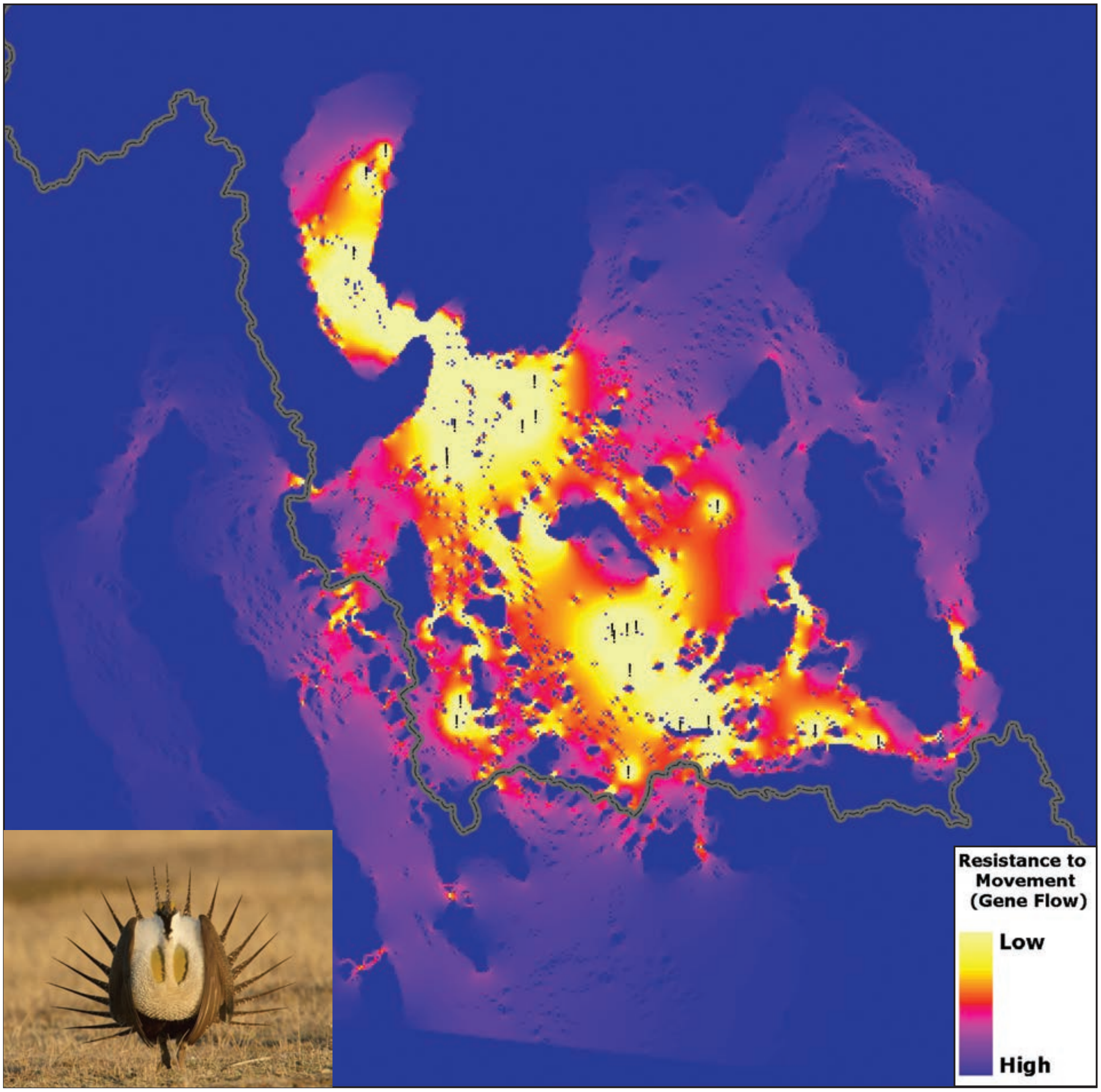
United States Department of Agriculture

Resistance-Surface-Based Wildlife Conservation Connectivity Modeling:

Summary of Efforts in the United States and Guide for Practitioners

Alisa A. Wade, Kevin S. McKelvey, Michael K. Schwartz



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Abstract

Resistance-surface-based connectivity modeling has become a widespread tool for conservation planning. The current ease with which connectivity models can be created, however, masks the numerous untested assumptions underlying both the rules that produce the resistance surface and the algorithms used to locate low-cost paths across the target landscape. Here we present a process to guide map creation, from conceptualization through validation, that seeks to better consider the complex biological issues inherent to connectivity modeling. Following this organized approach to connectivity modeling will help analysts prevent a plethora of issues common in recently created models, such as the failure to specify the temporal domain, purpose of the mapped connectivity, or the biological rationales for assigned pixel-level resistances. Following these steps will improve both the understanding and biological relevance of constructed connectivity maps.

Keywords: connectivity, resistance surface, least-cost path, cost distance modeling, validation, models, conservation.

Authors

Alisa A. Wade is a private consultant conservation scientist and an affiliate faculty with the University of Montana, Department of Geosciences, Missoula, Montana.

Kevin S. McKelvey and **Michael K. Schwartz** are research ecologists, U.S. Forest Service, Rocky Mountain Research Station, Wildlife and Terrestrial Ecosystems, Missoula, Montana.

Cover—Connectivity modeling of greater sage-grouse leks (black dots) in southwest Montana. Resistance of land cover to gene flow is hypothesized and connectivity models are generated by comparing landscape attributes to measures of genetic connectivity. The connectivity map is provided courtesy of Todd Cross (tbcross@fs.fed.us, 406-209-8633). The sage grouse photo is provided courtesy of John Carlson: Photo Copyright - John Carlson.

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Chapter 1. Introduction

> "Corridors are a hot topic, perhaps even a fad, in conservation planning these days. ... Planners...are busy drawing...habitat corridors...sometimes with only a vague awareness of the biological issues underlying the corridor strategy" (Noss 1987).

Despite originating in a seminal paper dating back a quarter century, Reed Noss's comment remains relevant today. During that time, the initial controversy surrounding whether wildlife corridors are cost or ecologically effective (the "corridor controversy" reviewed in Anderson and Jenkins 2006) has given way to general acceptance of the importance of landscape connectivity (Hilty and others 2006). Yet, there remains a lack of consensus about exactly what landscape connectivity entails (Crooks and Sanjayan 2006), how it should be modeled and quantified (Beier and others 2008; Kindlmann and Burel 2008; Huber and others 2010; Sawyer and others 2011; Zeller and others 2012), and whether sufficient biological understandings underlie current landscape linkage designs (Bélisle 2005; Chetkiewicz and others 2006; Beier and others 2009; Lowe and Allendorf 2010; Parks and others 2012). Here we primarily focus on connectivity defined as the degree to which a landscape facilitates wildlife movement (sensu Taylor and others 2006).

In the face of increasing habitat loss and fragmentation (Wilcove and others 1998), as well as the potential need for species range shifts under novel climates (Heller and Zavaleta 2009; Carroll and others 2010), the debate surrounding the definition, modeling, and implementing of connectivity has not stopped an explosion of research concerning connectivity for wildlife conservation (Crooks and Sanjayan 2006), nor has it slowed efforts amongst land use planners and managers to design connectivity projects. Implementing connectivity on-the-ground, however, has high political and economic costs, as well as large opportunity costs: finite resources invested in protecting a putative linkage will not be available for protecting other areas. Thus, it is imperative that linkages be modeled carefully; modeling should be rooted in the principles of both wildlife ecology and model uncertainty. Planning linkage-based conservation should follow a clearly defined process to ensure that the problems are properly framed, landscapes are properly modeled, and the correct methods and metrics have been applied.

Early in the process, conservation practitioners must clearly define their conservation goals and consider whether increasing connectivity is the highest priority management approach. Connectivity is not a panacea and is just one of many tools available to land managers (Simberloff and Cox 2005). Other landscape management options (reviewed in Lindenmayer and others 2008) include maintaining large patches of native vegetation, managing for structurally complex and heterogeneous habitats, and creating buffers surrounding sensitive and core habitat areas. Further, certain forms of connectivity may not be ecologically feasible or cost-effective for some species and landscapes (Simberloff and others 1992; Hannon and Schmiegelow 2002). However, recent studies have provided additional data to support thoughtfully planned connectivity (Collinge 1998; Tewksbury and others 2002; Damschen and others 2006; Worboys and others 2010; Gilbert-Norton and others 2010).

A clearly defined conservation goal supporting the decision to increase connectivity will guide practitioners in selecting from a large suite of connectivity modeling methods. Each method has its own unique set of assumptions and best practices, and each produces slightly different types of maps. Connectivity modeling is not a one-size-fits-all endeavor. For example, if the goal is to measure whether a landscape is connected, construction of landscape graphs between habitat patches may be sufficient (reviewed in Galpern and others 2011). Similarly, for some very coarse scale connectivity mapping, where connectivity is modeled at regional to continental scales, expert opinion may be the only option due to data limitations (e.g., Jongman 1995; process summarized in Beier and others 2011). At the other end of a complexity spectrum are spatially explicit population models (SEPM). These models link population processes and landscape features to assess demographic consequences of connecting populations, and may be particularly helpful in assessing scenarios of land cover or climate change (reviewed in Carroll 2006).

If spatially explicit connections are required—e.g., the goal is to design and implement linkages by purchasing or otherwise protecting specific areas—there remain many options. For example, individual Based Models (IBM) that simulate animal movement using species-specific behavioral rules (e.g., movement angles) and mortality risks in response to landscape elements can be applied. There are also IBM-like approaches that use observed animal movement data to assess landscape connectivity (e.g., "morphological image mapping," Vogt and others 2009).

However, the most common type of spatially explicit connectivity modeling uses resistance surfaces. Resistance-surface-based connectivity modeling is a relatively accessible method that does not require excessive data or computational resources. Resistance surfaces represent the degree to which some landscape feature impedes or facilitates some movement process (Adriaensen and others 2003), typically represented as a cell (pixel) value in a grid (raster) within a Geographic Information System (GIS). Linkages are then modeled in areas with lowest resistance to the movement process considered. The models are relatively easy to apply given existing data, and the approach offers the flexibility to develop models ranging from simple to complex, tailored to the specific conservation needs, and able to be refined as better data become available. A resistance surface is conceptually related to the idea of travel costs from behavioral ecology, and can therefore be designed to integrate ecological concepts important to successful wildlife movement such as an organism's perceptual range and susceptibility to competition and predation (Bélisle 2005).

Resistance-surface connectivity modeling assumes a relationship between surficial proxy measures and ease of animal movement. Unlike a SEPM—which requires specification of the biological needs and behaviors of the modeled organism—resistance surfaces can be posited without clear links to specific biological processes. It is common, for example, to equate resistance to habitat quality (e.g., Wikramanayake and others 2004; Beazley and others 2005; Kindall and Van Manen 2007; Gavashelishvili and Lukarevskiy 2008; Thatcher and others 2009; Castilho and others 2011; Atwood and others 2011). However, it is often not clearly stated whether the presumed low resistance through high quality habitat is due to ease of movement, ease of food acquisition, behavioral familiarity, predator avoidance, or any of a multitude of other potential biological factors. Given this, it is important that resistance surfaces be considered *hypotheses* reflecting a solid consideration of causal biology. Similarly, resistance modeling generally implies that an organism has a specific directional movement goal, which may or may not be biologically reasonable. In some resistance-surface approaches, such as when connectivity is modeled using circuit theory (McRae and Beier, 2007; McRae and others 2008, see Chapter 3), organisms are modeled as electrons being pulled from a source (anode) to a destination (cathode). In other methods, such as least-cost path (LCP) analysis (see Chapter 3), an organism's knowledge of landscape resistance is assumed to be perfect; the organism always knows the right path choice to minimize the overall cost and takes it. LCP analyses, like circuit analogies, generally assume a single goal: to travel from one cell to another, generally distant, one. The biological realism of these connectivity algorithms is largely unknown, but these levels of knowledge and motivation would surely be rare amongst organisms.

There is, however, nothing in the process of modeling resistance-surface-based connectivity that forces one to confront these biological issues explicitly, and the ease of creating resistance-surface models therefore presents a potential trap. Data layers in a GIS can easily be transformed into resistance surfaces through simple manipulations, and user-friendly software exists to apply common algorithms to build corridors. It is easy to build a resistance-based connectivity map. However, due to the abstractions and hidden assumptions associated with this process, we assert that it is difficult to build a good one; it remains largely unknown whether the current connectivity models or designs will meet conservation goals and reduce biodiversity loss (Vos and others 2002; Goodwin 2003; Sawyer and others 2011; Zeller and others 2012).

The primary objective of this report is to provide a thorough, yet concise and accessible, information summary and guidance for land managers seeking to employ resistance-surface-based connectivity modeling for terrestrial wildlife conservation. We note that connectivity for aquatic species is also critically important, but the methods for modeling connectivity in ocean (e.g., Treml and others 2008) or riverine (e.g., Fagan 2002) environments may not lend themselves to resistance-surface-based approaches (but see Landguth and others 2012).

There are several helpful reviews in the primary literature covering topics such as best uses for connectivity metrics (Calabrese and Fagan 2004; Kindlmann and Burel 2008; Rayfield and others 2011), best practices for modeling resistance surfaces (Spear and others 2010; Zeller and others 2012), and corridor and conservation network design guidelines (Beier and others 2008, 2011; Sawyer and others 2011). We synthesize, update, and expand on these efforts to achieve five goals: (1) briefly summarize the theoretical ecological concepts that underlie connectivity modeling and planning, (2) review connectivity modeling efforts in the primary literature, (3) review applied connectivity planning efforts in the United States, (4) detail the process of validating connectivity models, and (5) build on past and current connectivity modeling efforts and provide guiding questions to assist practitioners in modeling robust, ecologically grounded, resistance-surface-based wildlife connectivity. We note that these are not proscriptive guidelines because landscape connectivity is context dependent, depending on the species of concern, the landscape, and the conservation goal. What we provide is an organized approach to the problem of constructing resistance-based connectivity models. Each stage in this process is motivated by key critical questions that should be considered to ensure that connectivity designs are as ecologically relevant as possible.

Throughout this report, we direct practitioners to other key resources that provide helpful details. There are other general frameworks for connectivity planning available, providing guidance on steps from assembling the planning team, determining the goals of the project, establishing collaborative arrangements, selecting the study area, through assessing opportunities and limiting factors of the modeled linkages (Hilty and others 2006; see Anderson and Jenkins 2006; Beier and others 2011; summarized in Aune and others 2011). While some of these frameworks tend towards coarse scale regional connectivity modeling, many of the guidelines are helpful at any scale. Similarly, there exist in-depth reviews of theoretical foundations for connectivity modeling (e.g., Forman 1995; Bennett 2003; Hilty and others 2006; Lindenmayer and Fisher 2006) and technical details on specific steps in the larger process (e.g., Adriaensen and others 2003; Theobald 2005; Beier and others 2009; Spear and others 2010; Huber and others 2010; Parks and others 2012; Zeller and others 2012); we urge readers to consult these helpful works as necessary. Here, we seek to find the balance between detail and accessibility, providing a summary of existing efforts and detailed questions for modeling resistance-surface-based, spatially explicit linkage designs for terrestrial wildlife conservation. To accomplish our goal, we reviewed 47 recent publications that used resistance modeling and 31 recent efforts by planners and practitioners in the United States.

Chapter 2. Ecological Framework and Key Definitions for Modeling Connectivity

The Foundations of Resistance-Based Connectivity Modeling

Land cover conversion leading to **habitat loss** is one of the greatest threats to global biodiversity (Wilcove and others 1998; Sala and others 2000; Foley and others 2005; Cushman 2006) (see "Connectivity Terminology" at the end of Chapter 2 for definitions of words in **bold**). Associated with habitat loss is **habitat fragmentation**, the breaking apart of large contiguous blocks of habitat into multiple smaller **patches**. Habitat fragmentation has numerous negative effects on ecosystems (for a thorough treatment of the topic, see Saunders and others 1991; Lindenmayer and Fisher 2006). Fragmentation changes the shape and pattern of habitats throughout the landscape and tends to decrease habitat quality more than areal losses would indicate: fragmentation in and of itself reduces the amount of structural **core area**, where **edge** effects and external disturbances do not permeate. Fragmentation, and particularly "dissection" of habitats by roads and other human-built barriers, reduces **landscape connectivity** (Franklin and Forman 1987; Forman and Alexander 1998). Ultimately, habitat loss and fragmentation can lead to declines in wildlife populations (Ricketts 2001; Wiegand and others 2005; Hansen and DeFries 2007).

Reduced landscape connectivity leads to **isolation** of individuals or populations via reduced foraging, dispersal and reproduction, or migration movements (Lindenmayer and Fischer 2006). These effects of reduced landscape connectivity span multiple spatial and temporal scales affecting processes as varied as daily foraging, annual migrations, rates of genetic mixing, and population persistence. Reduced landscape connectivity may also alter food webs (Holyoak 2000) and ecosystem processes including microclimatic shifts and nutrient cycling (Collinge 1996). The degree of impacts from fragmentation depends on whether the organism in question is a habitat specialist or generalist, whether it prefers habitat core or edge areas (Bender and others 1998; Fahrig 2003), and the species' evolutionary predilection to cross "gaps" or barriers in the landscape (Lindenmayer and Fischer 2006).

Because land cover conversion, fragmentation, and habitat loss are prevalent, maintaining or restoring landscape connectivity is widely accepted as necessary, *but not sufficient*, for sustaining daily habitat, demographic, and genetic processes that support the persistence of local and peripheral populations and their evolutionary potential (Debinski and Holt 2000; Bennett 2003; Crooks and Sanjayan 2006; Taylor and others 2006; Pressey and others 2007). Connectivity may be particularly critical for species seeking suitable habitat under a changing climate (Lawler and others 2008; Heller and Zavaleta 2009; Carroll and others 2010; McKelvey and others 2011).

The term landscape connectivity was originally coined by Merriam (1984) and defined by Taylor and others (1993) as "the degree to which the landscape facilitates or impedes movement among resource patches." A landscape therefore only has **functional connectivity** relative to a single species' perspective. Functional connectivity is also dependent on the specific organisms' scale of movement (Wiens 1997), perception of the landscape (Lima and Zollner 1996), resource needs, and behavioral responses to landscape elements and patterns (Lima and Zollner 1996; Wiens 1997; Tischendorf and Fahring 2000; D'Eon and others 2002). In practice, because behavioral responses to the landscape are not always known for a specific species, connectivity models often focus only on the physical patterns, or **structural connectivity**, of the landscape. However, structural connectivity in no way ensures functional connectivity, and a functionally connected landscape may not appear on a map as having structurally contiguous habitat considered suitable for a species' movement (Taylor and others 2006).

Fundamentally, the concept of landscape connectivity is grounded in three primary ecological fields: island biogeography, metapopulation, and landscape ecology. Although the original development of the first theory, island biogeography (MacArthur and Wilson 1967), was related to actual islands, the theory later came to represent a general view of the landscape as habitat patches with high quality habitat that supported organisms surrounded by an inhospitable landscape of other, unsuitable habitats, commonly referred to as the **matrix**. The theory holds that biodiversity is positively related to size and proximity of patches (specifically, the theory developed functions to calculate the theoretical equilibrium number of organisms on an island in response to island size and distance from the mainland). Biologists eventually recognized that this theory was not a perfect fit for most terrestrial systems because patch/matrix differences are seldom as extreme as the original ocean/land dichotomy. In short, the matrix matters (reviewed in Franklin and Lindenmayer 2009), and the theory breaks down to the degree to which it matters. Nevertheless, the theory set up the view of the landscape as a binary "patch or matrix" system.

The second theoretical foundation for connectivity is metapopulation theory (Levins 1968, 1969a; Hanski 1998). The theory holds that local populations of organisms are connected by individuals moving (dispersing) between other local populations to create a larger, interconnected system of populations (metapopulation). In the simplest of terms, metapopulation theory quantifies the proportion of patches occupied as a function of the ratio of patch-level extinction and recolonization (Levins 1969a, 1970). Importantly, for all of the patches to be occupied, colonization rates need to be orders of magnitude higher than extinction rates; when extinction rates equal colonization rates, the entire metapopulation goes to extinction (Levins 1969a, 1970). Lande's (1987) individual occupancy model, which is a precise discretization of Levins' model (Noon and McKelvey 1996), examines the effects of metapopulation dynamics in the case where patches represent individual home ranges. Lande (1987) theoretically demonstrated that, for territorial organisms, sufficient fragmentation, even in environments with unlimited habitat, will lead to extinction.

The concepts of proximity and size of patches from island biogeography combined with the critical element of dispersal rates from metapopulation theory were incorporated into the third foundation of landscape connectivity, the growing field of landscape ecology. This field of study tends toward a patch-corridor-matrix view of the landscape (Forman 1995). In the terminology of landscape ecology, a patch is a relatively discrete area that differs from the surrounding matrix, where matrix is the primary, most extensive (and often most contiguous) land cover type. Patches may be connected through the matrix via **corridors**, linear landscape elements that differ from the land cover on either side (dissimilar from the matrix). Landscape ecologists see the pattern of patches, corridors, and matrix forming a hierarchy of landscape mosaics, that in turn, affect (and are affected by) ecological processes across a range of scales (Turner 1989). These landscape mosaics have more recently been viewed by landscape ecologists and conservation biologists as being made up of a series of patches along a gradient of habitat quality (Fischer and others 2004). Given a gradient of patchily distributed habitat qualities, in this paradigm habitat patches are subjectively defined for management convenience (Bennett 2003), and the matrix may be equally important for conservation (Ricketts 2001; Jules and Shahani 2003; Prevedello and Vieira 2010). However, while this paradigm does not formalize landscapes into arrangements of habitat islands in a sea of matrix, the flavor of the older island-biogeographic concept is often retained: animals are assumed to live within and move between patches of most preferred habitat seeking paths through a matrix of less preferred habitat. The physical paths taken through the matrix represent **functional linkages**, spatially explicit paths of any shape and form through the matrix that provide functional connectivity across the landscape.

Connectivity modeling naturally followed this trajectory of ideas: early connectivity modeling focused on creating narrow links between patches as suggested by the patch-matrix-corridor model. As the field evolved, however, and with landscapes increasingly viewed as containing gradients of habitat quality, the issue changed from the maintenance or creation of **structural linkages** in the shape of corridors, to nuanced linkages, identified using the **perceptual scale** of a given **conservation target** (Wiens and Milne 1989). Thus, connectivity was no longer understood in terms of the presence or absence of a single thin corridor (Bennett and others 2006), but rather a network of optional paths (that may or may not consist of a highly visible contiguous swath of habitat) to facilitate movement under different scenarios, responding directly to a clearly articulated conservation goal. Thus, connectivity modeling efforts have recently moved to mapping **potential linkages** (sensu Fagan and Calabrese 2006), which represent hypotheses about paths that provide functional connectivity. Potential linkages are determined by evaluating the spatial landscape structure given knowledge of an organism's likely behavioral response to the specific area's landscape elements.

The analysis of connectivity within complex habitat quality gradients requires assumptions about how landscape patterns affect and direct organismal movement and dispersal. Formalizing these relationships as **resistance surfaces** allows the application of flow algorithms to identify structural or functional linkages. Conceiving connectivity as flow rates across a variably resistant surface makes this approach extremely flexible: many things can flow. Thus, resistance (or cost) surfaces can represent the hypothesized relationships between landscape features and a variety of ecological flows, such as movement of organisms, genes, or processes. It provides a facile approach to determining the location and shape of functional linkages given the landscape-ecological paradigm of landscapes being mosaics of patches with different habitat qualities. Mapping patch qualities to resistance levels and thereby enabling the use of flow algorithms, makes the problem of determining how organisms might move across complex patchy landscapes tractable.

The Ecological Consequences of Connectedness

Although the consequences of habitat fragmentation and lost connectivity receive more attention, practitioners must be aware of the potential negatives to increased **connectedness**. In particular, there is a concern that increased connectivity for target organisms may also lead to increased connectedness for unintended organisms and processes, spreading invasive species, changing competition and metapopulation dynamics, and introducing disease (Bennett 2003; Crooks and Suarez 2006; McCallum and Dobson 2006; Blowes and Connolly 2012). As a result, practitioners should assess the potential for negative effects of connectivity, particularly in the presence of invasive species, and integrate specific mitigation measures into the planning process (Aune and others 2011). Further, higher movement rates may be associated with higher mortality rates for some species (Biro and others 2003; Frair and others 2005; Grilo and others 2011). However, there is growing evidence that, in most cases, the benefits outweigh the risks, and that thoughtfully designed or restored connectivity increases biodiversity in increasingly fragmented landscapes (Beier and Noss 1998; Bennett 2003; Worboys and others 2010; Gilbert-Norton and others 2010; Beckmann and others 2010).

First Principles for Modeling Wildlife Connectivity

Connectivity is species-specific. A forest may provide connectivity for squirrels, but may represent a barrier for meadow voles. Not only is habitat species-specific, but species also respond to landscapes at very different spatial and temporal scales depending on their size, mobility, sensory acuity, and the purpose of their movements. A road may present an impassable barrier or a minor nuisance depending on the size of an organism and whether their biological needs require successful road crossing once a day or once a decade. Therefore, one of the most critical ecological concepts to consider when modeling connectivity is that of **scale.**

The importance of the **grain** and **extent** of both temporal and spatial scales has long been recognized as critical for conservation biology (Wiens 1989; Levin 1992; Frankham and Brook 2004). Specifically, connectivity modeling results may be very sensitive to grain size and the extent of analysis (Graves and others 2007; Pascual-Hortal and Saura 2007), thus it is critical that the modeling be conducted at a spatial and temporal scale that matches the organism's perceptual scale (Wiens and Milne 1989; Baguette and Van Dyck 2007; Pe'er and Kramer-Schadt 2008; Galpern and Manseau 2013). Thus, the optimal scale of functional connectivity analysis arises from the intersection of species-specific traits and the **type of connectivity** being modeled. For example, Squires and others (2007) estimated a total population size of approximately 13 wolverines (*Gulo gulo*) occupying four mountain ranges in Montana. Any one of these mountain ranges, however, contains tens of thousands of chipmunks (*Neotamias* spp.). The spatial extent and grain of connectivity modeling to meet the daily needs of an individual wolverine would clearly be larger than those required for a chipmunk. Additionally, the wolverine population is so small that it requires both genetic and demographic connectivity to persist, and analysis would require a spatial extent of multiple mountain ranges. Between-mountain-range demographic and genetic connectivity is much less important for the larger chipmunk populations and, due to their comparatively small size and reduced mobility, is unlikely to occur with any frequency.

Temporal scaling is at least as important as spatial scaling in connectivity modeling. Temporal scaling affects both movement and population processes. In the wolverine/chipmunk example, wolverine's small population size within a range mandates nearly continuous movements between mountain ranges to avoid extinction due to chance events and to rapidly recolonize areas to avoid range shrinkage. These needs are demographic in nature, and temporally scale to years to decades. Chipmunks, on the other hand can persist in isolated mountain ranges for thousands of years. In the Spring Mountains, Nevada, a separate species, Palmer's chipmunk (*Neotamias palmeri*), has likely persisted in isolation since the Pleistocene, but retains levels of genetic variability not dissimilar to widely distributed species (McKelvey and others 2013). Thus, where local populations are larger and extirpation is not a frequent concern, the primary connectivity requirements may be to alleviate genetic rather than demographic stochasticity, and dispersal rate requirements scale to generation times rather than to population sizes (Lowe and Allendorf 2010). Both demographic and genetic processes, however, are short term when compared to the ebb and flow of climatic conditions that can render large areas that were habitat unsuitable and open up new areas of habitat in previously unsuitable landscapes. Connectivity at these time scales controls current ranges of species, and the process of speciation itself. These broad-scale and long-term connectivity needs have not been the historical focus of conservation biology. However, with the potential for rapid directional climate change in the near future, connectivity that allows movements at the regional to continental scale may be most critical for long-term population and species persistence (Heller and Zavaleta 2009; Shoo and others 2013).

Species-specific traits and the biological requirements facilitated by connectivity also determine the characteristics of potential linkages (Harrison 1992). If an organism moves rapidly, or if the biological requirements require short distance movements, connectivity may be achieved by a landscape whose only property is that it does not impede these movements. However, if movement is slower, or across greater distances, connectivity will require a landscape that provides food, water, and shelter or resting habitat in addition to allowing movement. If it takes generations to move across the space, then connectivity requires a landscape that provides for the entire life history needs of a species and is of sufficient areal extent and quality so as to support contiguous populations.

When planning for connectivity, careful consideration of species' needs and capabilities should be evaluated at a hierarchy of spatial and temporal scales. Further, the biological needs and associated movement requirements should be identified. We formalize these ideas by identifying six types of landscape connectivity: Structural Connectivity and five additional types of functional connectivity that are closely related to spatial and temporal scales of movement, **Daily Habitat, Seasonal Migration, Demographic, Genetic,** and **Range Shift**. We include brief definitions for these terms in "Connectivity Terminology" at the end of Chapter 2, but because these ideas are developed in this report, rather than being general to the literature, we discuss each of these ideas in detail.

1. Daily Habitat. This represents wildlife movement to meet daily food, water, and shelter needs, and it is the smallest temporal and spatial scale we consider. Daily movement connectivity is particularly important for species that shelter or breed in one habitat and forage in another type(s) of habitat separated by less suitable habitat, or for wide-ranging species that have home ranges that span a mosaic of habitat suitability (Bennett 2003). Improving daily habitat connectivity may be an important conservation goal for species or populations that have high mortality because of barriers (for example, roads) that hamper meeting basic resource needs. Because daily habitat movements occur at small spatial scales, they often follow tortuous paths (Crist and others 1992; Johnson and others 1992) and need to be modeled at an appropriately fine grain.
2. Seasonal Migration. This type of movement has many of the same motivations as Daily Habitat movement, but generally occurs at broader spatial extents (relative to each species' daily movements) and does not occur for all species. To separate this from Demographic movement (below), we define this as round-trip, seasonal movements. For species such as ungulates that require seasonal movements to obtain forage, seasonal migration routes may be some of the most critical to identify for conservation actions.
3. Demographic. Demographic movement is defined as being between sub-populations and occurring at relatively broad extents. These are dispersals from one sub-population to another rather than seasonal loops. Demographic movement rates that provide stability across sub-populations scale as the proportion of the census population, whereas genetic connectivity scales to the total number of migrants (Lowe and Allendorf 2010). In practice, this means that necessary rates of movement are at least an order of magnitude greater than are required to achieve genetic stability.
4. Genetic. Genetic movement, like demographic movement, occurs between sub-populations and happens at the same spatial scale. However, the temporal scale is much different. Genetic movement serves to maintain genetic variability across sub-populations by transferring genes at rates equal to rates of loss caused by genetic drift. So while demographic stability occurs if the number of migrants is sufficient to maintain a constant population on an annual basis, genetic stability

occurs if the number of migrants is sufficient for the next generation to have equal genetic variability when compared to the current generation (Mills and Allendorf 1996).

5. Range shift. Historical variability in climate, topography, and plant and animal communities has necessitated that species shift range for long-term species persistence. These are not movements made on an annual or even generational basis. However, with the possibility of rapid directional climate change (see Loarie and others 2009), introductions of exotic species, and other anthropogenic global changes, the rates of this type of movement may increase. Planned linkages between distant patches (such as pole-ward or elevational range shifts) may be required to help species adapt to unprecedented rates of change (Harris and Scheck 1991; Hobbs and Hopkins 1991; Tiebout III and Anderson 1997).
6. Structural. Landscape structure connectedness is assumed to increase long-term persistence of species without specifically defining a movement type or even which species are targeted. Although other connectivity requirements would generally be evaluated for a target organism, landscape structure is often evaluated for an unspecified group of organisms and includes broad concepts such as assumptions that biodiversity is increased when there are few human-built barriers (e.g., Theobald and others 2012). Therefore, in many cases, structural connectivity actually refers to lack of physical structures such as houses, roads, and parking lots. However, it can also refer to landscape features such as "facets" (Beier and Brost 2010), defined as landscape units with uniform topographic and soil attributes. This approach is well-suited for assessing general scenarios of land cover or ecosystem change (e.g., Wade and Theobald 2009; Brost and Beier 2012; Baldwin and others 2012).

These connectivity types are not independent; in a global sense, all are important for the long term conservation of a species. However, formal consideration of each type should lead to better and more comprehensive connectivity models and designs. For example, if the primary goal of a connectivity plan is to increase the likelihood that an organism can acquire its daily needs of food, water, and shelter, then these goals should be formally identified. A design that achieved this while also maintaining some level of between-population genetic connectivity would, however, be more likely to succeed in maintaining the species in that portion of its range.

In conclusion, resistance based connectivity modeling is the direct outgrowth of the fields of island biogeography and metapopulation dynamics when applied to complex, patchy, habitat gradients, the landscape-ecological view of landscapes. Transforming these quality gradients into resistance gradients allows the application of flow algorithms and makes computing connectivity tractable. However, because this transformation is intrinsically integrative and abstract, it can be accomplished without links to the specific biological behaviors, needs, and limitations of a target organism. To properly relate putative resistance factors to organism biology requires evaluating the spatial and temporal scales of the connectivity process in terms of the organism's own perceptual scale, density, and vagility. Further, it requires specificity concerning the type of movement being modeled. In the remainder of this report, we narrow our focus to the specific process of developing resistance-surface-based connectivity models, first providing a literature survey of published analyses, and then outlining an 8-step process which, if followed, will guide the analysis and avoid common pitfalls.

Connectivity Terminology

Connectivity

- **Landscape Connectivity:** Also called ecological connectivity (although usually applied to diffusion of ecological processes not movement of organisms), landscape permeability, (inverse of) **isolation.** This is a general term to represent the degree to which the landscape facilitates or impedes movement of organisms or processes (Crooks and Sanjayan 2006; Taylor and others 2006). Landscape connectivity can be represented as functional or structural connectivity. We note that some previous authors consider the term "landscape connectivity" to represent the connectivity of vegetation patterns or habitat, and to be a synonym of structural connectivity (e.g., Lindenmayer and Fischer 2006); however, we use the term as originally defined, above, as a general, umbrella term. We identify six total **types of connectivity**, one structural and five functional:
    - □ **Structural Connectivity:** Also called landscape pattern connectivity, habitat connectivity. Structural connectivity is the degree of physical, spatial contiguity of habitat types or elements in the landscape, assumed to increase flow of some processes, but generally considered independent of any specific organism (Collinge 1998).
    - □ **Functional Connectivity:** Also called actual connectivity. Functional connectivity is an emergent property of species-landscape interactions whereby the landscape, whatever its structure, allows sufficient organismal movement to provide some or all functional types of connectivity:
        - **Daily Habitat:** movement between resource patches to meet daily food, water, and shelter needs;
        - **Seasonal Migration:** annual or seasonal departure and return to breeding areas (Sinclair 1983);
        - **Demographic:** movement that leads to successful recruitment in new population (Lowe and Allendorf 2010) ;
        - **Genetic**: movement between populations that affects genetic structure, minimizes losses of genetic variability, and influences the evolutionary processes (Lowe and Allendorf 2010);
        - **Range Shift:** movement that allows species to track the shifting range of habitat availability resulting from factors such as climate change, large scale disturbances, novel pathogens, etc.
- **Connectedness:** Quantitative measure of connectivity; many metrics exist for quantifying connectedness (Calabrese and Fagan 2004; Kindlmann and Burel 2008; Magle and others 2009; Laita and others 2011). Connectivity is measured uniquely for a given type of functional or structural connectivity.

Conservation Target: Broadly, anything that one wishes to conserve. In this context, a biological element selected for conservation; this can be a single species or guild, at any level of biodiversity (e.g., individual, population, metapopulation, etc.).

Core Area: An area that is assumed to be vital to a specified conservation target. Often identified core areas represent specific types of habitat that are unique or rare in their abilities to provide habitat needs (e.g., foraging/prey, cover, reproduction), areas of particularly high productivity for the target, or simply large contiguous areas of habitat considered vital for metapopulation persistence. This idea differs from a habitat patch core that is more tightly defined as the center of a habitat patch, surrounded by a protective buffer, so that the core is not affected by edge effects or permeated by external disturbances.

Corridor: Originally defined as a relatively narrow strip of land cover that differs from the matrix on either side (Forman 1995); in its original meaning, the term represented only structural connectivity between patches and was not related to organism movement, but the term now refers to a human-built or naturally occurring linkage that is relatively short, usually linear, and dissimilar from the surrounding matrix and that may allow organisms to move between habitat patches (Beier and Noss 1998). In resistance modeling, corridors are associated with paths of low resistance that lie between predefined nodes representing source and destination locations for a specified conservation target.

Edge: The portion of a habitat patch near its perimeter where environmental conditions are more affected by the surrounding matrix as compared to the patch core (Turner and others 2001).

Habitat Fragmentation: Splitting of a single habitat patch into multiple, smaller patches; also generally entails habitat loss.

Habitat Loss: Reduction in total area of habitat.

Linkage: A spatially explicit representation of a physical path in the landscape, of any shape or form, through a landscape matrix. Linkages are not limited to narrow, linear connections between habitat patches (Bennett 2003). There are three primary types of linkages:

- **Structural Linkage:** a linkage drawn on a map based solely on structural vegetation or habitat patterns; does not consider species-specific behavioral responses to the landscape.
- **Functional Linkage:** a linkage that is empirically shown to provide a specific type of functional connectivity;
- **Potential Linkage:** often modeled as a structural element in the landscape (e.g., continuous swath of habitat) that, given assumed or known organismal behavioral response to landscape elements, is hypothesized to provide a functional linkage.

Matrix: In the terminology of landscape ecology, a matrix was originally defined as the primary, most extensive background land cover type (Forman 1995) and was generally considered the inhospitable binary opposite of habitat. Ecologists now view the matrix as a heterogeneous mix of land cover along a gradient from high quality, core habitat to completely inhospitable barriers; it is generally agreed that even less-than-suitable matrix is often used as habitat (Haila 2002; Berry and others 2005).

Patch: Also called habitat patch**.** A patch is a relatively contiguous land cover that differs from the surrounding land cover (Forman 1995); a habitat patch is a contiguous area in the landscape that meets specified habitat requirements for a given species.

Perceptual Scale: The grain and extent of an organism's response to heterogeneity in the landscape (Wiens 1989).

Resistance Surface: Also called cost surface. The resistance surface is the foundation of the modeling process, whereby land areas are assigned resistance (or cost) values representing the hypothesized relationship between ecological variables and the difficulty of animal movement across that cell. In common practice, these maps are GIS raster surfaces. Resistance values are proxies for ecological cost (also called functional cost, cost distance) and are generally assumed to represent either time (travel time), or fitness (physiological expenditure or likelihood of mortality) associated with traversing a specific area. However, in practice the ecological underpinnings of resistance are often poorly defined. Thus, resistance is often based on perceptions of habitat quality, correlations with known animal movements, or assumed impediments to movement (e.g., anthropogenic structures). In the case of structural connectivity (see Chapter 3), resistance is generally not formally linked to ecological cost.

Scale (**Grain**, **Extent)**: Scale is the spatial or temporal dimension of an object or process; there are two primary attributes of scale: grain is the finest level of resolution (e.g., in a GIS, the size of a cell, for time minutes vs. hours) and extent is the size of the study area or duration of time under consideration (Turner and others 2001).

Chapter 3. Resistance-Surface-Based Connectivity Modeling: Formalizing the Process and Reviewing the Literature

> "There are known knowns. These are things we know that we know. There are known unknowns. That is to say, there are things that we know we don't know. But there are also unknown unknowns. There are things we don't know we don't know."
>
> *Donald Rumsfeld*

Building a resistance-surface-based connectivity model based in actual functional connectivity requires both structured thinking concerning the ecological concepts discussed in Chapter 2 and a formalized process to make sure that important considerations have not been neglected. As noted both in the introduction and Chapter 2, there is nothing intrinsic to the process that forces one to address the issues that Donald Rumsfeld so pithily expressed. However, without formalizing our state of knowledge regarding the biological and ecological processes we seek to model, the chances of developing an accurate connectivity map are low. To provide a structure to help to achieve this, we identify eight critical steps for modeling resistance-surface-based linkage designs for terrestrial wildlife conservation (Figure 1; see Figure 2 for mapped examples of steps 2, 3, 4, and 5):

1. Define the type of connectivity to be modeled;
2. Create resistance layer(s);
3. Define what is being connected;
4. Calculate ecological distance;
5. Map potential linkages;
6. Validate potential linkages;
7. Assess climate change effects (optional);
8. Quantify connectedness (optional).

Assessing the uncertainty involved with each step is also a critical element of successful connectivity modeling (see more detailed discussion in Chapter 4). Although we discuss these steps in a linear fashion for convenience, the modeling process is seldom linear; decisions at each step may require that a decision made at a previous step be revisited.

Here, we focus on the modeling process, not the planning or implementation phases of linkage design. We do not consider pre-modeling planning, which includes clearly defining the conservation issue or problem, choosing conservation targets, and identifying collaborators, budgets, and timelines (Groves and others 2002). We also do not consider post-modeling implementation, which includes assessing feasibility of linkage designs, prioritizing linkages for protection, and estimating economic costs (Bennett 2003; Hilty and others 2006; for more details on these steps see Aune and others 2011; Beier and others 2011).

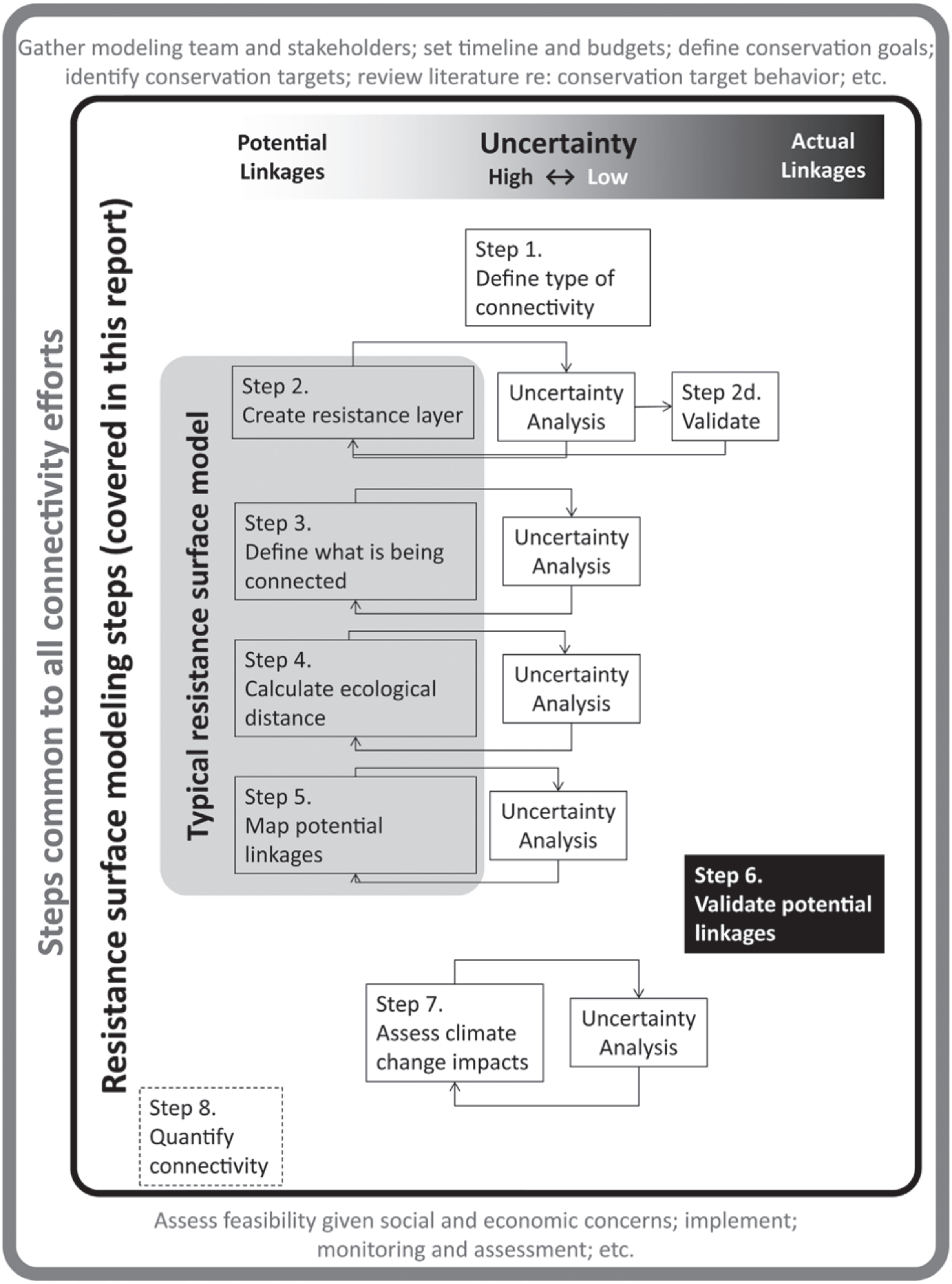


Figure 1—Resistance-surface modeling workflow. Workflow proceeds from top to bottom, but steps are not linear as decisions at each step may require revisiting previous steps; particularly, uncertainty analysis may suggest need to revamp methods. Methods from left to right reduce uncertainty in final mapped linkages. Step 8, quantifying connectivity, does not necessarily affect uncertainty.

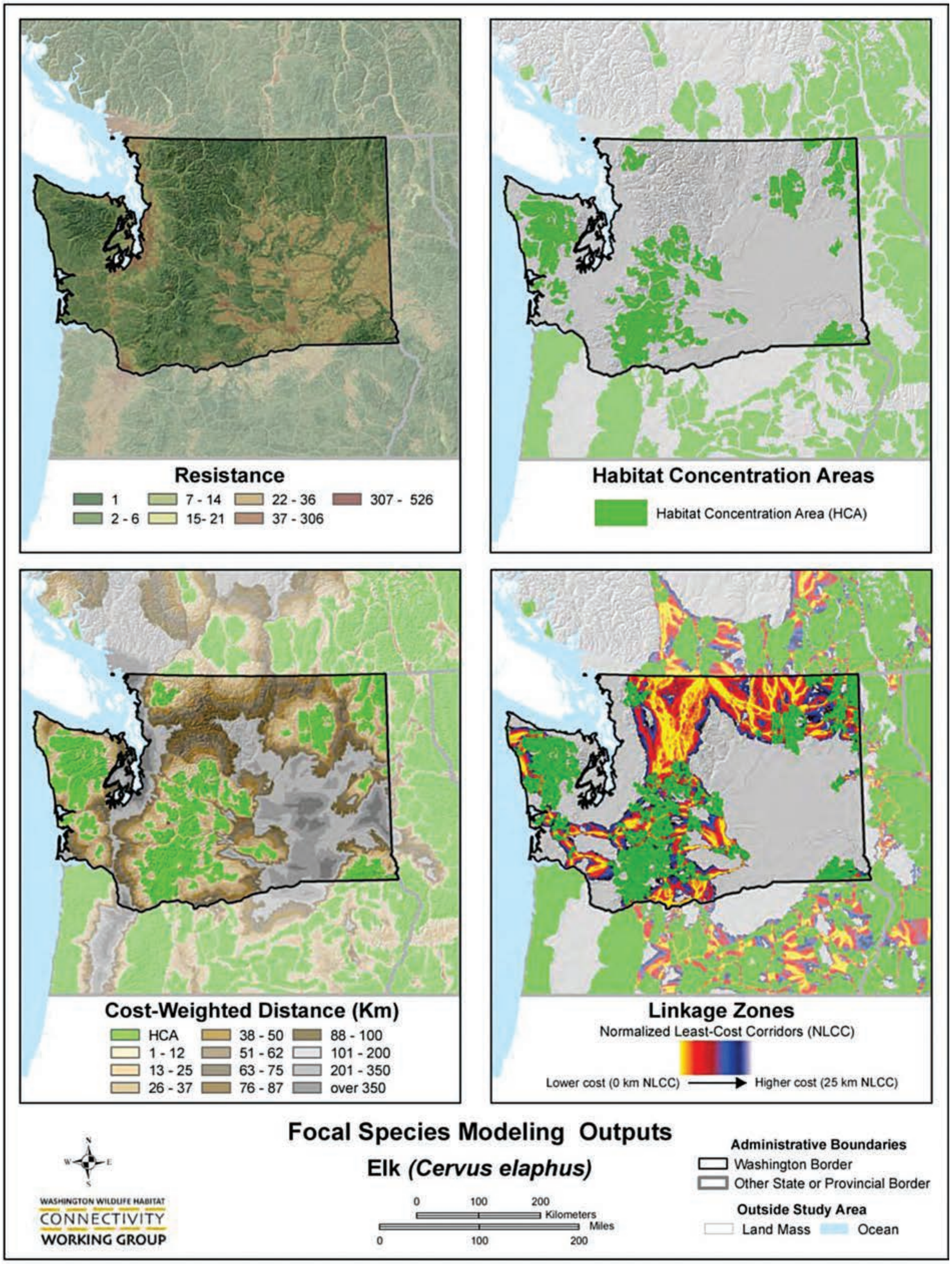


Figure 2—Example of steps 2 (top left; create resistance layer), 3 (top right; define what is being connected), 4 (bottom left; calculate ecological distance; here, least cost distance), and 5 (bottom right; map potential linkages; here using normalized least cost) in the process of resistance-surface-based connectivity modeling (here, for Elk; Figure ES.1 in WHCWG 2010; see Chapter 5 for a discussion of this project). (Permission to reprint figure granted by the Washington Wildlife Habitat Connectivity Working Group).

For each step, we include findings from a review of two types of literature: (1) papers seeking to provide guidance, critiques, or reviews for connectivity modeling and (2) papers that describe examples of resistance-surface connectivity modeling for conservation purposes. Although some papers covered both types of literature, we used our best judgment to determine their primary intent. The former papers are referenced in the discussion of each modeling step, below. The latter type of papers, those that describe connectivity modeling for conservation purposes, are summarized by each modeling step and listed in Appendix 1 (47 papers). In this report and in the table, we include several papers that did not have a primary intent of mapping linkages, but instead sought to more generally assess or quantify connectivity (17 papers, highlighted in grey in Appendix 1). We included these papers because they contribute something unique in their approach to modeling connectivity. To identify the papers discussed herein, we searched Web of Science and Google Scholar[1], followed citation leads, and relied on our own knowledge of the literature.

Steps for Modeling Resistance-Surface-Based Linkage Designs for Terrestrial Wildlife Conservation

Step 1. Define Type of Connectivity to Be Modeled

The conservation problem must be clearly defined in the pre-planning stages, and this in turn suggests the type of connectivity that should be modeled: in Chapter 2 we identified six movement types (also see "Connectivity Terminology" at the end of Chapter 2).

Many of the papers we reviewed, however, did not explicitly state the type of connectivity being modeled, but we were often able to infer the type from the stated intent. Several of the papers modeled more than one type of connectivity. The majority of papers' stated intent was to model "dispersal" (18 papers). This appeared to represent a combination of the second and fourth most commonly modeled connectivity types: genetic (specifically stated or intended in 10 papers) and demographic connectivity (9 papers). Structural connectivity was the third most commonly modeled (8 papers). Three papers sought to model daily habitat connectivity, and two sought to model migration connectivity. No authors stated or clearly implied they were modeling connectivity associated with range shifts. Two papers stated they were modeling "functional" connectivity, without further defining what that meant. In four of the papers we reviewed, the type of connectivity was not stated and could not be inferred (Appendix 1). In our view, this review identifies a clear deficiency in connectivity modeling to date. If the type of connectivity being modeled is not clearly specified, it becomes impossible to evaluate the quality of the resulting model either through direct validation (see Chapter 4) or even in the less demanding context of comparing the resulting linkage map to other constructs based on different resistance values, grain sizes, path algorithms, or nodal structures (below). Without specifying precisely what is trying to be achieved, there can be no related metric to judge success.

[1] We searched Web of Science for documents between January 1, 2002, and August 31, 2012, for the terms: Title = (linkage* OR corridor* OR landscape permeability OR conservation network OR connectivity OR landscape resistance) AND Topic = (least cost path OR least-cost OR least cost OR cost distance OR ecological distances OR resistance surface OR permeability OR isolation by resistance). This resulted in 425 citations. We reviewed abstracts to select the top 100 papers that most likely concerned resistance-surface connectivity modeling. We searched Google Scholar to identify any papers we may have missed with the terms: habitat connectivity, resistance layer, impedance layer, inverse of suitability, least cost path, least cost corridor, least cost distance, conservation area design, corridor map, Circuitscape, linkage mapper, FunConn, CorridorDesigner, Connectivity Analysis Toolkit, UNICOR, landscape integrity, MaxEnt connectivity, modeling connectivity, and functional connectivity.

Step 2. Create the Resistance Layer

The resistance layer is the foundation of the modeling process, whereby cells in a GIS raster surface are assigned a value representing the hypothesized relationship between ecological variables and the difficulty of animal movement across that cell. Zeller and others (2012) provide a comprehensive recent review of this critical step, and we recommend that practitioners refer to their manuscript for more detailed discussion of potential pitfalls. Here, we identify four sub-steps to creating the resistance layer: (a) determine the scale of the resistance layer, (b) identify ecological variables, (c) assign resistance values based on chosen ecological variables, and (d) validate the resistance surface.

Step 2a. Resistance layer extent and grain. The extent of the resistance layer should extend well beyond the area of interest. Mapping errors can occur at the edges of the resistance layer due to artificial truncation of landscape features, but more importantly, linkages will be artificially limited by the map edges (Koen and others 2010), which will be modeled as de facto barriers. Buffering beyond the area of interest reduces the likelihood that these errors will affect modeled potential linkages or that important potential linkages will be missed. Unfortunately, artificial boundaries constrain both political realities and data. Thus, if buffering the study area is intractable, it must be understood that connectivity analyses near the study area border are likely deformed and less dependable. Analysis extent must also reflect the level of organismal structure under consideration. For example, the extent of analysis for modeling demographic connectivity between multiple populations is very different from a model of daily habitat connectivity for a single organism.

The grain of the resistance surface, represented as the cell size in GIS, should reflect the perceptual grain of the species or conservation target given the type of connectivity being modeled. Often, however, there is a tradeoff between grain and extent for computational reasons (Lima and Zollner 1996), and commonly grain size is constrained non-biologically by the granularity of the available data.

Very few of the papers we reviewed specifically addressed the biological rationale associated with extent and grain. It was, for example, difficult to determine whether researchers extended analysis areas beyond the primary study extent to avoid mapping errors. For spatial grain, the majority of papers appear to set analysis grain on the basis of the resolution of available data rather than the perceptual grain of the conservation target. Therefore, the majority of researchers used between a 30 m – 100 m cell size, although several papers that modeled movement of smaller organisms used more finely resolved cell sizes (e.g., Stevens and others 2006; Driezen and others 2007; Wang and others 2009; Decout and others 2012) or larger cell sizes for larger animals (e.g., Falcucci and others 2008; Huck and others 2011; Carroll and others 2012; Ziółkowska and others 2012), in an effort to reflect an organism's perceptual grain. A few papers mention that cell size was chosen in response to computational limitations (e.g., Bunn and others 2000; Carroll and others 2012).

Several papers discussed scale mismatches associated with convenience-scaled resistance surfaces. For example, Pullinger and Johnson (2010) specifically discuss the potential implications arising from a mismatch between the inferred paths from telemetry (taken for caribou at >3 hour recurrence intervals) and modeled paths (using environmental variables with 25 m cell resolution). When cell resolution is arbitrary or differs from the scale of related occurrence data, a sensitivity test in which the analysis is run using a range of cell resolutions is a reasonable approach (Broquet and others 2006). Only five of the papers reviewed, however, considered various cell resolutions in their studies. For example, Walpole and others (2012) looked at correlation between resistance-surface cell size and occurrence data for lynx; they found that correlations existed for all cell sizes examined, and chose the finest resolution data for use in the remainder of the analysis. This level of analysis, although commendable, may not be sufficient to fully understand the sensitivities of putative corridors to cell size (Graves and others 2007; Pascual-Hortal and Saura 2007). For example, Schadt and others (2002) found that the size and shape of habitat patches were sensitive to grain size, and Carroll and others (2012) found the final modeled links were sensitive to analysis resolution.

An alternative to conducting a sensitivity analysis may be to use genetic (e.g., Cushman and Lewis 2010) or occurrence data (e.g., Janin and others 2009) in a model selection framework. Because organisms respond differently to various physical environmental properties at different scales, Zeller and others (2012) suggest that it may be best to determine an optimal grain for each ecological variable, rather than trying to find an optimum for all variables combined. This idea applies to temporal scales, as well. For example, Lowe and Allendorf (2010) reviewed the differences between demographic and genetic connectivity, noting the temporal mismatch in using genetic data to estimate resistance surfaces for modeling demographic connectivity.

It should be noted that grain size of the resistance surface is not the only way to reflect the perceptual grain of a species, and several of the papers we reviewed applied other approaches, such as defining patches, accumulating ecological costs, or mapping potential links on the basis of a species' assumed perceptual grain. We discuss those approaches below.

Step 2b. Determine ecological variables. Selection of ecological variables should be guided by state-of-the-science knowledge about a species' habitat relationships if the goal is to model a type of functional connectivity. For evaluating landscape structure, this isn't formally possible, as putative connectivity is not associated with specific organisms. However, the variables should still represent something thought to influence ecological flows, and the rationales for the choices should be clear. When assigning resistance levels to structural elements, this assignment unavoidably contains implicit understandings concerning the relationship between the element and organismal biology. For example, giving urban areas high resistance values implicitly indicates that the resulting connectivity models are not appropriate when applied to organisms common in urban areas. Inherently, even if guided by biological studies, variables are chosen using expert opinion and, from a practical standpoint, are driven by data availability. Optimally, the choice of variables should be comprehensive (Beier and others 2008), but there is no way to guarantee that all potential factors affecting species movement will be included, and, in truth, a relatively small subset of possible variables will be available as continuous spatial data. For this reason, almost all of the studies considered some form of land use or land cover (41), and many included a measure of human population density or locations (18), and/or road density (32). Ideally, studies should choose variables more specifically related to assumed relationship between an organism and potential for movement but, data availability generally dictate that rough proxies be used. Given this, if possible, a number of potential connectivity models should be compared within a coherent model selection framework. Of the 47 papers we reviewed, 14 used model selection to compare potential ecological variables.

In addition to considering the biological rationale for choosing a particular environmental variable, it is also important to consider data accuracy; restricting data layers to those with high accuracy rates is desirable (Zeller and others 2012). At a minimum, data sources should be listed and data accuracy should be incorporated into the discussion of the likely accuracy of the resulting modeled linkages. Only two of the papers reviewed explicitly considered uncertainty associated with data sources.

In many cases data reliability is affected by the scaling decisions associated with Step 2a, above. Different types of data are variably sensitive to scaling decisions. In general, classified data, such as the areal extent of forest cover, tend to be highly sensitive to scale when classification is based on achieving threshold value, and particularly when a classified type is rare on a landscape. For example, if a cell needs to be >50% tree covered to be classified "Forest," and forested areas are scattered within a largely agricultural landscape, as cell size increases, the area classified as Forest will predictably decrease—at some large cell size none of the cells will be 50% tree covered. Thus, when evaluating the accuracy of any mapped environmental variable, it is important to ascertain the degree to which its assumed value is dependent on scaling decisions.

Step 2c. Assign resistance values. In this step, each cell in the resistance surface is assigned a value denoting the ease of movement across that cell. This is generally the most critical step because the resistance values control the general nature of the final product. Zeller and others (2012) describe either a one or two stage process. The first step in either case is to assign initial resistance values either on the basis of expert opinion or empirical data. In the second stage, model selection, which requires empirical data, is used to finalize resistance values.

Fifty-four percent of the papers we reviewed were also reviewed by Zeller and others (2012); we both found an over-reliance on expert opinion to guide resistance value assignment. Three papers we reviewed used "landscape integrity," a Structural Connectivity metric associated with anthropogenic features coupled with expert opinion to quantify resistance values. The remaining papers sought to reflect (generally, the inverse of) "habitat suitability" in the resistance surface. Twenty papers modeled habitat suitability (and therefore resistance) using exclusively expert opinion.

The importance of resistance value assignment in connectivity analyses cannot be overstated. While other steps will define the spatial arrangement and exact locations of connection paths (Steps 3 and 4, respectively, below), the resistance surface defines landscape connectivity and all results are highly sensitive to the method of identifying resistance values (Sawyer and others 2011). Not surprisingly, expert opinion has not been shown to be a robust method for parameterization of resistance surfaces (e.g., Pullinger and Johnson 2010; and see discussion in Zeller and others 2012). While there are cases where the exigencies associated with a perceived conservation crisis may require the use of expert opinion (e.g., Compton and others 2007), a connectivity plan built on expert opinion must be viewed with circumspection absent further testing and refinement (see Chapter 4 on model validation). At a minimum, it is important to define who is an "expert" (Krueger and others 2012), and expert opinion should be questioned as being useful beyond a local range of knowledge (Murray and others 2009). Four papers that we reviewed used a clearly defined method for surveying and compiling expert opinion (such as Analytical Hierarchy Process), which is more likely to properly quantify expert opinion. However, properly investigating what people believe should not be confused with properly investigating the likelihood that their beliefs are correct.

Following Zeller and others (2012), we define resistance surfaces based on empirical data as any model that yields estimates of resistance based on patterns observed in biological data. When evaluating the nature of empirical support for resistance surface construction, Zeller and others (2012) defined the following categories:

1. Point selection function (PSF): correlation between presence data and ecological variables;
2. Home range selection function (HSF): correlation between home range data (generally based on telemetry of instrumented organisms) and ecological variables;
3. Matrix selection function (MSF): correlation between distance (genetic or individual occurrence locations) and ecological variables without assuming the actual movement paths between locations; and
4. Path selection function (PathSF): correlation between ecological variables (or the final resistance surface) to observed paths from empirical movement data (Figure 3).

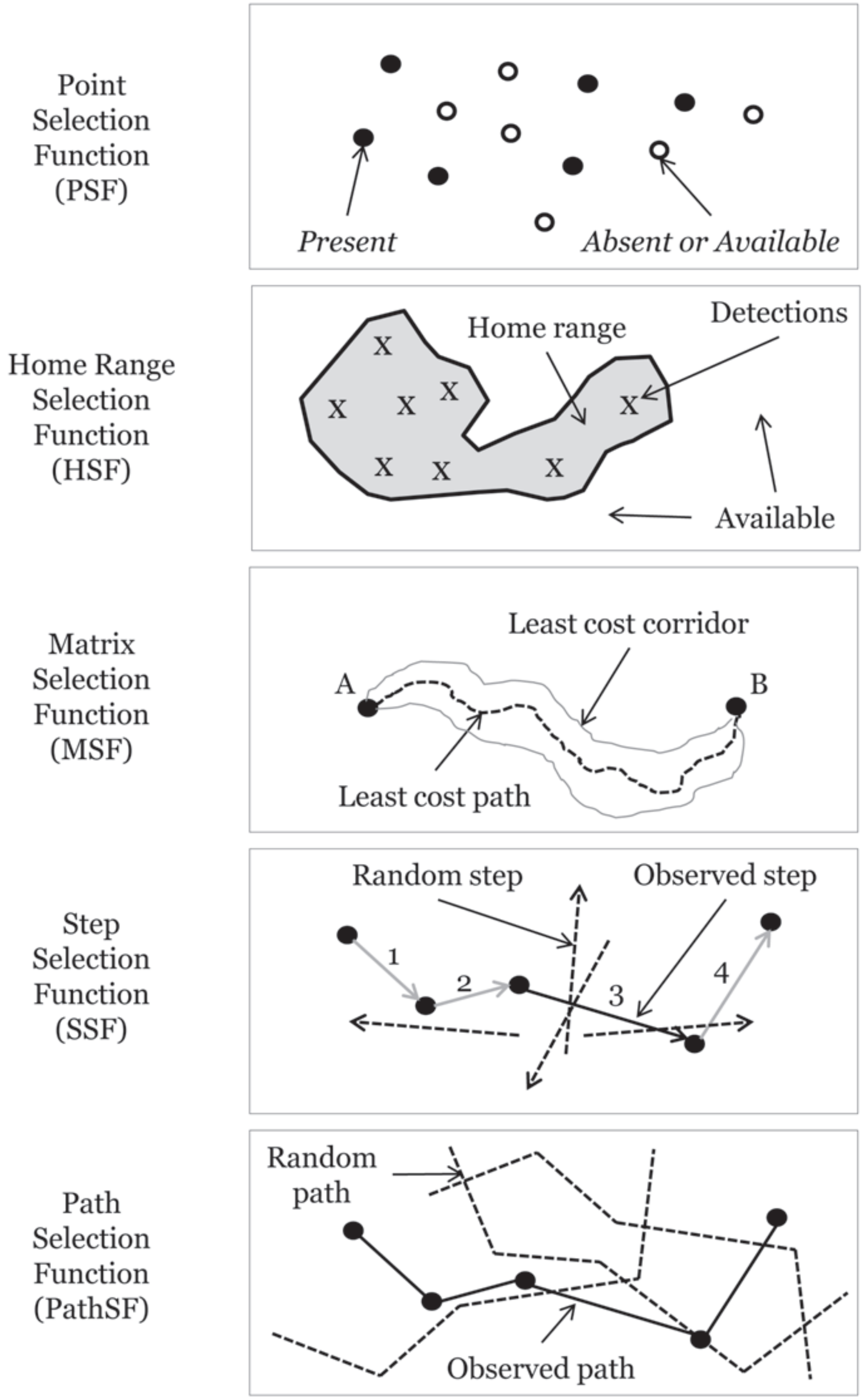


Figure 3—Examples of resource selection functions used to create resistance surfaces, from Zeller and others (2012, Figure 2). (Permission to reprint figure granted by Springer and by the authors.)

See Zeller and others (2012) for a discussion of the pros and cons associated with these approaches. Of the 24 papers that used empirical data to quantify resistance, 14 began with expert opinion and used empirical data for model selection, 9 conducted a single stage empirical analysis, and 1 paper used empirical data for both model creation and selection. Empirical PSF were most commonly used (14 papers), followed by MSF (6), HSF (3), and PathSF (1).

Although empirically based resistance surfaces are more closely tied to measured organism behavior than those derived from expert opinion, using habitat quality as a proxy for resistance (the most common approach in the literature) makes the implicit assumption that habitat suitability is a valid approximation for permeability to movement (Hagerty and others 2011). The extent to which this assumption is valid depends on the organism and movement type. For example, for an organism with low vagility, the organism can only move through habitats in which it can live for extended periods of time, possibly generations. In this case, movement corridors need to be habitat to be effective, and using habitat measure as a proxy for movement resistance is likely reasonable. Examples include the spread of plants and movement of small mammals along powerlines. On the other extreme are high vagility organisms and associated rapid movements. For example, the seasonal movements of ungulates from high elevation summer habitats to low elevation winter ranges may occur in hours or, at most, days; the habitat quality along the movement path is less relevant than the presence of actual physical barriers to movement.

This understanding underscores the need to think carefully about the functional biological underpinnings of animal movements and of the types of connectivity to be modeled. Of the four approaches that use empirical data to model resistance (above), only the path selection function transforms movement directly into resistance and therefore does not contain implicit assumptions concerning the relationship between landscape attributes and movement. However, although path selection functions clearly require fewer assumptions than do the other approaches, there is often a mismatch between measured movements and the movement type associated with the desired connectivity map. Within-home-range movement data are easiest to acquire, but are only directly pertinent to Daily Habitat movement analyses. Demographic movements, for example, occur between sub-populations and are generally rare in empirical datasets. Therefore, using path selection functions to inform resistance surfaces generally requires the assumption that the rules that guide within-home-range movements are identical to those that guide between-population movements. Because between-population movements by necessity require crossing areas not suitable for home range establishment, the validity of this assumption is tenuous.

In many cases, landscape resistance is assumed to be functionally related to a combination of multiple ecological variables. The transformation of any multivariate habitat model into a resistance surface will, for example, require combining variables. But the need to combine variables may occur in structural connectivity analyses as well. For example, a cell that contains a plowed field and a road may be considered to be more resistant to travel than a similar cell lacking a road. While the premise that combinations of factors can lead to differential resistance is reasonable, it leads to additional complexities and uncertainties. Specifically, decisions need to be made concerning how these elements should be combined, and whether they should be, in a relative sense, scaled (e. g., should roads and habitat quality be considered of equal importance). In essence, combining environmental variables to produce a resistance value requires the creation of a mathematical model in which resistance is the dependent variable, and environmental variables are associated through arithmetic operators (e. g., addition or multiplication) with each environmental variable multiplied by a scaling coefficient (in this context even the decision not to scale is an explicit scaling: all coefficients are set to 1.0). Because resistance controls putative movement and the operators used to combine variables control resistance values, these decisions translate directly into understandings of how multiple environmental factors affect organism movement. For example, summing the resistance values across variables reflects an assumption that variable effects are additive while using a product assumes that effects are cumulative; a geometric mean assumes additive effects with a log-scale transformation.

In general, there is very little to guide the choice of these weighting parameters and arithmetic operators unless they can be empirically derived from movement data (see Parks and others 2012) or represent the direct application of an a priori model. Combination of variables and weighting schemes should therefore not be taken lightly and, if model fitting is not possible, uncertainty analyses should consider the sensitivity of results to the chosen approach.

Step 2d. Validate the resistance surface. In connectivity modeling, there are two important validation steps. The first, discussed in detail in Chapter 4, is the validation of the final connectivity model. This is critical, as the entire process of connectivity modeling contains so many assumptions that resulting models and connectivity maps are best thought of as a hypotheses rather than predictions. Additionally, it is important to validate all intermediate steps to the extent possible, particularly the resistance-surface model. Six of the papers we reviewed conducted cross validation for their resistance values. We list these efforts under the "Uncertainty Analysis" column in Appendix 1, instead of under "Validation of Resistance Surface" because true validation requires independent data. Cross validation uses a subset of the model training data, not independent data, and therefore provides an assessment of the stability of the resistance model rather than its correctness. True validation of the resistance surface requires empirical movement data to assess how well a species moves through a given habitat type or barrier, and whether actual paths follow mapped corridors. Lacking this, various degrees of validation can be achieved through testing against independently collected proxy data. For example, assuming that the resistance surface was based on an expert-opinion-based habitat model, the model predictions could be checked using an independent data set of species occurrence data or to resource selection scores associated with independent studies. Even where habitat models are based directly on empirical studies, the habitat models generated by these studies generally use data types collected differently, at very different scales and in different times and locations. These models therefore have to be imperfectly crosswalked to available data, and this crosswalk needs to be validated. Similar to using rigorous methods to quantify expert opinion, validating a habitat model does not directly test the validity of a resistance surface. It does, however, avoid compounding errors associated with improper implementation of the habitat model. That is, whether a good habitat model serves as an adequate proxy for movement remains untested, but it is unlikely that a bad habitat model will serve this purpose.

A form of quasi-validation is model fitting, in which the resistance values and structure of the resistance surface is modified to maximize the fit to independent data. In the literature, this has most commonly been accomplished by correlating derived ecological distances with genetic distances. In this approach, resistance values are modified, connectivity models run, and the resulting ecological distances between location pairs compared to the genetic distances between organisms collected at those same locations. Historically, this has been done using Mantel tests and partial Mantel tests, but concerns have been raised about the validity of this approach given spatially autocorrelated data (Raufaste and Rousset 2001; Guillot and Rousset 2013). However, issues associated with the specifics of Mantel tests do not change the need to determine appropriate weightings for resistance surfaces. Without some form of fitting, there is no way to quantitatively determine appropriate weightings or to assert that one weighting scheme is superior to another.

Of the papers we reviewed, six papers used independent occurrence data for validation, with one of those papers using actual movement data (Driezen and others 2007). Other papers used alternative semi-validation approaches, including correlating ecological distance with genetic distance with the assumption that resistance surfaces would correlate with genetic structuring (7 papers), or comparison to a null model (2 papers), or more simply conducting an assessment of similarity between multiple model outputs (1 paper).

If validation is not possible, at a minimum sensitivity of the results to resistance values should be reported; 11 papers considered sensitivity of results to the contrast between resistance values, the resistance values themselves, or the habitat suitability models used to determine the resistance values. This left 24 (51%) of the papers with no discernible uncertainty analysis (excluding cross-validation) or validation of the resistance surface.

A properly validated model is judged not by the robustness of its design and underlying data and assumptions, but rather by its proven efficacy. However, lacking formal validation, there exists a hierarchy of resistance surface quality, such that model inference is likely to be more robust as one moves from expert opinion only to increasing reliance on empirical data. Within models that are based on empirical data, reliability increases to the extent to which utilized data directly describes the desired movement type (Figure 4). Further validation of the resistance surface, by comparing multiple methods, correlating with genetic distance data, or field studies of dispersability for a released individual continues to reduce uncertainty.

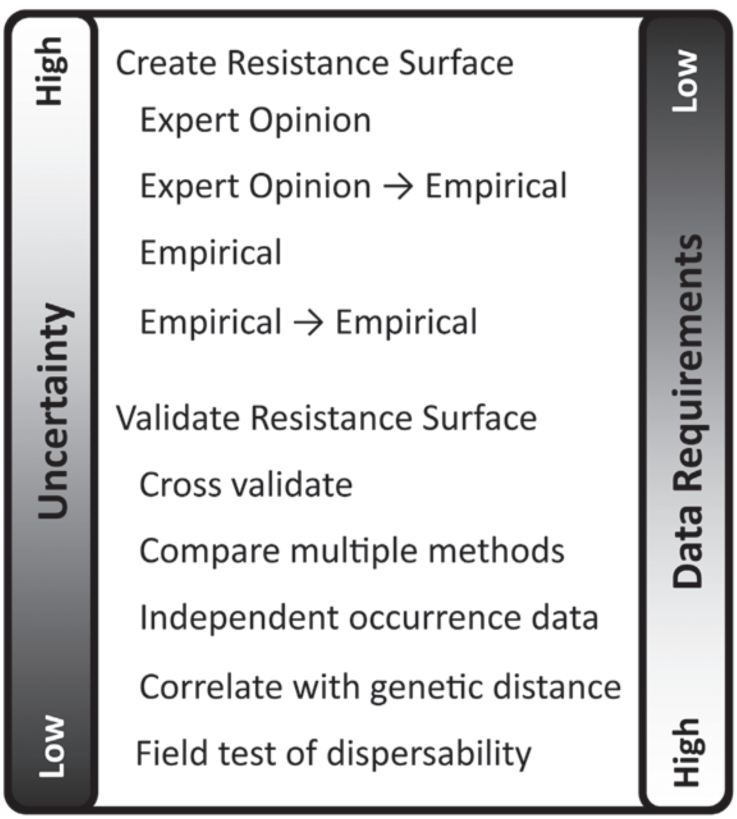


Figure 4—Hierarchy of uncertainty associated with resistance surface creation.

Step 3. Define What is Being Connected

This step is often listed as a first step, however we list this after creating the resistance surface because often linkage termini are derived from the resistance surface. For example, if a habitat model forms the basis for resistance, often linkage termini are limited to large, contiguous areas of high quality habitat. Additionally, the type of movement being modeled sets the context for choosing termini. For example, if modeling genetic connectivity, termini might be nesting or denning sites. This step, though often approached casually, is a critical step in the process—after definition of the resistance surface, likely the most critical because once linkage termini are selected, the range of potential corridors is largely defined (Laita and others 2011). Just as the resistance surface formally defines landscape connectivity, the selection of termini defines and limits the specific movements to be modeled (Figure 5).

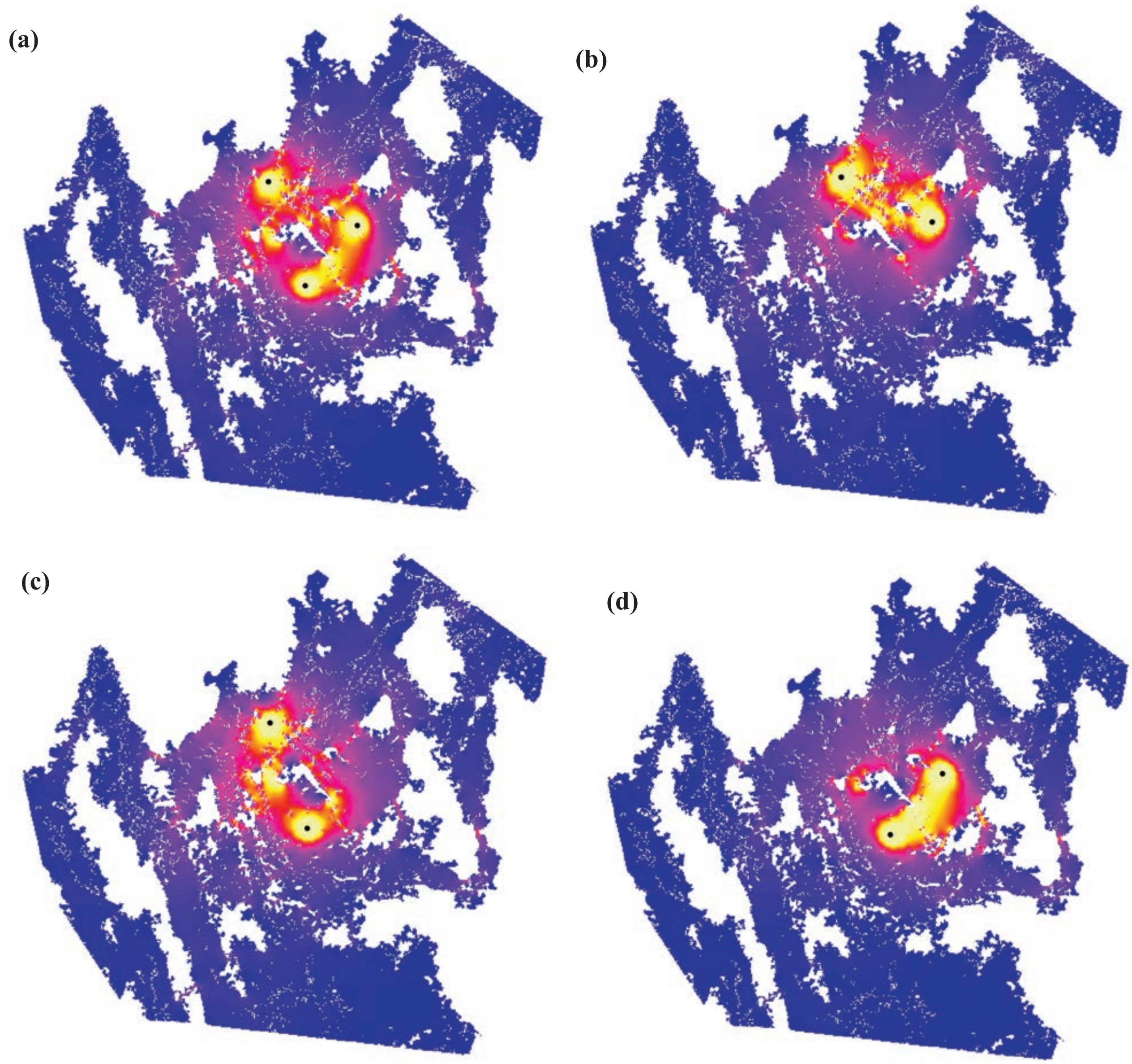


Figure 5—Placement of termini largely defines the modeled linkages: (a) Circuitscape run with 3 nodes on a forest / grassland ecosystem (white is grassland, purple is sage brush); (b-d) modeled linkages change when only two of three nodes are sampled.

We use the term "termini" (sensu, Beier and others 2008) instead of "patches" because connectivity can be modeled between points or polygons (3-dimensional patches in a GIS). Aune and others (2011) and Beier and others (2008) review multiple approaches for identifying what should be connected. For structural connectivity models, termini often represent known protected areas, areas of high "naturalness" (low human modification), unique topological or geomorphological landscape elements, or locations chosen using expert opinion. For functional connectivity modeling, termini can be defined as habitat patches or empirically derived species occurrence points. Advances in computational power also allow modelers to avoid choosing unique termini, instead calculating linkages between all possible combinations of cells in a GIS, or at least numerous randomly selected cells. Some approaches to accumulating ecological distance (discussed in step 4, below) avoid the identification of termini entirely.

Of the papers we reviewed, 27 applied some statistical or subjective rule set to the resistance surface to identify termini. Examples include applying a threshold value to the resistance surface to form patches, while others calculated a minimum value from a moving window analysis (grouping contiguous cells with mean neighborhood resistance values below some threshold). One paper overlaid a threshold habitat suitability index with representation of landscape types and special landscape elements, similar to a Conservation Area Design approach (Beazley and others 2005). One interesting approach was to use cost distance to "grow" home ranges out from known breeding sites through the resistance surface and use derived home ranges as termini (Decout and others 2012). Thatcher and others (2009) used an independent telemetry data set to determine the statistical distance between habitats in known home ranges versus modeled home range areas, and chose modeled home ranges with smaller statistical distances as termini. Twenty-three papers considered minimum size in determining patches containing termini, and required minimum sizes were often related to home range size. Avoiding patches all together, Cushman and Landguth (2012) used lowest resistance cells as termini, and Theobald and others (2012) iteratively and randomly selected cells with highest landscape integrity (in this case defined as an index of the amount of human activity in an area; see also McRae and others 2012; Figure 6a).

The other 21 papers identified termini through approaches not reliant on the resistance surface. Five papers used protected area boundaries to define linkage termini. One paper relied solely on expert opinion to define patches, while 11 papers used empirical occupancy data. Examples of empirical approaches included defining areas with some minimum probability of occurrence from empirical data (with data different than that used to develop resistance surface; 2 papers) or actual observed locations (2 papers). Three papers used the centroids of empirically determined population locations and 5 papers created polygon patches around population locations. Carroll and others (2012) calculated centrality (discussed below) between all cells, which does not rely on the identification of unique termini.

When choosing termini, scale is critical. It is important that if patches are used as termini, they reflect the perceptual grain of the conservation target. Often, patches are defined using patterns evident to humans; but these may not be evident to other organisms. Even a seemingly discrete patch, like a pond boundary, becomes a continuous gradient as one zooms in to finer and finer scales. Chetkiewicz and others (2006) provide a useful framework for considering patch size and structure in relation to connectivity type, summarized in Table 1.

A second caveat is that any "patch" is both spatially and temporally dynamic, and linkages modeled between fixed points may not persist into the future under changing climates, land uses, conservation policies, or species demographics. Modelers need to seek a balance between identifying structural landscape elements that are likely to persist and functionally defined patches that may be less spatially and temporally robust.

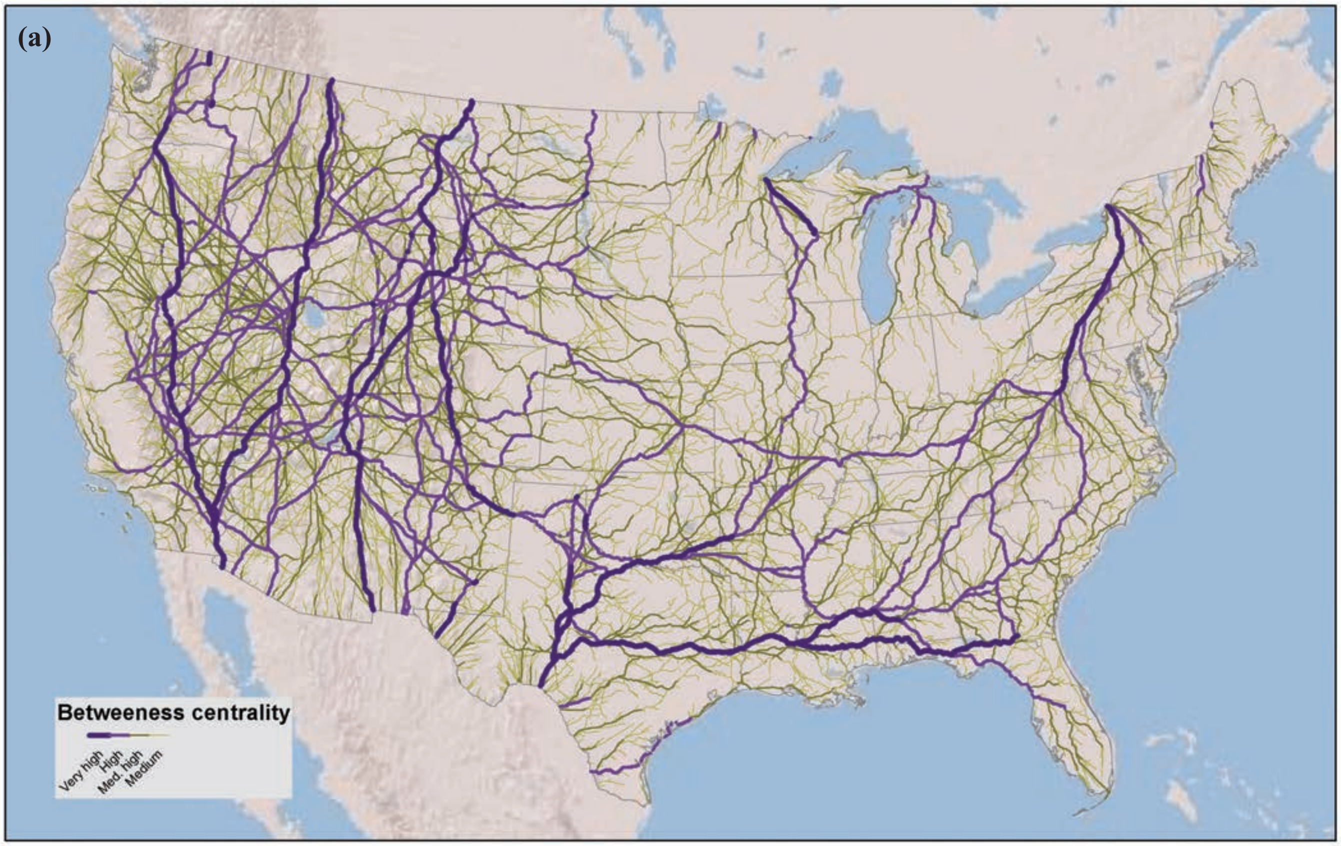
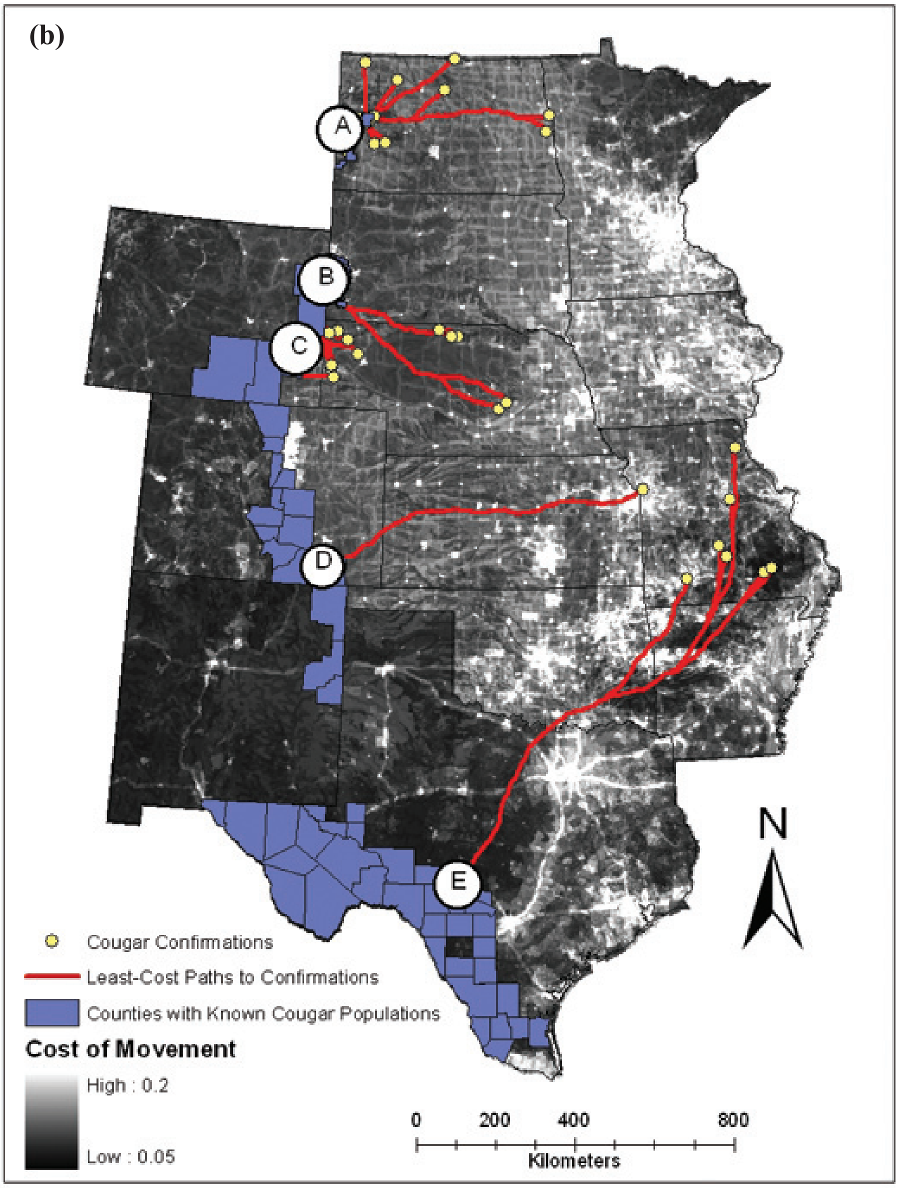


Figure 6—Examples of connectivity modeled between different termini: (a) iteratively, randomly selected cells of lowest resistance value (Figure 3 in Theobald and others 2012); (b) LaRue and Nielsen (2008) mapped Least cost paths from patch edges to confirmed cougar locations (Figure 3 in LaRue and Nielsen 2008); and (c) Cushman and others (2009) spaced termini along the northern and southern borders of Montana to model bear movement from Canada to the Greater Yellowstone Area (Figure 1 in Cushman and others 2009). (Permission to reprint figures granted by Wiley (a, c), Elsevier (b), and by the authors.)

The internal structure of the patch should also be considered when modeling linkages between patches. In patch-based connectivity models, it is common to use the border of the patches as termini (Figure 6b). Locating termini in this manner implicitly assumes all movement within the patch is uniform such that organisms occur at all locations along the patch borders with equal likelihood. If termini are located in this manner, the least cost path algorithm will identify the shortest ecological distance between two patch boundaries, regardless of the structure of the landscape at that point along the patch perimeter. For example, ravines and riparian waterways may funnel species to a certain point along the patch edge, yet the modeled least-cost path may connect to another location along the patch edge where there is an impassable cliff band. Another approach is to place the termini at the centers of patches. While this has fewer ramifications than termini along the patch peripheries, it makes the equally unlikely assumption that all organisms originate their movements at the patch centroid. Where possible, we note whether a termini was represented as a patch edge, centroid, or otherwise in Appendix 1.

Of the papers in which we were able to determine whether linkage source was at the patch edge or centroid, 31 were from the patch edge, and only 1 paper used a patch centroid. Three other papers used other approaches, either systematically placing points within patches (Schwartz and others 2009; Wasserman and others 2012) or modeling linkages between all points at regular intervals along a patch edge (Cushman and others 2009; Figure 6c).


(b)
A
B
C
D
E
N
Cougar Confirmations
Least-Cost Paths to Confirmations
Counties with Known Cougar Populations
Cost of Movement
High : 0.2
Low : 0.05
0
200
400
800
Kilometers

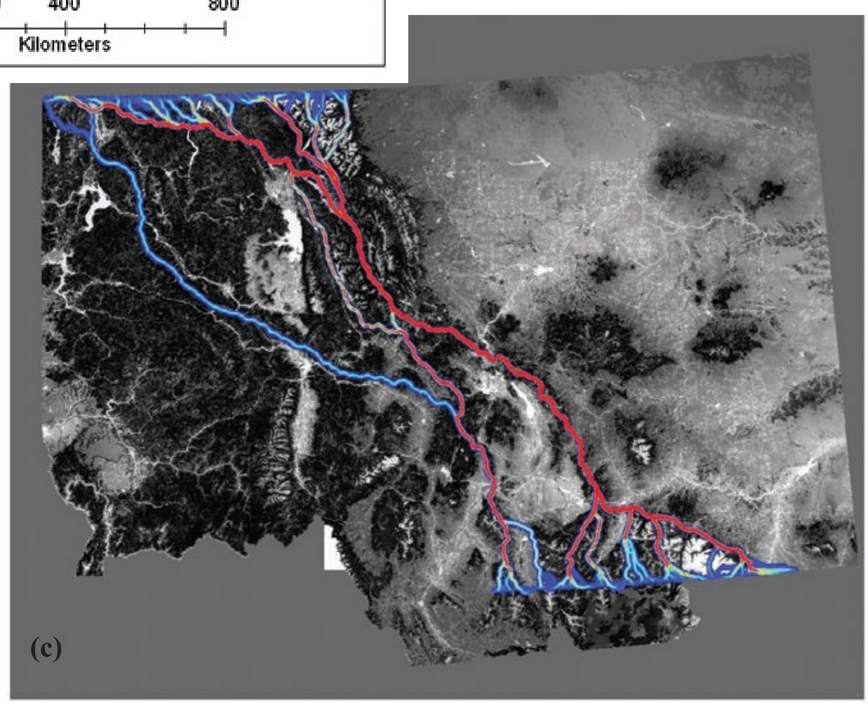

(c)

Table 1—Wildlife movement type, patch spatial structure, and analysis spatial and temporal grain in relation to connectivity modeling intent, adapted from Chetkiewicz and others (2006).

Connectivity type	Movement type	Spatial structure	Spatial grain	Temporal grain
• Daily habitat	• Food items search	• Food item distribution • Food patch shape and size • Small-scale obstructions	Resource patch	Daily
• Daily habitat	• Patch searching • Traplining • Territory patrolling	• Food patch configuration • Shelter • Abiotic factors and topography	Habitat patch	Weekly
• Demographic • Genetic	• Dispersal	• Patch distribution • Landscape features	Patch mosaic	Yearly or Decadal
• Genetic • Seasonal migration • Range shift • Landscape pattern	• Migration	• Large scale topography barriers	Region	Yearly or Decadal

Perhaps the greatest effect of termini location, however, is associated with the decision to place a terminus at all. In most connectivity algorithms, paths are forced to connect all termini. For example, in the connectivity modeling software Circuitscape (McRae and Beier 2007), termini are designated as anodes or cathodes, and simulated electrons flow from the anode termini to the cathode termini. If a patch is designated to be a terminus, then electricity will flow from or to it, and flows will be concentrated around it. If a patch contains no termini, then electrons will only flow through it to the extent that it represents a low-resistance route between other patches that have been designated as having termini. In general, connectivity models obligately link one terminus to other termini, no matter how high the intervening landscape resistance. This attribute is largely due to the common assumption (found in all but two papers), that all paths are of equal value (e.g., in Circuitscape, that an equal quantity of electrons flow between each pair of termini) regardless of the landscape resistance between termini. Thus, these types of connectivity maps are better thought of as asking the question “if an organism were to travel from terminus A to terminus B, what path would it take?” rather than “how likely is an organism to travel between termini A and B?”.

Given the potential sensitivity of modeled results to selection of linkage termini, modelers must give careful consideration to this step in light of the connectivity model goals. Connectivity analyses should test the effects of different assumptions about how patches are calculated, identified, and the effects of different grains and extents of patches being considered. At a minimum, the effect of internal patch structure should be considered when modeling potential linkages. The majority of papers we reviewed did not test sensitivity of results to patch locations. However, Epps and others (2007) assessed three different approaches to identifying patches: expert-opinion-defined patches, minimum convex polygons around empirical sampling locations, and an occurrence model from telemetry locations. Since their goal was to optimize resistance values, not map linkages, their results were not overly sensitive to these choices. It is primarily in the mapping of linkages where decisions regarding termini location become critical.

Step 4. Calculate Ecological Distance

Connectivity models seek to calculate the ecological cost of movement through the landscape (ecological distance) by associating paths or flows with the mapped resistance values given specific termini. The presumed relationship between the resulting patterns and actual movements lies in the assumption that the likelihood of movement between two termini is proportional to the ecological distance between them. In practice, there are three common models applied for calculating ecological distance over a resistance surface between termini: cost distance, current flow, and network flow. The benefits, weaknesses, and assumptions for each modeling approach are summarized in Table 2. In general, cost distance and network flow are route optimization algorithms, whereas circuit theory is a flow algorithm.

Cost distance models first calculate a cost surface, which represents the lowest accumulative cost distance for each cell in a raster surface, to the nearest terminus based on the resistance surface. Then, it uses the values in this surface to compute the least cost paths (LCP) between any 2 termini. As applied to mapping linkages for wildlife, least cost distance models assume that organisms have perfect knowledge of the landscape and therefore will choose paths that minimize cumulative ecological cost across the entire path. ***Resistant kernel*** modeling approaches are built on the same algorithm of cost distance models, but add a dispersal function to model expected density of dispersing organisms from each terminus, which declines with greater accumulated cost. The kernel values radiating out from each terminus are then summed to create a resistant kernel map.

Current flow models are based on circuit theory, whereby the resistance surface is analogous to a conducting surface in which resistance to current flow is uneven (e.g., a metal sheet of unequal thickness). Flow is approximated by modeling the surface as a web of resistors, where each resistor represents the local resistance to current flow associated with its location on the surface. When these ideas and methods are applied to the question of landscape connectivity, a landscape is viewed as a large complex circuit composed of a web of resistors; generally each cell in a resistance surface is a resistor with “wires” connecting it to its neighbor cells. Standard rules for electrical resistance calculation apply (e.g., resistors in series produce additive resistance to flow). Current is added at source nodes (termini) and flows toward ground nodes through the circuit. As related to wildlife movement, current represents the probabilistic movement across all possible paths in the landscape, assuming that organisms have no prior knowledge of that landscape, but are driven to move from a source terminus to a ground terminus and move from cell to cell based on the resistance values they encounter. While high flow areas are generally consistent with paths produced by LCP algorithms (most of the electrons will find the path that minimizes overall resistance between the anode and cathode), circuit designs are sensitive to the width of low resistance areas because resistance decreases when resistors are parallel in a circuit (based on Ohm’s law) whereas LCP are not (see Step 5 for a more complete discussion of these differences).

Network flow models visualize organismal movement as being similar to water flow through a connected network of pipes. Network flow resembles current flow, except that network flow algorithms seek to identify the optimum routing through the resistant surface that maximizes flow while minimizing accumulated ecological cost. The interpretation is therefore not probabilistic (it does not summarize the probability that a random walker will reach a termini) but, like cost paths, is an optimization problem. Network flow calculates the centrality of all termini in a network and therefore has the advantage of estimating the relative importance of each path to overall flow across the network. Thus, network analysis is particularly useful for problems that require prioritizing functional or structural linkages.

Table 2—Comparison of methods to calculate ecological distance over resistance surfaces. Portions of table adapted from Aune and others (2011), Carroll and others (2012), and McRae and others (2008).

Method	Advantages	Disadvantages	Assumptions	Best modeling applications
Cost distance	• Modest data needs • Incorporates influence of matrix and individual species behavior • Computationally inexpensive • Can incorporate dispersal distance into analysis (as a threshold only)	• Sensitive to termini locations • Sensitive to analysis grain • Cannot reflect differences in bi-directional costs (ease of walking uphill vs. downhill cannot be incorporated) • Can only calculate least cost path between one pair of termini at a time • Temptation to represent a linkage as a single, 1 cell wide, least cost path (do not succumb!) • Does not inherently incorporate dispersal distance • Paths are computed between termini regardless of total cost	• Organism has perfect knowledge of the entire landscape and moves with intent to minimize travel cost between two known locations • The organism is destination driven and wants to move from one terminus to the next	• Identify likely locations for further refinement and investigation • Movement behavior for a single individual between resource needs within a familiar territory
Resistant kernel distance	• Same as least cost distance • Inherently incorporates dispersal distance into analysis and can use any functional form (e.g., linear vs. exponential decline in likely dispersal with distance from terminus) • Can simulate population patterns by weighting termini where larger populations exist • Can calculate least cost distances between multiple termini pairs	• Same as least cost distance	• Organism has perfect knowledge of landscape within dispersal distance from source and moves with intent to minimize travel cost; areas with low cost distance back to multiple termini are likely to represent areas with higher probability of movement or use • The organism is destination driven and wants to move from one terminus to the next	• Identification of resource patches most likely to be used (breeding sites or water use) in familiar territory • Movement between populations or home ranges in familiar territory

(continued)

Table 2 (Continued)

Method	Advantages	Disadvantages	Assumptions	Best modeling applications
Current flow	• Modest data needs • Precise relationship with directed random walks • Can simulate populations patterns by injecting more current into circuit where larger populations exist	• Sensitive to termini locations • Sensitive to analysis grain • Cannot reflect differences in bi-directional costs (ease of walking uphill vs. downhill cannot be incorporated) • More highly resistant circuits in parallel reduce overall resistance (e.g., a 5-mile long cliff has less resistance to movement than a 2-mile long cliff) • Does not inherently incorporate dispersal distance • Computational limitations: a landscape with N cells is transformed into an NxN matrix. In practice this places severe constraints on the resolution of modeled landscapes • Current will flow between termini regardless of intervening resistance	• Organism follows movement pattern of random walker with no previous knowledge of the landscape; decisions are made at each step • The organism, while locally ignorant, is destination driven and wants to move from one terminus to the next	• Identify bottlenecks within broader linkages • Movement behavior for migration of a large population (e.g., many ungulates during a seasonal migration) • Flow of genes over time
Network flow	• Modest data needs • Can incorporate multiple, distinct criteria (such as habitat resistance and land purchase cost) into a single analysis • Can incorporate climate change scenarios	• Computationally expensive • Does not inherently incorporate dispersal distance	• Linkages that maximize the amount of flow across minimum distances reflect likely movement paths	• Comparison of results against other methods to identify sensitivity to model chosen • Produces network metrics to prioritize important nodes and linkages

It is likely that most animal movement reflects neither perfect knowledge (as in cost distance models) nor complete local ignorance of the surrounding landscape coupled with the overwhelming drive to move from one location to another (as in current flow models) (McRae and others 2008; Carroll and others 2012). However, the difference in assumptions concerning an organism's knowledge of the landscape associated with cost distance and current flow algorithms is often of low practical consequence, because, as in any circuit, all electrons will travel from the source to the ground and, probabilistically, most will travel along the same low cost paths that are identified by least-cost path algorithms. Both algorithms treat the termini as being of very special importance to the organisms, being both the only possible source and the ultimate obligate destination. As noted above, the generation of the resistance surface and decisions concerning valid termini to connect have far greater impacts on the understandings of landscape connectivity than the specific algorithm used to calculate ecological distance.

Of the 47 papers we reviewed, 46 applied some form of algorithm to model connectivity and 41 of them used a cost distance algorithm. Least cost distances from multiple sources often represent only the distance to the nearest neighboring terminus. Three of the papers we reviewed applied the resistant kernel approach. Seven papers applied circuit theory in their connectivity model. One of the papers modeled connectivity on the basis of network flow.

Only one paper compared current and network flow and also cost distance. Carroll and others (2012) found that some resulting linkages for wolves overlapped, while others did not (Figure 7). Three papers compared results from cost distance and current flow. Van Strien and others (2012) found that the best correlation between ecological (or Euclidean) distance and genetic distance for a species of damselfly varied depending on the ecological variables used in creating the resistance surface. They created a new approach, termed least cost transect analysis, whereby land cover variables were quantified along a transect centered on the path with the single shortest cost distance. Least cost transects had significantly better correlation with genetic distance when compared to least cost distance or current flow. Hagerty and others (2011) also found differences in correlation strength between ecological distance measured with least cost distances or current flow when compared to genetic distance for a tortoise; cost distance was better able to parse out barrier effects whereas current flow identified Euclidean distance as the primary control on genetic differences. Schwartz and others (2009) also found that cost distance approaches better correlated likely habitat preferences of wolverine and genetic distance than current flow, which again only identified the importance of Euclidean distance. Koen and others (2012) also found that Euclidean distance performed better than current flow ecological distance for modeling marten gene flow. These examples support the recommendation of Carroll and others (2012) that multiple approaches should be compared in an uncertainty analysis, and that for genetic distance at least, the additional null model of Euclidean distance should be considered.

Step 5. Map Potential Linkages

Results from the previous step provide comprehensive values of ecological cost across the entire analysis extent, which can be several million pixels in size. Modelers can simply provide a gradient map of the probability for movement within, or the priority for conservation of a specific area. However, for implementation of connectivity projects, often a spatially explicit sub-set of highest quality potential linkages must be identified. Thus, in this step, one takes modeled ecological costs (cost distances, current flows, or network flows) and applies some rule-set to map spatially explicit linkages or corridors. This requires species-specific design criteria that considers width, length, and types of suitable human activities within the linkage, given the life history needs and connectivity intent of species of interest (Harrison 1992; Cushman and others 2009).

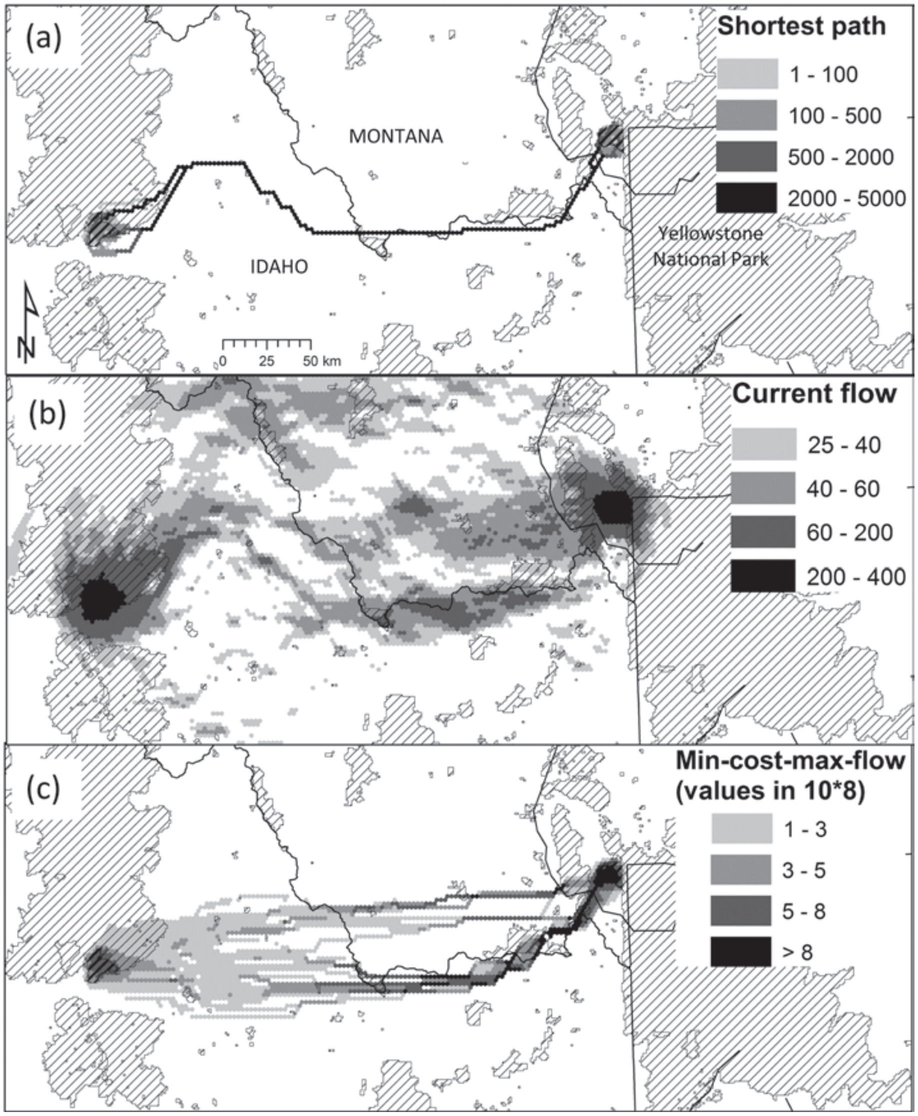


Figure 7—Carroll and others (2012) compared cost distance, circuit flow, and network flow methods for calculating cost distance and subsequently mapping linkages. They found results varied depending on method (Figure 3 in Carroll and others 2012). (Permission to reprint figure granted by Wiley and by the authors.)

In the case of cost distance analyses, the single path with the lowest total sum between two termini is called the ***least cost path.*** These models are sometimes called shortest path models as opposed to least cost paths to avoid confusion with monetary costs. Unfortunately, often modelers have presented only this single-pixel-wide least cost path connecting two termini as the "solution" to a connectivity analysis (Figure 8a), which has fueled the continuation of the timeworn "corridor controversy" (reviewed in Anderson and Jenkins 2006). A single-pixel wide linkage is unlikely to represent the exact path taken by an organism, and the LCP is very sensitive to the location of termini, which also are not exact. Further, an LCP can be identified through an area of completely inhospitable landscape as the result for a single misclassified cell in the resistance surface (Kautz and others 2006). Thus, LCPs may be sensitive to small map irregularities and the grain at which the landscape is modeled (Theobald 2005).

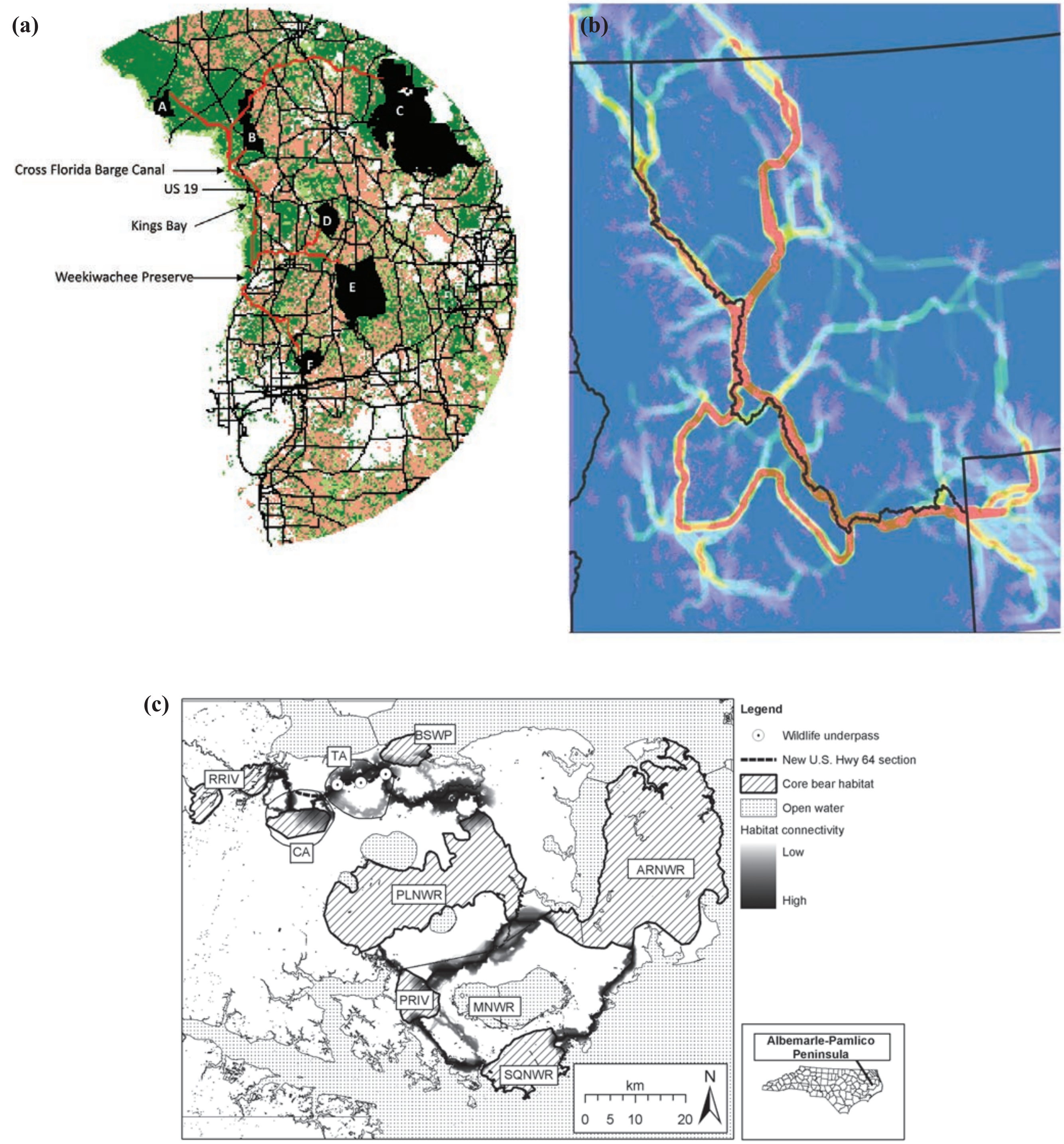


Figure 8—Examples of mapped linkages or paths from the literature; (a) Larkin and others (2004) used simple least cost paths (LCP) to model cougar movement in Florida (Figure 3 in Larkin and others 2004); (b) Schwartz and others (2009) placed termini on a grid and computed all pairwise LCP, buffering each path with an arbitrary kernel and adding kernel heights associated with each pixel; (c) Kindall and Van Manen (2007) calculated the cost surfaces and then mapped areas of connectivity by using thresholds based on relative cost (Figure 4 in Kindall and Van Manen 2007; upper 10% least cost paths displayed); d) Cushman and Landguth (2012) used resistant kernels centered at fixed map locations to generate cost surfaces (Figure 3c in Cushman and Landguth 2012); and (e) Hagerty and others (2011) used cumulative current flow between populations to model connectivity for desert tortoises in the Mojave Desert (Figure 3 in Hagerty and others 2011). (Permission to reprint figures granted by Wiley (a, c), Elsevier (d), Springer (e), and the authors.)

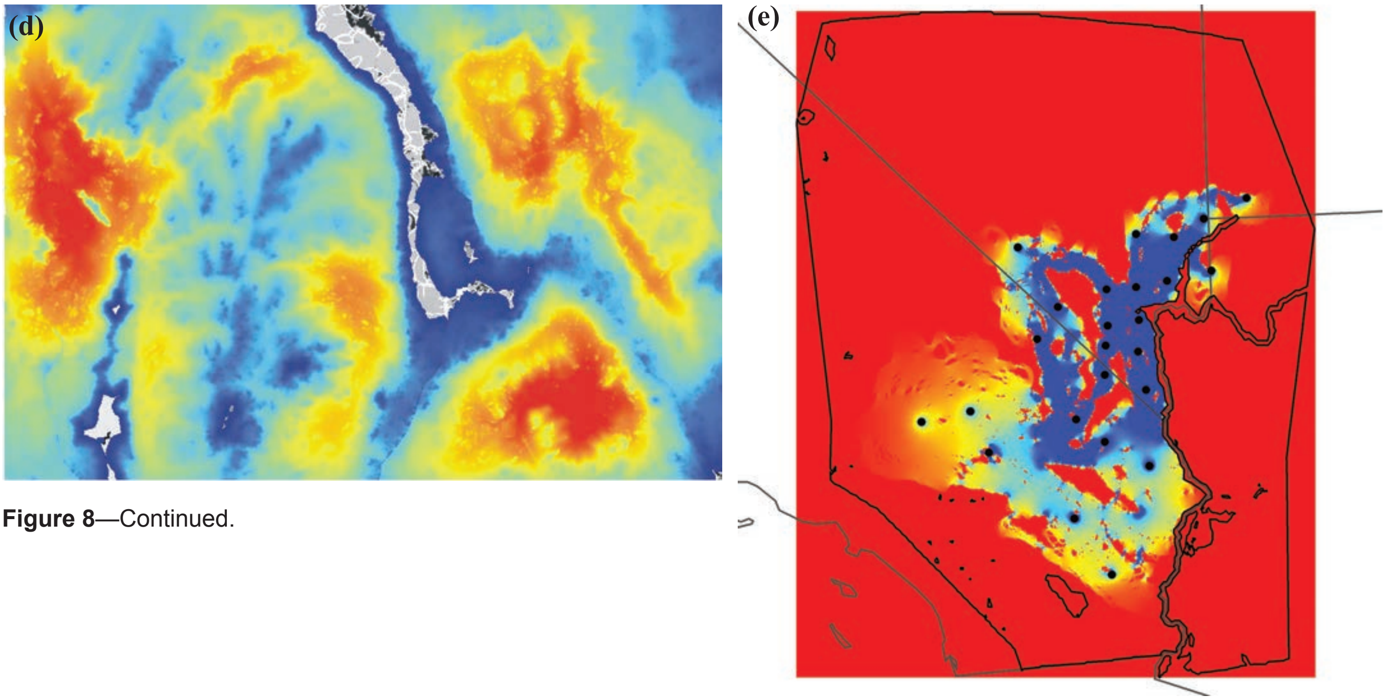


Figure 8—Continued.

We believe that mapping techniques that display areas of very good connectivity have merit when compared to techniques that only map the very best connectivity routes. Ideally, connectivity maps should illustrate multiple potential linkages, reflecting the likelihood that wildlife experience the landscape as a shifting gradient of possible movement paths given their life history traits and movement needs (Cushman and others 2009). In the case of cost distance modeling, a ***least cost corridor*** can be designated by buffering the LCP to select a broader swath of landscape neighboring the LCP. However, buffering the LCP (Figure 8b) does not resolve the sensitivity of the LCP to resistance layer errors or uncertainty. Creating a least cost corridor by taking the top nth percentile of least cost paths better reflects the idea that, while an organism may not know the ideal route, it can find a route that is among the best (Figure 8c,d; Figure 9).

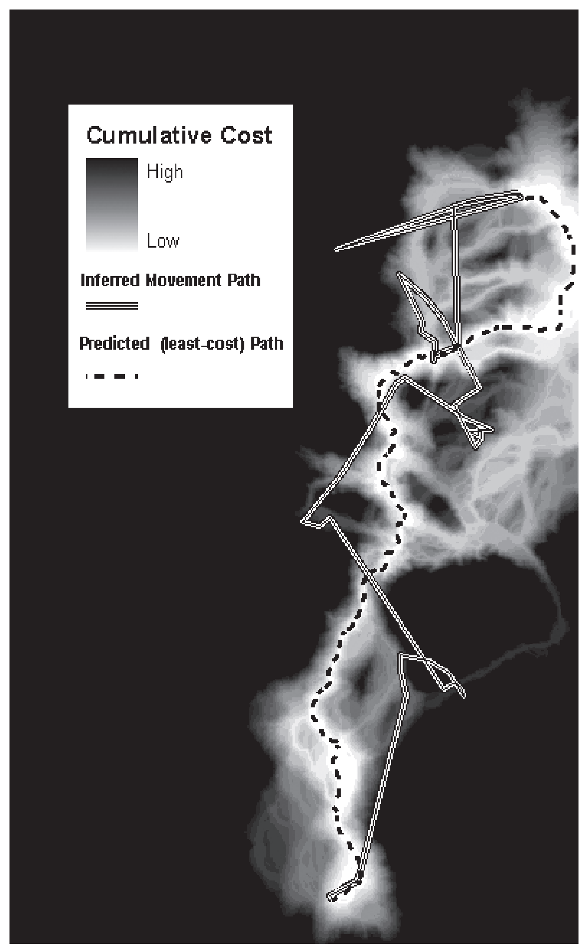


Figure 9—Even a well-modeled LCP does not necessarily represent the actual path taken by a species. In this map, Pullinger and Johnson (2010, Figure 6) illustrate the inferred movement path for caribou from telemetry points versus the modeled LCP. Considering the top percentile least cost paths, out to some species-specific width around the LCP, may provide a more reasonable representation of a linkage modeled using cost distances. (Permission to reprint figure granted by Springer and the authors.)

Because circuit theory maps current flows, and virtually all cells have some level of flow, the least cost corridor idea is also intrinsic to the mapping of multiple linkages in circuit theory. Connectivity areas can be identified through a cutoff in proportional current flow (e.g., cells in the top 20th percent of current flow; Figure 8e). A primary difference between using thresholds to map linkages or corridors with current flow as compared to cost distance methods is that circuit theory inherently places greater value on wide paths or alternative paths. When resistances are in series (such as when an organism travels down a narrow corridor made up of multiple resistance cells), resistances are additive. When resistances are parallel (such as would occur in a corridor wider than a single cell) resistance decreases with increasing numbers of parallel paths (the reciprocals of the resistance along each path are added). Thus, the circuit analogy will indicate that wide corridors are more favorable for travel than are narrow corridors and that termini connected by multiple corridors will be better connected than termini that only are connected by a single corridor. One of the distinct advantages of using current flow models is the ability to map a "pinch point," which is a relatively restricted area representing a landscape feature through which dispersers must pass. It should be noted that while the idea that wider corridors are better has a long history and is biologically reasonable, the biological rationales for this idea have little to do with electron flow through parallel circuits. In a circuit, multiple paths or wider paths (e.g., thicker wires) allow more electron flow and hence lower resistance. However, connectivity is not generally limited by organisms queuing up at pinch points. Rather, the assumed lower resistance associated with wide corridors is due to corridor width being in and of itself a desirable property; it allows a corridor to function as habitat, provides protection from threats associated with the matrix, or perhaps is simply perceived as less hostile by the dispersing organism. The intrinsic quality of cells is conditioned by the quality of adjacent cells. These differences may be subtle, but they should not be dismissed; while equivalent electron flow can occur across a broad area of medium resistance or a narrow band of low resistance, these 2 landscapes may not be identical to the target organism. For a more complete discussion of current flow applications for connectivity modeling, see McRae and others (2008).

Six of the papers that were reviewed categorically mapped cost distance (3), resistant kernel results (2), or current flow (2). Of the 30 papers that provided a map of potential linkage locations, 23 applied a cost distance approach (plus an additional 2 papers that used a resistant kernel and 3 papers that compared cost distance with current flow or another approach). Of those 24 papers, 6 used only the LCP, and only one of those conducted some form of validation on the potential LCP linkage. Two additional papers mapped the LCP, although the primary intent was to compare ecological distance to genetic distance or to use ecological distance to weight a graph (see step 8; Figure 9).

One paper used buffered LCPs to identify likely highway crossing locations. Two papers used home range as a minimum width to buffer the LCP. This is likely over simplistic, but a better approach than the four papers that used arbitrary buffers surrounding the LCP. Three papers categorically mapped the nth top percentile least cost paths; however, it is difficult to find biologically relevant means for selecting the nth percentile cutoff threshold for LCP inclusion. Two papers used a parabolic kernel smoothing of the LCP, whereby likelihood of use of a linkage drops off with distance from the LCP, accounting for the surrounding habitat quality. Kautz and others (2006) used telemetry data, literature review, and the surrounding habitat quality to buffer the LCP by a width that was likely to support movement for panthers in Florida.

In addition to identifying the spatial extent (width) of the potential linkage, it is often useful to prioritize the importance of each linkage. One prioritization approach is to map the redundancy of linkages as an estimate of likelihood of use. Schwartz and others (2009) mapped (parabolic kernel smoothed) LCP between all pairwise combinations of wolverine locations, then categorized linkage potential by the number of times a given cell was part of a pairwise linkage; Li and others (2010) used a similar methodology. Similarly, the use of resistant kernel models overlays cost distances from multiple termini to help prioritize those areas with lowest cost distance to multiple termini. As mentioned above, network analysis allows linkage prioritization. To prioritize linkages, Theobald and others (2012) categorically mapped the betweenness centrality for every cell. Betweenness centrality accounts both for the ecological distance between two termini and the position of each terminus within the network of the termini. This approach could be applied to functional connectivity as well, using habitat quality in lieu of landscape naturalness, as was done by Carroll and others (2012).

Prioritization of linkages, however, depends on the likelihood of use for any specific linkage. LCP and LCC compute the best possible paths between termini, but do not discriminate between short, easy routes and long difficult routes. The same is true of circuit theory. It is, however, not difficult to factor the ecological costs into the evaluation of linkage importance. The resistant kernel approach, for example, assumes that the ecological cost to move from one point to another represents the probability of organisms making that movement (e.g., Compton and others 2007). Epps and others (2007) eliminated paths based on a cost threshold based on the measured correlation between cost distance and genetic relatedness; paths with costs associated with genetic independence (and therefore no evidence of movement) were eliminated. Parks and others (2012) proposed a general framework for linking the movement types modeled to a linkage weighting scheme using the LCC approach. They note that for movement types where the total number of organisms moving is important (e.g., demographic connectivity), mapped linkages should strongly discount paths with large ecological costs as it is unlikely that many organisms will use them. However, for other movement types such as long term persistence (e.g., range shift connectivity), these longer paths are of critical conservation importance. Thus, the weighting scheme should be linked to the purpose of the connectivity that is being modeled. In all cases, it is probably a good idea to set a maximum allowable path cost representing an insurmountable barrier for the organism and to eliminate any paths with costs above this threshold.

Lastly, it should be noted that many factors other than putative ecological costs affect the use of areas by wildlife for linkages. Lindenmayer and Fischer (2006) list 13 factors that influence wildlife linkage use, including target species life history traits, gender, biotic interactions, edge effects, food availability, vegetation attributes in the linkage, linkage width and length, vegetation gaps, size of termini connected, linkage redundancy, matrix condition, and dispersal behavior of organism.

Step 6. Validate Potential Linkages

Modeled wildlife linkages represent hypotheses about where habitat and open space should be protected or restored to provide functional connectivity. All hypotheses require testing. Unfortunately, many reviews of connectivity modeling approaches fail to discuss validation in depth. We detail options for validation in Chapter 4. In this section we review the papers in Appendix 1 in light of linkage validation efforts. We only considered a study as having validated potential linkages if the researchers directly compared modeled linkages to *independent* data describing wildlife movement paths. We considered all other efforts to be either sensitivity analyses or validations of the resistance surface. Two of the studies we reviewed had the stated intent of testing the validity of modeled linkages. Driezen and others (2007) used a path selection function and model selection to build a robust resistance surface and identify the LCP for hedgehog dispersal in Belgium. Subsequently, they compared the LCP to independent radio-tracked movement data for a single hedgehog. Although the hedgehog followed lower resistance cells, its movement path was substantially different from the LCP. The authors recognized the need to test with more independent hedgehog data, but noted that animals are searching for food and avoiding predators, illustrating the improbability of an organism following the optimum LCP. Pullinger and Johnson (2010) also found that the LCP was a poor predictor of the precise spatial location of movement paths for woodland caribou. They found no statistically significant improvement in modeling movement paths when comparing straight line paths between termini versus those indicated by LCP.

Of the 29 papers that sought to map potential linkages for specific species, 23 attempted no validation. Of the studies that attempted validation, most were qualitative in nature and may have been more akin to uncertainty tests as opposed to true validation. Carroll and others (2012) used a weight-of-evidence approach to qualitatively compare potential linkages resulting from three separate modeling approaches. Chetkiewicz and Boyce (2009) compared LCP maps to known highway crossing locations for both bears and cougars in Canada (of the small number of telemetry monitored animals, none crossed at the modeled LCP location). Epps and others (2007) compared sheep populations putatively linked based on connectivity modeling to those with empirical evidence of linkage (telemetry, mark/recapture), and Meegan and Maehr (2002) visually compared telemetry data for panthers with a single modeled LCP. Rabinowitz and Zeller (2010) conducted field searches for signs of jaguar presence along modeled linkages (areas of high conductance). Walpole and others (2012) applied the most quantitative approach, statistically comparing known lynx movement paths with modeled conductance values. They found that lynx traveled through areas with higher modeled current flow. They did not map specific linkages, but categorically mapped conductance values. Thus this test indicated that the movement model was correlated with independent lynx movements, but represents a very different test from one that tests for use of a specific path or group of paths.

Step 7. Assess Climate Change Impacts (Optional)

For some applications, evaluating current connectivity is sufficient. However, many applications involve high-cost one-time management actions. In these cases, it is important to assess not only the current landscape but likely future landscapes when prioritizing management activities. Protecting current functional linkages without an eye on the likely future landscape conditions greatly increases the odds of creating expensive "bridges to nowhere." No papers sought to map connectivity for the purpose of assessing longer term persistence against climate change (i.e., range shift connectivity), although a well-connected landscape is likely to be important for climate induced range shifts (Heller and Zavaleta 2009; Hodgson and others 2009, but see Hodgson and others 2011). However, Wasserman and others (2012) considered the effects of climate change, assessing scenarios involving elevation shifts in suitable habitat on potential genetic connectivity for marten. Similarly McKelvey and others (2011) modeled expected changes in connectivity for wolverines based on modeled changes in spring snowpack. They used understandings derived from Schwartz and others (2009) where linkages were based on relating snow cover to genetic patterns. McKelvey and others (2011) looked at the change in location of the paths given climate change, and the changes in ecological cost associated with moving between termini.

Integrating climate change and connectivity is a relatively nascent area of research, but we expect a coming explosion of new tools. Analyses of wildlife connectivity under climate change are currently being conducted using landscape arrangement optimization algorithms (Carroll and others 2010; Faleiro and others 2013), and Nuñez and others

(2013) have developed approaches to create linkages between habitat patches that support continuity along projected climatic gradients over time. There are, however, many impediments to projecting connectivity over time. One is the availability of downscaled data for those variables that define the resistance surface and the reliability of those data if available. A second is the question of whether and how termini should change. If, for example, an organism was, in the future, extirpated from much of its current range, many of the current termini would be obsolete. Given the importance of both of these components in resulting connectivity maps, high levels of future uncertainty are problematic. However, even if formal landscape futuring and connectivity modeling is not possible, this issue should be given thoughtful consideration prior to management actions.

Step 8. Quantify Connectivity (Optional)

Quantifying connectivity can provide a summary value to assist in prioritization of critical linkages or habitat patches for protection or to assess scenarios of landscape or climatic change on connectivity. There are many metrics for quantifying connectivity of landscape patches, and nearly as many papers reviewing the options (Calabrese and Fagan 2004; Fagan and Calabrese 2006; Kindlmann and Burel 2008; Rayfield and others 2011). We will not review them again here, but instead will focus on common methods applied in the resistance-surface connectivity literature. Most frequently, graph theory is used as a means of quantifying connectivity (Urban and Keitt 2001; Garroway and others 2008). Graphs are mathematical structures made up of nodes and edges; for connectivity purposes, these are generally represented as termini and linkages, respectively (Bunn and others 2000). Graph theoretic connectivity metrics are especially helpful in assessing the effects of adding or deleting particular termini or linkages (see Table 3 for a brief summary of metrics).

Table 3—A brief summary of graph theory connectivity metrics, adapted from Garroway and others (2008).

Betweenness: the number of shortest paths that a particular node or edge lies on. Assuming that interactions take place through the shortest path, then betweenness is a measure of the importance of a node or edge in terms of the bottleneck it creates.

Centrality: a measure of the relative position of a node or an edge in terms of connectivity or facilitation of node interaction (e.g., betweenness, degree, eigenvector centrality).

Characteristic path length: the mean of all pairwise graph distances connecting nodes. It can be used as a 'fitness' measure describing the ease of node communication.

Clustering coefficient: a measure of the probability that two nodes connected to a particular other node are themselves connected.

Degree: the number of edges connected to a node. If the edges are weighted, then edge weights are summed and this measure is generally termed 'strength'.

Degree distribution: the distribution of node degree values of a network. The degree distribution is a particularly important measure of network topology and together with other metrics is diagnostic of certain classes of networks and some general properties of network topology.

Graph distance: the sum of the shortest number of distinct edges (or edge weights) connecting a pair of nodes.

Bunn and others (2000) and Ziółkowska and others (2012) illustrate the application of graphs to identify thresholds of change in connectivity given node and edge removal, and the sensitivity of connectivity given assumptions about maximum dispersal distances. O'Brien and others (2006) also assessed model sensitivity to dispersal distance assumptions using a measure of graph cluster size. Betweenness, a measure of the importance of each node given the number of linkages that pass through that node, is also a commonly applied metric to prioritize linkage or termini importance. This can be applied to patches (e.g., Goetz and others 2009), or to every cell in a resistance surface, thereby functioning less as a means of quantifying connectivity for a graph, but as a means of mapping potential linkages as part of Step 6 (e.g., Carroll and others 2012; Theobald and others 2012). The betweenness measure can also be weighted by the area or habitat quality of the termini, providing a useful means of incorporating both the ecological distance between, as well as the importance of the termini being connected.

Other graph measures can be applied to summarize overall connectivity, although different metrics reflect different properties of connectivity, and modelers should be aware of these implications (see Laita and others 2011 for a review). Decout and others (2012) calculated the integral index of connectivity to calculate overall landscape connectivity for the common frog. Alternatively, non-graph based metrics can be calculated, such as the number of habitat patches connected in the landscape or the largest patch index of connected habitat patches (sensu McGarigal and others 2002), as was used by Wasserman and others (2012) to assess connectivity changes under various climate change scenarios.

We conclude by noting that very few extant connectivity analyses carefully followed these six-eight steps. We acknowledge that some, such as formal validation and modeling future landscapes, are difficult and may not be feasible for many analyses. However, if you follow these steps, we believe both that your connectivity analysis will be as conceptually solid and robust as is possible and that you will be fully aware of those areas where untested assumptions are being applied and the effects of these assumptions on derived connectivity linkages. Alternatively, failure to formalize the processes associated with developing resistance-surface-based connectivity models can, and has led to a series of conceptual omissions that not only render the ultimate reliability of an analysis speculative, but also preclude any clear statement concerning what is being modeled in the first place.

Chapter 4. The Importance of Validating Wildlife Connectivity Models[1]

It is clear, from the logic presented in Chapter 3, that resistance-based connectivity modeling relies on many assumptions. The first assumption is that movement rules can be collapsed to pixel-level resistance factors based on precisely mapped landscape features. The second is that organisms are goal oriented—they are actively trying to move from the source to the destination. This is perhaps most obvious in electron-flow algorithms where current (dispersing organisms) is drawn from the origin to the destination. The third is that most models assume organisms are uniform in behavior (e.g., age and phenotype are irrelevant). Lastly, there are assumptions about the levels of organismal knowledge of the landscape. Least cost paths, for example, assume absolute knowledge. All steps taken are chosen to minimize the total cost of passage from the source to the destination; locally optimal, but globally sub-optimal paths are never taken. It is also clear, based on the literature review in Chapter 3, that these assumptions, while perhaps reasonable for some species and movement types, are almost entirely untested.

Given the complexity of species habitat requirements during dispersal and movement, and the many untested assumptions associated with most connectivity models, much care is needed in translating models into local, regional, and national connectivity maps. Specifically, we suggest that broad-scale connectivity modeling used to inform management would be strengthened by (1) evaluating the robustness of the connectivity models and subsequent maps to resistance parameterization and patch definition, (2) evaluating the connectivity algorithm through a sensitivity analysis, and (3) validation using independent datasets, especially when connectivity models were initially derived from expert opinion. Here validation specifically is associated with the application of independent data to determine the degree to which a connectivity model accurately represents use patterns and movement trajectories of target organisms. In this review we discuss model validation and ways in which independent data can be used to provide confidence in connectivity modeling efforts.

Agencies and private conservation entities have proven willing to overhaul land management strategies to prioritize wildlife connectivity based on information derived from connectivity models (Schultz and others 2013) —information that inherently has some degree of uncertainty. Yet, given the fiscal costs and lost opportunities associated with imprecise corridor placement, it is important that we apply some validation approaches to existing models prior to using them to guide management plans on landscapes.

Validation

Models can be validated many ways, but, in ecology, are most often validated with the use of independent data (Schlesinger and others 1979). For example, habitat use models (e.g., resource selection functions) are based on the probability of use or occurrence in focal areas and are statistically based on observed occurrence frequencies. These are typically internally validated using subsets of the total data (e.g., k-fold cross validation or withholding data from model development to use as test data) and may be

[1]This chapter presents ideas associated with a forthcoming journal article on validation of resistance models. Contributors include Winsor H. Lowe, David Theobald, Kim T. Scribner, Leona K. Svancara, Meredith Rainey, Erin Landguth, Stephen Spear, Todd Cross, and John Pierce.

externally validated using fully independent data collected at a different time and place (Pearce and Ferrier 2000). Resistance-based connectivity models are not usually data-derived statistical models. Even if components of the model have been fit to data (e.g., LCP costs correlated with genetic relatedness), the overall model structure is likely to contain untested assumptions (e.g., that genetic relatedness captures the relevant movement types). In this, they have more in common with conceptual models—sometimes called process or mechanistic models—in which a logical framework is constructed to describe a process. Whereas statistical models are directly built from data, process models are built from concepts and then validated with data. Thus, until validated, process models are best thought of as elaborate hypotheses that may be partially or entirely incorrect. Recognizing connectivity models as a type of process model, we recommend a general validation framework that applies across many model types This framework acknowledges the many interdependent steps involved in model development, from formulating the problem, to developing a conceptual model, to building and verifying computer code to validating the outputs (Table 4).

Table 4—Categories of data that can be used to validate connectivity models, specific data types within each category, descriptions of common uses, and examples of these types of data in the literature. Note that examples are not cases where these data have been used to validate connectivity models.

Categorical approach	Data type for validation	Description of common uses	Examples
Inferential	Genetic markers	Often collected to estimate population structure, genotypic diversity, and inbreeding, or to evaluate biogeographic hypotheses.	Keyghobadi and others 1999; Schwartz and others 2003; McRae and Beier 2007; Trumbo and others 2013
Inferential	Biogeochemical markers	Using trace element concentrations or stable isotopes to infer geographic origins and movement patterns.	Marra and others 1998; Rubenstein and Hobson 2004; Brattström and others 2010; Muhlfeld and others 2012
Occurrence based	Occurrence	Collected at multiple scales, often presence / detection of a species. Sometimes absence data or associated probabilities of detection also available.	Nichols and others 2007; Gil-tena and others 2009; Zanini and others 2009; Russell and others 2012
Occurrence based	Radio / satellite telemetry	Collected to describe habitat use or evaluate survival and reproduction. Can be used as paths if collected frequently enough, or devolved to point occurrence data.	Copeland and others 2007; Jonsen and others 2007; Squires and others 2007; Vashon and others 2008; Klaassen and others 2010; Mate and others 2011
Occurrence based	Historical (museum)	Historical specimens from museums can be useful for rare or difficult-to-detect species. Must be spatially referenced.	Marra and others 2009; Schofield 2009
Occurrence based	Species distribution (camera traps, casual observations, non-invasive genetic sampling, etc.)	Occurrence data is modeled to produce maps of species distribution.	Manel and others 1999; Guisan and Thuiller 2005; McKelvey and others 2008; Varela and others 2009
Path Based	Satellite telemetry	Unlike telemetry occurrence data (above), here the path of animal movement is the unit of measurement.	Horne and others 2007; Patterson and others 2008; Sawyer and others 2009; Colchero and others 2011

We believe there are three validation techniques most appropriate for connectivity models: Event/Predictive Validity, Face Validity, and Comparison to Other Models (nomenclature from Sargent 2009, 2012;). Event Validity is the comparison of events predicted in the model to events that occur in the actual ecological system, whereas Predictive Validity tests models ability to forecast in space and time. For example, Event Validity can be assessed using the correlation between predicted movements and actual movements within the modeled landscape, whereas Predictive Validity might be assessed based on movements in an area outside of the modeled landscape. At least for broad, regionally based connectivity models, it is unlikely that independent data detailing actual movements will be available across the modeled landscape. Rather, these data are likely to be limited to particular places and times, and will only allow partial validation. However, because process models are not directly constructed from data, partial validation is, however, the norm and its utility should not be dismissed. We reiterate: process models contain assumptions that are not supported by data, and without validation, model reliability is largely unknown. Thus, any validation even if partial or anecdotal is important.

Face Validity is another term for expert opinion, where those knowledgeable about the system evaluate whether the model behavior seems reasonable. All models should have some level of Face Validity, but we suggest that this approach provides only weak or minimal validation, especially if expert opinion was used overtly (e.g., the model was formally based on expert opinion) or covertly (e.g., landscape variables associated with resistance scores were based on expert opinion) to construct the model. Comparisons to Other Models can be a useful approach when other independent models exist. A good example comes from short-term climate modeling, where multiple statistical and process models are used to produce consensus predictions (Murphy and others 2004). If independently built model results converge, this can be considered strong validation because convergence is unlikely to occur due to random chance (weather forecasters often frame their confidence in future weather based on the degree of model consensus). Validation through model comparison, however, suffers from the same weaknesses as does Face Validity; true independence between models is difficult to achieve. For example, comparing corridors that were created using circuit theory and cost path methods will tend to converge because both are constrained by the same resistance surfaces and termini. Validation of connectivity models is therefore not likely to be a binary, comprehensive process (e.g., the model was or was not validated). It is important to understand the degree to which the model has been validated and to provide clarity as to which approaches were used. It is equally important to assess the relative strengths and limitations of those approaches in the specific context of the modeled landscape and organism.

Data Types For Connectivity Model Validation

Wildlife and fisheries biologists collect many types of data suitable for validating connectivity models through event or predictive validation techniques (Table 4). These data can be grouped into three categories: inferential, occurrence, and path (Figure 10). These categories and their applications to model validation are described below.

Inferential Data

Inference-based data refers to either biological or biogeochemical markers used to make indirect evaluations of movement (Rubenstein and Hobson 2004). Biological markers are morphological, behavioral, or genetic markers used to track individual movement, or groups of individuals of similar type, across large landscapes. For instance,

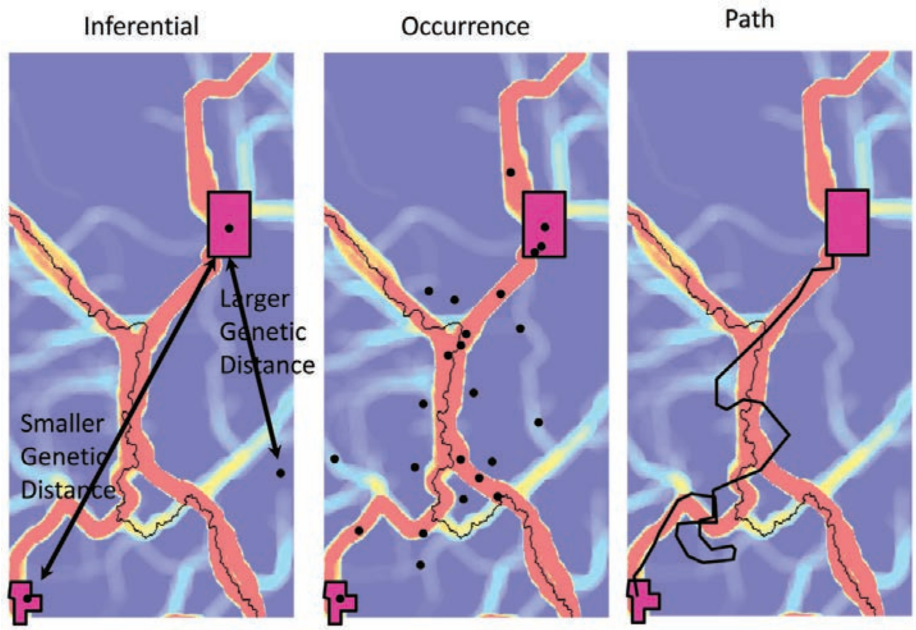


Figure 10—A conceptual framework for model validation adapted from Sargent (2009, 2012).

biogeochemical markers use trace element concentrations or stable isotope signatures associated with particular areas and diets (Rubenstein and Hobson 2004; Muhlfeld and others 2012). These markers have been especially useful for assessing movement in species producing large numbers of propagules that cannot be individually marked (Thorrold and others 2001) and in species that disperse especially long distances (Groves and others 2002; Sepulveda and others 2009).

Landscape genetic data are the most common form of inferential data used to validate connectivity models (Manel and others 2003; McRae and others 2008). Here an index of relatedness (or its inverse, genetic distance) can be calculated between individuals across a landscape. Genetic distance is inversely related to gene flow and gene flow occurs when organisms successfully disperse and breed; high rates of successful dispersal are assumed to reflect low movement costs. Thus, high levels pairwise genetic distance between samples or populations serve as proxies for low rates of movement and are assumed to represent high landscape resistance. Pairwise genetic distances between samples can therefore be correlated with putative cost distances between sample locations, and resistance models having higher correlations are considered better supported (Cushman and others 2006). For example, Short Bull and others (2011) examined 36 different resistance hypotheses on how black bears moved through a Rocky Mountain landscape and found gene flow, as estimated by molecular genetic data, was best explained by elevation, forest cover, and roads.

There are many advantages to using genetics to validate connectivity models. Gene flow is mediated by the movement and subsequent successful breeding of an organism. Because the movement of an organism across the landscape is limited by passable landscape features, so too is the resultant gene flow. Therefore, genetic samples and molecular markers have been used to validate connectivity models by calculating connectivity/isolation metrics at a population and individual level from a single sampling occasion. Data can be obtained relatively easily and at low cost; sampling can be systematic (e.g., non-invasive genetic sampling grid) and/or opportunistic (e.g., sportsman-contributed samples); samples are useful so long as spatial coordinates are collected at a resolution appropriate to the connectivity question (Galpern and others 2012). Additionally, genotyping data are precise; genotyping error rates are low and quantifiable, species-level misidentification is virtually non-existent, and major modeling assumptions (e.g., marker neutrality) are testable.

Several additional approaches can be taken to infer movements from genetic data. At a fine scale, one can establish multi-generational parent-offspring relationships to document the movement, breeding, and subsequent gene flow resulting from demographic connectivity (Peery and others 2006; Araki and others 2007; Hudy and others 2010). This approach has several advantages, perhaps the most important is that the temporal frame is well defined. When using inferential data, it is important to remember that movement is, by definition, inferred rather than measured and genetic distance does not change instantaneously with changes in the landscape; there is a lag time. For example, several generations must pass before a new landscape obstruction is detected through genetic analyses (Landguth and others 2010). Additionally, inferential data may be insensitive to certain types of movements that direct movement data would detect. Seasonal migrations or habitat patch utilization may be entirely absent from relatedness patterns revealed by genetic data (Spear and others 2010).

Occurrence Data

There are many potential sources of occurrence data for connectivity model validation, including satellite and radio telemetry data, ground and aerial observation, noninvasive sampling, museum specimens with associated spatial locations, and remotely triggered wildlife cameras (Table 4). Occurrence data can be invaluable for validation of connectivity models because they provide a direct means of assessing whether a species and, in some cases, an individual moves across a landscape as predicted, by noting when an observation is within a corridor or area of likely movement.

Telemetry data: We distinguish telemetry data from other forms of occurrence data because the ability to collect multiple point locations for a specific individual at regular intervals is particularly useful in this context. Telemetry data are uniquely able to capture critical movements of individuals, including long-distance migration and dispersal, if collected on an appropriate temporal scale. However, we note that telemetry data are generally not used to infer paths (see below) but instead are seen as a series of detections or occurrences.

While telemetry would appear to be an excellent choice to validate connectivity models, there are few examples in the literature. Most studies utilizing telemetry for model validation have done so opportunistically, making *post hoc* comparisons of model predictions with available data. As such, results tend to be more anecdotal than confirmatory. In an exploration of landscape restoration opportunities for the Florida panther, Meegan and Maehr (2002) noted that their predicted least cost path crossed a river within a 4-km reach known to have been crossed by three radio-collared individuals. Similarly, Chetkiewicz and Boyce (2009) noted the frequency of least cost paths that fell near known grizzly bear and cougar highway crossing sites.

While the straightforward use of telemetry data is for Event Validity, it can also be used in a Model Comparison framework. For example, Cushman and Lewis (2010) compared landscape resistance surfaces estimated from genetic data with black bear occurrence based on telemetry. They found that both telemetry and landscape genetic data predicted that bear movement was sensitive to forest cover, development and roads, and elevation (Cushman and others 2006; Cushman and Lewis 2010). Pullinger and Johnson (2010) used two alternative resistance maps to compare least cost paths to caribou migration movements from GPS data. Observed and predicted paths were compared for path sinuosity and a path deviation index, which gives the average distance between paths.

Critical to validation with telemetry data is the degree to which these data capture within versus between home-range movements. Habitats that animals use to move within a home range can be vastly different from habitats that they chose to move between home ranges. Further, we must also acknowledge that not all movement outside home ranges is beneficial. Often, exploratory movements are taken by inexperienced sub-adults or other individuals that are socially excluded from suitable habitat (e.g., Roznik and others 2009). In these cases, choice of dispersal habitat may not provide short-term fitness advantages or long-term demographic benefits; using telemetry data from these individuals to validate a connectivity model may prove misleading. Inferential genetic data are stronger for separating beneficial movements; gene movement only occurs when dispersals are successful. This is one reason that using genetic and telemetry data in a Model Comparison framework is potentially so powerful; Telemetry detects movements missed by genetic indices and results are relevant to the current landscape, but fails to differentiate between harmful and beneficial movements. Genetic indices ignore all movements except for those movements with the known benefit of producing viable offspring but contain a multi-generation time lag. Thus, these two approaches provide contrasting windows into organism movement patterns. Relating this to the movement types defined in Chapter 2, telemetry is ideal for assessing Daily Movement and Seasonal Migration, whereas genetic patterns are optimal for Demographic, Genetic, and Range Shift movement types.

Understandings from telemetry data are not, however, instantaneous. Time is required to generate use patterns. A statement such as “the organism uses areas within the corridor preferentially” requires a sufficient number of relocations to support this statement statistically. Using location data in this manner to validate corridor use represents a type of resource selection function (RSF; Manley and others 1993). In RSFs, importance is inferred through frequency of use. When based on regularly or randomly collected occurrence data, frequency is a measure of time spent in an area, which may or may not be a pertinent metric to describe movements. Just as it is critical to think carefully about the types of movements and nature of linkage use when building a connectivity model, these same understandings will inform the utility of various data for the purpose of model validation.

Non-telemetry occurrence data: Occurrence data can come from multiple sources. For example, organisms may be identified during formal survey activities, accidentally or intentionally killed and subsequently recorded, captured on remote camera sets, or seen by casual observers. One important source of occurrence data is museum specimens (Graham and others 2004; Jackson and others 2012). In the last decades, museums have become repositories of spatially referenced tissue samples that can be analyzed genetically to verify species identification. Other repositories of occurrence data are Natural Heritage databases, where state-level species occurrence data is often collated, proving a wealth of opportunities for validating connectivity models. However, many movements will be poorly represented by non-telemetry occurrence data. For example, if an animal moves quickly through a corridor, the likelihood of casually detecting it while in the corridor may be low. Similarly, non-telemetry occurrence data are often limited spatially (e.g., adjacent to roads) and are therefore frequently non-representative; presence or absence of occurrences within corridors could be functions of sampling intensity rather than landscape condition. In general, casually collected occurrence data will therefore provide weak anecdotal validation. These data, however, should not be ignored. Often they are freely available and therefore can provide quick and inexpensive checks on model expectations. For example, if occurrence data showed no relationship to putative linkages, this could indicate a serious error in one or more of the model assumptions.

Path Data

Most conventional telemetry data devolve into point or occurrence data largely because the time between detections was large and telemetry error great, preventing inferences about the actual path taken. However, with newer GPS-based telemetry devices, both of these issues can be resolved allowing inferences to be made of the actual path used by an organism (Brown and others 2012). These paths will provide strong validation for connectivity models. Unlike occurrence data, which are scalar, path data are composed of movement vectors, having properties such as velocity and direction.

Paths are the movement data themselves and, therefore, do not require the steady-state assumptions needed when transforming telemetry data to movement data (see Moorcroft and others 2006; Patterson and others 2008). Because paths approximate actual movements, movement rules can be tested directly by comparing expectations to path structures (Chetkiewicz and others 2006). For example, if certain landscape features are considered to have high resistance (e.g., major highways), then, when faced with alternatives, organisms should choose to avoid crossing these areas (e.g., Whittington and others 2005).

Path data can also be used to track rapid movements through areas for which, because cumulatively little time is spent there, occurrence data will be sparse. However, unless the instrumented organisms represent the population adequately, path data will be anecdotal in nature.

Path data are not commonly used to validate connectivity models; however, we expect this to change with the development of new state-space models, which are a class of time-series model that predict a system's future state based on a probabilistically derived process model (Horne and others 2007; Patterson and others 2008). State-space models estimate the probabilities of a particular state (e.g., location) and model variables (mean speed and turn-angles) and subsequently incorporate these parameters into a flexible future forecasting model. The combination of these models with fine-scale satellite telemetry data is rapidly improving our understanding of animal dispersal and movement (Horne and others 2007). For example, Vergara and others (2013) used state-space models and translocation experiments with austral thrushes to show that the use of riparian strips for connecting between habitat patches is highly influenced by the surrounding landscape. We believe that state-spaced models will provide one of the best ways to validate connectivity.

The Case for Monitoring

Connectivity modeling is popular today due to perceived threats to natural linkages due to urbanization, land conversion, and climate change. Areas where conservation decisions are urgent may not be areas with large quantities of extant data on a specific target species. Thus, it is likely that connectivity models used to inform decisions will be largely or wholly unvalidated. However, there is no reason that this situation should be permanent. Targeted monitoring (Nichols and Williams 2006) provides an efficient and coherent approach to collect pertinent data, especially in a model-testing framework. Monitoring underpass and overpass structures in Banff provides a straightforward example.

In Banff National Park, Alberta, Canada, an extensive system of underpasses, overpasses, and wildlife fences were constructed to prevent vehicle collisions with wildlife and to provide connectivity across Canada 1, the major east-west highway in the country. However, at the time of construction, the efficacy of these structures was unknown. The simplest indication of efficacy is the presence of occurrences in the corridors. To this end, a series of track beds and cameras were monitored; across the first 10 years, track beds indicated more than 84,000 occurrences within the structures (Clevenger 2007). Thus, this monitoring indicated that corridors were being used. Importantly, however, use increased over time as animals learned how to take advantage of the structures (Clevenger 2007). More recently, genetic monitoring has begun in the areas adjacent to Canada 1. A recent study indicated that, for bears (*Ursus spp.*), genetic connectivity across the road appeared adequate (Sawaya and others 2014). Note that elapsed time was required for both of these evaluations; occurrence was conditioned by learning, and genetic patterns require several generations to reflect barrier removal (Landguth and others 2010).

Conclusions

Connectivity is a critical requirement for conserving native biological diversity. With the high probability of directional climate change in the near future, connectivity has emerged as perhaps the primary conservation need, supplanting the conservation of specific habitats. A number of high profile connectivity modeling exercises are in progress (e.g., WGA 2009), with the anticipation that results will drive policy at state and regional levels, and in both agencies and private conservation organizations. Given the importance of maintaining connectivity for conservation biology, and the potential high costs associated with implementing these models, robust validation of connectivity models is essential.

Ultimately, we believe that testing connectivity models with a combination of genetic and path-based methods will provide the best opportunities for model validation. Path approaches will reveal movements within home ranges and dispersal events; genetic data will provide information on the outcomes of important movements, such as effects on fitness and population growth. A combination of these approaches will be most powerful. We also note that the direct evaluation of linkages is likely to involve the long-term collection of specific data. However, given the preponderance of non-validated connectivity models, even weak validation using any available data would represent a step forward.

Model Validation Framework

A useful conceptual framework for model validation is that of Sargent (1982, 2009, 2012). Figure 11 is adapted from Sargent (2009, 2012), where the first stage is to establish a "Problem Entity," which is the system, idea, situation, policy, or phenomena to be explored with models (e.g., enhanced landscape connectivity for a particular threatened species). Subsequently, a "Conceptual Model" is built that provides the logical or mathematical construct of the problem entity. In developing conceptual models, decisions are made concerning the intrinsic nature of the problem, which will dictate which mathematical paradigm it approximates and, given this, acceptable levels of simplification and abstraction (e.g., parameterizing resistance surfaces). The step of collapsing a complex phenomenon (evaluating species connectivity) into a conceptual model requires simplification and abstraction and occurs in an "analysis and modeling phase" (e.g., choosing a connectivity algorithm to use in a GIS environment and statistical metrics to evaluate its output). It is during this phase that the model is subject to verification, the process of ensuring that algorithms within the computer model are performing as intended. Verification identifies coding errors, numerical instabilities, and errors in translation between the conceptual model and the computerized model (Schmolke and others 2010).

Once verified, the model then produces inference about the initial problem entity through computer experiments and tests (e.g., connectivity maps). Validation also occurs in this last phase, when external data are used to assess whether the model accurately reflects the system under study. While coding and code verification need to be correctly executed, it isn't until the validation step that the extent to which the decisions made in the conceptual model are assessed. The process of model creation, presented above as a linear progression from problem to validated model, is an iterative process (Figure 11).

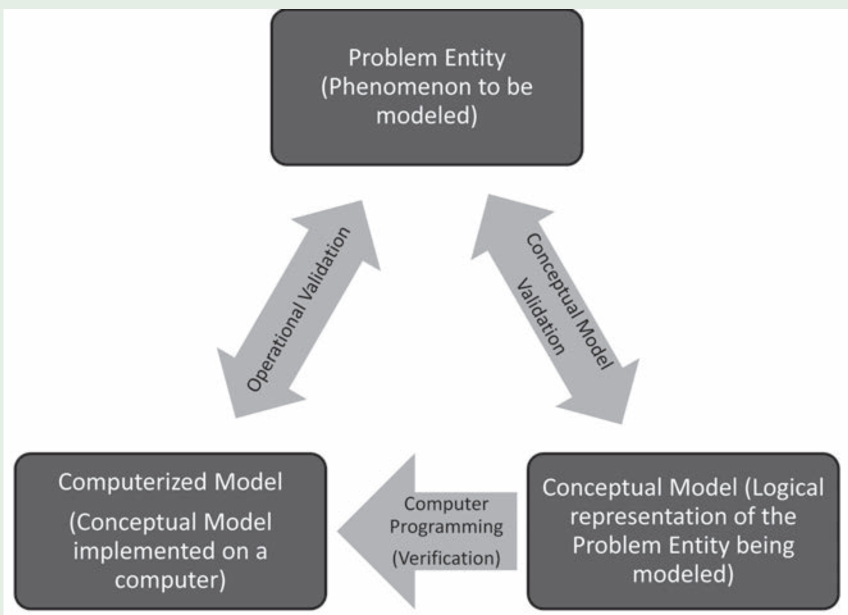


Figure 11—Graphic depicting the three data types that can be used for validating connectivity models. The pink shapes are source and destination nodes, while the color map is predicted corridors from resistance modeling efforts. In all cases, validation is through the degree of correlation between the putative corridor and applied data. (Adapted from Sargent 2009, 2012.)

Overall, a model is created to represent a specific reality and for a specific purpose, and is validated with respect to its intended accomplishments (Sargent 2009). There are multiple approaches to test the validity of a model. The most common is to have the development team make the decisions based on internal tests conducted during model development. This approach has been criticized for a lack of independence and excessive reliance on expert opinion (Tropsha and others 2003). A second approach is to have the model users validate the model independent of the model developers; independence is also an issue here. A third approach, which substantially increases model credibility, is to involve an external peer group to independently validate the model using independent data.

Chapter 5. Practitioner Efforts

In this chapter, we review 31 resistance-surface-based connectivity projects in the United States (Appendix 2). All of these projects have a primary purpose of mapping potential wildlife linkages to guide conservation efforts. Most of the projects are published as agency or organizational reports, although several are also published in the conservation planning literature. Although not an exhaustive review, our summary represents the majority of relatively broad extent, resistance-surface connectivity planning efforts since 1998. The primary organizations conducting these projects were state agencies (8 projects), non-governmental organizations (NGO, 8), or Federal agencies (6). Nine of the projects were conducted by a consortium of organizations, primarily state (6) or Federal agencies (4) in collaboration with NGO (6) and/or academic institutions (7). Seven of the projects are in the early phases of development, and some methodological details are unknown (marked with a question mark in Appendix 2). We review practitioner efforts following the eight steps outlined in Chapter 3.

There are a number of additional efforts inside the United States that apply alternative methods, such as using actual path data, like the Wildlife Conservation Society's Path of the Pronghorn project, http://www.wcsnorthamerica.org/WildPlaces/Yellowstone-andNorthernRockies/PronghornFieldProgram.aspx, or the State of Colorado's efforts to map lynx roadway crossings (Crooks and others 2008). Simulated annealing models are also applied (see From Adirondacks to Arcadia http://www.twp.org/sites/default/files/Adirondacks_to_Acadia_08Mar07.pdf, or the Heart of the West Plan http://wildutah-project.org/programs/heartofthewest) while other projects use expert-opinion-delineated linkages (for example, see Connecting Alaska Landscapes Into the Future http://www.snap.uaf.edu/resource_page.php?resourceid=5). The Western Governors Association (WGA) is currently funding a western state-wide Crucial Habitat Assessment Tool (CHAT) program, with an expected completion in 2013 http://www.westgov.org/initiatives/wildlife/380-chat/#CHAT_states. CHAT will provide internet-accessible information on crucial habitats and linkages. Much of the current CHAT connectivity work applies maximum entropy models or expert opinion. Additionally, across the United States, numerous projects are underway or have been completed to map wildlife road-crossing corridors, including efforts in Alaska, Arizona, Colorado, Florida, Idaho, Maine, New Hampshire, New Mexico, Oregon, Utah, Vermont, Virginia, and Wyoming. Many of these efforts are summarized by Feinberg (2007). There is also an active effort to map linkages for wildlife conservation abroad, and we provide some examples in Table 5. Worboys and others (2010) also provide a useful summary of a number of international connectivity modeling efforts.

Table 5—Examples of international connectivity modeling projects.

Project Title	Lead organization	Organization type	Author, year	Map extent	Species	Resistance layer type	Variables used for resistance surface	Resistance score basis	Calculate ecological distance and map potential linkages	Sensitivity analysis or validation?	Website
Canada Inland Temperate Rainforest Conservation Area Design	Yellowstone to Yukon	NGO	Craighead et. al. , 2004	Canada inland temperate rainforest	Multiple focal species	Focal species habitat Suitability	Human modification land cover types + topographic features	Expert opinion	Least cost corridor	No	http://www.y2y.net/
Taku River Area Conservation Design	Round River Conservation Studies	NGO	Heinemeyer et. al. , 2003	Taku River watershed, northwestern British Columbia	Multiple focal species	Habitat suitability models	Vegetation type + forest age + topography + human impact	Scientific expert opinion, traditional ecological knowledge, telemetry data	Least cost path	Validated habitat model	http://www.roundriver.org/index.php/taku-river
Forest Habitat Networks Scotland	Forestry Commission Scotland	Federal	Moseley et. al. , 2008	Scotland	Generic focal species	Habitat suitability models for generic focal species	Forest cover type + quality, based on expert opinion	Expert opinion	Least cost path	Sensitivity of results to resistance values	http://www.forestry.gov.uk/fr/INFD-69PF6U
Connecting priority conservation areas in the main island of Puerto Rico	The Nature Conservancy	NGO	Leidner, 2004	Puerto Rico	NA: linking natural landscapes and protected areas	Landscape integrity	Forest Cover type + human impact	Expert opinion	Least cost path	No	http://www.conservationgateway.org/Files/Pages/connecting-priority-conse.aspx
Establishing Connectivity in the Southwest Amazon	World Wildlife Federation	NGO	WWF , 2002	Southwest Amazon	NA: linking protected areas	Landscape integrity	Forest Cover type + human impact	Expert opinion	Least cost path	No	http://science.natureconservancy.ca/centralinterior/docs/ERAtoolbox/11/Standard11_casestudy_SWAmazonConnectivity.pdf
Snow Leopard Connectivity	Snow Leopard Conservancy	NGO	Jackson et. al. , 2011	Snow Leopard Range, Mongolia	Snow Leopard (Panthera uncia)	Focal species habitat suitability	Elevation + topography	Expert opinion	Least cost corridor, circuit theory	Planned	http://www.arcgis.com/home/item.html?id=f00522011f144a49ab1f5c84b6c05b71
Canada Inland Temperate Rainforest Conservation Area Design*	Craighead Institute	NGO	Craighead et. al. , 2004	Inland temperate rainforest, Canada	Multiple focal species	Focal species habitat suitability	Human population density + road density + land cover + slope + elevation +	Expert opinion	Least cost distance	No	www.savethecedarleague.org/docs/Inland%20Rainforest%20CAD.pdf

Resistance-Surface Connectivity Modeling Steps

Below we go through the eight steps in resistance-surface connectivity modeling and relate each of these to the identified practitioner's connectivity modeling.

Step 1. Define Type of Connectivity to Be Modeled

The majority of practitioner connectivity efforts (Appendix 2) modeled structural connectivity (11 projects), with one of these assuming that landscape connectivity would also provide for long-term persistence, given climate change (Range Shift Connectivity). Although these projects developed resistance surfaces from measures of landscape integrity, several discussed their intent to represent "dispersal" or "functional" connectivity. The California Essential Habitat project (Spencer and others 2010) is a good example of a project with the goal of modeling functional connectivity, but that begins the process with broad extent landscape pattern connectivity with planned additional phases to model species specific linkages at finer scales. One project sought to model "dispersal" and genetic connectivity, but did so without reference to any specific species, using landscape integrity to quantify the resistance surface instead. The remaining papers all used focal species (generally a suite of species) to model undefined "dispersal" (four) or functional (two) connectivity, dispersal and daily habitat (one), or dispersal and genetic (one) connectivity. One project conducted a conservation area design (CAD), and three projects sought to represent all forms of connectivity in the mapped linkages (Washington Connected Landscapes Project [WHCWG 2010], with a focus on genetic and range shift connectivity; Staying Connected Initiative [SCI Ongoing]; Montana Connectivity Project [Herbert and others 2011]). Two projects looked at connectivity as a range shift against climate change. One project did not define the type of connectivity to be modeled and four were too early in development to infer connectivity intent.

As is often the case, efforts to model functional connectivity types relied mostly on structural landscape measures, but sought to include process-based understanding for species-specific modeling. For example, two projects led by Beier and others (2007; SCW 2008) included numerous focal species (20-100) to represent a broad-spectrum of potential connectivity types. Focal species were chosen to be taxonomically diverse, sensitive to habitat fragmentation, represent diverse ecological interactions, and to include both corridor dwellers and passage species (ability to move through a linkage within a day).

Step 2. Create the Resistance Layer

Step 2a. Resistance layer scale. Of the projects where analysis extent was set by a state or other political boundary, we assessed whether the extent had been buffered beyond the arbitrary boundary to avoid mapping errors. Buffered extents were used in nine projects and un-buffered in seven projects. The majority of projects did not consider the analysis grain from a species' point of view; 30-100 m cell resolutions were most often applied. There were six projects that did explicitly discuss scale issues. The Southern Rockies Wildlands Network Project (Miller and others 2003) reviews issues with scale in the introduction, and both the Washington (WHCWG 2010) and Montana (Herbert and others 2011) connectivity projects do an excellent job of discussing how scale affects analysis results and interpretability. Both reports further discuss how, for some species, lack of data limit the ability to model certain functional types of connectivity. The Washington (WHCWG 2010), Montana (Herbert and others 2011), Linking Colorado's Landscapes (Kintsch and others 2005), and California Essential Habitat Connectivity (Spencer and others 2010) projects all provide examples of a hierarchical scale approach, where modeling began with a coarse scale analysis intended to be followed by further analysis at finer scales. The Arizona Missing Linkages (Beier and others 2007) project is an example of a secondary analysis using finer-scaled data.

Step 2b. Determine ecological variables. As in the literature review (Chapter 3), most of the applied projects relied on land cover (24) and a measure of distance to roads or road density (15). While human population density or urban development was also included in 7 projects, a measure of topography was more common for practitioner projects (15 projects). Ten projects only used a combination of these four variables, and 3 additional projects only used a variable (or variables) representing land cover. Other commonly used variables included hydrology (6) and conservation or protection status (6). Only one report (Great Northern Landscape Connectivity (GNLCC Ongoing)) considered the sensitivity or modeling results to the quality of the ecological data, and two projects (South Coast Missing Linkages [SCW 2008]), and Linkage Network for California Deserts [Penrod and others 2012]) ground-truthed land cover data.

Step 2c. Assign resistance values. Of the 31 projects reviewed, 5 were too early in development to determine the method of assigning resistance values, and 23 used expert opinion to model resistance surfaces on the basis of either landscape integrity (13, see Figure 12 for example) or habitat suitability (8). Two modeled both. These projects used various approaches to combine multiple ecological variables into the resistance surface, including taking the sum, product, geometric mean, or maximum of the variable values. Five projects applied empirical methods to modeling resistance. The Washington Connected Landscapes Project (WHCWG 2010) used expert opinion to develop a suite of models and compared circuit-theory-generated distances to genetic data for model selection for one focal species (mountain goat). The other four projects used occurrence data. Both the Montana Connectivity Project (Herbert and others 2011) and Mapping Habitat

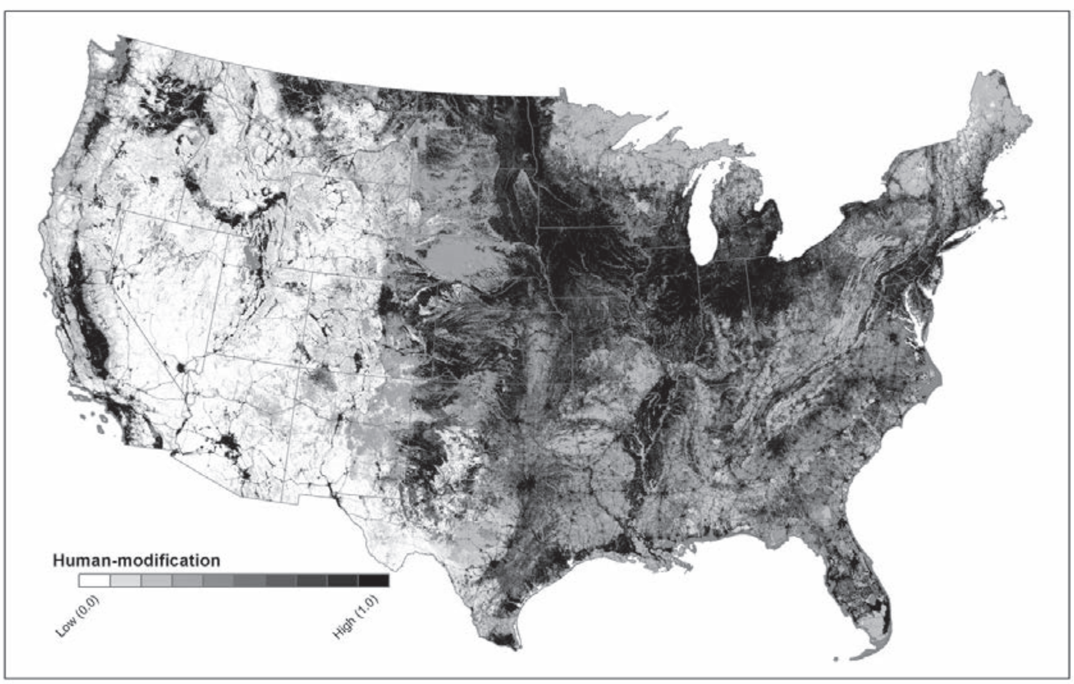


Figure 12—Fields and others (2010) used human modification to create a resistance surface for a structural connectivity analysis. Construction of this surface is fully described in Theobald and others (2011); figure is a reprint of Figure 1 in Theobald and others (2011). (Permission to reprint figure granted by Springer, Wildlands Network, and the authors.)

Connectivity Around Military Installations (Moody and others 2011) used the maximum entropy program MaxEnt (Phillips and others 2006) to predict realized ecological niches from presence only data and, in turn, inverted the resulting habitat suitability model to create the resistance layer. The California Landscape Connectivity (CLCC Ongoing) project is currently conducting occupancy modeling with species presence data, and the Pathways project in the Hudson Valley (Howard and Schlesinger 2012) used occurrence points and randomly generated pseudo absences to conduct random forest (Liaw and Wiener 2002) bioclimatic niche modeling.

Step 2d. Validate resistance surface. Of the projects using expert opinion to create a resistance surface, one project conducted semi-validation of the resistance surface. The Northeastern Resilience Network (Anderson and others 2012) calibrated the expert-opinion-derived resistance surface to known movement paths. The Washington Connected Landscape Project (WHCWG 2010) plans to validate expert-opinion-derived resistance values for sage-grouse with genetic data. For empirically based efforts, the Mapping Habitat Connectivity Around Military Installations (Moody and others 2011) project conducted field experiments testing target species' movement behavior in different habitat types and across habitat boundaries to validate their resistance surface values (Figure 13), and the California Landscape Connectivity project (CLCC Ongoing) plans to validate their occupancy modeling with genetic distance data. Seven other projects conducted uncertainty analysis on the resistance surface, including testing various resistance val-

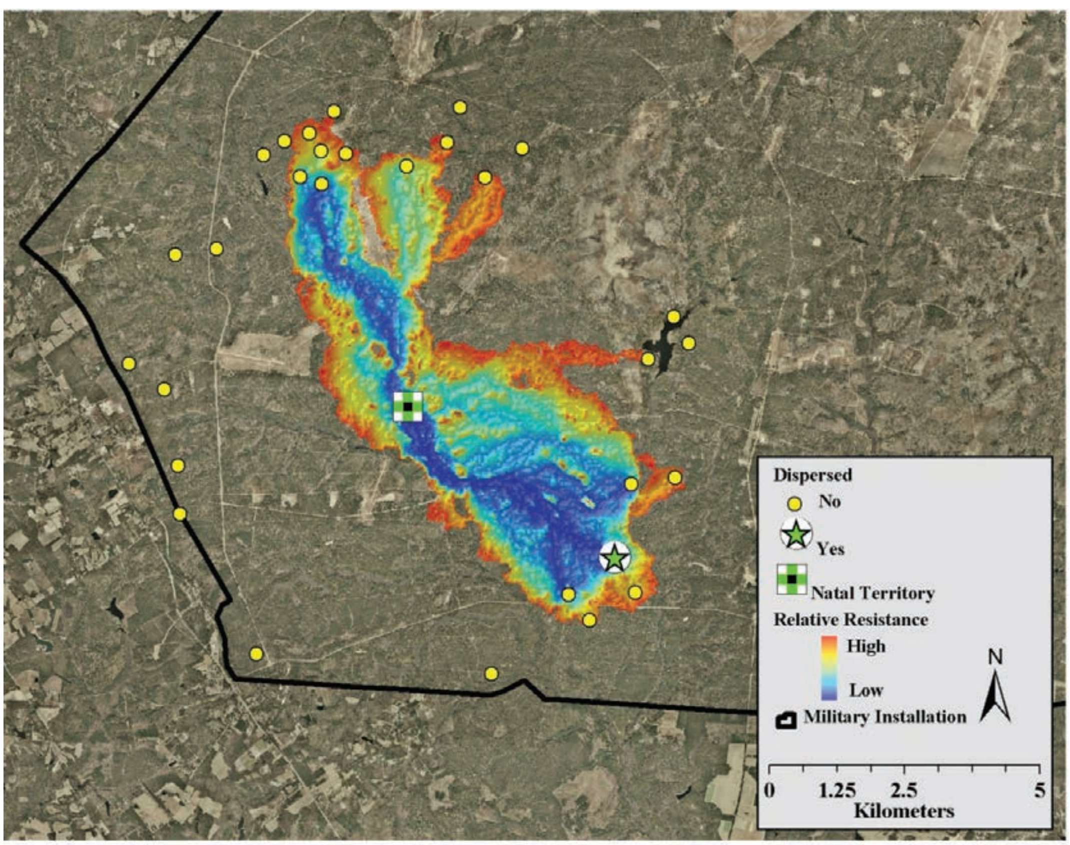


Figure 13—Moody and others (2011) evaluated resistance surfaces by comparing independent species dispersal data against cost-distance models. Here (Figure 11 in Moody and others 2011), a long-distance dispersing juvenile red-cockaded woodpecker is compared to the 25% least-cost corridor. (Permission to reprint figure granted by the authors.)

ues (5 projects, 2 of which used a factorial design to test multiple resistance values) or conducting cross-validation of the resistance surface (1 project). One project, Mapping Habitat Connectivity on and Around Military Installations (Moody and others 2011), assessed uncertainty related to resistance variables and values, as well as the functional form of the relationship between habitat suitability and resistance. The Pathways project (Howard and Schlesinger 2012) provides a good example of conveying uncertainty, providing a ranking of relative confidence of model fit for each species.

Step 3. Define What Is Being Connected

Most projects applied rules to the resistance layer to delineate patches used as linkage termini. Approaches included simulated annealing or expert opinion to create patches that clustered areas with high levels of focal species habitat suitability (from resistance surface), species representation, and special elements (CAD, 2 projects) or moving window analyses over the resistance surface to group high quality habitat into patches (which then served as termini) for 4 projects. Of the moving window analyses, two projects (Arizona Missing Linkages (Beier and others 2007) and Linking Colorado Landscapes (Kintsch and others 2005) used different sized windows to represent focal species' perceptual grain. Arizona Missing Linkages was further notable in that the researchers lowered the resistance values in some of the patches so as to encourage "stepping stone" behavior whereby species movement would follow paths of smaller patches linking larger patches. Three projects applied threshold values to the resistance surface and grouped contiguous cells above the threshold (high habitat suitability or landscape integrity); one of these projects (Montana Connectivity Project [Herbert and others 2011]) defined "contiguous" dependent on whether cells were within a species-specific "perception distance." They also grouped several species with similar patch characteristic and movement behaviors into guilds to reduce the number of models computed. Three projects applied the resistant kernel approach, with lowest resistance cells serving as termini in two cases, and in one project, resistant kernels were run from all cells out to a limited distance to ensure computational feasibility. Wild Life Lines (Fields and others 2010) iteratively identified lowest resistance cells to serve as termini in modeling multiple pair-wise linkages.

For projects that identified termini independent of the resistance layer, several papers used protected areas or natural areas, not directly derived from resistance layer but often using similar variables. One paper identified patches using habitat quality models for vegetation types (forests, grasslands, wetlands; Minnesota Terrestrial Habitat Connectivity [Richardson 2010]). Two projects used occurrence data points as centroids for at least some species (Great Plains Landscape Connectivity [Cushman and others 2010], Mapping Habitat Connectivity Around Military Installations [Moody and others 2011]). The Washington Connected Landscape Project (WHCWG 2010) applied three different approaches to delineating termini: known centers of distribution for well-documented species, moving window analysis to identify patches of relatively low resistance surface values for less well defined populations, and contiguous cells of relative natural land cover for landscape pattern connectivity.

Overall, of the projects where methods were identifiable, 17 connected patches from their edge, and 8 projects used a patch centroid, occurrence data point, or cell as linkage termini. One project accounted for resistance patterns internal to a patch by using a point 1 mile within a patch on either side of a road to identify road crossing locations (Locating Potential Cougar Corridors in New Mexico [Menke 2008]). Thirteen projects applied a minimum size threshold to patches. Two projects conducted some form of uncertainty analysis regarding termini identification. The Montana Connectivity Project (Herbert and others 2011) tested multiple patch delineation methods for some species, all of which were reviewed and selected by experts prior to the final model runs. Linking Colorado's Landscapes (Kintsch and others 2005) project tested various moving window analysis sizes and minimum patch sizes.

Step 4. Calculate Ecological Distance

We were unable to determine the method of calculating ecological distance for 5 nascent projects. For the remainder, 20 projects used cost distance, 2 applied resistant kernels (Figure 14), 1 project used circuit theory, and 3 projects used a combination of these approaches. Two of the projects that applied a resistant kernel approach tested the sensitivity to the assumed maximum dispersal distance for species of interest; one project is still ongoing, and the other found high sensitivity (Cushman and others 2010). The Pathways project in the Hudson River Valley (Howard and Schlesinger 2012) used a unique method of converting the resistance surface into a triangulated irregular network (TIN), calculating the least cost paths between neighboring patches, and then calculating cost distance between all pairs along the TIN to increase computational efficiency. The Montana Connectivity Project (Herbert and others 2011) also extended the traditional cost distance approach by calculating pairwise cost distances between all pairs of patches and then combining those; we assume additively, but the method is unstated. The researchers for the project also tested circuit and graph theory-based approaches, and used the software program CorridorDesigner (www.corridordesign.

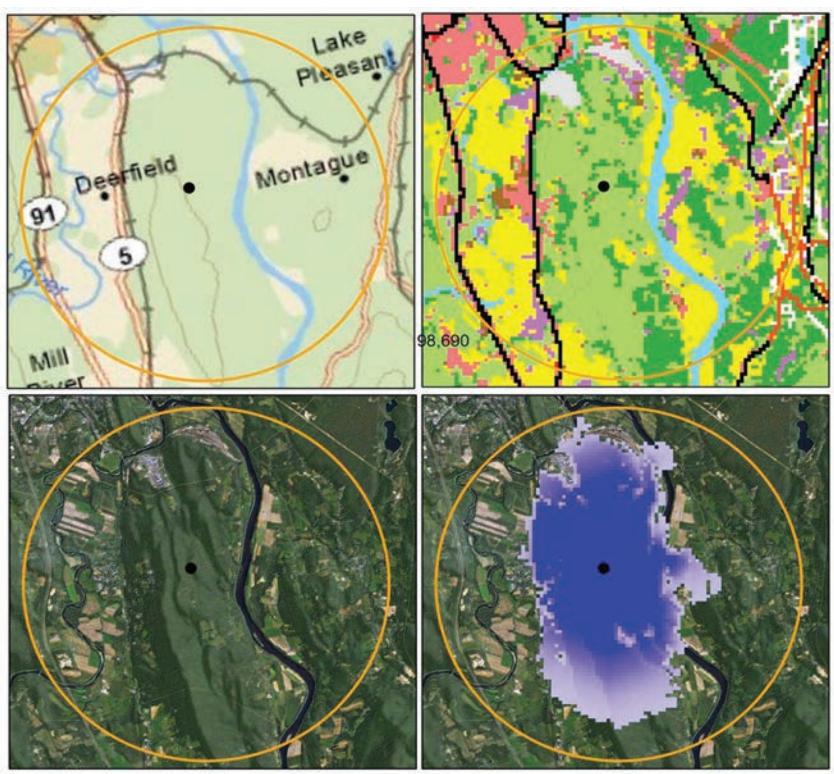


Figure 14—Example of a resistant kernel spreading out to a maximum constrained distance (bottom image) given the underlying resistant layer (top image; here, land use) (Figure 3.6 in Anderson and Sheldon 2012). (Pemission to reprint figure provided by The Nature Conservancy and the authors.)

org) early in the project, but found none suited their modeling purposes. The authors of Mapping Habitat Connectivity Around Military Installations (Moody and others 2011) also found that current flow approaches, when compared to cost distance and individual based movement models, did not work for their purposes, because they failed to suitably represent species with low dispersability.

Step 5. Map Potential Linkages

Only three projects mapped least cost paths directly. The Pathways project (Howard and Schlesinger 2012) also included maps of the LCP; however, the emphasis was on prioritizing importance of land parcels for multi-species linkages. The use of tax parcels to map the number of intersecting linkages provided a mapping unit more useful for planning; however, the use of the LCP fails to recognize the possibility of multiple potential linkages. Five projects buffered the LCP with a minimum width that was not justified in external documents. South Coast Missing Linkages and Arizona Missing Linkages projects (Beier and others 2007; SCW 2008) mapped the union of all focal species' LCP and then buffered by a minimum width (Arizona used an arbitrary 500 m; South Coast tailored buffer width to surrounding habitat type and species dispersability, Figure 15).

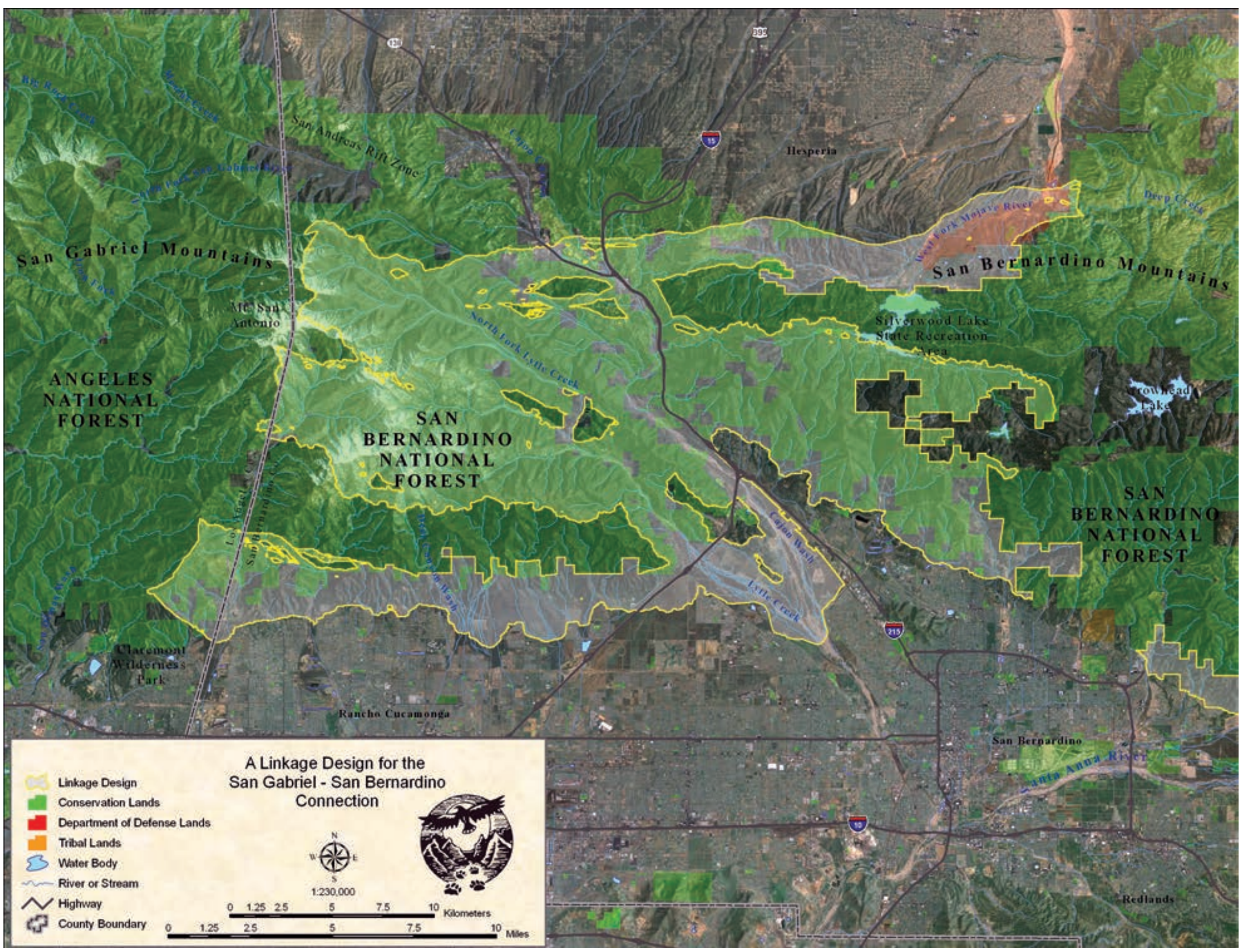


Figure 15—South Coast Missing Linkages mapped linkages by adding a variable buffer around the LCP based on surrounding habitat quality and species-specific needs (page 18 in SCW 2008). (Permission to reprint figure provided by Science & Collaboration for Connected Wildlands.)

Eleven projects categorically mapped cost distance results, with two projects mapping resistant kernel modeling results (path density), one categorically mapping cost distance, two categorically mapping the nth lowest percentile distances, and one categorically mapping the redundancy of LCP between areas of high naturalness (network centrality). The California Essential Habitat project (Spencer and others 2010) only calculated least cost distances within a 5-km buffer around natural landscape blocks, and then mapped the lowest 5% of cost distances within the buffers. The Montana Connectivity Project (Herbert and others 2011) first combined the cost distance maps from all pairwise patch combinations and then categorically mapped the nth percentile lowest distance paths. The Montana project also identified stepping stone patches within identified linkages that could provide stop-over habitat for species with lower vagility. The Mapping Habitat Connectivity Around Military Installations project (Moody and others 2011) categorically mapped cost distance outputs, and then combined all cost distance surfaces using a weighted zonation approach to prioritize linkages across multiple focal species (Figure 16). The Washington Connected Landscape Project (WHCWG 2010)

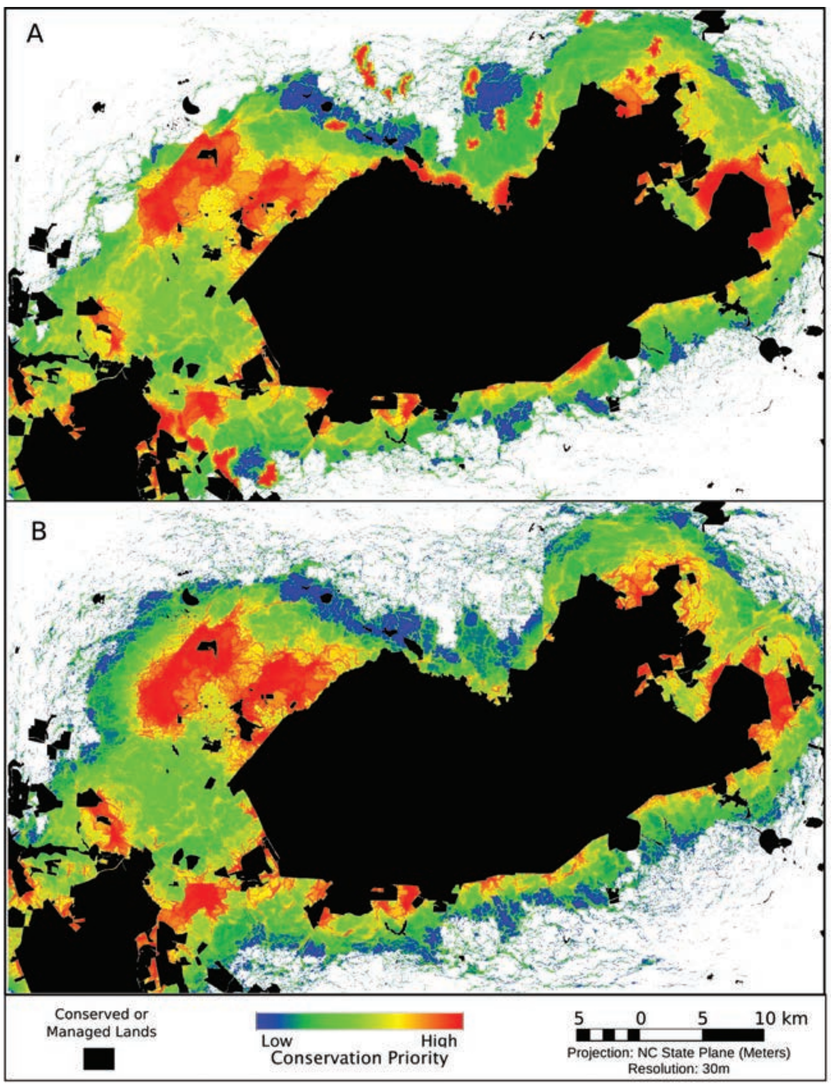


Figure 16—Moody and others (2011) combined calculated least cost distances for all focal species using a weighted zonation approach (Figure 45 in Moody and others 2011); red areas are higher, blue are lower conservation priorities, respectively. (Permission to reprint figure granted by the authors.)

mapped cost distances from four different hypothesized resistance surfaces for species, and then normalized each potential linkage by the least cost path between each pair of natural area patches, categorically mapping linkages by normalized cost distance below a maximum dispersal distance threshold.

Step 6. Validate Potential Linkages

Of the 27 reports reviewed where we could determine validation efforts, 19 did not attempt to validate modeled linkages. However, Fields and others (2010) discuss the potential of the Wild Life Lines project to serve for comparison against other broad extent connectivity models (such as Yellowstone to Yukon). Two connectivity efforts had plans to conduct validation, and 6 remaining studies conducted some form of Model Comparison validation, 5 of which were primarily visual comparisons between potential linkages that were modeled using different approaches. The Washington Connected Landscape Project (WHCWG 2010) compared mapped linkages between focal species and landscape integrity approaches, and they also inspected sensitivity of mapped linkages to underlying assumptions about landscape resistance (Figure 17). Three other projects visually compared linkages to other modeled outputs. Although neither Herbert and others (Montana Connectivity Project; 2011) nor Howard and Schlesinger (Pathways project; 2012) conducted validation per se, both efforts provide exemplary uncertainty reporting, detailing confidence in modeled linkages for each focal species.

The Mapping Habitat Connectivity Around Military Installations project (Moody and others 2011) conducted the most substantial validation. They considered multiple modeling approaches (IBM, current flow, and cost distance) and compared them all to field observation data about species movements. They found current flow was not as robust as other approaches for their organisms of interest. The report also provided excellent graphics mapping both priority areas for connectivity conservation, as well as uncertainty associated with those areas (Figure 18).

Step 7. Assess Climate Change Impacts (Optional)

Of the 3 projects with intent to measure connectivity as a range shift for species persistence under a changing climate, 2 have not yet completed the planned climate change analyses. The third, the Pathways Project (Howard and Schlesinger 2012), used a random forest (Liaw and Wiener 2002) analysis to correlate occurrence point with climatically static (geology, soils, elevation, etc.) and dynamic variables (temperature, precipitation, snow depth). Based on this climate model, habitat suitability was then projected using model-based climate change scenarios. The project provides maps of land parcels that intersect either a suitable habitat patch or a linkage between patches for current and future time periods and demonstrates a clear northward/upward shift in high priority parcels. A few project reports recommend the application of climate analyses for future, finer-scale connectivity modeling efforts. Great Plains and North Pacific Forest Landscape Connectivity projects are currently conducting climate analysis [NPLCC Ongoing; Cushman and others 2010]) and are modeling habitat conditions under three different emissions scenarios and mapping connectivity for each. The Linkage Network for California Deserts (Penrod and others 2012) project uses the Land Facet approach (Brost and Beier 2012), identifying connectivity within areas of relatively similar topographic position, solar insulation, steepness, and elevation, assuming contiguity through these areas represents continued connectivity under a changing climate.

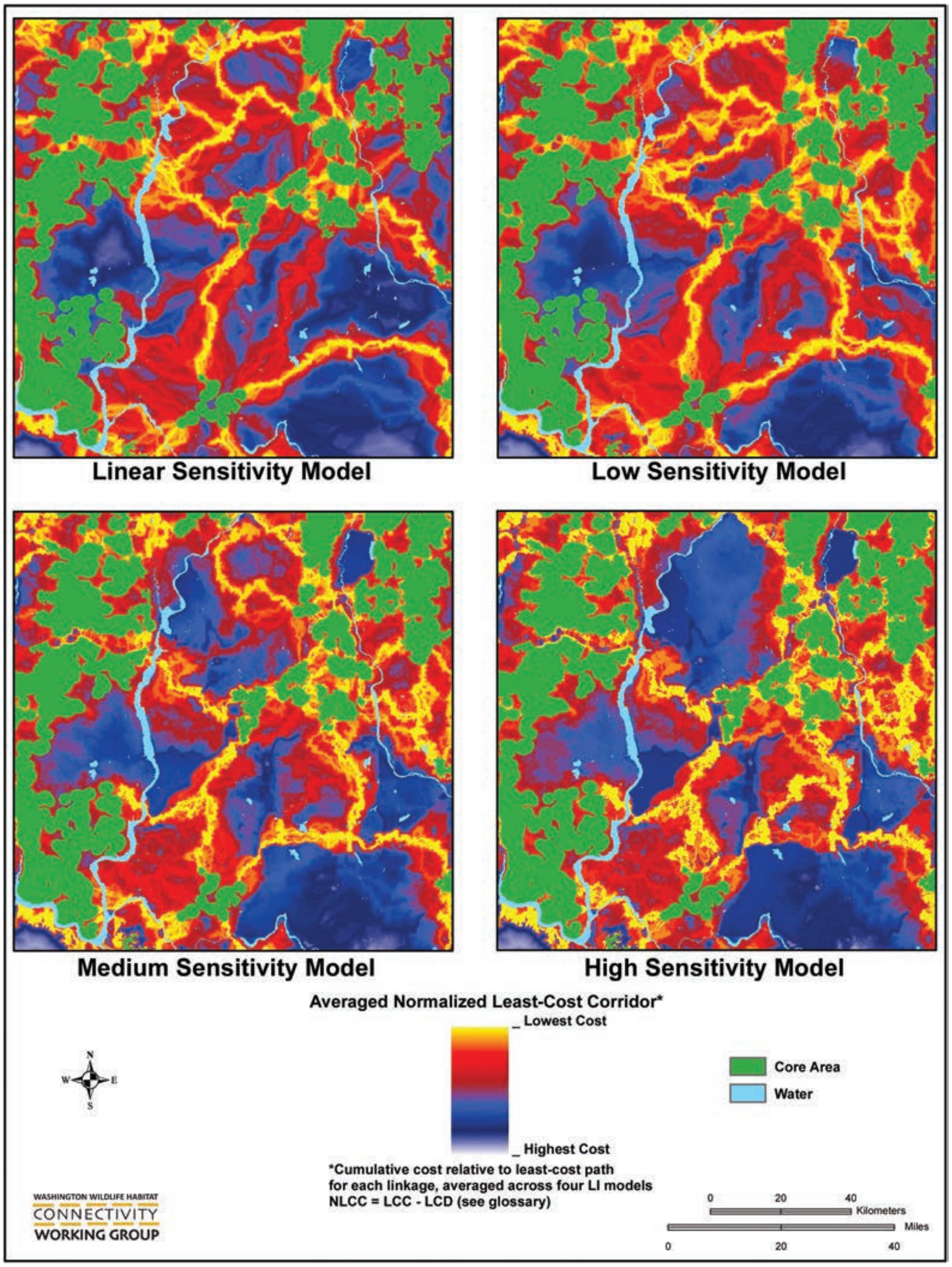


Figure 17—The Washington Connected Landscapes Project compared modeled potential linkage sensitivity to underlying assumptions about species sensitivity to landscape resistance (Figure 3.69 in WHCWG 2010). (Permission to reprint figure granted by the Washington Wildlife Habitat Connectivity Working Group.)

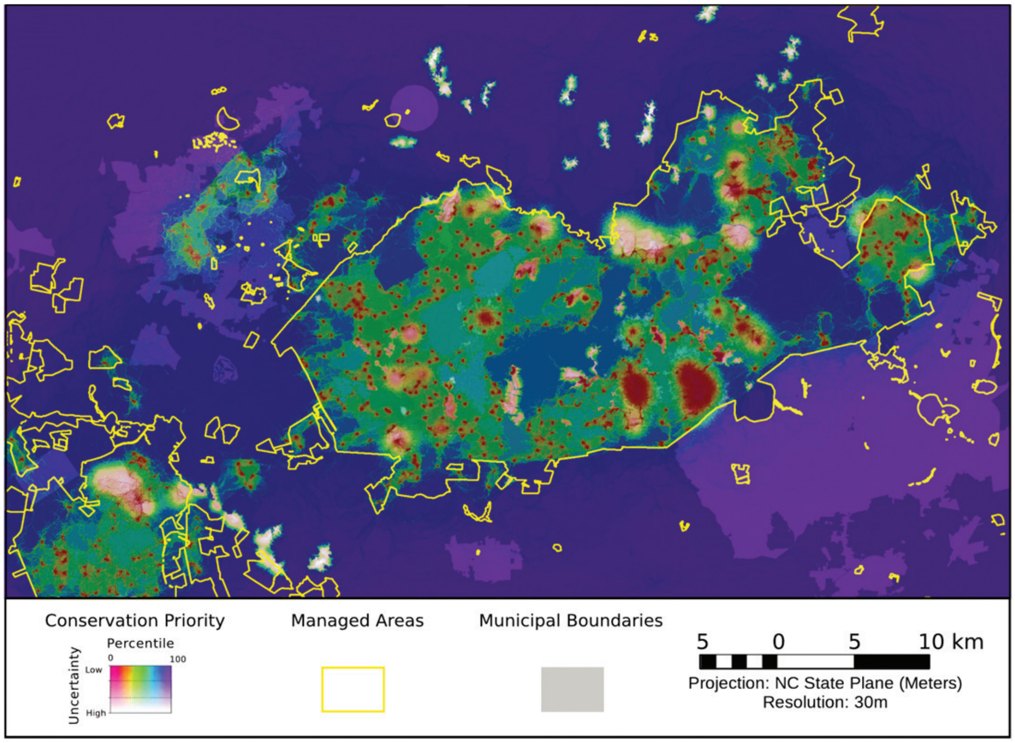


Figure 18—Moody and others (2011, Figure 48) provided excellent graphics mapping both priority areas for connectivity conservation, as well as uncertainty associated with those areas. (Permission to reprint figure granted by the authors.)

Step 8. Quantify Connectivity (Optional)

Both the Delaware Ecological Network and Maryland Green Infrastructure projects (Weber and others 2006; Weber 2007a) prioritized natural areas and linkages by summarizing a number of ecological variables for each, including rare species habitat, unfragmented forest area, and distance to roads. Three projects weighted the edges in a graph network using cost distance. The Linking Colorado's Landscape projects (Kintsch and others 2005) calculated patch connectedness and link importance, weighting edges by 10th percentile cost distance. The Pathways project (Howard and Schlesinger 2012) measured betweenness centrality for each patch, and then mapped that back to the tax parcels to provide a more management-relevant mapping unit. Mapping Habitat Connectivity Around Military Installations (Moody and others 2011) assessed changes in graph connectivity given assumptions about maximum dispersal distances.

We preface our conclusions by noting that many of these practitioner efforts were still in process at the time we compiled these lists. As with the published scientific literature, we note that very few extant connectivity analyses have followed all of these eight steps. However, in general we would argue that these efforts were more aware of the problems and limitations associated with the applied data and methodologies and in many cases applied thoughtful approaches to at least evaluate the associated uncertainties. We think that most of these projects would have benefited from a formal evaluation against a checklist such as our eight steps provide. Even if, ultimately, one decides that a step either is not relevant or cannot be assessed given data limitations, comparison with an *a priori* list of criteria ensures that these decisions are made explicitly; it makes sure that the right questions have been asked. In Chapter 6 we provide specific approaches to guide this process.

Chapter 6. Guiding Questions for Practitioners

Each connectivity modeling project has unique conservation goals. No set of guidelines will ensure success for all connectivity modeling efforts; we urge modelers to review available "best practices" lists in addition to this report (Beier and others 2008, in particular, 2011; Sawyer and others 2011; Rudnick and others 2012). However, we believe that the eight steps we have identified, if closely followed, will ensure that all important aspects of model development and validation have been addressed. Here, we provide a set of guiding questions and suggestions to assist practitioners in modeling robust wildlife linkages with resistance-surface methods. Think of these questions as a kind of check-list. You may answer the question with "I don't know" or "We didn't do that," but it is important to make these knowledge gaps and process omissions explicit. Once explicit, one can begin to ask ancillary questions such as: "Can we find out?" and "Can we and should we do that?"

Step 1. Define Type of Connectivity to Be Modeled

1. What is the conservation problem? How important is connectivity?
2. What is (are) the species of concern?
3. What type of movement(s) will best respond to the conservation problem for the given organism(s)? See chapter 2 for a complete discussion of the type of organism movement and hence connectivity being modeled. Specifically state the type(s) of connectivity to be modeled.
4. Specifically, how will retaining or enhancing this type of movement improve the organism's fitness or resilience?
5. How will this movement change the probability of persistence of the organism in a patch?
6. What is the state of the knowledge about the given organism's habitat preferences, life history, genetic, and demographic needs, and associated movement behaviors?
7. What biological requirements are associated with the modeled movement?
8. What data are available, empirical or qualitative, about the organism's movement behaviors? What data are available that could be used as proxies for these behaviors, and do they represent appropriate proxies?
9. Will one model be adequate to represent all types of movement or are different movement types sufficiently diverse to require different modeling approaches?
10. Draw a conceptual model linking conservation problem, organism's fitness needs, type of connectivity, resistance layer development, and linkage modeling. What are the assumptions at each step?

Step 2. Create the Resistance Layer

Step 2a. Resistance layer scale

1. Is a hierarchical modeling approach, starting with coarse scale models, qualitative data, and general assumptions and refined with finer scale models an appropriate paradigm? If so, how does this affect the generation of a resistance layer? Where is this particular modeling effort intended to fit into the hierarchy?
2. What modeling extent is appropriate for the type of movement modeled? What modeling extent is sufficient to maximize the number of potential links identified to avoid mapping artifacts? Are data beyond the target area available?

3. What is the organism's perceptual grain? How does it see the world, given the type of connectivity being modeled? What cell size, in a GIS, best represents this perceptual grain? What other methods could be considered to represent the organism's perceptual grain?

Step 2b. Determine ecological variables

4. What, specifically, are resistance-surface values intended to represent? Travel time? Fitness costs (e.g., mortality risks)? Search time? Difficulty in travel (e.g., physical barriers)? Habitat suitability?
5. List all of the biotic and abiotic influences on movement behavior. What variables would best serve as proxies for these influential effects?
6. What data are available that relate to the identified proxy measures? Are these data available at an appropriate scale and resolution?
7. How does the scale (temporal and spatial) of the data relate to the organism's perceptual grain and extent? How can mismatches between spatial and temporal scales be minimized?
8. How good are the data? How do classification and other errors in the available data affect model performance and inference? How sensitive are the data to scaling decisions?

Step 2c. Assign resistance values

9. What are the best available data and how can they best be applied to minimize uncertainty in the relationship between resistance-surface values and hypothesized movement behavior (see Figures 3 and 4)?
10. Are empirical data available for developing resistance values in either a one-step (model development) or two-step (model selection) framework?
11. If no empirical data are available, how can expert opinion be obtained and quantified to incorporate and minimize uncertainty?
12. How certain is the relationship between modeled resistance values and movement behavior?
13. How certain are you regarding the contrast between different resistance values?
14. How do multiple ecological influences combine to affect likely resistance to organism movement? How should ecological variables be combined to best represent these relationships? Do they need to be combined, or can empirical data be used in a matrix regression to evaluate data?
15. See Zeller and others (2012) for additional decision support.

Step 2d. Validate resistance surface

16. How sensitive are results to the analysis grain? (Select a reasonable grain on the basis of organism size, dispersability, movement type, etc., and conduct sensitivity test against finer and coarser grains.)
17. How sensitive are results to the quality of ecological variable data?
18. How sensitive are results to the incorporation of different ecological variables used in creating the resistance surface?
19. How sensitive are results to the resistance values assigned and the contrast between different values?
20. How sensitive are results to the method used to combine multiple ecological variables into a single resistance surface?

21. What empirical data are available to test stability (cross-validation) of resistance-surface model?
22. Are independent empirical data available for validation of the resistance surface? Are the available data directly related to the type of movement being modeled (e.g., genetic data may not be appropriate for daily life history movement)? What are the potential mismatches between the resistance surface intent and the available validation data?

Step 3. Define What is Being Connected

1. What type of habitat or landscape element requires connectivity to address the conservation problem?
2. How does the organism perceive these habitats or landscape elements? How can termini be represented to reflect the organism's perception (both temporal and spatial; see Table 1)?
3. If the termini represent some form of patch (polygon), how will modeling account for movement dynamics internal to the patch? How much of the landscape lies within patches?
4. Are there empirical or qualitative data to support the termini choice (e.g., do occurrence data suggest these termini are used by the organism)? Similarly, are there empirical or qualitative data to support the decision not to place termini in specific areas (e.g., evidence that the organism does not exist in certain areas)?
5. How does the distance between termini reflect the movement behavior of the organism? Are the distances appropriate for the type of movement?
6. How sensitive are results to the placement of termini? Size of termini? Number of termini? How sensitive are results to using the centroid of the termini versus the edge?
7. How temporally and spatially robust are the termini? How are they likely to shift or change over time, and how does this affect modeled linkages?

Step 4. Calculate Ecological Distance

1. What ecological distance method best corresponds to the organism and movement type (see Table 2)? How well do the methods reflect an organism's knowledge and perception of the landscape?
2. Test two or more methods. How sensitive are results to the chosen methods?
3. Is one method best for one aspect of movement? Should results combine ecological distances from multiple approaches, or does one method appear better for the modeling purposes?
4. Is the goal to locate the least cost path, a pinch-point, or to evaluate general connectivity across a broad area?

Step 5. Map Potential Linkages

1. How will map of connectivity be used in conservation planning? Is categorical mapping of ecological distance sufficient for intended map purposes? Are spatially explicit linkages necessary? How will the map be perceived by policy makers, funders, and the public? Are there legal ramifications associated with corridor mapping?
2. Is there any scenario under which a single LCP is a suitable representation for potential linkages? If so, how sensitive is the resulting path to likely errors in the underlying data used to build the resistance surface?

3. How do the mapped linkages incorporate the surrounding landscape and account for habitat quality, organism's life history needs during movement, and potential for multiple linkages (e.g., corridor dwellers, use of stepping stones, edge effects from neighboring land uses)?
4. What is the width of a mapped linkage and how does that affect its potential for use as a movement path?
5. What is the length of a mapped linkage and how does that affect its potential use? Does the resulting linkage map reflect the vagility of the organism?
6. How sensitive are the results to assumed functional relationship between ecological distance and likelihood of linkage use for wildlife movement?
7. How should linkages be prioritized?

Step 6. Validate Potential Linkages

1. Are there independent occurrence, inferential, or path data (Chapter 4) available for validating models?
2. If empirical data are available are they independent of the data used to build the initial map?
3. Are validation data collected at (or relevant to) the same temporal and spatial scale of the map to be validated?
4. What are the biases associated with the collected data (e.g., occurrence data only on public land)?
5. If validation is not possible, how should sensitivity be tested? What key variables should be allowed to vary for sensitivity testing?

Step 7. Assess Climate Change Impacts (Optional)

1. Do downscaled climate data exist at scales relevant to the connectivity modeling effort?
2. What is the projected magnitude and rate of climatic change for the study area?
3. Will potential linkages remain robust under shifting temperature and precipitation regimes?
4. Are there landscape elements or ecological variables that should be included in the resistance surface to account for climate change? Can modeling be conducted with multiple scenarios of projected climate change?

Step 8. Quantify Connectedness (Optional)

1. What are the assumptions underlying the chosen measure of connectedness? How does the measure relate to the organism's perception of a connected landscape?
2. How sensitive is model inference to the measure of connectedness?

Chapter 7. Conclusions and Synthesis

Connectivity is important for the long-term persistence of many organisms. Maintaining or enhancing connectivity has become a common conservation goal to offset increasingly fragmented habitat throughout the world. Furthermore, connectivity is essential for organisms to respond to changes in climate, large scale disturbances, and ecological changes due to factors such as the invasion of exotic species. If we experience rapid directional climate change during the next several centuries, large spatial shifts in optimum climatic niches are anticipated for many—probably most—organisms; if species are to keep pace with shifting habitats, dispersal through well connected habitats will be essential (e.g., Iverson and Prasad 1998).

Ecologists have long understood that connectivity is critical for species persistence (Levins 1969b, 1970), but the study of connectivity has been fraught with controversy. Much of the debate surrounding landscape connectivity concerns whether linkages are likely to be effective (both financially and ecologically) given the uncertainties concerning organism movement behavior. The advent of cost-path modeling, geographic information systems, and nationally available ecological resource datasets has revolutionized the field of connectivity modeling, providing numerous approaches for evaluating landscape permeability. Thus, connectivity modeling has become common. The resulting graphics are attractive and detailed, and the maps provide precise locations for presumed linkages, potentially facilitating directed conservation activities.

The emerging field of landscape genetics (Manel and others 2003) has also provided impetus for renewed interest in connectivity modeling. The movement of genes is closely linked to the movement of organisms and, in many cases connectivity maps have been generated based on correlations with genetic patterns.

In this manuscript, we have given overviews of the various methodologies and a framework within which to organize connectivity modeling, implementation, and validation. Additionally, we have provided extensive references both to published journal articles and on-the-ground applications of these methods. However, we have provided relatively little information concerning the efficacy of these methods; the relationship between these maps and actual animal movement patterns remains largely unknown.

Basing connectivity on genetic patterns or other movement-based data (e.g., the output from state-space models) is clearly desirable; using these types of data provides some rationale for considering one connectivity map to be better than another. It does not, however, indicate in any absolute sense the quality or sufficiency of the modeled corridors. While recent work has questioned the model selection process (e.g., Guillot and Rousset 2011; Cushman and others 2013), many more fundamental issues surround the use of resistance surfaces to evaluate connectivity. Critically, these models do not incorporate important, but likely ephemeral biological exigencies: the need to locate food, avoid predators, or invade a dominant competitor's territory. Population dynamics, which strongly drive both dispersal dynamics and desirable destination locations, are also not generally considered.

All resistance-surface-based connectivity algorithms assume a directional force that drives movements; organisms are dedicated to moving from one terminus to another and in some cases know the perfect route to follow. This very specific drive, when applied to a resistance surface and given a finite and fixed group of specified termini, channels movement into tightly defined linkages, reinforcing the idea that these structures have both reality and merit. However, this is not necessarily the case. If we relax these assumptions then both movement patterns and our general perception of them become very different. If, for example, movements across areas lacking suitable habitat were largely random, there would be no formal corridors. Similarly the locations of source and destination termini may be highly artificial. Organisms disperse, seeking better habitat, and settle based on a local evaluation of habitat quality—locations that may or may not be identified as containing a pre-defined terminal patch.

None of this is to say that connectivity modeling using resistance surfaces is not a useful and appropriate activity, especially when combined with efforts to validate these surfaces. Quite the contrary; it is a much better approach than previous strategies, such as drawing lines on maps based solely on consensus opinion. Among other things, it requires formalization of connectivity assumptions and their quantification, and is both understandable and repeatable.

However, any connectivity map based on the approaches examined here must, lacking strong external validation, be considered to be a largely untested hypothesis rather than a tested solution to a problem. As we have noted, validation of connectivity maps is virtually non-existent. In part, this may be due to the relative nascence of wildlife connectivity modeling. While efficient algorithms for least cost paths have been around since the 1980s (Fredman and Tarjan 1987) with current approaches based on accumulated cost surfaces dating to the mid 1990s (Douglas 1994), the utilization of these methods to identify connectivity patterns for wildlife is quite recent (Walker and Craighead 1997). As such, it is only recently that land management agencies have broadly embraced this approach and begun to apply it to actual land management problems.

Perhaps a simpler explanation for the lack of connectivity validation is that it is difficult. Movement data, and particularly between-population movement data, has been notoriously hard to collect. New technologies to sample (forensic and environmental DNA, digital infrared cameras) and locate (reliable, energy efficient GPS) organisms coupled with advances in population and landscape genetics now allow us to better estimate movements and evaluate the efficacy of putative linkages. However, these new technologies do not remove the need for long-term targeted monitoring of putative linkages to determine how well they actually are working.

From our review of connectivity modeling, we can now provide some broad advice to those thinking of embarking on a connectivity modeling exercise for their region. First, is the recognition that not all connectivity modeling efforts are equal. Nearly anyone can download a raster coverage, reclassify the pixels to create a resistance surface, identify termini, and produce a seemingly meaningful connectivity map. However, efforts that are spent articulating objectives, understanding data limitations, and considering how the focal species may view the landscape (if that is, indeed, the objective) produce far better products that are more justifiable than efforts that fail to complete these steps. Due to this recognition, we delineated the eight connectivity steps detailed previously and listed guiding questions for each step. If followed, these provide a logical framework for conducting connectivity modeling. Following this process ensures that appropriate measures to improve model quality have not been overlooked. For example, in reviewing extant connectivity modeling, it is surprising the degree to which basic ideas such as the type of movement and even the target species have not been well defined. Clearly, the formal clarification of model objectives will improve both model quality and facilitate model validation.

In closing, our advice is to take advantage of the strengths of resistance-surface connectivity analyses; these methods provide valuable tools to avoid resource conflicts and provide clear rationales for management prioritization. However, it is essential to remain aware of their weaknesses, assumptions, and methodological quirks. Lastly, we believe that wildlife movement monitoring is required prior to making any declarations or assumptions concerning actual linkage efficacy.

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Appendix 1—Resistance-surface connectivity modeling literature reviewed in this report. Papers highlighted in grey did not have the primary intent of mapping linkages, but we include them because they offer something novel in their approach to general resistance-surface-based connectivity assessment. For details on individual columns, refer to the discussion in the text for the appropriate related modeling step.

Paper Title	Author, Year, Journal	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Modeling connectivity of black bears ...	Atwood et al., 2011, Biological Conservation	Map linkages / Undefined	Occupancy Model to score Habitat Suitability Model	Land Cover, Topography, Distance to Roads, Distance to Water	Expert Opinion with Occurrence Data (hair snag sample locations PSF) for model selection	No	Patch Edge	Cost Distance	Buffer LCP accounting for habitat quality within home range width	No	No	No	No
The use of focal species in designing a habitat Network	Bani et al., 2002, Conservation Biology	Map linkages / Undefined	Habitat Suitability Model	Forest Cover Type	Occurrence Data (transect search for signs PSF)	No	Patch Edge	Cost Distance	Map LCP	No	No	No	No
Biodiversity considerations in conservation system planning...	Beazley et al., 2005, Ecological Applications	Conservation area design and map linkages/ Migration and "Dispersal"	Habitat Suitability Index	Forest Cover, Road Density	Expert Opinion with Occurrence Data (moose pellets PSF) for model selection	No	Patch Edge	Cost Distance	Buffer LCP by home range width	No	No	No	No
Landscape connectivity: a conservation application of graph theory	Bunn et al., 2000, Journal of Environmental Management	Calculate graph / "Dispersal"	Habitat Suitability	Land Cover, Human Development	Expert Opinion	No	Patch Edge	Cost Distance Graph	Weight graph by dispersal probability function	NA	No	Yes	Methods of graph edge weighting
Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of Gray Wolf...	Carroll et al., 2012, Conservation Biology	Calculate graph connectivity and map linkages/ "Functional"	Habitat Suitability	Land Cover, Primary Productivity, Slope, Road Density, Human Population Density	Expert Opinion	No	All hexagon centroids in GIS lattice	Compared output from: Cost Distance, Circuit Theory, Network Flow	Map betweeness centrality	Some	No	Yes	Analysis grain size, connectivity methods
Landscape genetics of mountain lions...	Castilho et al., 2011, Mammalian Biology	Assess connectivity and map linkages / Genetic	Habitat Suitability	Land Cover	Expert Opinion	Correlated ecological distance with genetic distance	Protected Areas, Sample Collection Locations	Circuit Theory	Categorically map conductance	No	No	No	No
Use of resource selection functions to identify conservation corridors	Chetkiewicz and Boyce, 2009, Journal of Applied Ecology	Map linkages / Undefined	Seasonal Habitat Suitability Model	Land Cover, Subregion, Food Resources, Topography, Road Density	Occurrence Data (telemetry PSF)	No	Patch Edge	Cost Distance	Buffer LCP	Some	No	No	Resistance surface cross-validation

Paper Title	Author, Year, Journal	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Use of empirically derived source-destination models to map regional conservation corridors	Cushman et al., 2008, Conservation Biology	Map linkages / "Dispersal"	Habitat Suitability Model, Barriers	Elevation, Forest Cover, Roads	Expert Opinion with Genetic Distance (MSF) for model selection	Assessed similarity of top models selected	Systematic placement of points	Cost Distance	Buffer LCP with parabolic kernel smoothing	No	No	No	No
Movement behavior explains genetic differentiation ...	Cushman and Lewis, 2010, Landscape Ecology	Identify resistance factors / "Dispersal"	Habitat Suitability Model, Barriers	Elevation, Canopy Cover, Roads, Human Structures	Expert Opinion for model development with Movement Data (telemetry PathSF) for model selection	Compared RS from movement data with RS from genetic distance	NA	NA	NA	NA	No	NA	Analysis grain size
Multi-taxa population connectivity ...	Cushman and Landgruth, 2012, Ecological Modeling	Assess connectivity and map linkages / "Dispersal"	Habitat Suitability , Barriers	Elevation, Forest Cover, Roads	Expert Opinion (representing hypothetical species)	No	Lowest resistance cells	Resistant Kernel Analysis	Categorically map resistant kernel	NA	No	No	Dispersal distances
Integrative approach for landscape-based graph connectivity analysis...	Decout et al., 2012, Landscape Ecology	Assess connectivity / Life history and demographic	Habitat Suitability , Barriers	Land Cover, Road Traffic Counts	Expert Opinion	No	Breeding Sites	Cost Distance Graph within "Suitable Habitat* corridor connecting breeding sites	Limit graph edges to dispersal thershold	Some	No	Yes	No
Evaluating least-cost model predictions with empirical dispersal data...	Driezen et al., 2007, Ecological Modeling	Assess resistance / "Dispersal"	Habitat Suitability, Barriers	Land Cover, Roads, Railroads, Streams	Expert Opinion with Movement Data (radiotracked PSF) for model selection	Compared ecological distance from source at known location along path vs. all other cells at same Euclidean distance from source	Release Sites	Cost Distance	Map LCP	NA	No	No	No
Optimizing dispersal and corridor models using landscape genetics	Epps et al., 2007, Journal of Applied Ecology	Assess connectivity and map linkages / "Dispersal"	Binary Slope Threshold, Barriers	Slope, Anthropogenic Barriers	Expert Opinion with Genetic Distance (MSF) for model selection	No	Patch Edge	Cost Distance	Map cost distance under dispersal threshold over which gene flow detected	Some	No	No	Resistance contrast, patch delineation, slope threshold , gene flow

Paper Title	Author, Year, Journal	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Land-cover change and the future of the Apennine brown bear...	Falcucci et al., 2008, Journal of Mammalogy	Assess connectivity / Landscape (habitat) pattern	Deductive Model Habitat Suitability	Land Cover, Elevation	Expert Opinion	No	Patch Edge	Cost Distance	Categorically map least cost distance	No	No	Semi	Habitat suitability models
Modelling the habitat requirements of leopard...	Gavahelishvili and Lukarevskiy, 2008, Journal of Applied Ecology	Assess connectivity and map linkages / Undefined	Habitat Suitability Model	Climate, Topography, Natural Land Cover, Human Disturbance	Expert Opinion with Occurrence Data (presence/ absence PSF) for model selection	No	Occurrence Data	Cost Distance	Map LCP	No	No	No	Resistance surface cross-validation
Connectivity of core habitat in the northeastern United States...	Goetz et al., 2009, Remote Sensing of Environment	Assess connectivity and map linkages / Landscape pattern	Landscape Integrity	Forest Cover, Human Modification, Water	Expert Opinion	No	Patch Edge	Cost Distance Graph	Weight graph by cost distance	No	No	Yes	No
...Landscape genetics of the Mojave desert tortoise	Hagerty et al., 2010, Landscape Ecology	Assess connectivity and map linkages / Demographic and genetic	Habitat Suitability Model	Topography, Vegetation Cover, Climate	Occurrence Data (presence PSF) split for model building and selection	Correlated ecological distance with genetic distance	Occurrence Data	Cost Distance Graph, Circuit Theory	Weight graph by cost distance	No	No	No	Con-nectivity methods
Ecological networks as a new approach for nature conservation ...	Hepcan et al., 2009, Landscape and Urban Planning	Map linkages / Landscape (habitat) pattern	Habitat Suitability	Vegetation Cover, Carrying Capacity , Road Density	Expert Opinion	No	Patch Edge	Cost Distance	Buffer LCP by minimum width	No	No	No	No
Spatial genetic structure and dispersal of giant pandas on a mountain-range scale	Hu et al., 2010, Conservation Genetics	Assess connectivity / "Dispersal"	Habitat Suitability Model	21 Ecogeographical variables	Occurrence Data (telemetry PSF)	No	Occurrence Data	Cost Distance	NA	NA	No	No	No
Analyses of least cost paths for determining effects of habitat types on landscape permeability...	Huck et al., 2011, Acta Theriologica Sinica	Assess connectivity / "Dispersal"	Habitat Suitability Model (Ecological Niche Factor Analysis) , Barriers	Land Cover, Roads	Expert Opinion , Occurrence Data (presence, signs HSF)	Compared LCP between populated and unpopulated patches and using genetic distance	Patch Edge	Cost Distance	NA	NA	No	No	No

Paper Title	Author, Year, Journal	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Assessing landscape connectivity with calibrated cost-distance modeling...	Janin et al., 2009, Journal of Applied Ecology	Assess resistance / Migration and "Dispersal"	Habitat Suitability Model, Barriers	Land Cover, Rivers, Roads	Expert Opinion with Occurrence Data (presence/ absence PSF) for multi-scale model selection	Independent Occurrence Data	Patch Edge	Cost Distance	NA	NA	No	No	Hierarchal approach to analysis grain size, resistance surface cross-validation
...Landscape-scale conservation for the Florida Panther	Kautz et al., 2006, Biological Conservation	Map linkages / Life history	Habitat Suitability Model	Land Cover (with urban including roads and power lines)	Occurrence Data (telemetry PSF & HSF)	No	Patch Edge	Cost Distance	Buffer LCP by minimum width based on telemetry paths and surround-ing landcover type	No	No	No	Resistance values of water and roads, habitat suitability modeling approach
Identifying habitat linkages for American black bears...	Kindall and Van Manen, 2007, Journal of Wildlife Management	Map linkages / Landscape (habitat) pattern	Habitat Suitability Model	Forest Cover	Weights of Evidence of Occurrence Data (telemetry PSF)	Comparison to a null model	Patch Edge	Cost Distance	Categorically map least cost distance	No	No	No	Telemetry location error, resistance surface cross-validation
Functional habitat connectivity of the American Marten ...	Kirk and Zeilinski, 2010, USFS White Paper	Map linkages / "Dispersal"	California Wildlife Habitat Relationship Model	Vegetation Cover, Topography, Rivers, Highways, Burned Areas	Expert Opinion	No	Patch Edge	Cost Distance	Map top 10th and 25th percentile paths	No	No	Yes	No
Landscape resistance and American marten gene flow	Koen et al., 2012, Landscape Ecology	Assess connectivity / Genetic	Habitat Suitability	Forest Cover	Expert Opinion	Correlated ecological distance with genetic distance	NA	Circuit Theory (and Euclidean Distance)	NA	NA	No	No	Resistance values contrast, con-nectivity method
Landscape linkages and conservation planning for the black bear...	Larkin et al., 2004, Animal Conservation	Map linkages / Demographic and genetic	Habitat Suitability, Barriers	Land Cover, Roads	Expert Opinion	No	Patch Edge	Cost Distance	Map LCP	No	No	Yes	Resistance value contrast
Modeling potential dispersal corridors for cougars...	LaRue and Nielsen, 2008, Ecological Modeling	Map linkages / "Dispersal"	Habitat Suitability	Land Cover, Human Density, Distance to Roads, Slope, Distance to Water	Expert Opinion (Analytical Hierarchy Process)	Independent Occurrence Data (LaRue 2007)	Patch Edge	Cost Distance	Buffer LCP	No	No	No	No
Landscape conservation and regional planning for the Florida panther	Meegan and Maehr, 2002, Southeastern Naturalist	Map linkages / Demographic	Habitat Suitability	Forest Cover, Urban Areas, Roads	Expert Opinion	No	Patch Edge	Cost Distance	Map LCP	Some	No	No	No

Paper Title	Author, Year, Journal	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Testing the importance of spatial configuration of winter habitat for woodland...	O'Brien et al., 2006, Biological Conservation	Calculate graph connectivity / Landscape (habitat) pattern	Habitat Suitability Model	Forest Cover, Stand Age, Topography, Water	Occurrence Data (telemetry PSF)	Independent Occurrence Data	Patch Edge	Cost Distance Graph	NA	NA	No	Yes	Error in resistance surface, dispersal distances
Beyond the least-cost path: evaluating corridor redundancy...	Pinto and Keitt, 2009, Landscape Ecology	Assess effects of habitat clustering on connectivity / "Dispersal"	Landscape Integrity	Forest Cover, Human Footprint, Agriculture	Expert Opinion	NA	Patch Edge	Cost Distance	Categorically mapped con-ditional minimum transit cost, multiple shortest paths	NA	No	No	No
Maintaining or restoring connectivity of modified landscapes: evaluating the least-cost path model...	Pullinger and Johnson, 2010, Landscape Ecology	Assess validity of least cost path methods / Dispersal ("long distance movement")	Habitat Suitability Model	Land Cover, Distance to Predation Risk, Distance to Water bodies, Distance to Roads, Elevation, Topography	Expert Opinion (Analytical Hierarchy Process) OR Occurrence Data (telemetry PSF) for model selection	Independent Occurrence Data	Telemetry Points	Cost Distance	Map LCP	Yes	No	No	Resistance surface cross-validation
A range-wide model of landscape connectivity and conservation for the jaguar...	Rabinowitz and Zeller, 2010, Biological Conservation	Map linkages / "Dispersal"	Habitat Suitability	Natural Land Cover, Percent Tree and Shrub Cover, Elevation, Human Population, Roads	Expert Opinion	No	Patch Edge	Cost Distance	Map lowest 0.1% of cell values	In Progress	No	Yes	No
Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx	Schadt et al., 2002, Ecological Applications	Map linkages / Landscape (habitat) pattern	Habitat Suitability	Frag-mentation, Barriers (rivers, highways, urban), Forest Cover	Expert Opinion	No	Patch Edge	Cost Distance	Map LCP	No	No	Yes	Grid cell size used in determining Frag-mentation
Wolverine gene flow across a narrow climatic niche	Schwartz et al., 2009, Ecology	Assess connectivity and map linkages / "Dispersal"	Habitat Suitability	Spring Snow Cover	Expert Opinion	Correlated ecological distance (and Euclidean Distance) with genetic distance	Systematic placement of points	Cost Distance, Circuit Theory	Buffer LCP with parabolic kernel smoothing and map redundancy	No	No	No	Resistance value contrast, connectivity method

Paper Title	Author, Year, Journal	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Proposed conservation landscape for giant pandas...	Shen et al., 2008, Conservation Biology	Map linkages / Demographic	Habitat Suitability	Land Cover, Forest Cover, Elevation, Slope, Aspect, Distance to Roads, Distance to Residential Area	Expert Opinion (Analytical Hierarchy Process)	No	Patch Edge	Cost Distance	Map cells under (unstated) accumulated cost threshold	No	No	No	Resistance values, land cover classes
Using weighted distance and least-cost corridor analysis to evaluate regional-scale large carnivore habitat connectivity ...	Singleton et al., 2001, International Conference of Ecology and Transp. Proceedings	Map linkages / Life history, genetic, demographic	Habitat Suitability	Land Cover, Human Density, Roads, Slope	Expert Opinion	No	Patch Edge	Cost Distance	Categorically map least cost distances within "fracture zones"	No	No	No	No
Landscape permeability for grizzly bear movements ...	Singleton et al., 2004, Ursus	Assess permeability / Demographic and genetic	Habitat Suitability	Land Cover, Human Density, Roads, Slope	Expert Opinion	No	Patch Edge	Cost Distance	Categorically map lowest 10% of cost surface	No	No	No	No
Gene flow and functional connectivity in the natterjack toad	Stevens et al., 2006, Molecular Ecology	Assess connectivity / "Dispersal"	Habitat Suitability Model	Land Cover, Water, Buildings	Movement Efficiency and Preference (MSF)	Correlated ecological distance with genetic distance	Patch Edge	Cost Distance	NA	NA	No	No	Resistance values, measures of gene flow
A habitat assessment for Florida Panther population expansion ...	Thatcher et al., 2009, Journal of Mammalogy	Map linkages / Demographic	Habitat Suitability Model	Natural Land Cover, Road Density, Human Population Density, Floodedness	Expert Opinion with Occurrence Data (telemetry HSF) for model selection	Independent Occurrence Data	Patch Edge	Cost Distance	Categorically map least cost distance	No	No	No	Resistance surface cross-validation, habitat patches
Connecting natural landscapes using a landscape permeability model...	Theobald et al., 2012, Conservation Letters	Assess permeability and map linkages / Landscape pattern	Landscape Integrity	Land Cover, Housing Density, trans-portation Infrastructure, Highway Traffic, Resource Extraction, Canopy Cover, Slope	Expert Opinion	No	Iterative, random selection of lowest resistance cells	Cost Distance (calculated for entire map extent)	Categorically map network centrality	No	No	Yes	Resistance values

Paper Title	Author, Year, Journal	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
A conservation design for the central coast of California ...	Thorne et al., 2006, Natural Areas Journal	Map linkages / Landscape (habitat) pattern	Habitat Suitability	Forest Cover, Road Density	Expert Opinion	No	Patch Edge	Cost Distance	?	No	No	No	No
A new analytical approach to landscape genetic	Van Strien et al., 2012, Molecular Ecology	Assess resistance / Genetic	Habitat Suitability Model	Land Cover, Streams	Expert Opinion with Genetic Distance (MSF) for model selection	No	Patch Edge	Cost Distance, Circuit Theory, Least Cost Transect	NA	NA	No	No	Resistance value contrast, connectivity method
Functional connectivity of lynx ...	Walpole et al., 2012, Landscape Ecology	Assess resistance and map linkages / "Functional"	Occupancy Model to score Habitat Suitability Model	Forest Cover, Forest Age, Snow Conditions, Distance to Roads, Distance to Forestry, Time Since Snowfall	Expert Opinion with Occurrence Data (telemetry PSF) for model selection	Independent Occurrence Data	Patch Edge	Circuit Theory	Categorically map conductance	Yes	No	No	Analysis grain size
Landscape genetics and least-cost path analysis reveal unexpected dispersal routes for salamander...	Wang et al., 2009, Molecular Ecology	Assess resistance and map linkages / Genetic	Habitat Suitability Model	Land Cover	Expert Opionion with Genetic Data (MSF) for model selection	No	Occurrence Data	Cost Distance	Map LCP	No	No	No	No
Simulating the effects of climate change on population connectivity of American marten ...	Wasserman et al., 2012, Landscape Ecology	Assess connectivity under a changing climate / Genetic	Habitat Suitability Model	Elevation	Expert Opionion with Genetic Data (MSF) for model selection	No	Systematic placement of points	Resistant Kernel Analysis	NA	NA	Yes	Yes	No
Designing a conservation landscape for tigers in human dominated environments	Wikramanayake et al., 2004, Conservation Biology	Map linkages / Genetic and demographic	Habitat Suitability	Natural Land Cover, Human Modification	Expert Opinion	No	Patch Edge	Cost Distance	Map top 10th, 20th, and 30th percentile paths	No	No	No	No
Potential habitat connectivity of European bison...	Ziółkowska et al., 2012, Biological Conservation	Calculate graph connectivity / "Dispersal"	Habitat Suitability Index	Forest Cover, Forest Frag-mentation, Distance to Roads, Distance to Settlements , Roads, Rivers, Topography	Depending on herd: Expert Opinion or Occurrence Data (telemetry PSF)	No	Patch Edge	Cost Distance Graph	Weight graph by dispersal probability function	NA	No	Yes	Resistance value contrast, dispersal distance

Appendix 2—Resistance-surface connectivity modeling in practice.

Project Title	Author, Year	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Florida's Ecological Greenways Network	Hoctor et al., 2000	Link natural areas / Landscape Pattern	Landscape Integrity	Maximum resistance of: Previously identified biodiversity hotpsots and conservation areas + Land Cover + Roadless Areas + Hydrography	Expert Opinion	No	Patch Edge	Cost Distance	Buffer LCP up to 25% of length	No	No	No	No
Southeastern Ecological Network	Carr et al., 2002	Link natural areas / Landscape Pattern	Landscape Integrity	Maximum resistance of: Previously identified biodiversity hotpsots and conservation areas + Land Cover + Road Density + Distance to Water	Expert Opinion	No	Patch Edge	Cost Distance	Buffer LCP	No	No	No	No
Southern Rockies Wildlands Network	Miller et al. , 2003	Conservation Area Design / "Dispersal"	Focal Species Habitat Suitability	Power function rescale of product of: Human Population Density + Road Density + Land Cover + Slope	Expert Opinion	No	Patch Edge	Cost Distance	Categorically map cost distance	No	No	No	No
Maryland's Green Infrastructure Assessment	Weber et al., 2003	Link natural areas / Landscape Pattern	Landscape Integrity	Sum of: Land Cover + Roads + Slope + Protected Status + Edge + Distance to Development	Expert Opinion	No	Patch Edge	Cost Distance	Buffer LCP by minimum width	Visually compared output map to Expert Opinion derived linkage maps	No	Calculated ecological variables within network to rank linkage importance	No
Linking Colorado's Landscapes - Phase I	Kintsch et al., 2005	Link habitat patches and identify road crossing linkages / Life History and "Dispersal"	Focal Species Habitat Suitability	Product of: Land Cover + Patch Structure + Distance From Roads and Development + Slope	Expert Opinion	No	Patch Edge	Cost Distance	Categorically map top Nth percentile paths	Visually compared output map to Expert Opinion derived linkage maps	No	Graph theoretic patch connectance and link importance	Moving window size and minimum area in identification of a source patch
Delaware Ecological Network	Weber, 2007	Conservation Network Design / Landscape Pattern	Landscape Integrity	Maximum resistance of: Land Cover + Landscape Structure + Roads + Protected Status + Topography + Hydrography	Expert Opinion	No	Patch Edge	Cost Distance, Expert Opinion	Buffer LCP by minimum width	No	No	Calculated ecological variables within network to rank linkage importance	No

Project Title	Author, Year	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
Virginia Natural Landscape Assessment	Weber., 2007	Link natural areas / Landscape Pattern	Landscape Integrity	Unknown combination of: Human Modification + Forest Land Cover Types Topographic Features + Conservation Status	Expert Opinion	No	Patch Edge	Cost Distance	Map LCP	No	No	No	Resistance values
South Coast Missing Linkages	SCW, 2008	Link protected areas / "Dispersal"	Focal Species Habitat Suitability	Sum of weighted: Elevation + Land Cover + Topography + Road Density	Expert Opinion	No	Patch Edge	Cost Distance	Map uion of focal species' LCP and buffer minimum width to ensure sufficient habitat given dispersability	No	No	No	Ground-truth cover and barriers in linkages
Arizona Missing Linkages Project	Beier et al., 2007-2008	Link protected areas / "Functional"	Focal Species Habitat Suitability	Geometric mean of weigthed: Land Cover + Elevation + Topography + Distance from Transportation Corridor (+ Threshold distance from species-specific critical factors)	Expert Opinion	No	Patch Edge	Cost Distance (for vagile species with available data; Patch Configuration Analysis for others)	Map union of focal species' LCP and buffer minimum width of 500 m	No	No	No	No
Locating Potential Cougar Corridors in New Mexico	Menke, 2008	Link habitat patches / "Dispersal"	Cougar Habitat Suitability	Weighted sum of: Land Cover + Human Population Density + Distance to Roads + Topography	Expert Opinion	No	Point 1 mile within patch on either side or pre-identified road crossing	Cost Distance	Categorically map top 10th percentile paths	No	No	No	No
Pennsylvania Forest Habitat Connectivity Analysis	Zimmerman et al., 2008	Link natural areas / Landscape Pattern	Landscape Integrity	Sum: Land Cover + Roads + Railroads + Hydrography + Utility ROW + Slope	Expert Opinion	No	Patch Edge	Cost Distance	Map LCP	No	No	No	No
Wild Life Lines	Fields et al., 2010	Link natural areas / Landscape Pattern	Landscape Integrity	Maximum proportion in moving window of: Land Cover + Distance to Roads + Traffic Volume + Housing Density	Expert Opinion	No	Cell	Cost Distance	Categorically map network centrality	No	No	No	Resistance values
Great Plains Landscape Connectivity	Cushman et al., 2010	Link natural areas and Link habitat patches / "Dispersal"	Landscpae Integrity and Focal Species Habitat Suitability	Sum: Land Cover + Roads + Biome Vegetation	Expert Opinion	No	Cell	Resistant Kernel Analysis (Cost Distance + Dispersal Model)	Categorically map path density	No	No (planned)	No	Resistance values in a factorial design, dispersal distances

Project Title	Author, Year	Step 1: Connectivity Type	Step 2: Resistance Layer Type	Step 2b: Resistance Variables	Step 2c: Resistance Values	Step 2d: Resistance Validation	Step 3: Termini	Step 4: Ecological Distance	Step 5: Map Linkages	Step 6: Linkage Validation	Step 7: Climate Change	Step 8: Connectivity	Uncertainty Analysis
California Essential Habitat Connectivity Project*	Spencer et al., 2010	Link natural areas / Landscape Pattern	Landscape Integrity	Sum of weighted: Land Cover + GAP Conservation Status	Expert Opinion	No	Patch Centroid	Cost Distance	Map top 5% of paths within 5km buffer around and between source patches and add riparian connections	Visually compared output map to other linkage maps	No	No	No
Minnesota Terrestrial Habitat Connectivity Index	Richardson, 2010	Link natural areas / Landscape Pattern	Landscape Integrity	Land Cover	Expert Opinion	No	Patch Edge	Cost Distance	Buffer LCP, shorter distances given greater width	No	No	No	No
Washington Connected Landscapes Project	WHCWG, 2010	Link natural areas and Link habitat patches/ All Connectivity Types (focus on genetic and precautionary hedge)	Landscape Integrity and Focal Species Habitat Suitability	Sum of: Land Cover + Elevation + Slope + Roads + Housing Density (for some sp.) Forest Cover (for some spe.)	Expert Opinion or Expert Opinion with Genetic Data (MSF) for model selection for Mountain Goat	Planned compar-ison with genetic data for for sage-grouse	Patch Edge	Cost Distance	Categorically map paths normalized by shortest LCP - combined output from 4 resistance models connecting patches within cut-off distance or multiple paths out to maximum dispersal distance and an abitrary maximum corridor witdth for a given species	Planned using telemetry data for sage-grouse; Compared outputs and quantified overlap between landscape integrity and focal species-based analyses	No (planned)	No	Resistance values (for landscape integrity analysis)
Mapping Habitat Connecivity for Multiple, Rare, Threatened, and Endangered Species on and Around Military Installations	Moody et al., 2011	Link habitat patches/ "Dispersal"	Focal Species Habitat Suitability	Maximum resistance of: Land Cover + Forest Structure	Occurrence Data (PSF) (via MaxEnt)	Field experiment validation of movement probability	Patch Centroid	Individual-Based Models, Cost Distance, Circuit Theory	Categorically map top 25th percentile paths	Compared outputs from IBMs and Circuitscape	No, but considered scenarios of land use change	Graph theoretic patch connectance under varying dispersal distances	Resistance variables and values and non-linearity of relationship between habitat suitability and resistance

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Montana Connectivity Project	Herbert et al., 2011	Link habitat patches/ Functional	Landscape Integrity or Focal Species Habitat Suitability	Land Cover (+ Topography + Various others for focal species)	Expert Opinion for Landscape Integrity; Occurrence Data (PSF) (via MaxEnt) for Habitat Suitability	No	Patch Edge	Cost Disatnce	Mosaic all pariwise combinations of least cost distance and categorically map top Nth percentile paths; Identified stepping stones for species requiring stop-over habitat	No	No	No	Connectivity model, Patch identification, summary of confidence ratings for each species/ guild
Forest Matrix Blocks and State Forest Connectivity	Messenger and Perry, 2011	Link natural areas / Landscape Pattern	Landscape Integrity	Moving window (300m radius) analysis of percent of natural: Land Cover	Expert Opinion	No	Patch Edge	Cost Distance	Map LCP; Identified state forests near LCP for priority management	No	No	No	No
Pathways: Wildlife Habitat Connectivity in the Changing Climate of the Hudson Valley	Howard and Schlesinger, 2012	Link habitat patches / Precautionary Hedge	Focal Species Habitat Suitability + Roads	Random Forest Model: Land Cover + Elevation + Topography + Solar Radiation + Terrain Wetness + Soils + Geology + Summer Temperature + Spring Precipitation + Spring Snow Depth	Occurrence Data (PSF)	No	Patch Edge	Cost Distance along a Triangulated Irregular Network	In addition to mapping LCP, summarized multiple species "richness", betweeness centrality, and number species occurring in two or three time periods by tax parcel	No	Map habitat suitability and connectivity for current and two future scenarios	Betweeness Centrality	Resistance surface cross-validation, model fit statistics
A Linkage Network for California Deserts	Penrod et al., 2012	Link habitat patches / "Functional"	Focal Species Habitat Suitability	Weighted geometric mean of: Land Cover + Elevation + Topography + Distance to Streams + Road Density	Expert Opinion	No	Patch Edge	Cost Distance	Map union of focal species' LCP and buffer to minimum width of 2km	No	Map land facet (similar elevation/topography) corridors assumed to retain connectivity under climate change	No	Ground-truth cover

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Northeastern Resilience Network	Anderson et al., 2012	Assess landscape permeability and Link natural areas / Landscape Pattern and Precuationary Hedge	Landscape Integrity	Maximum of: Land Cover + Roads	Expert Opinion	Calibrated surface to known links	Local - Cell Regional - ?	Local - Resistant Kernel Analysis (Cost Distance + Dispersal Model) Regional -Circuit Theory	Map resilient areas on the basis of connectivity and other properties; did not map linkages	No	No	No	No
Beginning With Habitat	BWH, 2012; Ongoing	Identify road crossing linkages / Undefined	Focal Species Habitat Suitability	Unknown combination of: Land Cover + Edge Effects + Hydrography + Dispersal Distance + Elevation	Expert Opinion	No	Patch Edge	Roads dividing highly suitable habitat, Circuit Theory	NA	No	No	No	No
New Jersey Landscape Project	NJDFW; Ongoing	?	?	?	?	?	?	?	?	?	?	?	?
Staying Connected Initiative	SCI; Ongoing	Link habitat patches and Identify road crossing linkages / All Connectivity Types	Focal Species Habitat Suitability	?	Expert Opinion	?	?	Circuit Theory, Cost Distance	?	Planned road crossing validation	No	?	?
North Atlantic Landscape Connectivity	NALCC, 2012; Ongoing	Assess landscape permeability /Undefined connectivity	?	?	?	?	?	?	?	?	?	?	?
North Pacific Forest Landscape Corridor Project	NPLCC, Ongoing	Assess landscape connectivity / "Dispersal" and Genetic	Landscape Integrity	Sum: Land Cover + Elevation + Human Footprint	Expert Opinion	No	Cell	Resistant Kernel Analysis (Cost Distance + Dispersal Model)	Categorically map path density	No	Mappped connectivity for 3 scenarios of future land cover	No	Resistance values in a factorial design, dispersal distances
California Landscape Connectivity	CLCC, Ongoing	Link habitat patches / Precautionary Hedge	Focal Species Habitat Suitability	?	Occupancy Modeling (PSF)	Genetic distance	?	?	?	?	Planned	?	?
Terrestrial Habitat Connectivity	SALCC, Ongoing	Link habitat patches / ?	Focal Species Habitat Suitability	?	?	?	?	?	?	Compare connectivity methods	?	?	?
Southern Rockies Landscape Connectivity	SRLCC, Ongoing	?	?	?	?	?	?	?	?	?	Planned	?	?
Great Northern Landscape Connectivity	GNLCC, Ongoing	Link habitat patches / ?	Focal Species Habitat Suitability	?		?	?	?	Cost Distance	?	Planned	?	?