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Biological corridors and connectivity

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hring utan ymbbearh, þæt heo þone fyrdhom ðurhfon ne mihte, locene leoðosyrcan laþan fingrum.

On his shoulder lay braided breast-mail, barring death, withstanding entrance of edge or blade.

Beowulf (Old English epic poem, c. 10th Century)

Introduction

The ability of individual animals to move across complex landscapes is critical for maintaining regional populations in the short term (Fahrig 2003; Cushman 2006), and for species to shift their geographic range in response to climate change (Heller & Zavaleta 2009). As organisms move through spatially complex landscapes, they respond to multiple biotic and abiotic factors to maximize access to resources and mates while minimizing fitness costs such as mortality risks. Habitat fragmentation decreases dispersal success (Gibbs 1998), increases mortality (Fahrig et al. 1995) and reduces genetic diversity (Reh & Seitz 1990; Wilson & Provan 2003). Local populations may decline if immigration is prevented (Brown & Kodric-Brown 1977; Harrison 1991) and may prevent recolonization following local extinction (Semlitsch & Bodie 1998).

The goal of this chapter is to describe the state of the art in quantitative corridor and connectivity modelling. We will review several critical issues in modelling, and provide expert guidance and examples to help practitioners implement effective programmes to preserve, enhance or create connectivity among wildlife populations. We first

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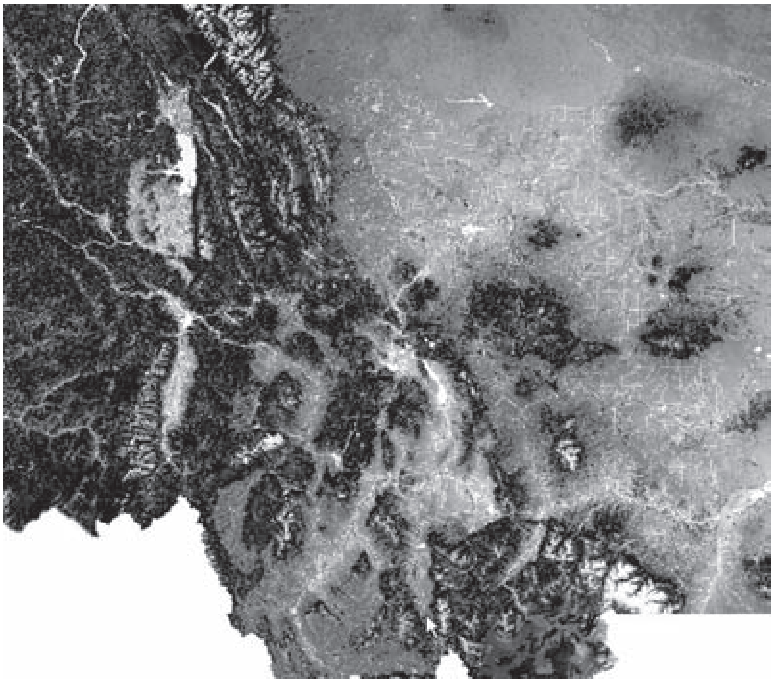


Figure 21.1 Example landscape resistance map for American black bear in an area of the US northern Rocky Mountains encompassing Montana and northern Idaho. Dark areas are low resistance for movement, while light areas are high resistance for movement. The resistance map was developed by Cushman et al. (2006) and validated with independent data by Cushman & Lewis (2010) and in multiple independent study areas by Short Bull et al. (2011).

review the fundamental task of estimating landscape resistance, comparing expert opinion and empirical methods. Next, we describe current methods of predicting connectivity from resistance surfaces. Then we discuss how to develop linkage designs that can maintain connectivity for multiple species, and under changing climate. We conclude with discussion of how effectively to validate connectivity model predictions.

Estimating landscape resistance

Most current methods of predicting population connectivity and mapping areas significant in facilitating animal movements begin with landscape resistance maps (Figure 21.1). Landscape resistance maps depict the cost of movement through any location in the landscape (pixel cell in a raster map) as a function of landscape features of that cell (e.g. high resistance might be assigned to a road or a body of water). In its most basic sense, landscape resistance reflects the local movement cost incurred by an animal. More formally, the resistance reflects the step-wise cost of moving through each cell for least-cost analyses (Singleton et al. 2002) or the relative probability of moving into the cell for circuit theory-based analyses (McRae et al. 2008).

Expert versus empirical estimation

Most published studies using landscape resistance maps have estimated resistance of landscape features to movement based on expert opinion alone (e.g. Compton et al. 2007). However, non-human species perceive landscapes in ways that may not correspond to human assumptions concerning connectivity and habitat quality (With et al. 1997). Using unvalidated expert opinion to develop resistance maps has been a major weakness of most past landscape resistance modelling efforts (Seoane et al. 2005).

Methods for empirically estimating resistance

Habitat quality as surrogate for landscape resistance

Habitat quality can be predicted based on patterns of occupancy in relation to ecological conditions, such as through resource selection functions (e.g. Guerry & Hunter 2002; Weyrauch & Grubb 2004). The simplest way to estimate relationships empirically between population connectivity and environmental conditions is to assume that habitat quality directly equates to population connectivity. Predictions of habitat quality based on patterns of occurrence studies are limited because they do not directly measure biological responses such as mortality, movement and productivity (Cushman 2006). Patterns of species occurrence do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns (Van Horne 1983). More importantly, in the context of connectivity modelling, suitability for occupancy and suitability for dispersal may not be driven by the same factors at the same scales (e.g. Shirk et al. 2010; Wasserman et al. 2010). Habitat selection reflects the behaviour of individual organisms to maximize fitness within home ranges, while population connectivity is driven by dispersal, migration and mating events. These are functionally and biologically different processes. Few studies have formally evaluated the performance of habitat suitability models as surrogates for landscape resistance, but those that have generally have found them to perform poorly (e.g. Shirk et al. 2010; Wasserman et al. 2010). This highlights the importance of not assuming that habitat relationships optimally reflect the landscape features governing population connectivity.

Mark-recapture and experimental movement studies

By quantifying movement rates, distances travelled and routes of animals through complex environments, researchers can quantitatively describe species-specific responses to environmental conditions and landscape structure. For example, a study by Gamble et al. (2007) quantified dispersal in relation to topography and vegetation for several pond-breeding amphibians, demonstrating the value of mark-recapture approaches to evaluating population connectivity. In addition, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. For example, Haddad & Baum (1999) used a large-scale experiment to find that three habitat-restricted butterfly species reached higher densities in patches connected by corridors than in similar, isolated patches.

These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal & Cushman 2002). Unfortunately, large-scale manipulative field experiments and mark-recapture meta-population studies are expensive, take several years, and generally suffer from small sample sizes. Another potential limitation is that these studies focus on short-term, fine-scale movement path selection of individual animals, which may not scale up to population-level effects on migration and gene flow.

Telemetry

Advances in wildlife telemetry technology have enabled collection of very accurate and frequent location data for individual animals. Landscape resistance modelling based on telemetry is a powerful technique to address the factors that affect organism movement directly on scales of space and time greater than are possible with mark-recapture and experimental movement studies (e.g. Osborn & Parker 2003; Cushman et al. 2005, 2010a). GPS telemetry data enable direct assessment of the influences of landscape features on movement path selection. For example, Cushman et al. (2010a) modelled the influence of landscape features on elephant movement path selection using telemetry data, showing that elephants (*Loxodonta africana*) select movement paths near water, avoid human settlements and do not cross wildlife cordon fences. Similarly, Cushman & Lewis (2010) used satellite telemetry data to show that American black bears (*Ursus americanus*) choose movement paths that avoid roads and human residences and concentrate activity in forested areas at middle elevations. Directly associating movement paths with landscape features enables the development of species-specific landscape resistance models that are more reliable than those produced by expert opinion.

Landscape genetics

Gene flow among populations is necessary to support the long-term viability of populations, as it maintains local genetic variation and spreads potentially advantageous genes. Thus it is important to infer the functional connectivity among populations and across landscapes (van Dyck & Baguette 2005). The ultimate validation of any method of estimating functional connectivity lies in how well it explains gene flow (Cushman et al. 2006; Shirk et al. 2010; Wasserman et al. 2010; Short Bull et al. 2011). Genetic methods can directly measure dispersal and immigration (Waples 1998; Landguth et al. 2010). Logistical and financial costs associated with tracking individual animals are obviated and because genetic data integrate time and space, slow rates of dispersal through complex landscapes are measurable. Landscape genetic analyses enable direct association of movement cost across resistance surfaces with genetic differentiation, which enables empirical derivation and validation of connectivity maps. For example, Wasserman et al. (2010) used non-invasive monitoring to collect genetic data from several hundred individual American marten (*Martes americana*) across a 4000 square kilometer study area, and were able to use multivariate landscape genetic modelling to identify the landscape features that affect gene flow.

Combining multiple methods to produce robust estimates of resistance

Every method of estimation has its own limitations, so it is valuable to use multiple methods and independent data sets to estimate resistance. The strongest inferences are derived from multiple analyses of different kinds of data that produce a consistent result (Cushman & Lewis 2010). For example, landscape genetics and GPS telemetry are two complementary analyses that can be combined to produce robust estimates of landscape resistance. Using movement data to predict landscape resistance, and comparing that to landscape resistance predicted from landscape genetic analyses of the same species in the same study area, is a useful way to verify the robustness of landscape connectivity hypotheses (e.g. Cushman & Lewis 2010). In addition, such analyses would illuminate the multi-scale drivers of population connectivity, since mating and dispersal movement behaviours are the mechanisms through which gene flow operates in animal populations. At the present time, only a few research programmes have estimated resistance from a combination of approaches (Coulon et al. 2008; Cushman & Lewis 2010; Shanahan et al. 2011; see Box 21.1).

From landscape resistance to population connectivity

While resistance is point specific, connectivity is route specific (Cushman et al. 2008). Therefore, while resistance models can provide the foundation for applied analyses of population connectivity, they do not, in themselves, provide sufficient information to evaluate the existence, strength and location of barriers and movement corridors. Connectivity must be evaluated with respect to the paths, costs and success of moving across a landscape. The resistance model is the

Box 21.1 Combining landscape genetics and telemetry to estimate landscape resistance for American black bear

Cushman et al. (2006) used causal modelling with landscape genetics data to evaluate support for 110 alternative hypotheses describing the effects of landscape variables on population connectivity in an American black bear (*Ursus americanus*) population in northern Idaho, USA. Their analysis rejected hypotheses of isolation by distance and isolation by a geographical barrier, and affirmed a landscape resistance model which predicts that rates of gene flow are related to elevation, forest cover, roads and human development. Cushman & Lewis (2010) used conditional logistic regression to predict landscape resistance based on black bear GPS telemetry data in the same landscape. They used a path-level spatial randomization method to assess the effects of multiple landscape features on movement path selection (e.g. Cushman et al 2010a). The path-level randomization approach provides a robust means to compare the landscape features an animal encounters in its actual path with those that would be encountered in a large sample of available paths of identical length and topology. They found that consistent landscape factors influence genetic differentiation and movement path selection, with strong similarities between the predicted landscape resistance surfaces. Genetic differentiation among individual American black bears is driven by spring movement (mating and dispersal) in relation to residential development, roads, elevation and forest cover. The real value of this study is that it used two independent data sets and different kinds of analyses to validate the results, and it quantified the scale and strength of bear behavioural response to several landscape features. For example, it showed that gene flow is maximum at middle elevations due to impassable snow pack at high elevations in the dispersal season, and concentrated human populations in low-elevation valleys, and that bears strongly avoid roads and human resistances (e.g. near-total avoidance within a 200 m radius buffer around human structures).

foundation for these analyses, but it is explicit consideration of movement paths across the resistance surface that provides the key information for conservation and management.

Identifying corridors using least-cost modelling

In recent years least-cost (LC) modelling (part of graph theory, see below) has become the dominant modelling tool to evaluate functional landscape connectivity, especially in applied studies. This is mainly because:

- it produces an unambiguous corridor or path as an output, whereas most other approaches do not
- it is available in most commercial GIS packages as well as open source software
- LC models generate visually attractive and easy to communicate representations of connectivity (maps) and quantitative metrics of effective distance (cost values) in the same units (meters) as Euclidean distance (Adriaensen et al. 2003; Fagan & Calabrese 2006).

These attributes make LC modelling very well suited for quantitative landscape analyses and for evaluating effects of future scenarios on connectivity.

In LC models the only inputs are the map of sources and targets and the map of resistance values (R; Figure 21.2a). The cost layer is the first and central level of output of a LC analysis (see Figure 21.2a), and provides the functional cost distance values from the designated source to all locations in the geographical extent of the analysis. The least-cost path (Figure 21.2b) is the series of cells in the landscape which results in the minimum cumulative cost value (LC path value) to move from a source cell/cells to the target cell/cells under investigation. The LC path indicates the location of the cheapest route, but gives no information on how cost values are distributed over the landscape. For example, it does not indicate other zones in the landscape resulting in comparable costs (Figure 21.2c) or how wide the LC path zone is (Adriaensen et al. 2003; Pinto & Keitt 2009).

There are several methods available to produce biologically informative measures of landscape connectivity from such cost surfaces. One of these is the combination of several cost

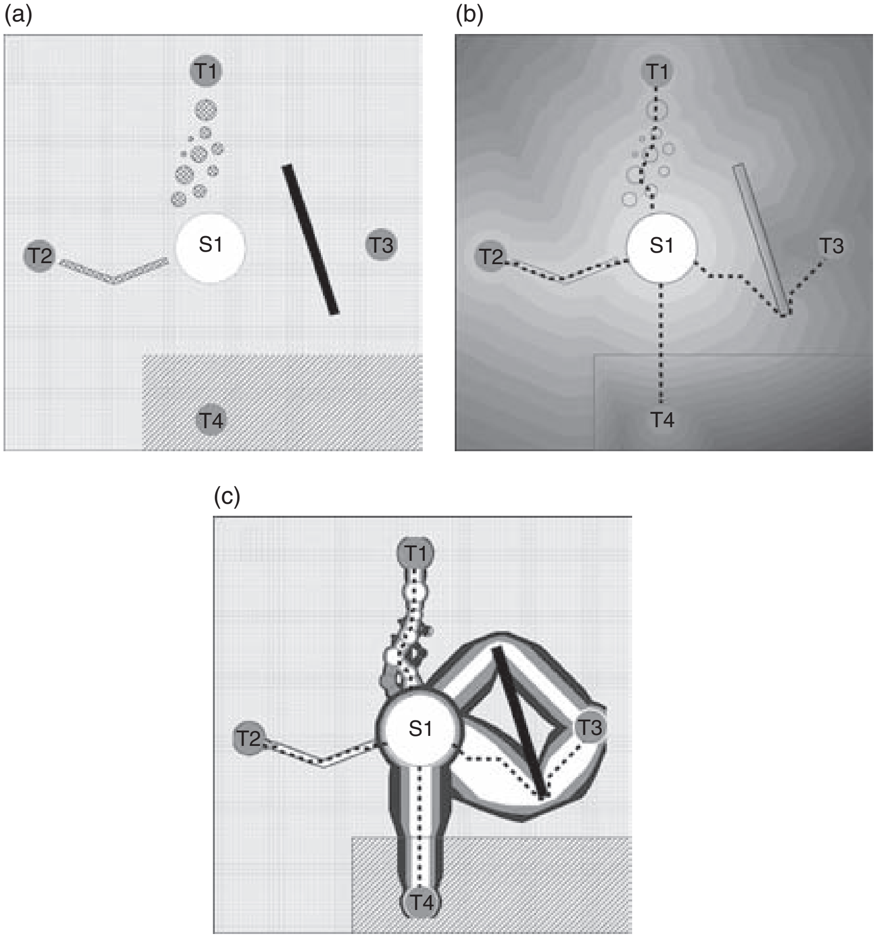


Figure 21.2 Input (a) to output (b-c) in LC modelling using a simple virtual landscape to show the basics of this modelling approach. (a) Landcover map showing a hypothetical landscape (source area S1: forest; target areas T1–4: woodlots; grassland (dotted); intensive cropland (hatched); hedgerow and bushes (cross-hatched); open water (solid black). (b) Cost layer from source area S1 and LC path to 4 target areas (dashed lines). (c) Corridor map showing 1–10% corridor buffers derived from bidirectional cost layers from source area S1. Result of 4 corridor analyses superimposed (targets=T1–4): white, increase in minimum cumulative cost less than 1% of LCP; light grey 1–5%; dark grey 5–10%.

layers into one ‘corridor’ layer (other names: bidirectional cost layer, conditional minimum transit cost [CMTC, Pinto & Keitt 2009]; see Figure 21.2c), in which the value of each cell is the overall cost to reach the target cell T from source cell S, but with the constraint to go through the cell under investigation. The LC path is a special case of this (with all cells having a value equal to the LC path value and thus the minimum present in the corridor layer). The LC path will always be the path of minimal corridor values but elsewhere in the landscape, there could be other zones with nearly equal cost values (see Figure 21.2c). Corridor maps give a more realistic view of the functionally cheapest routes in the landscape from the designated source to the destination (Adriaensen et al. 2003) (Box 21.2). For example, the width of corridors can be determined by taking percent slices of the landscape representing the lowest cumulative resistance (e.g. Singleton et al. 2002; Spencer et al. 2010) or by limiting

Box 21.2 Landscape connectivity in the Taita Hills

The Restoration and Increase of Connectivity among Fragmented Forest Patches in the Taita Hills, South-east Kenya project (CEPF project 1095347968; Adriaensen et al. 2007) included a detailed analysis of functional landscape connectivity in the area. In this project, evidence of the distribution and population status of bird species in the remaining small cloud forest patches on the hill tops (black patches) was successfully combined with output of LC models to support and prioritize habitat restoration actions in plantations with exotic trees (white patches). Forest restoration is now being implemented in a set of five pilot projects.

Least-cost models were used to model the location of exotic tree plantations in relation to modelled connectivity corridors for forest interior birds (dark grey zones), in order to evaluate their potential roles as stepping stones to promote recolonization after rehabilitation of the plantations. In the map shown, corridors between all pairs of remaining forest plots were superimposed (resistance set R1S5 for eco-type 'sensitive interior forest bird', including the critically endangered Taita thrush *Turdus helleri*).

corridors to a maximum cost-weighted cut-off distance above that of the LC path (WHCWG 2010). Regional connectivity assessments can require mapping corridors between hundreds to thousands of core area pairs (e.g. Spencer et al. 2010; WHCWG 2010). The development of GIS tools to automate corridor mapping, including decisions of which pairs

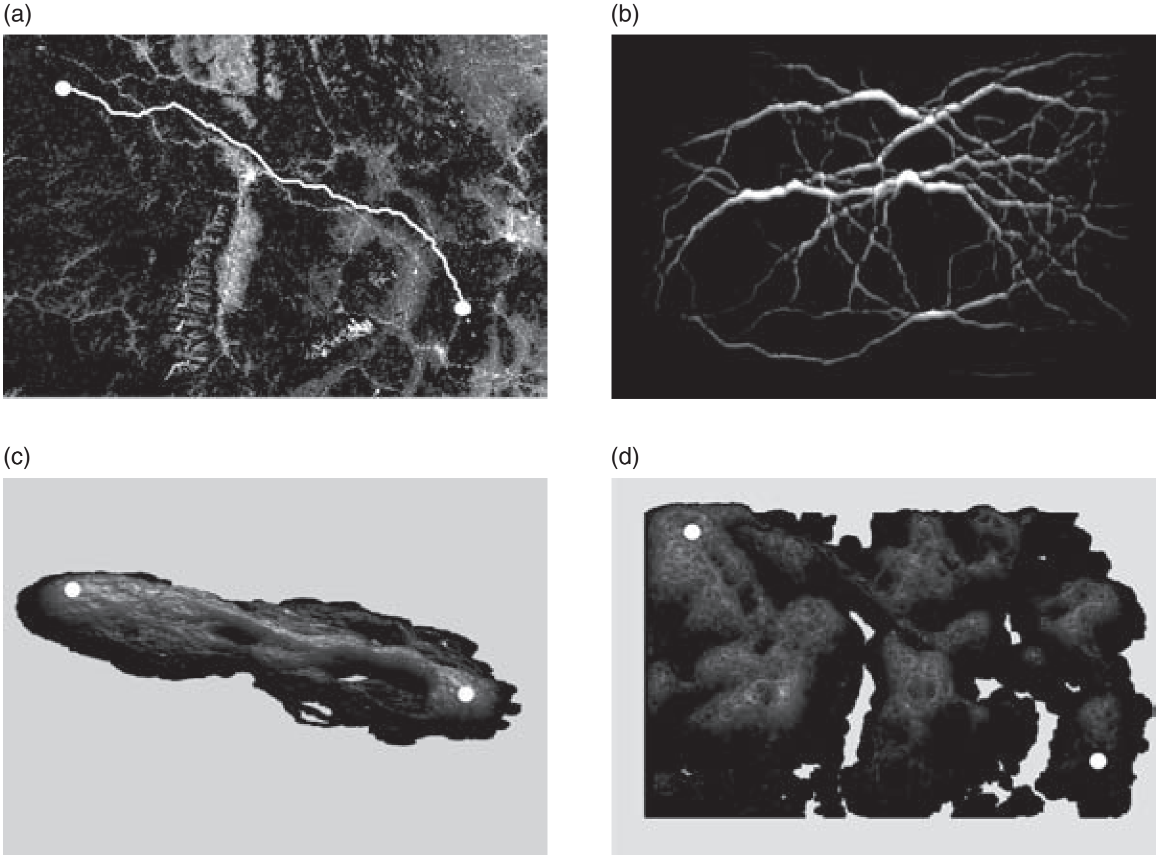


Figure 21.3 Comparison of four connectivity modelling methods applied to a single study area and resistance map. The study area is northern Idaho, USA. The resistance map is shown in panel (a) as a colour scale from blue (low resistance) to red (high resistance), and reflects landscape resistance to black bear gene flow (Cushman et al. 2006). Panel (a) shows a single least-cost path (white line) between two point locations (white dots). Panel (b) shows a factorial least-cost path analysis between several hundred source points. Panel (c) shows the least-cost corridor between the same two source points as in (a). Panel (d) shows the cumulative resistant kernel model of synoptic landscape connectivity.

of core areas to connect (e.g. McRae & Kavanagh 2011), makes this easy.

Factorial least-cost paths

One limitation of traditional LC path and LC corridor analyses is that they are limited to prediction of connectivity between single sources and single destinations (Figure 21.3a). While this may be ideal in the case where one is interested in the lowest cost routes between two focal conservation areas, there are many situations where a more synoptic analysis of connectivity is valuable. For example, it may be that there is a need to calculate corridor connectivity between thousands of sources and a single destination (e.g. Cushman et al. 2010a) or between hundreds of sources and hundreds of destinations distributed across a complex landscape (e.g. Cushman et al. 2008, Cushman et al. 2011; Figure 21.3b). For example, Cushman et al. (2008) used factorial least cost path analysis to predict the most important movement routes for bears between Yellowstone National Park and the Canadian border in the United States Northern Rocky Mountains, showing that there are few major connections and locating several dozen potential barriers. This, in turn, focuses attention on where restoration and mitigation efforts would be most effective. A factorial implementation of least cost paths (e.g. UNICOR; Landguth et al. 2011) permits integration of a vast number of least cost paths to show synoptic connectivity across large and complex landscapes (Figure 21.3b). For example (Cushman et al. 2011) mapped regional corridor networks for several species of conservation concern across a vast area of the United States great plains using UNICOR (Landguth et al. 2011). The analysis identified which species have the most fragmented populations and mapped the most important corridor linkages among population core areas, focusing conservation efforts on the most important locations.

Other ways to analyse connectivity

Ecologists often use the term *graph theory* to refer to a family of analyses in which patches are reduced to nodes at patch centroids, with centroids connected by lines or 'edges' (e.g. Bunn et al. 2000; Urban & Keitt 2001; Minor & Urban 2007). Such graphs underlie many methods in connectivity analysis, including LC corridor modelling. Advances in computing and algorithms borrowed from other disciplines have allowed applications of graph algorithms to continuous landscapes instead of simple networks. Rayfield et al. (2011) review graph-based connectivity measures and provide a framework for classifying them as applications to connectivity conservation.

Circuit theory

Connectivity analyses based on electrical circuit theory use networks of electrical nodes connected by resistors as models for networks of populations, habitat patches or locations on a landscape connected by movement. Because connectivity increases with multiple pathways in electrical networks, distance metrics based on electrical connectivity are applicable to processes (e.g. gene flow; McRae 2006) that respond positively to increasing numbers of pathways. Additionally, previous work has shown that current, voltage and resistance in electrical circuits all have mathematical relationships with random walks (Doyle & Snell 1984; Chandra et al. 1997). Random walks can predict the expected routes that an animal with a preference for low-resistance habitat will take as it moves through a landscape. The precise relationships between circuit theory and random walks mean that circuits can be related to movement ecology and population genetics via random walk and coalescent theories, providing concrete interpretations of connectivity measures (McRae 2006; McRae et al. 2008).

Circuit and LC models represent two extremes in assumptions about movement and connectivity. Least-cost corridors calculate the routes expected to be taken by animals with perfect or near-perfect knowledge of the landscape, whereas current maps generated from circuit models predict movement routes taken by random walkers, with all possible paths contributing to connectivity. Neither will entirely correctly predict movement behaviour of real animals (Spear et al. 2010, and see below) but there are benefits to both models, as we show in the example in Figure 21.4. Least-cost analyses can show what routes/zones would permit the most efficient movement, which can be important for conservation planning; if a large portion of a landscape is likely to be developed, identifying those areas which, if conserved, provide the easiest movement routes will be important. Circuit theory has the advantage of identifying and quantifying 'pinch points' (see Figure 21.4), i.e. constrictions in corridors that, if lost, could sever connectivity entirely. Such areas can be prioritized for early conservation action because options are limited. Circuit algorithms also integrate across all movement pathways to

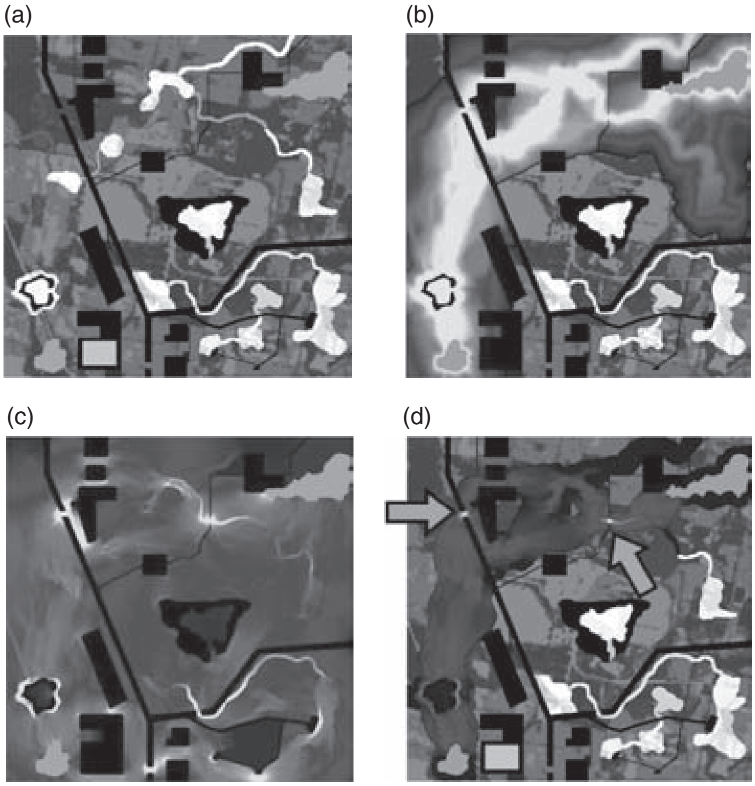


Figure 21.4 Example of how circuit theory can be used to identify and prioritize important areas for connectivity conservation. (a) Simple landscape, with two patches to be connected (green) separated by a matrix with varying resistance to dispersal (low resistance in white, higher resistance in darker shades, and complete barriers in black). (b) Least-cost corridor between the patches (lowest resistance routes in yellow, highest in blue). (c) Current flow between the same two habitat patches derived using Circuitscape (McRae & Shah 2009), with highest current densities shown in yellow (from McRae et al. 2008). Circuit analyses complement least-cost path results by identifying important alternative pathways and ’pinch points’, where loss of a small area could disproportionately compromise connectivity. (d) A promising application is restricting circuit analyses to least-cost corridor slices to take advantage of the strengths of both approaches (from McRae & Kavanagh 2011). This hybrid approach shows both the most efficient movement pathways and critical ‘pinch points’ within them,which glow yellow. These could be prioritized over areas that contribute little to connectivity, such as the corridor at the top right of the map that has been coloured dark blue because it does not provide connectivity between the patches.

provide measures of redundancy, i.e. availability of alternative pathways for movement (see Figure 21.4). New applications allow identification of barriers that have a strong effect on connectivity, which can be useful for highlighting opportunities to restore connectivity, e.g. through re-establishment of natural vegetation or installation of highway crossing structures (McRae, unpublished data).

Centrality analyses

A promising graph-theoretic approach to connectivity modelling is centrality analysis, which ranks the importance of habitat patches or corridors in providing movement across an entire network, i.e. as ’gatekeepers’ of flow across a landscape (Carroll et al. 2011). Centrality analyses can be based in LC path, circuit theory or other connectivity analysis methods. The difference is that, instead of mapping corridors or current flow between single pairs of core areas, they add up results from connectivity analyses between all pairs of nodes (sites or cells) on a landscape. Centrality analyses can be applied to raster GIS data or networks to identify core areas, linkages or grid cells that are particularly important for overall connectivity. Because centrality metrics can incorporate connectivity between all pairs of nodes on a landscape, they can eliminate the need to identify specific pairs of habitat patches to connect. For example, betweenness centrality (Freeman et al. 1991) identifies the shortest paths connecting all pairs of nodes in a network, and sums the number of such shortest paths involving each intervening node. This procedure identifies areas lying on a large proportion of the shortest paths in a network, the loss of which can disproportionately disrupt connectivity across the network as a whole. The Connectivity Analysis Toolkit (Carroll 2010) specializes in centrality analysis, and supports metrics based on betweenness, current flow (Newman 2005), maximum flow (Freeman et al. 1991) and minimum-cost flow (Ahuja et al. 1993). It also allows time-series analyses of connectivity across landscapes where habitats shift through time (Phillips et al. 2008).

Resistant kernels

The resistant kernel approach to connectivity modelling is based on least-cost dispersal from some defined set of sources. The model calculates the expected density of dispersing individuals in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010b). Once the expected density around each source cell is calculated, the kernels surrounding all sources are summed to give the total expected density at each pixel (see Figure 21.3d). The results of the model are surfaces of expected density of dispersing organisms at any location in the landscape. For example, Cushman et al. (2010b) used resistant kernel modelling to evaluate the interactive effects of roads and human land use change on population connectivity for a large number of pond-breeding species in Massachusetts (USA). The resistant kernel approach quantified expected density of dispersers in the upland environment as functions of breeding population size, dispersal ability and quantified the relative impacts of roads and land use on population connectivity (Figure 21.5).

The resistant kernel approach to modelling landscape connectivity has a number of advantages as a robust approach to assessing current population connectivity (Compton et al. 2007; Cushman et al. 2010b, 2011). First, unlike most approaches to mapping corridors , it is spatially synoptic and provides prediction and mapping of expected migration rates for every pixel in the whole study area, rather than only for a few selected 'linkage zones' (e.g. Compton et al. 2007). Second, scale dependency of dispersal ability can be directly included to assess how species of different vagilities will be affected by landscape change and fragmentation under a range of scenarios (e.g. Cushman et al. 2010b). Third, it is computationally efficient, enabling simulation and mapping at a fine spatial scale across large geographical extents (e.g. Cushman et al. 2010b, 2011).

Individual-based movement models

Individual-based (IB) models explicitly simulate the processes acting on the individual to predict movement. IB models predict movement paths of simulated dispersers based on parameters such as energetic cost of movement in different patch types, turning angles within patches and at patch transitions, movement speeds, duration of movement events, mortality risks in different patch types, and likelihoods of movements between patch types. Thus, IB models usually incorporate much more detail and thus greater realism than other

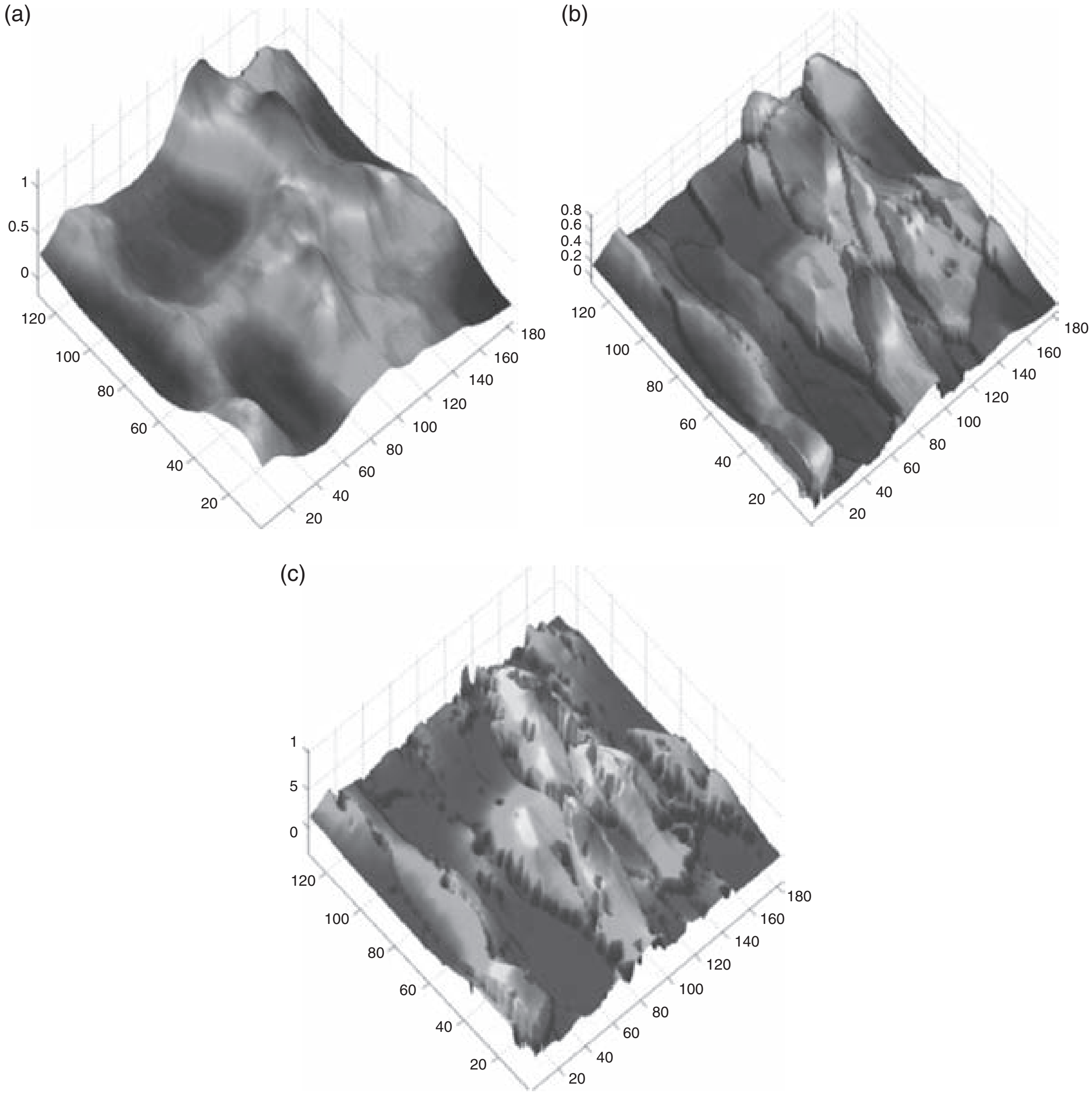


Figure 21.5 Example of resistant kernel results from Cushman et al. (2010b) showing predicted density of dispersing individuals in upland habitat under three hypotheses: (a) connectivity is unaffected by land use and roads and only a function of distance, (b) connectivity is reduced by roads but not by differences in land cover and land use, (c) connectivity is affected by roads and land use/land cover.

connectivity models, such as demographic and dispersal data, in addition to landscape characteristics.

There are three broad categories of models that simulate individual movement (raster based, vector based and network based), which differ according to whether the landscape is represented as fields, features or graphs. Conceived as fields, a landscape is a continuous surface defined by one or more variables (layers) that can be measured at any point within the field. Fields usually model continuous data such as elevation, or temperature gradients, but can also represent categorical data such as habitat classification. If movement through the landscape is dependent on the variables of the field, then raster-based movement rules are most appropriate. Features are discrete entities that occupy positions in space, such as lines (rivers, roads, hedgerows) and polygons (lakes, woodland). The interiors of polygons are considered to be homogeneous. Movement between features is usually simulated using vector-based models. Finally, graphs represent the positional relationship between discrete elements in a landscape; a graph consists of a set of nodes that may represent continuous or categorical data, and a set of edges, which are dimensionless but describe how the nodes are connected to one another. Edges may be temporally referenced, indicating changes in graph connectivity over time. Network-based models are used to simulate IB movement in graphs. Examples of all three of these categories are discussed below.

Movement rules and models

Regardless of whether movement models are raster, vector or network based, they encode a series of rules that predict how the dispersal behaviour of individual animals is expected to interact with the spatial pattern of landscape structure (King & With 2002). Variations in patch quality, boundaries between patches, the nature of the mosaic, and overall landscape connectivity all affect the permeability of the landscape to dispersing individuals (Wiens 1997). The limited empirical information on the behavioural responses of animals to landscape structure (Turner et al. 1995; Lima & Zollner 1996) means that model parameters are usually based on observed habitat preference, dispersal rates in different patches, and how the energetic costs of crossing a landscape affect distance moved as well as direction taken. For example, the rules employed by Boone & Hunter (1996) simulated IB searching behaviour in grizzly bears by encoding permeability into the cells of habitat patches. Highly permeable habitat patches produced straight paths and long distance movements whereas patches of low permeability caused convoluted paths and short displacement.

Raster-based models

Raster- or grid-based representations of the landscape permit the greatest flexibility with which movement interacts with the landscape, and are appropriate where the dispersal matrix is heterogeneous (Wiegand et al. 1999). The landscape is represented as a series of tessellated shapes, usually square grid cells, and the model animal moves through each cell based on movement rules.

An advantage of this approach to modelling is the inclusion of a clear relationship between a cell and its neighbours, facilitating the description of local interactions by state transition rules. Each cell stores its own state variables that influence the decisions made by individuals through the landscape it represents. However, there are three principal disadvantages to raster-based models.

- The resolution of the grid is limited by memory capacity and simulation speed, and raster-based models have a tendency to be computationally demanding.
- The fixed spatial structure implies a fixed relationship between the spatial scale in the simulation and the scale of individual movements of the organism investigated.
- The geometry chosen to represent landscape in raster-based models (i.e. square grid, hexagonal grid, Dirichlet tessellation, etc.) can substantially affect the simulated behaviour of the individual dispersers even if the rules for movement and settlement are the same between different geometries (Holland et al. 2007).

Vector-based models

Vector-based models simulate organisms dispersing through continuous or homogeneous landscapes. If the motivations for these movements are random or quasi-random search patterns, they can be simulated using correlated random walk algorithms (Kareiva & Shigesada 1983). Alternatively, if individual movements are targeted searches for resources with a particular spatial or temporal distribution, movement decisions will be informed by the underlying landscape structure. Finally, if motivation for movement is prompted by the desire to avoid or join conspecifics, it will result in density-dependent movement rules. Where motivations for movement are known and appropriate, IB models benefit from vector-based dispersal simulations, which are less computationally demanding than the raster-based alternative.

Network-based models

Network-based models differ from the other types in that they do not include a continuous representation of the landscape. Rather, connectivity between locations is represented by an edge between nodes. Network-based models usually specify an *a priori* representation of patch size, patch adjacency and other criteria (e.g. Lookingbill et al. 2010). Edges are formed when movement is possible between nodes. Dispersal corridors can be represented as nodes as well as edges in network visualizations of a landscape used as analytic connectivity models (McRae et al. 2008). They calculate walks through the network that minimize total weight, suggesting optimal pathways for dispersal. In IB models, network-based landscapes are utilized probabilistically (Lookingbill et al. 2010; Morzillo et al. 2011), and may result in biologically plausible but analytically suboptimal solutions. Graph-theoretic approaches to network analysis can be applied to the utilized networks of IB models to identify the nodes and edges that maintain cohesion of the network. For example, Gurnell et al. (2006) identified routes of entry for invasive grey squirrels into potential conservation areas for the endangered red squirrel in northern England through network analysis.

Corridors based on shifting climate envelopes

This approach produces ’temporal corridors’ that track how a species’ climatic envelope (suitable temperature and moisture regimes) might move across a landscape under climate change scenarios. Like some types of individual-based models, this approach avoids the concept of resistance that is central to most previous approaches. The heart of this approach is either a dispersal chain model (Williams et al. 2005) or a network flow model (Phillips et al. 2008), either of which identifies cells with suitable climate envelopes that are spatially contiguous for long enough to allow the species to establish new populations in cells as they become suitable. Although dispersal chain and network flow models are conceptually sound, they depend completely on the outputs of three other models, namely models of future emissions of greenhouse gasses, models of future climate resulting from how the atmosphere and oceans respond to these emissions, and climate envelope models for the focal species. Unfortunately, each of these latter three models is plagued with massive uncertainty (summarized in Beier & Brost 2010). In the future, ensemble modelling (building many alternative corridors based on various combinations of emission scenarios, circulation models and climate envelope models) might identify corridors robust across the range of assumptions in the ensemble.

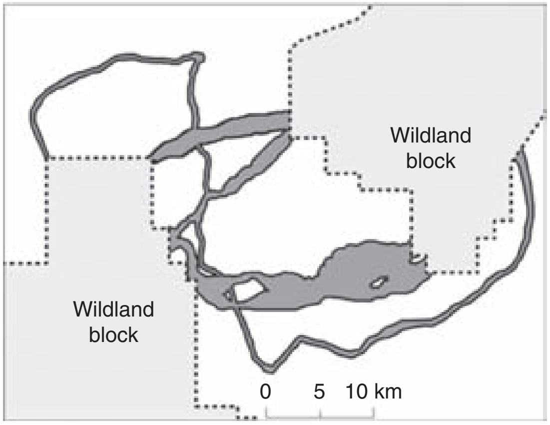
Beyond single species

From optimal corridors for single species to linkage designs for multiple species

Up to this point, we have described methods of mapping an optimal corridor, or areas important for connectivity, for a single species. Beier et al. (2008) proposed the term *linkages* to denote lands intended to support movement of

Box 21.3 Example of optimizing multispecies linkage

A hypothetical linkage design including optimal corridors for eight focal species, expanded to include patches of modelled breeding habitat for an additional five focal species for which corridor models were not appropriate, and a narrow riparian strand for fishes. Each strand needs to be >1 km wide in order to create large interior spaces free of edge effects, support meta-populations of species needing multiple generations to achieve gene flow through the corridor, and support ecological processes more complex than animal movement.



multiple focal species and ecosystem processes. To design linkages, conservation planners can select a suite of representative focal species suitable to serve as a collective umbrella for the entire biota. For instance, each of 27 linkage plans in California and Arizona (Beier et al. 2006, 2007) was designed to meet the needs of 10–30 focal mammals, reptiles, fishes, amphibians, plants and invertebrates. Focal species included species requiring dispersal for metapopulation persistence, species with short or habitat-restricted dispersal movements, species tied to an important ecological process (e.g. predation, pollination, fire regime), and species reluctant to traverse barriers in the planning area. Although large carnivores are appropriate focal species and flagships (Servheen et al. 2001; Singleton et al. 2002), most of them are highly mobile habitat generalists and thus inadequate umbrellas for other species (Beier et al. 2009; Minor & Lookingbill 2010).

A simple unweighted union of single-species corridors is an obvious way to produce a linkage design to promote the goal of 'no species left behind' (Beier et al. 2006, 2007; Adriaensen et al. 2007; Cushman et al. 2011) (Box 21.3). But corridor models are not appropriate for some focal species, such as many flying animals, that do not move across the landscape in pixel-to-pixel fashion. To support movement of these species, Beier et al. (2008) recommend draping maps of known or modelled breeding habitat over the union of corridors, and enlarging the union to include patches that would decrease the interpatch distances that dispersers would need to cross. The linkage design should be further expanded to include major riverine connections, which provide natural corridors for aquatic and some upland organisms, and promote other ecological processes and flows such as movement of sediment, water and nutrients.

Coarse-filter linkage designs for climate change

Climate change poses a challenge to all types of conservation planning, including linkage design. As climate changes, existing land covers in some planning areas will not merely shift but will disappear as plant associations reassemble (Hunter et al. 1988; Lovejoy & Hannah 2005). Linkage designs should be robust to such changes, and should allow species to shift their ranges into and out of the planning area. To address this, one could attempt to model corridors for the shifting climate envelopes of all species (above). A simpler alternative is to design linkages with a coarse-filter approach based on the abiotic drivers of land cover and species distributions (Hunter et al. 1988; Anderson & Ferree 2010). This idea is grounded in the foundational ecological concept (Jenny 1941; Amundson & Jenny 1997) that biodiversity at any point in time is determined by the interaction of the recent species pool with climate, soils and topography.

Beier & Brost (2010) and Brost & Beier (2012) developed multivariate procedures to identify *land facets*, defined as recurring landscape units with uniform topographic and soil attributes, from readily available digital maps of elevation and soils. They used multivariate dissimilarity as a measure of pixel resistance for each land facet type. Finally, they used least-cost modelling to design land facet corridors, and joined these corridors into a linkage design. Other coarse-filter approaches are feasible. For instance, Rouget et al. (2006) suggest that species will shift their ranges by sequentially colonizing areas that lie along the most gentle and monotonic temperature gradients. Assuming these gradients in temperature are conserved in a changing climate, it may be possible to identify corridors along today's most gentle and monotonic temperature gradients, without the need for uncertain models of future climate.

Linkage designs should be produced by a combination of coarse-filter and focal species approaches. In each of three landscapes, Beier & Brost (in preparation) developed two linkages designs – one based on land facets and the other on focal species. The land facet linkage designs included optimal corridors for 25 of 28 focal species, whereas the focal species designs encompassed optimal corridors for 21 of 32 land facets. Neither approach on its own was likely to meet all conservation goals.

Validation of predicted corridors

Corridors resulting from models have sometimes been criticized because they lack supporting movement data (Simberloff et al. 1992; Rosenberg et al. 1997) and because they may contain errors in model parameters or incorrect assumptions (Spear et al. 2010). Therefore, additional vetting of modelled corridors in the field is strongly recommended.

Many field studies have evaluated the efficacy of existing corridors, such as corridors that follow linear features like fencerows or rivers (Hill 1995; Castellón & Sieving 2006), or that were constructed as part of experimental landscapes (Berggren et al. 2002; Haddad et al. 2003). There have also been tests of species' response to conservation action in established corridors (Duke at al. 2001; Shepherd & Whittington 2006). But field testing of modelled corridors, like the ones described in this chapter, have been scarce.

Modelled corridors may cover large spatial extents and span multiple land ownerships and management types, or even national borders, making the collection of field data logistically complex and resource intensive. If corridors are modelled for dispersal movement, capturing infrequent dispersal events is akin to finding a needle in a haystack, so collecting sufficient data to reliably test predicted corridors can be difficult. Finally, modelled corridors can only be truly validated if movement through the corridor is documented along with the outcome for which the corridor was intended, whether that be by successful migration to summer or winter ranges, successful recolonization of habitat patches, safe passage across a road, demographic rescue, or successful breeding and gene flow.

Even if all aspects of linkage cannot be validated, a partial field study will add confidence and transparency to a corridor project. For example, Clevenger et al. (2002) developed two habitat models for black bears, one based on expert opinion and the other based on data from the literature. They identified road crossing zones from these models, and using data on crossings by real bears, they tested if the predicted linkages were used more than would be expected by chance. They found that the linkage models based on data from the literature outperformed the expert opinion models. The authors indicated that the expert opinion models may not have performed as well due to an overestimation of the importance of riparian habitat.

As an additional example of empirical field validation of corridors, Quinby (2006) used existing data from the annual breeding bird survey to test the utility of a proposed corridor. More bird species were found inside the corridor than outside it, confirming its validity. Chardon et al. (2003) used presence/absence data on the speckled wood butterfly from two different landscapes to compare the explanatory power of Euclidean distance and effective-distance connectivity models. They found that cost-distance was better able to predict connectivity than Euclidean distance. Zeller et al. (2011) used interviews with local residents to collect detection/non-detection data on jaguars and seven prey species in a grid-based design. The data were analysed by a site-occupancy model to determine probability of habitat use inside and outside the modelled corridor. It was found that probabilities of habitat use were mostly higher outside the modelled corridor, a conclusion which prompted a redesign of the final corridor.

The fact that there have been few studies to validate corridor models calls for more attention to this topic. Corridor validation techniques not only need to be improved upon, they need to be accessible to researchers and land managers working at different scales and on various species. Bridging the gap between corridor identification and corridor implementation will increasingly depend upon these validation studies, since land managers do not want to be left to implement a corridor of questionable efficacy, or be blamed for creating a sub-par corridor while more appropriate lands are unprotected from development and fragmentation (Hess & Fischer 2001; Morrison & Boyce 2008).

Conclusions

Population connectivity is critical for maintaining viable regional populations in the short term and to enable species to shift their geographic range in response to future climate change and other pressures such as land use change. In this chapter, we described the state of the art in quantitative corridor and connectivity modelling approaches. The first step in most quantitative connectivity analyses is to estimate and map landscape resistance. Traditional expert opinion is less useful for developing landscape resistance maps now that new and effective approaches using empirical data provide a much more reliable and robust means to map landscape resistance. There are a number of ways to predict or describe connectivity from resistance surfaces. Least-cost paths, least-cost corridors, circuit theory, centrality analyses, and resistant kernels are all powerful approaches suitable for different objectives. The efficient application of corridor analyses to future applied conservation problems must develop corridor designs to maintain connectivity for multiple species, and under changing climate. Finally, empirical validation of predicted corridors and linkages is essential to demonstrate their functionality and guide improvement of future corridor designs.

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