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The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities

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The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities

SUMMARY

Landscape connectivity, the extent to which a landscape facilitates the movements of organisms and their genes, faces critical threats from both fragmentation and habitat loss. Many conservation efforts focus on protecting and enhancing connectivity to offset the impacts of habitat loss and fragmentation on biodiversity conservation, and to increase the resilience of reserve networks to potential threats associated with climate change. Loss of connectivity can reduce the size and quality of available habitat, impede and disrupt movement (including dispersal) to new habitats, and affect seasonal migration patterns. These changes can lead, in turn, to detrimental effects for populations and species, including decreased carrying capacity, population declines, loss of genetic variation, and ultimately species extinction.

Measuring and mapping connectivity is facilitated by a growing number of quantitative approaches that can integrate large amounts of information about organisms' life histories, habitat quality, and other features essential to evaluating connectivity for a given population or species. However, identifying effective approaches for maintaining and restoring connectivity poses several challenges, and our understanding of how connectivity should be designed to mitigate the impacts of climate change is, as yet, in its infancy.

Scientists and managers must confront and overcome several challenges inherent in evaluating and planning for connectivity, including:

- characterizing the biology of focal species;
- understanding the strengths and the limitations of the models used to evaluate connectivity;
- considering spatial and temporal extent in connectivity planning;
- using caution in extrapolating results outside of observed conditions;
- considering non-linear relationships that can complicate assumed or expected ecological responses;
- accounting and planning for anthropogenic change in the landscape;
- using well-defined goals and objectives to drive the selection of methods used for evaluating and planning for connectivity;
- and communicating to the general public in clear and meaningful language the importance of connectivity to improve awareness and strengthen policies for ensuring conservation.

Several aspects of connectivity science deserve additional attention in order to improve the effectiveness of design and implementation. Research on species persistence, behavioral ecology, and community structure is needed to reduce the uncertainty associated with connectivity models. Evaluating and testing connectivity responses to climate change will be critical to achieving conservation goals in the face of the rapid changes that will confront many communities and ecosystems. All of these potential areas of advancement will fall short of conservation goals if we do not effectively incorporate human activities into connectivity planning. While this *Issue* identifies substantial uncertainties in mapping connectivity and evaluating resilience to climate change, it is also clear that integrating human and natural landscape conservation planning to enhance habitat connectivity is essential for biodiversity conservation.

Cover photos: *Examples of ways different species move through landscapes and depend on connectivity. Clockwise starting on the upper left: a) The interconnection of ocean surface current patterns provides pathways for dispersal of larvae between coral reefs. b) A network of riparian corridors used by wildlife to move through an agricultural landscape. c) Continuous grasslands are used by migrating wildebeest in eastern Africa. d) Intact lowland forest is used by endemic forest birds for dispersal between mountain ranges.*

Photos credits: *a) NASA Goddard's Scientific Visualization Studio. b) Adina Merenlender. c) Flickr user Abeeeer. d) Flickr user Daniel Lane.*

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Introduction

What Is Landscape Connectivity and How Does It Affect Conservation Objectives?

Connectivity is the extent to which movements of genes, propagules (pollen and seeds), individuals, and populations are facilitated by the structure and composition of the landscape. A landscape's connectivity is defined relative to the requirements of the organisms that live within it and move through it. Therefore, connectivity is species and context dependent. Consider the interconnection of ocean surface current patterns providing pathways for dispersal of larvae between coral reefs; a network of riparian corridors used by wildlife to move through an agricultural landscape; the continuity of grasslands used by migrating wildebeest; intact lowland forest through which endemic forest birds move (see cover photos). Each of these examples demonstrates that connectivity is measured relative to the ease or difficulty with which a particular species is able to move across a particular land or seascape.

Connectivity has both *structural* and *functional* components. *Structural connectivity* describes the physical characteristics of a landscape that allow for movement, including topography, hydrology, vegetative cover, and human land use patterns. *Functional connectivity* describes how well genes, propagules, individuals, or populations move through the landscape. Functional connectivity results from the ways that the ecological characteristics of the organism, such as habitat preference and dispersal ability, interact with the structural characteristics of the landscape. The examples provided on the cover depict the ways that different species move through and depend on the landscape and demonstrate both functional and structural connectivity, whereby ecological requirements of individual species interact with the composition and configuration of the landscape. These interactions influence the ability of individuals and populations to move among locations to find key resources, such as food, water, appropriate substrates for sessile organisms, or breeding partners.

The destruction and degradation of natural habitats on which all organisms rely – including humans – is occurring at an unprecedented rate across most regions of our planet. As humans convert land for resource extraction and for urban and agricultural uses, and as our impacts on global climate continue to grow, we profoundly change the physical, chemical, and biological character of these landscapes. Land use changes may reduce the amount of a habitat or fragment it, breaking it up into smaller or differently arranged units. This process changes not only the size of habitat patches but also other landscape features, such as patch geometry or the amount of edge habitat, that may be of fundamental importance to species, communities, and ecological functions. Because human-caused disturbances often occur in shorter timeframes and over larger areas than do natural disturbances, ecological communities face challenges of how to adapt and respond to novel rates and scales of disturbances that are quite different from those with which they may have evolved.

Fragmentation, habitat degradation, and habitat loss are the dominant mechanisms by which connectivity is reduced or lost, and are widely recognized as major drivers of the present global biodiversity crisis. Fragmentation, the subdivision of habitat into smaller or more isolated remnants, can directly impact species persistence and accelerate local extinction rates. Habitat fragmentation is frequently associated with habitat loss. However, fragmentation can also eliminate dispersal or gene flow without causing impacts on a population's core habitat – for example, a highway bisecting a movement corridor.

For any given species, some parts of the landscape provide better opportunities than others to fulfill its ecological requirements, such as food, breeding habitat, or refuge from predation. Fragmentation and degradation can further increase the patchiness of the landscape in terms of meeting a species' needs. Conserving connectivity in this context requires identifying, maintaining, and possibly enhancing the linkages between suitable patches of habitat in the landscape. Corridors, which are generally linear spaces that facilitate movement between patches, are frequently used as a tool for conserving or enhancing linkages. The creation or protection of corridors can maintain connectivity for mobile species, such as ungulates or large felines that typically have large territories.

Corridors provide structural connectivity and are consistent with the functional connectivity needs of animals that can take advantage of linear spaces to move among disparate habitat patches. However, landscape connectivity is highly diverse and species-dependent, and other forms of connectivity may be more relevant to other types of organisms; for example, a linked mosaic of small wetlands for breeding populations of amphibians, continuity of vegetated intertidal rocky substrate along a coastline for a marine snail, or a heterogeneous assemblage of meadow plant communities with different flowering times for a population of pollinators. The challenge of matching connectivity patterns to ecological requirements becomes even greater when we expand our thinking to consider maintaining or restoring connectivity for multiple species or entire communities.

Many populations and ecosystem functions are dependent on extensive, well-connected habitats; however, understanding the factors that contribute to landscape connectivity for specific populations, species, or communities is challenging. This *Issue* reviews the importance of habitat connectivity, summarizes current science-based strategies for mitigating the negative ecological effects of fragmentation, explores data gaps and limitations of connectivity models, and describes obstacles and opportunities for developing policies and management approaches that improve connectivity and reach conservation goals.

Case Study 1. Managing for Marine Connectivity: Marine Protected Areas in the Gulf of California, Mexico

The growing movement toward ecosystem-based management, including networks of no-take zones in marine ecosystems (marine protected areas, or MPAs) requires that these conservation areas be deliberately and adequately spaced to allow for connectivity. The performance of a network of sites designed with the two-fold purpose of protecting commercial species and allowing for spillover effects (movement of organisms from protected areas into harvestable areas) will largely depend on whether sites in a network are functionally and structurally linked to each other by both biological (e.g., dispersal of organisms) and physical (e.g., currents) processes. Although the number and extent of MPAs has increased recently, studies have shown that, on a global scale, average distance between neighboring MPAs exceeds the distance of reef organism propagule dispersal. This distance suggests that some taxa could become genetically isolated if populations cannot reach each other, undermining the viability of populations in the MPAs.

The conservation of species, habitats, and ecoregions depends on developing practical, efficient, and effective planning strategies. This is especially true in the marine realm, where threats are diffuse and difficult to both identify and quantify. Well-designed networks should include MPAs and other conservation and management areas that support each other by taking advantage of oceanic currents and movement/migration capabilities of species. They also provide much-needed resilience against a range of threats. Because establishment of isolated marine reserves may not alone suffice for the conservation of biodiversity, identifying the level of connectivity between the areas is a critical aspect in network design.

In the Gulf of California, Mexico (GOC), two organizations, Comunidad y Biodiversidad and The Nature Conservancy, recently completed a marine ecoregional assessment to identify priority conservation sites and establish a network of conservation areas. This analysis identified 54 conservation areas that are deemed critical to marine conservation objectives, which cover 26% of the ecoregion. An important step towards implementing the assessment will be to account for connectivity between putative sites. To move from connectivity assessments based exclusively on structural attributes of connectivity to a detailed assessment of actual connectivity, models are used to track species' dispersal from site to site as well as movement through the matrix (for example, satellite tracking and the development of oceanographic models for the entire ecoregion). Pop-up satellite archival tags are being used globally for many marine species (e.g., the Tagging of Pacific Predators Program, http://www.topp.org/) and can greatly enhance knowledge of the dispersal of focal species. For example, sea turtle, cetacean, and whale shark tagging programs are already underway in the ecoregion, and expanded versions of these programs are expected to provide a more complete understanding of connectivity throughout the ecoregion. Integrating data from these tagging programs into the GOC ecoregional assessment is an important priority in understanding the role of connectivity in marine spatial planning.

How Fragmentation Affects Movement: From Genes to Species

Landscape fragmentation affects ecological communities at multiple levels of organization. Here, we briefly explore these effects, ranging from the movement of individuals and gene flow within and between populations to shifts in species range and species persistence.

Landscape connectivity is important for dispersing or migrating individuals. Dispersal increases resilience to disturbances by allowing organisms to track their shifting habitats, and it promotes the spread and expansion of populations. In some species – for example, wildebeest in Africa, bison in North America, a wide variety of bird species – seasonal migration has evolved as a means of maximizing access to critical resources as ecological conditions change throughout the year. Habitat fragmentation can disrupt dispersal and migration in several ways. First, edges of the remnant habitat patches may act as filters or barriers that discourage or impede movement. Second, increased distances between suitable habitat patches may influence the likelihood of successful movement. Last, the composition and structure of the intervening landscape mosaic may influence the permeability of the landscape to movements by different organisms. If fragmentation impedes seasonal migration, wildlife may be cut off from seasonal resources. If dispersal routes are blocked or altered, organisms may experience higher rates of mortality when trying to disperse, or they may be stopped completely, leading to unsustainably high densities of organisms in remnant patches, resulting in increases in mortality.

Habitat fragmentation may impede gene flow and lead to genetic isolation. Gene flow is critical to population viability, as it helps maintain local genetic variation and spreads potentially adaptive genes. Genetic isolation can be a mechanism for the creation of new populations and even species; however, small remnant populations inhabiting fragmented landscapes are more likely to suffer from inbreeding and low genetic variation, which can increase vulnerability to other stressors and lead to local extinctions. Retaining or restoring connectivity counteracts these negative effects of genetic isolation.

Landscape connectivity is essential across large areas (connectivity across ecoregions or continents is critical for some species) and over long timeframes (connectivity over many years or generations) to allow species' range shifts in response to long-term ecological change. Projected climate change over the next few decades will change ecosystem structure, species composition, and diversity. Changes in biophysical conditions will likely lead to species replacement in communities (community turnover) and latitudinal and elevational shifts in geographic ranges. During episodes of climate change since the Pleistocene, vegetation zones or communities did not move as a whole in response to climate shifts; rather, species responded individually to climate change, according to their own individual and largely independent environmental tolerances, dispersal abilities, and responses to biotic interactions. Current climate change appears to be occurring substantially faster than in the pre-historical record, meaning that the ecological conditions required by many species (their niches) may be shifting faster than species can adapt. These pressures, caused by changes in climatic conditions encountered by species in their current distributions, are compounded by habitat loss and fragmentation. The resulting obstacles to migration may impede species' abilities to adapt to climate change, to such an extent that many species could be driven to extinction.

Effects of Connectivity on Disease and Biotic Invasions

The extent to which landscapes are connected or fragmented may also affect the rate and pattern of disease spread and invasion by non-native species. Species introductions, which can radically alter ecosystems, include plant and animal diseases as well as competitors and predators against which native communities may not have evolved defenses. It is important for managers to consider how changes in connectivity and fragmentation may influence the spread of diseases and invasive species, and to recognize that these influences are not necessarily unidirectional, but rather depend on the characteristics of the particular species and landscape in question.

Intact, well-connected landscapes can serve as conduits for many invasive species if they disperse in similar ways to native species. In other cases, processes that fragment habitats for native species may simultaneously provide connections that can facilitate biotic invasions. For example, the recent Asian carp invasion (including grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys*

Box 1. Habitat Fragmentation and Increased Disease Transmissivity

An important consequence of fragmentation in forested habitats is the loss of species diversity. Those species that thrive in fragmented habitats tend to be more generalist or opportunistic, or have traits such as smaller home range requirements and tolerance for higher densities. Fragmentation can actually increase connectivity from the perspective of a disease-causing pathogen. Higher densities of hosts increase opportunities for transmissivity, and the host population is the true "landscape" across which pathogen movement occurs. This is the case for the tick-transmitted bacterium (*Borrelia burgdorferi*) that causes Lyme disease. Its host, the white-footed mouse (*Peromyscus leucopus*), has become increasingly common in small forest fragments (<2 ha) in New England, likely resulting from its small home range requirements combined with release from competitors and predators in smaller forest patches. *P. leucopus* is the principal natural reservoir for Lyme disease. Higher densities of ticks infested with *B. burgdorferi* are found in smaller forest fragments (Figure 1), which may result from higher densities of white-footed mouse in these smaller fragments, presenting more opportunities for ticks to feed on the mice. Consequently, humans living near these small forest fragments may have a higher risk of exposure to Lyme disease relative to those near larger forest fragments.

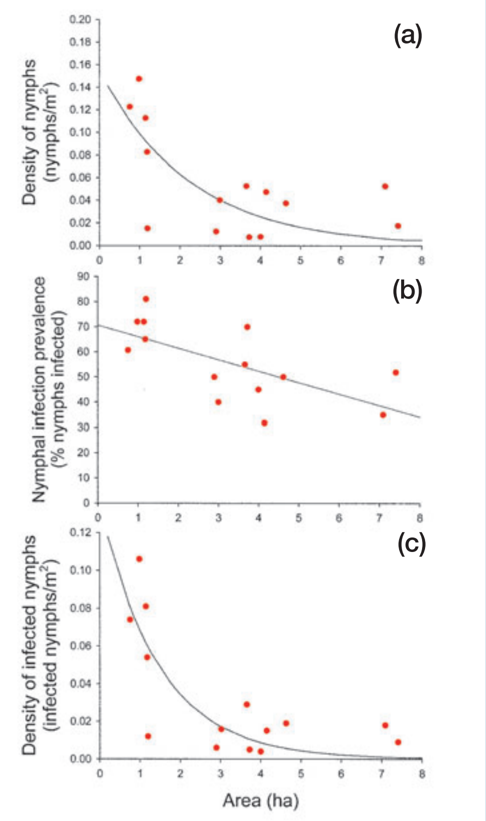


Figure 1. Relationship between measures of Lyme disease risk and forest patch area in a fragmented landscape in New York state. a) Density of nymphal ticks is higher in smaller forest fragments. b) Percentage of nymphal ticks infected with the bacterium Borrelia burgdorferi *is higher in smaller forest fragments. c) Density of nymphal ticks infected with the* B. burgdorferi *is higher in smaller forest fragments. (Source: Allan, B.F., F. Keesing, and R.S. Ostfeld. 2003. Effect of forest fragmentation on Lyme disease risk.* Conservation Biology. *17: 267–272). Image used with permission of John Wiley and Sons.*

molitrix), and bighead carp (*H. nobilis*)) in the Mississippi River watershed, and their potential spread into the Great Lakes, illustrate how human-constructed connections (canals) can both fragment the terrestrial environment and provide new corridors between aquatic systems. Similarly, while roads can fragment vegetated habitats, they can simultaneously serve as conduits for some invasive species, such as cheatgrass (*Bromus tectorum*), yellow star thistle (*Centaurea solstitialis*), and other invasive species that benefit from the openings created by roads.

Connectivity for pathogens and parasites is largely a function of host distribution and abundance. While disease persistence benefits from increased host connectivity, it does not necessarily follow that these conditions are optimized only in well-connected landscapes. Landscape disturbance and fragmentation can increase host abundance and alter host distribution, and these changes can increase connectivity for pathogens and parasites for which the hosts constitute the true "landscape" across which movement occurs (Box 1). However, fragmentation may also lead to the isolation of smaller host subpopulations, which then may become more susceptible to disease or invasions. In other situations, isolation resulting from landscape fragmentation may protect a population from disease. For example, plague (*Yersinia pestis*) in Colorado prairie dog (*Cynomys ludovicianus*) populations was shown to be less prevalent in more remote, isolated populations than in those more closely grouped together.

Measuring, Analyzing and Designing Landscape Connectivity

Measuring structural connectivity has increasingly become a routine objective of researchers and policy makers, as Geographic Information

System (GIS) and remote sensing tools become more widely available, affordable, and scalable. However, measuring functional connectivity using the movements of individual organisms can be logistically complicated. Even the largest studies using the most appropriate technologies can track only relatively few individuals over modest time periods, and controlled experiments addressing movements and dispersal at relevant scales are extremely difficult to implement. One way to address this difficulty is to measure gene flow, which may more accurately and efficiently reflect functional connectivity across large landscapes. Genetic studies avoid the logistic and financial costs of tracking individual animals and integrate only those movements that produce meaningful population impacts – dispersals that result in breeding or emigration. A shortcoming of this approach is that current genetic patterns may not reflect the impact of current landscape features, especially for species with large population sizes or long generation times, or species affected by unobserved events, such as genetic bottlenecks caused by past epidemics or human persecution. In addition, genetic connectivity may be masked in some instances by local adaptation, which can drive genetic distinctiveness even in a well-connected landscape, by selecting for particular characteristics of the local environment.

A common product of connectivity analysis is a map of predicted core areas, linkage zones, or barriers. Such maps often become the basis for management actions. Several tools can be used to map these features, and each has unique strengths and weaknesses. All of the approaches described in the next section depend on accurately defining landscape resistance (an indication of how well a landscape can be traversed by a given species), a challenging task when only a limited amount of information about species habitat preferences is available. Furthermore, connectivity models can be difficult to validate.

Several research teams are working to develop methods to rigorously estimate species-specific resistance from data on gene flow, genetic distances, habitat use, and movement paths. Simple estimates of resistance, based on the extent to which landscapes are impacted by roads, loss of natural land cover, increased edge effects, spread of invasive species, and other direct human impacts measures may be useful for some generalist species, but are insufficient for addressing species-specific movements and habitat needs. Thus, recent developments in connectivity modeling combine a structural landscape approach, identifying both the potential for and obstacles to long-term habitat shifts, with a functional approach that highlights the specific connectivity needs of species with restricted habitat requirements.

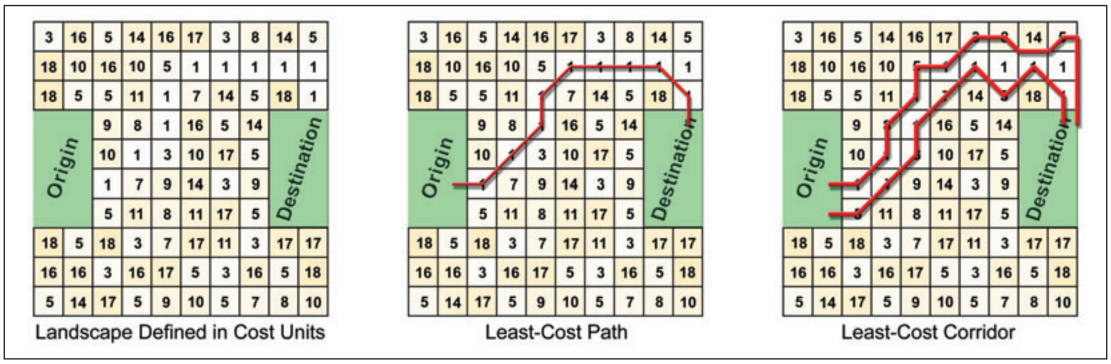
Modeling Approaches for Identifying and Quantifying Landscape Connectivity

We describe five widely-used analytical approaches, all implemented in a GIS environment, to assist planners in mapping and prioritizing landscape connections. Each approach has specific data requirements that often require input from biologists to help define model parameters. In addition, each approach is designed to meet different objectives and will, therefore, produce different outcomes.

Least-cost analysis identifies the least costly route that an animal can take from one area to another. The method assumes that the animal incurs a cost as it moves over an area, where "cost" may reflect the actual energy expended to move over the area, mortality risk, or impact on future reproductive potential. In practice, cost is usually estimated simply as the inverse of habitat suitability. Habitats that the animal favors are assigned low cost while unsuitable habitats are assigned high cost.

The least-cost path is the contiguous collection of cells that has the lowest cumulative cost as the path crosses from one endpoint (such as a park, natural area, or known population; sometimes referred to as a node or patch) to the other endpoint. Computers using GIS software can easily identify this path. Because the least-cost path is only one cell wide (for example, the center panel in Figure 2), it is often not a realistic area to propose for conservation. Therefore, analysts usually identify the least-cost corridor (shown in red in the panel on the right in Figure 2), which is a swath of cells expected to provide a low-cost route for movement.

Increased distance between two nodes or patches also results in higher costs. This latter assumption is important, in that some species may be able to identify and take advantage of shorter linkages, while others operate at a finer scale of perception and therefore may not be able to consider total corridor length. Correctly assigning these cost values (also referred to as



Landscape Defined in Cost Units

Least-Cost Path

Least-Cost Corridor

Figure 2. *A least cost path analysis.*

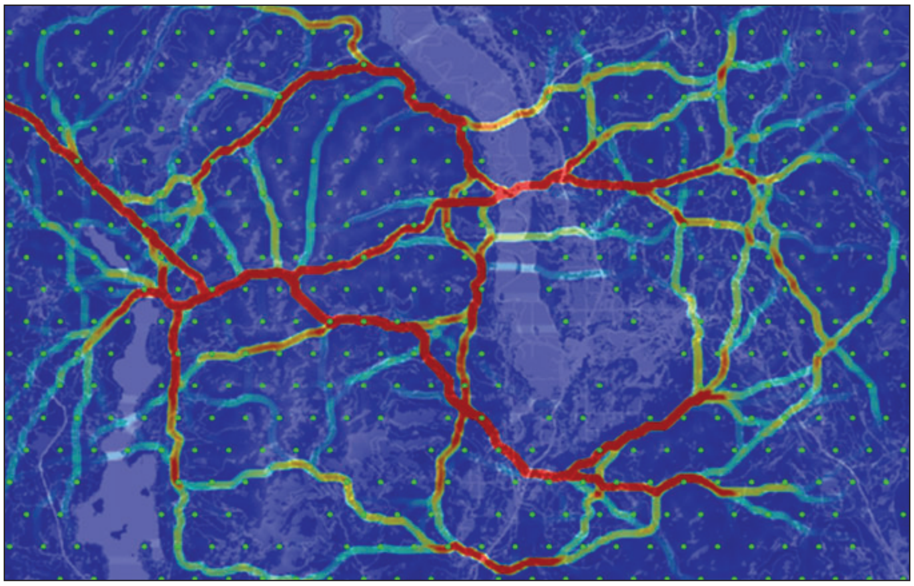
resistance or permeability values) is the most problematic aspect of least-cost analysis and the other approaches described here.

Factorial least-cost paths address one major limitation of traditional least-cost path and least-cost corridor analyses in that they are limited to predictions of connectivity between single sources and single destinations. While this may be ideal in the case where one is interested in the lowest cost routes between two focal conservation areas, many situations require a more comprehensive analysis of connectivity. For example, corridor connectivity may need to be calculated between thousands of sources and a single destination, or between hundreds of sources and hundreds of destinations distributed across a complex landscape. A factorial implementation of least-cost paths integrates a vast number of paths to show a network of connectivity across large and complex landscapes, such as a factorial least-cost path analysis among hundreds of points across a resistance surface (Figure 3). Densities of paths are shown in a gradient from yellow to red, with red paths representing routes that are predicted to contain the least-cost paths between many pairs of source and destination points. Additionally, while factorial approaches are most common among least-cost approaches, they can also be integrated into graph and circuit analysis as well.

Circuit theory treats the landscape as if it were a large electrical circuit, in which all cells in the landscape can support movement. An important distinction between this and other methods is that while circuit approaches can be used to delineate corridors (with additional processing), they are most useful in analyzing and describing how well connected source and destination habitat patches may be, given multiple movement pathways. Well-connected habitat patches have wide, continuous habitat between them, while paths between poorly-connected habitat patches might have constrictions and bottlenecks, each of which can be identified using a circuit based approach.

Current maps (Figure 4) can be a useful way to visualize a circuit-theoretic analysis. Current strength reflects the predicted probability of movement between the two points or habitat patches. Current maps can be difficult to interpret: higher current (usually depicted in yellow) may occur in a cell because resistance is low, because most paths are forced through that area because of high resistance elsewhere, or because the analysis is spatially constrained (Figure 4a). Lower current (usually depicted in blue), in turn, may imply either high resistance in the underlying layer, or simply that there are many equally good alternate paths for movement. In this way, circuit models may more accurately approximate how organisms move through real landscapes. Despite their relative complexity, these maps are useful for evaluating connectivity and identifying constrained areas (bottlenecks) for possible conservation action. In Figure 4a, where the

Figure 3. *A factorial least-cost path analysis, evaluating least-cost paths (lines in blue to red, with red showing paths with the lowest costs) among many source areas (green points).*



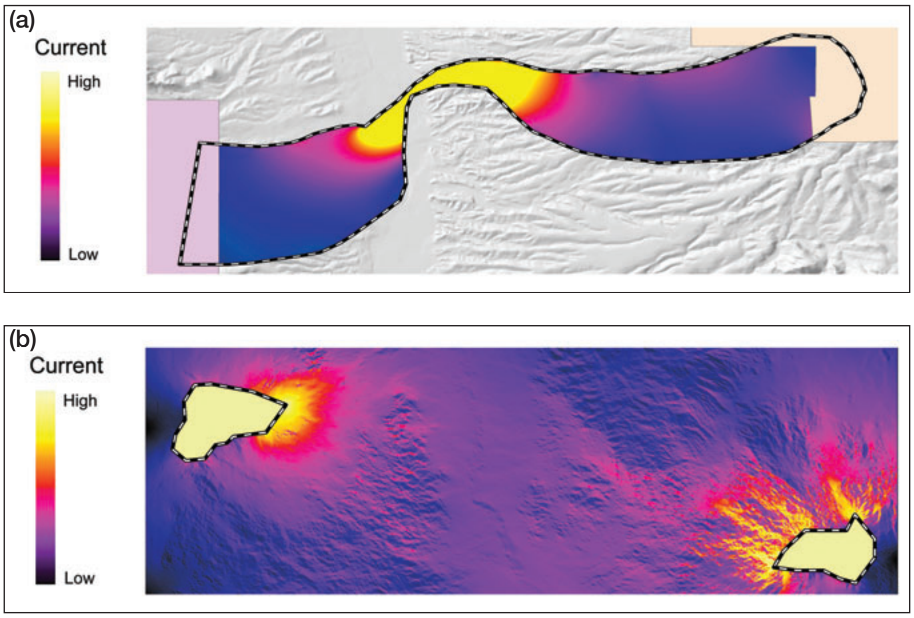


Figure 4. Current maps, illustrating a) a landscape where analysis was confined to a corridor and b) a different landscape where the analysis was not confined to a corridor.

model was confined to a particular habitat corridor, high current values clearly indicate a bottleneck where movement is funneled into a narrow space. In Figure 4b, where the analysis was conducted in a different landscape and not constrained to a corridor, few major bottlenecks are apparent but some areas have higher current due to lower resistance or proximity to the nearest edges of the habitat patches, which are shown in beige.

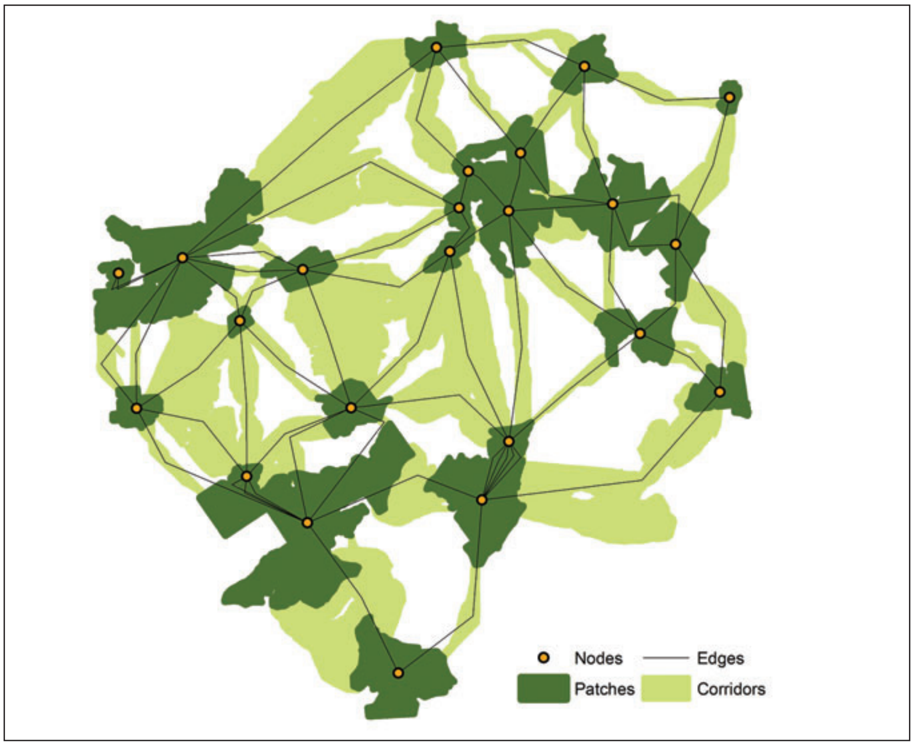


Figure 5. A graph theory model depicting connectivity between habitat patches.

Graph theory combined with least-cost modeling or circuit theory provides several useful enhancements to landscape connectivity assessment and modeling. The landscape itself can be likened to an interlaced web or network that is composed of habitat patches (graph theory modeling uses centers, or "nodes," of these patches as points of connection) and the connections between these patches (the linear representations of which are described in graph theory language as "edges") (Figure 5). Once identified, nodes and edges can be prioritized based on their overall contribution to the landscape network, for instance by evaluating how many potential connections rely on each node or edge. This approach allows for multiple least-cost pathways to be evaluated for their contribution to the configuration of the overall network. This approach is particularly useful when modeling connectivity between large reserve sets (assemblages of patches, parks, or protected areas), identifying isolated reserve sets within the context of the modeled landscape, evaluating the robustness of multiple connections within the landscape network, node/connection prioritization, and evaluating the consequences of losing nodes due to competing factors such as development pressure or fiscal constraints.

The resistant kernel approach to connectivity modeling is based on least-cost dispersal from a defined set of sources. The model calculates the expected relative density of dispersing individuals in each cell around the source, given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape. Once the expected density around each source cell (the smallest unit of space that is modeled containing individuals dispersing to other parts, or cells, in the landscape) is calculated, the kernels surrounding all sources are summed to give the total expected density at each cell. The results of the model are surfaces of expected density of dispersing organisms at any location in the landscape, in contrast to the physical delineation of linkages or corridors.

The resistant kernel approach has a number of advantages for assessing population connectivity. First, unlike most corridor prediction efforts, but similar to circuit-based approaches, it is spatially comprehensive, provides prediction and mapping of expected migration rates for every cell in the study area extent, and can do so for large geographic extents rather than only for a few selected linkage zones. Second, this approach allows assessment of how species with different movement patterns and disper-

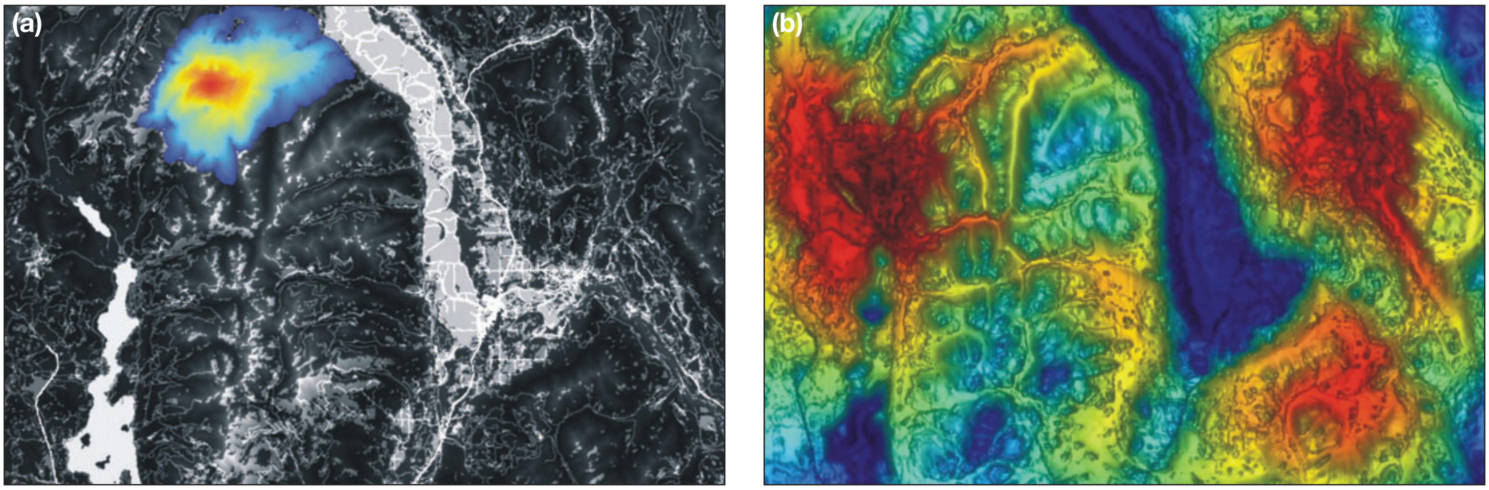


Figure 6. Resistance kernel modeling: a) single-kernel analysis and b) the cumulative resistance surface of all kernels across the landscape.

sal abilities are affected by a range of landscape change and fragmentation scenarios. This approach is useful for characterizing connectivity across continuous surfaces but does not identify individual linkages or corridors without additional analyses.

Figure 6 shows an individual resistant kernel around a) a single source cell and b) the cumulative resistant kernel surface created from summing all individual kernels for all habitat cells. Red areas are predicted to have high frequency of occupancy by dispersers, while blue areas are predicted to experience low rates of dispersal. Case Study 2 provides an example of the use of the resistant kernel approach in evaluating fragmenting effects of roads on amphibian populations.

Considering Resolution and Focus in Connectivity Design

The resolution at which connectivity is ecologically meaningful varies enormously, depending on the species in question. For example, consider the scale of connectivity relevant to a beetle versus a bison. In practice, we tend to design and plan for connectivity at a human scale, meaning that we visualize connectivity in terms of landscape management units in a policy framework. Spatially extensive maps (thousands of kilometers), with coarse grained resolution (for example, in the hundreds of meters per pixel or measurement unit) can depict a network of numerous habitat blocks and the connections among them. Such maps may serve as decision-support tools for managers, or provide a high-level vision of landscape connectivity. They may be used to alert decision-makers to potential threats to large-scale connectivity as well as conservation opportunities. However, these types of maps are often too coarse to inform specific conservation action plans. Examples include the Yellowstone to Yukon initiative, Arizona Wildlife Linkage Assessment, California Essential Habitat Connectivity, Two Countries-One Forest (Case Study 3), Washington Connected Landscapes, and the Bhutan Biological Corridor Complex. The two largest challenges for coarse-grained analysis and mapping are the identification and delineation of core habitat blocks (areas whose conservation value derives from the species and ecological processes within them) and determining which pairs or sets of blocks can feasibly be connected in a way that promotes functional connectivity and meets conservation goals. Once habitat blocks have been identified, various techniques may be used to map the connections (or linkages) among them, including least-cost path analysis, graph theory, or individual-based movement models.

Finer-grained linkage designs can guide site-specific actions to conserve connectivity between specific habitat areas that are relevant to the distances and ways in which species of interest move across the landscape. To develop maps for these plans, landscape connectivity planners typically select a suite of focal species and use the union of their corridors or movement pathways (usually produced by least-cost modeling) to serve as a preliminary linkage design for the entire biota. For instance, each of the 27 linkage plans in California (South Coast Missing Linkages project, available at www.scwildlands.org) and Arizona (the Arizona Missing Linkages project, www.corridordesign.org) was designed to meet the needs of several focal species including mammals, reptiles, amphibians, plants, and invertebrates. Focal species included area-sensitive species, species with short or habitat-restricted dispersal movements, and species

Case Study 2. Effects of Habitat Fragmentation on Vernal Pool Amphibian Populations

The resistant kernel approach for modeling connectivity is well suited to assessing how species with different dispersal abilities will be affected by landscape change and fragmentation. Cushman and colleagues used the resistant kernel modeling approach to evaluate the effect of habitat fragmentation by roads and residential development on a broad range of hypothetical population sizes and dispersal abilities of vernal pool breeding amphibians in western Massachusetts. The analysis compared habitat connectivity among 100 combinations of population size and dispersal ability, across three scenarios. The scenarios included a null scenario, in which the landscape is uniformly suitable for movement, and two scenarios of landscape fragmentation. The fragmentation scenarios included the effects of roads and effects of roads and land use combined.

The amount of habitat that was predicted to be occupied in the null scenario was strongly related to population size and dispersal ability. Figure 7 shows cumulative resistant kernel surfaces for a small portion of the study area for one combination of dispersal ability and population size for (a) the null scenario, (b) the roads scenario and (c) the roads and land use scenario. Areas in red are predicted to have high densities of dispersing individuals, while dark blue areas are predicted to have very low occupancy rates. The amount of habitat predicted to be connected by dispersal in the roads scenario decreased dramatically, with most simulated populations experiencing at least a 75% reduction in connectivity compared to the null scenario. Somewhat counter-intuitively, the largest reductions in the extent of connected habitat were for species with relatively large dispersal abilities; this finding is consistent with a number of empirical studies that have examined the effects of fragmentation on species with varying dispersal abilities. With the combined effects of roads and residential/urban development, the proportion of the simulated populations predicted to experience over 85% reduction in habitat connectivity increased from less than 10% to nearly 50%.

These results suggest that past road building and land use change may have had profound effects on the population connectivity of some vernal pool breeding species. This modeling exercise highlights the importance of landscape-level studies that explicitly include species-specific movement, abundance parameters, and the spatial patterns of the environment in a representation relevant to the organisms in question.

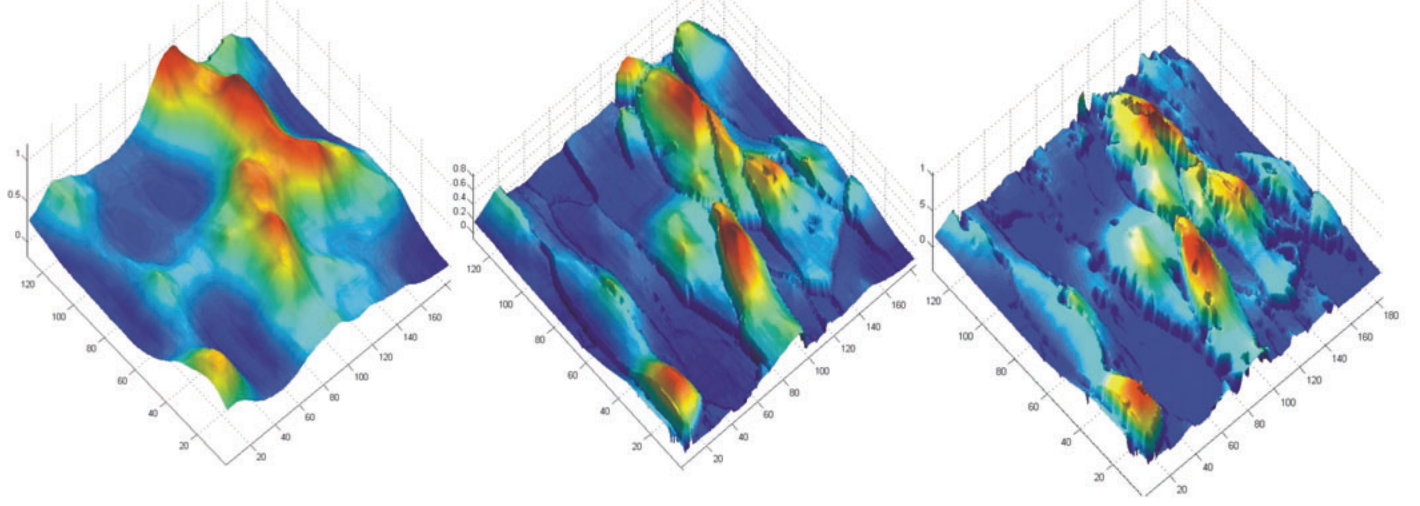


Figure 7. Cumulative resistant kernel surfaces for amphibian dispersal under a) a scenario in which the landscape is assumed to be uniformly suitable for movement, b) a scenario in which roads are resistant to movement, and c) a scenario where roads and different land-cover types (forest, agriculture, urban, residential, for example) are differentially resistant to movement. In all three scenarios, areas with the highest densities of organisms are in red, and those with lowest densities are in blue. The x and y axes represent longitude and latitude, and the z axis (height) represents expected density of dispersing individuals in each cell. The figure shows differences in densities of dispersing individuals across a 16 km^2 area under the three different scenarios described above.

reluctant to traverse barriers in the planning area. Large carnivores are commonly used as focal species because they can require large areas of habitat, but many are habitat generalists whose ecological requirements may not sufficiently encompass other focal species. To create a final multi-species linkage design, this union of pathways is expanded to 1) include patches large enough to support successful breeding in species for which corridors could not be modeled, 2) minimize edge effects, 3) provide sufficient space for animals and plants that require multiple generations to achieve gene flow, and 4) include physical and biological elements that may help support ecological processes that are more complex or operating at scales that differ from those of animal movements.

A complementary approach to restoring or retaining landscape connectivity based on the perceived requirements of focal species is based instead on the abiotic drivers of land cover and species distributions. This approach is grounded in the ecological concept that biodiversity at any point in time is determined by the interaction of the recent species pool with climate, soils, and topography. For example,

Case Study 3. Northern Appalachian/Acadian Ecoregion-Scale Connectivity Assessment

The Northern Appalachian/Acadian ecoregion spans 330,000 square kilometers across four states within the U.S. and all or part of four provinces in Canada, and contains large expanses of wilderness within close proximity to large human populations. As development within the region continues, and the demand on forest resources continues to increase, the ecoregion faces the very real threat of large-scale landscape fragmentation. Two Countries, One Forest (2C1Forest) is a highly collaborative international consortium of 50 conservation organizations, researchers and foundations dedicated to using landscape conservation to protect and maintain the forests and natural heritage of the ecoregion. To date, initiatives have been undertaken to inventory natural resources, evaluate human impact, project future growth, and identify priority locations for conservation action. Recent efforts have focused on identifying priority linkages among key portfolio conservation areas within the ecoregion.

As part of these efforts, Perkl and colleagues developed and evaluated landscape networks connecting target habitat areas arising from four plausible conservation scenarios for the Northern Appalachian/Acadian ecoregion (Figure 8). A graph-theoretic approach was used, applying the best available data on human settlement, access, land use change, and electrical power infrastructure, as a cost surface. Models indicated that while local connectivity was potentially retained at several sub-ecoregion scales, widespread ecoregional connectivity was not evident even in this extensive, forest-dominated region. Furthermore, the spatial dimensions of these modeled landscape networks were staggering in scale and pose substantial challenges to implementation. Among the four scenarios, total network lengths ranged from 2,589 to 4,190 km, with total corridor areas ranging from 13 to 18 million hectares.

This analysis was a first pass at evaluating ecological connectivity for the region and among the first to assess and model connectivity at this scale. While this initial work was not intended to serve as a prescription for landscape or connectivity design, it has proved a valuable first step in developing plausible scenarios that can be further refined to test assumptions for large swaths of the ecoregion that might serve a connectivity function.

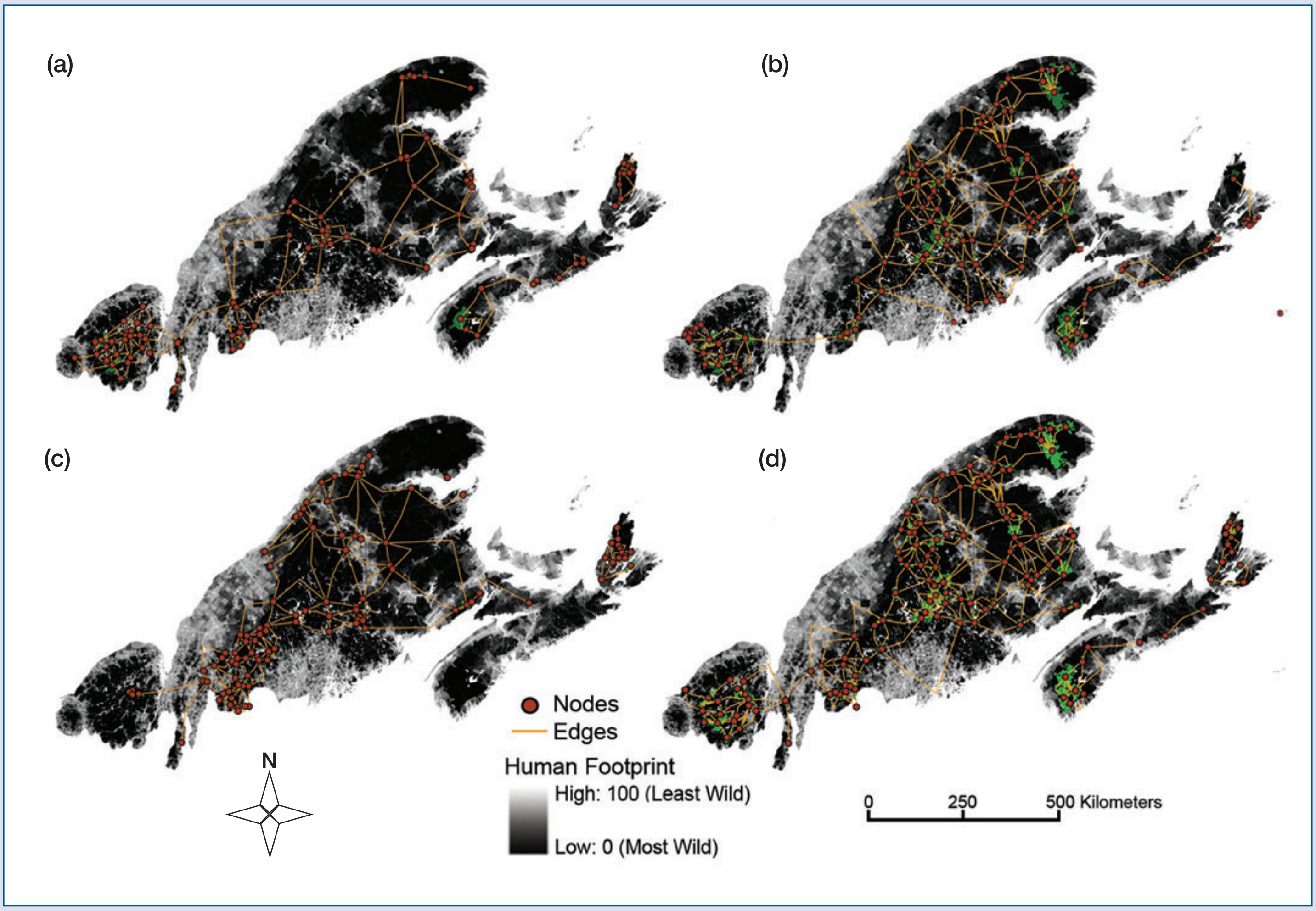


Figure 8. Evaluation of landscape networks using four different scenarios to select habitat targeted for conservation: a) biodiversity conservation (n=95), b) Last of the Wild areas (an evaluation of human influence across ecosystems to identify remaining large wild places, n=120), c) modeled habitat patches for mature-forest focal species (n=105), and d) a composite viability scenario which was composed of selected sites from each of the previous scenarios (n=143).

Case Study 4. Evaluating Landscape Connectivity for Prioritizing Restoration Opportunities in the Delaware Estuary

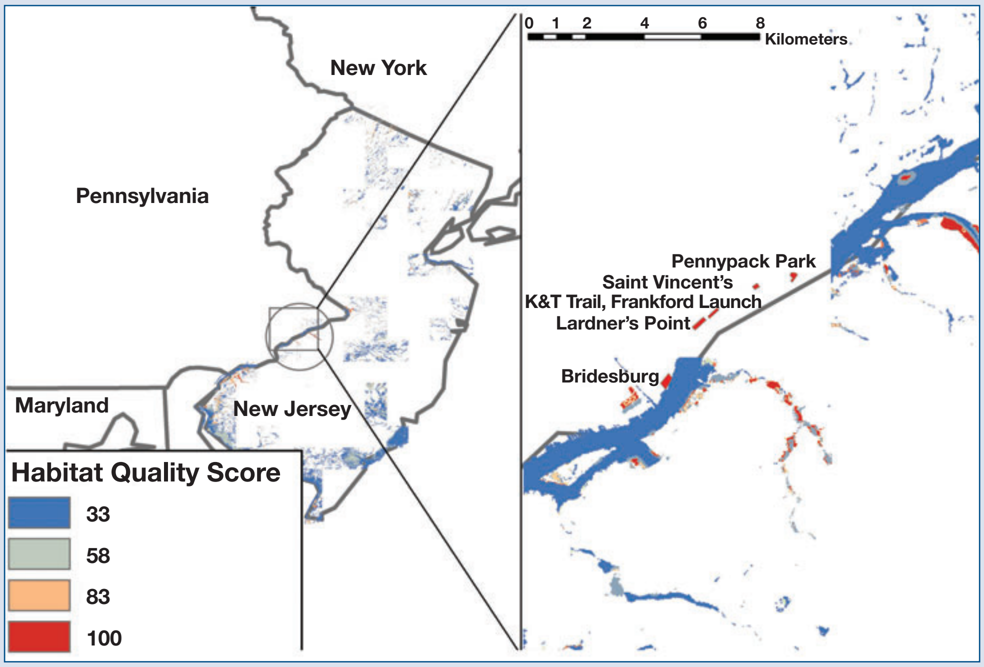


Figure 9. Maps identifying habitat quality based on dispersal requirements of the Least Bittern, used in evaluation of candidate restoration sites in the Delaware Estuary. Habitat quality scores are created by evaluating multiple, species-specific habitat characteristics, including how the patch contributes to overall population growth, the ability to provide opportunities for dispersal, and the extent to which the habitat patch may serve as a stepping stone to other patches (traversability).

Landscape connectivity analysis can be a valuable decision tool for prioritizing restoration opportunities, helping to identify areas that hold the greatest potential for increasing connectivity for focal species. In the Mid Atlantic region of the U.S., interest in restoration opportunities in the Delaware Estuary is increasing. For scientists, planners, and the public, a chief challenge has been to plan for the estuary in a manner that ensures that the value of regional restoration efforts is maximized to improve habitat quality for and persistence of wildlife populations, against a backdrop of an increasingly urbanized ecosystem.

To address this need, researchers modeled landscape connectivity for six candidate restoration sites under consideration by the Delaware Estuary Regional Restoration Work Group (DERRWG). The approach integrated data on home ranges, dispersal requirements, and habitat quality to evaluate suitable habitat for black duck (*Anas rubripes*), least bittern (*Ixobrychus exilis*), and marsh wren (*Cistothorus palustris*). The relative connectivity value for each habitat patch was determined through the calculation and comparison of three value parameters for each potential restoration site: (1) production, defined as the relative ability of a patch to contribute to overall recruitment as determined by local natality or mortality rates, which are influenced by patch area or habitat quality; (2) dispersal, the relative importance of a patch to the dispersal flux of individuals away from their natal patches or as part of a home range, and (3) traversability, the relative importance of a patch as a stepping stone between isolated patches. Species-specific information was used to assign habitat suitability scores based on several characteristics, including dominant vegetation community, similarity to target species preferences for vegetative types, proximity to wetlands, and species habitat and area requirements.

The ability of the six restoration sites to provide high-quality habitat was species-specific: all restoration sites showed potential for provision of high-quality habitat for black duck, three restoration sites showed particularly good potential habitat quality for marsh wren, and all six sites showed high traversability scores for this species. However, only two of the six sites met the dispersal requirements of the least bittern (St. Vincent's and Pennypack Park, Figure 9), and these two sites were highlighted as potentially serving an important function for connecting isolated populations of least bitterns across the landscape. These landscape-scale measures of the species-specific ecological value of each restoration site were provided for consideration by the DERRWG in the evaluation of potential restoration sites across the Estuary.

least-cost path analysis can be used to identify corridors that optimize continuity among recurring landscape units – areas with specific topographic, bedrock and soil attributes. Similar to identifying corridors for individual species, landscape units can be included in a linkage design with multiple, broad corridors that are likely to facilitate the movements of multiple species. These areas will, theoretically, support ecological and evolutionary processes, including species' range shifts in response to climate change, because they contain both the resources that species need, and the means for individuals to move among multiple potentially appropriate habitat blocks to buffer against the loss or degradation of habitat due to landscape change.

The challenges of moving from maps and designs to implementation

Connectivity maps and linkage designs are useful for conservation only to the extent that they can support decision-making, guide management, or otherwise be implemented. If municipalities, transportation agencies, and land management agencies are to integrate these designs into their own land use and plan-

Case Study 5. Using Science to Evaluate Compromises During Implementation of a Linkage Design

In June 2009, the Arizona state wildlife agency released a detailed plan to conserve a wildlife corridor between the Tortolita Mountains and the Santa Catalina Mountains, just north of Tucson, Arizona. The plan (linkage design) included corridors for 9 focal species, as well as habitat maps for several other focal species for which corridor models could not be created. In a proactive response, the local land-use planning agencies (Pima County, Town of Oro Valley, and the State Land Department) modified a proposed 14,000-acre urban development project so that the project would conserve one of the three main corridors of the linkage design. Their modified development plan also proposed to destroy another corridor and defer the fate of the third.

The planners asked ecologists to assess how well their compromise plan would serve each of the nine focal species, compared to the full 3 corridors in the optimal linkage design. Using newly developed corridor evaluation tools (available at www.corridordesign.org), the ecologists provided biologically meaningful comparisons of both designs. They concluded that the compromise was virtually as good as the optimum for 7 of the 9 focal species. They quantified the degradation in utility for the other 2 species in terms of the gap lengths between patches of breeding habitat that each species would have to cross. The analysis allowed stakeholders and decision-makers to act with detailed appreciation of the ecological costs of compromise. The agencies proceeded with the compromise corridor plan. From a conservation perspective, the outcome was a fully protected corridor nearly a mile wide for its entire length, an $8 million commitment to build one wildlife overpass where a highway crosses the corridor, high confidence that the corridor is as good as possible for 7 species, and moderate degradation in corridor utility for the other 2 species. The cost of land acquisition was reduced by > $50 million, and the decision to proceed was made less than 6 months after the start of deliberations. Although not everyone agreed, most conservation advocates, developers, and land-use planners felt that a good compromise had been reached without prolonged litigation and clashes of expert opinion.

ning efforts, conservation professionals must provide specific guidance on how to use connectivity maps and designs in land use, zoning, transportation, and other types of plans.

Teams that engage stakeholders from the project outset and remain focused on the purpose and need for connectivity analyses are more likely to produce useful maps and data (for example, Case Studies 4 and 5). It is important to understand how organizations interact to achieve connectivity goals, particularly where different agendas may operate in the same landscape. If groups operate independently, and the fundamental needs of each organization are widely divergent, simply embracing the same long term objectives may not be sufficient. Differences in organizational needs or agendas can be constrained by political or land ownership boundaries. Recognizing these differences up front and explicitly addressing them in a connectivity strategy is vital to stakeholder agreement and project success. Finding agreement and compromise among stakeholder agendas helps in reducing conflict and the time spent on decision-making to pursue a conservation strategy, which in turn can reduce the overall costs and timeframe of implementation.

Recognizing and Addressing Uncertainties

Connectivity modeling involves uncertainties and challenges, all of which should be directly addressed. All models are abstract and partial representations of reality. However, if models or data are wildly incorrect, modeled corridors and other inferences about landscape connectivity may do more harm than good. Here, we discuss points to consider when applying connectivity models to achieve conservation goals.

Uncertainty and error can be introduced into the modeling process through a number of avenues, including inaccurate or incomplete characterization of species' biology, incomplete theoretical basis for model development, inappropriate data extrapolation, uncertainty in future landscape change, and changes in design goals during the planning process. Taken together, these sources of error increase uncertainty and signal the need for targeted collection of empirical data or, at a minimum, indicate that greater caution must be exercised when crafting conservation actions from the models.

The following points provide a framework for examining and addressing potential uncertainties in the context of connectivity planning.

Pay special attention to correct characterization of the biology of focal species in the ecosystem under analysis. For example, core habitat requirements should be as correctly and completely identified as possible. If habitat requirements are not well understood and are not accurately parameterized, even good models of movement or gene flow will result in erroneous linkage designs. If the core habitat requirements of a given focal species are not well understood, it may be a good idea to substitute a different focal species whose biology is better understood, so that the model can be parameterized with more confidence.

Understand the strengths and limitations of the connectivity models. For example, does the model predict movement solely from habitat-use data? If so, the model may underestimate long-distance movements of individual dispersers. Models based on inferences from movement behavior or patterns of landscape genetics may provide better predictions of connectivity.

Consider the effects of spatial and temporal extent in all of the analytical approaches described above. Temporal aspects of ecological function may range from daily changes in foraging habitat to seasonal migrations, to inter-annual fluctuations in climate, disturbance, and site productivity. Spatial considerations can range from removing specific barriers to local animal movement, to facilitation of long-distance dispersal, to regional plans that consider regional connectivity. For example, individual property owners may remove fences at lot lines. Neighborhood considerations may include street design, such as reducing curb height, which can be a significant barrier for smaller, less mobile species such as turtles. Municipal connectivity initiatives may incorporate greenway delineation as part of the comprehensive planning process. State and regional initiatives may incorporate system-wide processes, such as watershed planning and ecoregional connectivity assessments. The spatial extent of connectivity planning may even transcend national boundaries, as in the Yellowstone to Yukon initiative linking wildlands in western North America, or an ecoregional connectivity assessment in the Appalachian/Acadian region (Table 1 and Case Study 3). The challenge for connectivity management is ensuring that multiple levels of effort complement each other in a coordinated way, and that the selected analytical method or methods are appropriate relative to the intended management or conservation objectives. Mismatches between the scale of the ecological processes of interest and the scale of analysis may result in failure to conserve connectivity.

Be aware of uncertainties that emerge when trying to extrapolate results outside of the originally observed conditions. While some degree of extrapolation is inevitable, given that comprehensive information about the needs and responses of all individuals of all species in every location could never be obtained, extrapolation to other locations or species should be based on empirical results relevant to the species and landscape under consideration. For example, if the goal of connectivity modeling is to understand the movements of a rare temperate forest songbird, but a surrogate species is identified for modeling due to the constraints of available data, one should look first to another temperate forest songbird whose taxonomy and ecological requirements are likely to be similar to the target species. Extrapolation across scales, both temporal and spatial, is an additional challenge. Knowing the physical characteristics that influence patterns of movement across short distances or short periods of time may not be representative of how an organism makes decisions regarding long-distance movements or movements that extend over periods of time measured in seasons or generations.

Be aware that relationships among ecological and landscape variables may not be linear. Extrapolation requires an assumption about the nature of the relationship among factors outside the range of what is actually known. Because nonlinearities can take almost any form, assumed relationships stand a great chance of being incorrect.

Try to account for anthropogenic landscape change and the processes that drive it. Anthropogenic influences will continue to greatly affect many species' habitats and their movements; modeling should incorporate anthropogenic drivers of change and how these drivers affect habitat and movements.

Address the random variation that is inherent in many biological processes. It often is helpful to present a range of potential outcomes or the likelihood of certain outcomes (such as population persistence) under different assumptions about such variation, rather than a single "best" solution.

Regularly refer back to the stated goals of the analysis throughout the project duration so that data inputs, assumptions, and methods remain consistent with these goals. While researchers and practitioners alike may seek to produce a linkage map that captures the movement needs of all wildlife species and can be applied to landscape-scale and local planning efforts, one linkage design cannot encompass all possible connectivity goals and objectives at all planning scales. For example, a linkage design that captures landscape-scale connectivity of natural habitats across large ecoregions (for example, Case Study 3) may address broader or different conservation goals than a design based on local-scale connectivity between pairs of core areas (for example, Case Study 4). Similarly, an ecoregional analysis may prioritize connections that do not emerge in a continental-scale analysis. Through regular reference to the stated goals, the tendency for the focus to shift or the scope of a project to widen ("mission creep") can be avoided.

Plan for increased connectivity and conserve existing corridors to account for changing landscape conditions and threats. Because many changes are not predictable, adaptive management is critical. Monitoring is essential for adaptive management, because monitoring helps managers to keep track of what is changing in real time – such as the arrival of a new invasive species in the landscape, or changes in stream discharge that may affect fish habitat connectivity – and informs quick and appropriate responses. Managers and planners should be willing to expend resources on the adaptive management process, including not only making decisions about priority linkages, but also following through to monitor the status, function, and trends of these linkages, evaluate and assess the observed changes, and adapt future connectivity planning accordingly.

In the long term, data gaps and areas of high uncertainty can be reduced with better data and models or a stronger conceptual approach. At a minimum, practitioners should exercise caution when crafting conservation actions from connectivity models. Articulation of these uncertainties does not, however, diminish the usefulness of these tools. Explicit acknowledgment of uncertainties allows results to be inter-

Table 1. Examples of connectivity maps and their utility.

Extent	Project*	Map Type	Application
Individual linkage	**South Coast Missing Linkages**	Linkage design and specific conservation plans for each of 11 key linkages in California's south coast ecoregion.	Over 25 partners have used the plan to help secure over 100,000 ha of land, modify current land-use plans, and plan wildlife-friendly infrastructure.
State-wide	**Washington Connected Landscapes**	Coarse-grained analysis identifying broad connectivity patterns for Washington and adjacent areas. Maps depict suitable habitat and linkages for 16 focal species complemented by an ecological integrity analysis.	Used to identify where highway mitigation dollars can provide greatest wildlife benefits and to inform actions by state and federal land management agencies, NGOs, and other parties.
Ecoregional	**Staying Connected in the Northern Appalachians** **Two Countries, One Forest**	Coarse-grained identification of critical movement areas for wildlife spanning several states and provinces, especially across the U.S./Canadian border.	Used by 21 public and private partners as a framework to engage local stakeholders in in each area to further refine and identify key areas of local connectivity and reduce risks of habitat fragmentation to wildlife movement.
National	**Wild LifeLines**	Coarse-grained analysis of potential wildlife dispersal pathways across the coterminous 48 states. Uses multiple layers including land cover, distance to roads and housing density as proxies for habitat permeability and potential for wildlife movement.	Prioritizes a network of naturalness-based connections in terms of the contribution of each pathway to the flow of connectivity across the network. Model favors pathways that avoid fragmented and human-modified landscapes.

* For more information about each project:

South Coast Missing Linkages	http://scwildlands.org
Washington Connected Landscapes	http://waconnected.org
Staying Connected in the Northern Appalachians	http://www.conservationregistry.org/projects/3837
Two Countries, One Forest	http://www.2c1forest.org/en/mainpageenglish.html
Wild LifeLines	http://www.wildlandsnetwork.org/what-we-do/scientific-approach/wild-lifelines

preted honestly and can suggest future directions for research and critical evaluation. Further, models can be useful even when underlying data are sparse or weak, such as using predictions to compare scenarios (which among a set of strategies is likely to lead to greater gene flow?) rather than stating absolute responses (if a strategy is implemented, it will increase gene flow by a specific amount).

Future Directions for Connectivity Science

Although connectivity science has evolved considerably in the last twenty years, much still needs to be learned in order to improve the effectiveness of design and implementation. Research on species persistence, behavioral ecology, and community structure is needed to increase the accuracy and reduce the uncertainty associated with connectivity models. Also, evaluating and testing connectivity responses to climate change will be fundamental to achieving conservation goals in the face of the rapid changes that will confront many communities and ecosystems. And all of these potential areas of advancement will fall short of conservation goals if the interdependence of humans with natural landscapes is not recognized and human activities are not effectively incorporated into connectivity planning.

1. Species persistence

One of the most important directions for connectivity science is to incorporate the likelihood of species or population persistence into conservation plans. Persistence is a vital concept for evaluating what happens to species and communities when connectivity is lost and which connections are most important to maintain. Most reserve design is based on static maps of species distributions, in an attempt to maximize the potential number of species conserved across a reserve network. However, it is important to incorporate species persistence into conservation plans, particularly when planning for a network of reserves or habitat patches in which populations of species may be distributed as metapopulations – groups of subpopulations that are linked by some gene flow.

Persistence metrics, such as mean time to extinction or probability of extinction within a given timeframe, are necessary for determining the relative merits of different connectivity configurations. In theory, such methods could also be used to prioritize linkages in the landscape according to their influence on dispersal between patches and the importance of those dispersal pathways to species persistence. However, the construction of complete models can require many years for a single species, making these methods infeasible for applications to large numbers of species. An important way to address this constraint is to develop spatially explicit, stochastic, demographic meta-population models that can be parameterized for many species. Simulation models can be used to compare how the subtraction of each patch and linkage in a complete network influences mean time to extinction. Only through this type of persistence modeling will it be possible to examine the trade-offs between corridor conservation and augmenting the size of existing protected areas for long-term biodiversity conservation. Importantly, this approach can incorporate economic trade-offs, allowing prioritization of how conservation dollars are applied within a network of core areas and corridors.

2. Behavioral ecology

Current methods for identifying connections among habitat areas and estimating the costs to organisms of moving through a landscape are largely based on habitat suitability modeling, which uses information on habitat requirements or the extent to which species avoid human-altered landscapes, such as the built environment. However, current information regarding species' behavioral responses to habitat modifications at the local and landscape scale is inadequate. For example, understanding how wildlife species are impacted by roads and how they possibly avoid them is critical because roads are widespread and increasing in density in many areas. Land use changes may lead to behavioral responses that differ widely even within taxa. For example, some monkey species adapt quickly to human alteration of the landscape for agriculture, migrating through and even benefitting directly from agricultural crops by foraging in them, while other species in the same area that specialize on mature forests will not use and may actively avoid farmed areas. Other potential barriers, such as noise or light pollution, may have profound effects on animal behavior and functional landscape connectivity, but are even less well studied and understood. Preliminary research suggests that even supposedly unobtrusive forms of human activities, such as low-impact recreation, can affect animal behavior; for example, bird-watching activities have been shown to contribute to marked declines in the detection rate of mesocarnivores in California. Equally important is the continued study of local habitat characteristics that are required to maintain functional habitat connectivity. Some bat species, for example, appear to be more sensitive to local habitat features such as suitable roosting structures and wet areas for foraging, than to changes in large-scale vegetation cover patterns.

The influence of many human activities on wildlife behavior and connectivity is still not well understood. Habitat mapping and simulations are often less expensive than fieldwork and hence form the basis for much of the work done in connectivity science to date; however, the need for more fieldwork to fully inform such models cannot be overstated. Local field studies are essential for improving connectivity models and, ultimately, on-the-ground conservation outcomes.

3. Community structure

Habitat loss and fragmentation strongly influence predator-prey and competitive interactions that help shape ecological communities, with variable impacts on individual species or populations. If habitats are reduced in size and connectivity to the extent that apex predators cannot persist, this process can lead to trophic disruption or collapse, and many such trophic cascades have been documented in both terrestrial and marine systems. For example, loss of connectivity has facilitated trophic collapse in some African landscapes: habitat fragmentation and loss has caused declines of lions and other apex predators, leading to rapid increases in mesopredators, such as baboons. These baboon populations are in turn able to sustain themselves by taking advantage of human-altered landscapes through crop-raiding. Theoretical studies have shown that interactions between competitors are very sensitive to the structure of the landscape. These studies also demonstrated that habitat fragmentation can either stabilize interspecific competition, allowing for the coexistence of similar species or, as fragmentation increases, it may increase competition to a level where one of the species is eliminated. In these cases, coexistence or exclusion of species results from a tradeoff between dispersal rate and competitive ability, in relation to the degree of habitat modification and fragmentation. The key factors underlying each case are the interactions of behavioral and life-history characteristics of particular species with the scales and patterns of variability of the landscapes in which they live.

4. The challenges of climate change

Connectivity is one of the most commonly advocated strategies to help species adapt and survive rapid climate change. The idea is that connectivity may allow species to shift their ranges in response to changing climate, and thereby allow evolutionary and ecological processes to be sustained. However, connectivity designs based on current land cover patterns may not allow species to adapt to a changing climate and shifting ecological zones. During the next century of climate change, habitats will not simply shift or shrink, but many will disappear as species shift their ranges, adapt, evolve, or go extinct in idiosyncratic ways.

Connectivity designs can incorporate the ability to respond and adapt to climate change in several ways, although none have been rigorously tested. One approach tracks how a species' climatic envelope (suitable temperature and moisture regime) moves across a landscape under several decades of simulated climate change. The predicted corridor is the chain of locations that were (during the simulation) contiguous for enough time to support range shifts, with new populations becoming established in locations that transition into the envelope while other populations go extinct. Such models are conceptually sound but depend on at least four other highly uncertain and often only partially predictive models: 1) predictions of future carbon emissions, 2) models of how the atmosphere and oceans respond to these emissions, 3) climate envelope models for the focal species, and 4) dispersal abilities of these species. In addition, the most problematic aspect of these models is that, under climate change, novel types of climates are expected to occur, and forecasting how suitable these novel climates will be for existing species cannot be reliably conducted.

A simpler alternative, which avoids the inherent uncertainties in a species-based approach, is to design linkages based on the expected rates of climate change and the distribution of climates across space and time. This approach examines different characteristics of climate (such as rate of change, diversity, and low temperatures) that are potentially influential for reserve network resilience, based on the following assumptions: 1) the advantages of connectivity are greatest for areas that will experience faster rates of change, 2) a reserve network that harbors greater climatic diversity will allow for greater adaptation, and 3) maintaining access to cooler climates is a high priority. For example, if the distribution and representation of climates contained in a protected area is expected to change quickly and dramatically, then species in those locations may have to move, and corridors may be critical for their survival. This approach prioritizes the maintenance of reserves with greater climate stability. Another equally reasonable assumption is that a reserve network that harbors greater climatic diversity will provide refugia that allow for adaptation, so targeting links that add climatic diversity to the network is another possible approach.

An even simpler approach builds on the idea that rivers and their associated valleys provide a gentle and monotonic temperature gradient that may allow species to shift their ranges by sequentially colonizing areas along that gradient. Because such valleys will support riparian vegetation in nearly all climate regimes, they should be part of any connectivity map.

In some instances, short distance movement may be all that is required for species to shift their range and persist, in which case additions to existing protected areas may prove more effective and efficient than establishing corridors. Hence, additional research is needed to determine under what conditions adding area to existing reserves is more effective than adding linkages for increasing climatic diversity within a reserve network. Recent efforts by physical scientists to downscale climate change models may allow ecologists to explore these questions. Approaches using landscape units, temperature gradients, and river valleys are coarse-filter approaches and, therefore, are unlikely to meet the needs of all terrestrial species, especially the most extreme habitat specialists. However, even the best fine-filter (species-based) approach will not be able to serve the needs of species that cannot shift their range fast enough in response to rapid climate change.

5. Putting people back on the landscape

The interaction between land use and natural systems affects not only biodiversity but also human livelihoods. Quantification of the ecosystem service benefits that result from well-connected habitat, as compared to fragmented landscapes, may help leverage public and political support. In particular, hydrologic connectivity can provide increased water quality and aquatic species diversity upon which humans and other terrestrial species rely. Multidisciplinary teams can use surveys of resource use and attitudes, and analysis of political structure to complement connectivity maps and plans, supporting a holistic understanding of the landscape and the organisms that inhabit it.

Further knowledge about how connectivity benefits ecological services can, in turn, improve the public's understanding of the importance of protecting connected wildlands. Ecosystem services, such as water and air quality or pollination, provide additional value beyond species movement and persistence. As connectivity conservation continues to become more prevalent, planning efforts need to be directed beyond simply quantifying the facilitation of species movement towards quantifying these additional positive conservation outcomes as well.

Conclusions

Landscape connectivity is of fundamental importance to the maintenance of populations and species, as it enables organisms to move among habitat patches to access the ecological resources they need. In this *Issue*, we have explored the issues that conservation scientists face in trying to evaluate, plan, and implement habitat connectivity for biodiversity conservation, today and into the future. We stress the importance of protecting structural and functional connectivity, to the extent that function can be measured, at multiple scales. However, processes such as biological invasion also highlight the complexity of understanding how connectivity influences the persistence of a given population or species. Increasing connectivity for one species can facilitate the spread of invasive species and disease, under some conditions, while fragmented landscapes and high levels of disturbance can also lead to similar results in other situations. Various methods exist to measure connectivity and identify priority linkages, and all point to the importance of scale for identifying linkages that can be restored or conserved through practical on-the-ground management. While increasing habitat connectivity remains a primary adaptation strategy for biological conservation, more research is needed on how best to assess the effectiveness of corridors for facilitating migration and providing overall reserve network resilience at the necessary scales, given expected rates of landscape change. Field studies that address how well linkages function for different species, and identify potential barriers to movement, are important to inform linkage design.

In the end, much remains to be learned about how configurations of reserves and linkages are likely to influence species conservation, how this may change under future climate scenarios, how species respond to site-level disturbances, and what management guidelines are most likely to protect the connectivity functions that linkages are designed to provide. Despite these data gaps and uncertainties, we believe that researchers and managers can successfully navigate many of the challenges in maintaining and restoring landscape connectivity by using the guidance we have outlined. First, approach connectivity at scales relevant to conservation targets. Second, incorporate flexibility and anticipatory approaches into connectivity planning through the use of tools including sensitivity analyses, uncertainty analyses, and adaptive management. Last, move forward on connectivity plans with stakeholder agreement and coordination, towards a common set of well-articulated goals that are scale-appropriate and account for major drivers in landscape connectivity, including anthropogenic influences and climate change.

For Further Reading

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