic variation in alpine plants is driven by temperature and precipitation. *Molecular Ecology* **21**, 3729–38.
- McElroy, B., DeLonay, A., & Jacobson, R. (2012) Optimum swimming pathways of fish spawning migrations in rivers. *Ecology* **93**, 29–34.
- McRae, B.H. (2006) Isolation by resistance. *Evolution* **60**, 1551–61.
- McRae, B.H. (2012) Pinchpoint Mapper User Guide. [Online] Available at: <http://www.circuitscape.org/linkagemapper>.
- McRae, B.H. & Beier, P. (2007) Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, vol. **104**, pp. 19885–90.
- McRae, B.H., Dickson, B.G., Keitt, T.H., & Shah, V.B. (2008) Using circuit theory to model connectivity in ecology, evolution and conservation. *Ecology* **89**, 2712–24.
- McRae, B.H., Hall, S.A., Beier, P., & Theobald, D.M. (2012) Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. *PloS One* **7**, e52604.
- McRae, B.H., A.J. Shirk, and J.T. Platt. 2013. Gnarly Landscape Utilities: Resistance and Habitat Calculator User Guide. The Nature Conservancy, Fort Collins, CO. Available at: <http://www.circuitscape.org/gnarly-landscape-utilities>.
- Michels, E., Cottenie, K., Neys, L., De Gelas, K., Coppin, P., & De Meester, L. (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modeling of the effective geographical distance. *Molecular Ecology* **10**, 1929–38.
- Moore, J.A., Tallmon, D.A., Nielsen, J., & Pyare, S. (2011) Effects of the landscape on boreal toad gene flow: does the pattern–process relationship hold true across distinct landscapes at the northern range margin? *Molecular Ecology* **20**, 4858–69.
- Munshi-South, J. (2012) Urban landscape genetics: canopy cover predicts gene flow between white-footed mouse (*Peromyscus leucopus*) populations in New York City. *Molecular Ecology* **21**, 1360–78.
- Murphy, M.A. & Evans, J.S. (2011) Boreal toad (*Bufo boreas boreas*) population connectivity in Yellowstone National Park: quantifying matrix resistance and model uncertainty using landscape genetics. In: Drew, C.A., Wiersma, Y.F., & Huettmann, F. (eds.), *Predictive Species and Habitat Modeling in Landscape Ecology*. Springer.
- Murphy, M.A., Evans, J.S., Cushman, S.A., & Storfer, A. (2008) Representing genetic variation as continuous surfaces: an approach for identifying spatial dependency in landscape genetic studies. *Ecography* **31**, 685–97.
- Murphy, M.A., Evans, J.S., & Storfer, A. (2010) Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* **91**, 252–61.
- Murray, J.V., Goldizen, A.W., O'Leary, R.A., McAlpine, C.A., Possingham, H.P., & Choy, S.L. (2009) How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. *Journal of Applied Ecology* **46**, 842–51.
- Parisod, C. & Holderegger, R. (2012) Adaptive landscape genetics: pitfalls and benefits. *Molecular Ecology* **21**, 3644–6.
- Phillips, S.J. & Dudik, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**, 161–75.
- Rayfield, B., Fall, A., & Fortin, M.-J. (2010) The sensitivity of least-cost habitat graphs to relative cost surface values. *Landscape Ecology* **25**, 519–32.
- Rebaudo, F., Rouzic, A., Dupas, S., Silvain, J.-F., Harry, M., & Dangles, O. (2013) SimAdapt: an individual-based genetic model for simulating landscape management impacts on populations. *Methods in Ecology and Evolution* **4**, 595–600.
- Reding, D.M., Cushman, S.A., Gosselink, T.E., & Clark, W.R. (2013) Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (*Lynx rufus*). *Landscape Ecology* **28**, 471–86.
- Richardson, J.L. (2012) Divergent landscape effects on population connectivity in two co-occurring amphibian species. *Molecular Ecology* **21**, 4437–51.
- Richards-Zawacki, C.L. (2009) Effects of slope and riparian habitat connectivity on gene flow in an endangered Panamanian frog, *Atelopus varius*. *Diversity and Distributions* **15**, 796–806.

- Row, J.R., Blouin-Demers, G., & Lougheed, S.C. (2010) Habitat distribution influences dispersal and fine-scale genetic population structure of eastern foxsnakes (*Mintonius gloydi*) across a fragmented landscape. *Molecular Ecology* **19**, 5157–71.
- Sawyer, S.C., Epps, C.W., & Brashares, J.S. (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *Journal of Applied Ecology* **48**, 668–78.
- Schumaker, N.H. (2012) *HexSim*. United States Environmental Protection Agency, Environmental Research Laboratory, Cornvallis, OR. <http://www.hexsim.net/index.html>.
- Schwartz, M.K., Copeland, J.P., Anderson, N.J., Squires, J.R., Inman, R.M., McKelvey, K.S., Pilgrim, K.L., Waits, L.P., & Cushman, S.A. (2009) Wolverine gene flow across a narrow climatic niche. *Ecology* **90**, 3222–32.
- Shafer, A.B.A., Northrup, J.M., White, K.S., Boyce, M.S., Côté, S.D., & Coltman, D.W. (2012) Habitat selection in mountain goats. *Bulletin of the Ecological Society of America* **93**, 170–2.
- Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A., & Vosper, S.B. (2013) Energy landscapes shape animal movement ecology. *The American Naturalist* **182**, 298–312.
- Shirk, A.J., Wallin, D.O., Cushman, S.A., Rice, C.G., & Warheit, K.I. (2010) Inferring landscape effects on gene flow: a new model selection framework. *Molecular Ecology* **19**, 3603–19.
- Shirk, A.J., Cushman, S.A., & Landguth, E.L. (2012) Simulating pattern–process relationships to validate landscape genetic models. *International Journal of Ecology* **2012**, 539109.
- Singleton, P.H., Gaines, W.L., & Lehmkuhl, J.F. (2002) *Landscape Permeability for Large Carnivores in Washington: A Geographic Information System Weighted-Distance and Least-Cost Corridor Assessment*. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Spear, S.F. & Storfer, A. (2008) Landscape genetic structure of coastal tailed frogs (*Ascaphus truei*) in protected vs. managed forests. *Molecular Ecology* **17**, 4642–56.
- Spear, S.F. & Storfer, A. (2010) Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. *Biological Conservation*, **143**, 778–86.
- Spear, S.F., Peterson, C.R., Matocq, M.D., & Storfer, A. (2005) Landscape genetics of the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). *Molecular Ecology* **14**, 2553–64.
- Spear, S.F., Balkenhol, N., Fortin, M.-J., McRae, B.H., & Scribner, K.T. (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology* **19**, 3576–91.
- Stevens, V.M., Leboulengé, E., Wesselingh, R.A., & Baguette, M. (2006a) Quantifying functional connectivity: experimental assessment of boundary permeability for the natterjack toad (*Bufo calamita*). *Oecologia* **150**, 161–71.
- Stevens, V.M., Verkenne, C., Vandewoestijne, S., Wesselingh, R.A., & Baguette, M. (2006b) Gene flow and functional connectivity in the natterjack toad. *Molecular Ecology* **15**, 2333–44.
- Storfer, A., Murphy, M.A., Evans, J.S., Goldberg, C.S., Robinson, S., Spear, S.F., Dezzani, R., Delmelle, E., Vierling, L., & Waits, L.P. (2007) Putting the “landscape” in landscape genetics. *Heredity* **98**, 128–42.
- Trumbo, D.R., Spear, S.F., Baumsteiger, J., & Storfer, A. (2013) Rangewide landscape genetics of an endemic Pacific northwestern salamander. *Molecular Ecology* **22**, 1250–66.
- Vandergast, A.G., Bohonak, A.J., Weissman, D.B., & Fisher, R.N. (2007) Understanding the genetic effects of recent habitat fragmentation in the context of evolutionary history: phylogeography and landscape genetics of a southern California endemic Jerusalem cricket (Orthoptera: Stenopelmatidae: *Stenopelmatus*). *Molecular Ecology* **16**, 977–92.
- van Strien, M.J., Keller, D., & Holderegger, R. (2012) A new analytical approach to landscape genetic modeling: least-cost transect analysis and linear mixed models. *Molecular Ecology* **21**, 4010–23.
- Vignieri, S.N. (2005) Streams over mountains: influence of Riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*). *Molecular Ecology* **14**, 1925–37.
- Vuilleumier, S. & Fontanillas, P. (2007) Landscape structure affects dispersal in the greater white-toothed shrew: inference between genetic and simulated ecological distances. *Ecological Modeling* **201**, 369–76.
- Wall, J., Douglas-Hamilton, I., & Vollrath, F. (2006) Elephants avoid costly mountaineering. *Current Biology* **16**, R527–R529.
- Walpole, A.A., Bowman, J., Murray, D.L., & Wilson, P.J. (2012) Functional connectivity of lynx at their southern range periphery in Ontario, Canada. *Landscape Ecology* **27**, 761–73.
- Wang, Y.-H., Yang, K.C., Bridgman, C.L., & Lin, L.K. (2008) Habitat suitability modeling to correlate gene flow with landscape connectivity. *Landscape Ecology* **23**, 989–1000.
- Wang, I.J., Savage, W.K., & Bradley Shaffer, H. (2009) Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (*Ambystoma californiense*). *Molecular Ecology* **18**, 1365–74.
- Washington Wildlife Habitat Connectivity Working Group (2012) Washington Connected Landscapes Project: Analysis of the Columbia Plateau Ecoregion. [Online] Available at: <http://wacconnected.org> [01 Oct 2014].
- Wasserman, T.N., Cushman, S.A., Schwartz, M.K., & Wallin, D.O. (2010) Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology* **25**, 1601–12.

- Wasserman, T.N., Cushman, S.A., Shirk, A.S., Landguth, E.L., & Littell, J.S. (2012) Simulating the effects of climate change on population connectivity of American marten (*Martes americana*) in the northern Rocky Mountains, USA. *Landscape Ecology* **27**, 211–25.
- Wright, S. (1931) Evolution in Mendelian populations. *Genetics* **16**, 97–159.
- Yang, J., Cushman, S.A., Yang, J., Yang, M., & Bao, T. (2013) Effects of climatic gradients on genetic differentiation of Caragana on the Ordos Plateau, China. *Landscape Ecology* **28**, 1729–41.
- Zeller, K.A., McGarigal, K., & Whiteley, A.R. (2012) Estimating landscape resistance to movement: a review. *Landscape Ecology* **27**, 777–97.