Landscape Connectivity and Ecological Effects

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Abstract
Landscape connectivity is the degree to which the landscape facilitates or impedes movement among resource patches. This movement is crucial for a number of different ecological processes including migration, dispersal, and colonization of locally extinct habitat patches. Hence, landscape connectivity has been of great interest to ecologists for at least two decades. Landscape connectivity is studied at the level of individual habitat patches as well as at the much larger landscape scale; it is modeled and empirically observed. Many different metrics have been developed to study the effect of landscape connectivity on a variety of organisms. Here, we give a brief overview of the different ways landscape connectivity has been defined and measured and highlight some important findings about the impact of connectivity on ecological and evolutionary processes, conservation, and natural resource management.

INTRODUCTION

Landscape connectivity is broadly defined as the "degree to which the landscape facilitates or impedes movement among resource patches."[1] Movement across the landscape is crucial for a number of different ecological processes including migration,[2] dispersal,[3,4] and colonization of locally extinct habitat patches.[5,6] These movements have serious implications for gene flow and long-term evolutionary processes[7–9] as well as biological conservation.[10,11] For that reason, landscape connectivity has been of great interest to ecologists for at least two decades.[1,12,13] However, it has also been the source of confusion because, as Calabrese and Fagan[14] wrote, "connectivity comes in multiple flavors." Here, we give a brief overview of the different ways landscape connectivity has been defined and measured and highlight some important findings about the impact of connectivity on ecological processes, conservation, and natural resource management.

DEFINITIONS

Structural versus Functional Connectivity

Structural connectivity is based on the amount and physical configuration of landscape elements, including habitat patches, corridors, and stepping stones (Table 1, Fig. 1). These elements are typically thought of as being embedded in a matrix of unsuitable habitat, through which movement may be limited or restricted.[15] Some studies have suggested that corridors or stepping stones can be established to increase connectivity between habitat patches.[3,16–20] However, these landscape elements may facilitate movement of some organisms more than others or more movement in some landscapes than others.[17,21,22] *Functional connectivity* incorporates an organism's behavior or response to elements such as corridors or stepping stones. Functional connectivity may also depend on a species' response to the matrix between landscape elements.[23,24] For example, corridors may be particularly important for species with a low capacity to move through the matrix.[25] Therefore, functional connectivity is species specific, and a single landscape can have different levels of connectivity depending on the species or process in question. Habitat that is functionally connected may not be structurally connected, and vice versa.[26]

Patch- versus Landscape-Level Connectivity

Connectivity can be measured at many different scales. On one hand, researchers or managers may want specific information about the connectivity of a single patch to the rest of the landscape. For example, studies of American pika (*Ochotona princeps*) have used incidence function models (IFMs)[27] to predict patch occupancy and population turnover in a large network of habitat patches.[28] On the other hand, researchers or managers may have questions about the connectivity of the entire landscape, perhaps to compare one landscape to another, or perhaps to identify whether

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Table 1 Landscape elements that affect landscape connectivity

Element	Definition
Habitat patch	A contiguous area of relatively homogeneous land cover that is suitable for the species of interest.
Corridor	Continuous strips of habitat that structurally connect two or more patches.
Stepping stone	Ecologically suitable patch (typically small in size) that may act to connect larger patches of habitat. Stepping stones may function at two different time scales. First, at the shortest time scale, they may provide a temporary stopping location for an organism moving through the landscape. Second, at the longer time scale, they may provide a breeding location so that an organism's offspring can move to more distant patches.
Matrix	The intervening area between habitat patches in a landscape mosaic, usually characterized by being the most extensive cover, having high spatial continuity, or having a major influence on the landscape dynamic.

Source: Modified from Forman.[15]

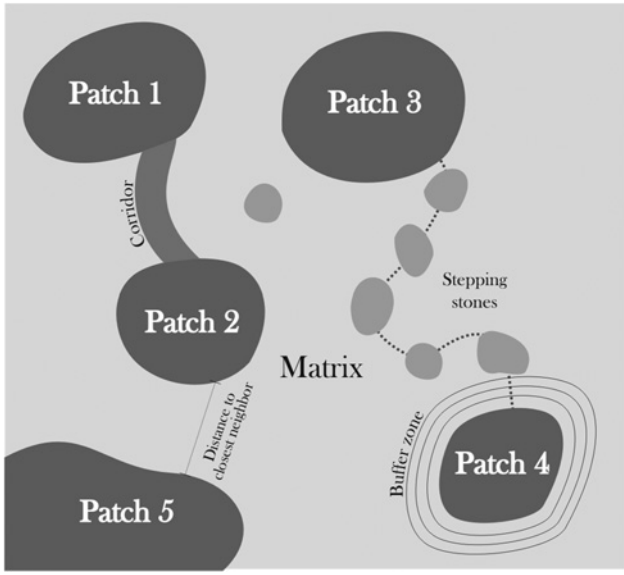

Fig. 1 Landscape structure and elements.

connectivity is sufficient for a species of concern. For instance, a study of protected area networks in the United States found that certain ecoregions had greater landscape-level connectivity than others and that protected area networks were consistently more connected for large mammals than for small mammals.[29] Different metrics are used for patch- and landscape-level connectivity, and we describe some of these in the following section.

MEASURING LANDSCAPE CONNECTIVITY

Dozens of different metrics exist for measuring landscape connectivity, and a number of reviews have been published on the topic.[26,30–35] Metrics may describe structural or functional connectivity, at the patch or the landscape level, or a combination of both (summarized in Table 2). One common approach that combines both patch- and landscape-level analyses involves patch-removal "experiments," in which researchers calculate a landscape-level connectivity metric, simulate the removal of a particular patch, and then recalculate the landscape-level metric once that patch has been removed. The difference between the first connectivity estimation and the second can be used to rank individual patches in terms of their importance for connectivity across the entire landscape.[36,37]

In general, structural connectivity measures may be calculated simply by examining a map. One of the simplest measures of patch-level structural connectivity is nearest-neighbor distance, which is the Euclidean distance to the nearest patch.[2] This measure was shown to be a useful predictor of the incidence of a frugivorous beetle in forest fragments.[38] This simple measure can be infused with more ecological information by measuring distance to the nearest occupied patch rather than distance to any patch,[2] but the more comprehensive measure is not always an improvement on the simpler one.[38] Another common way to measure patch-level structural connectivity is to examine the amount of habitat in a buffer around the focal patch. This measure was found to be much better than nearest-neighbor distance for predicting colonization events in two butterfly species but was very sensitive to buffer size.[32] At the landscape level, structural connectivity can be measured, for example, based on percolation or lacunarity. In these approaches, the landscape is considered as a two-dimensional grid where each cell in the grid is classified as either habitat or non-habitat. Landscape connectivity is then measured as the physical connection of habitat, in the case of percolation,[39] or as the variability and size of inter-patch distances, in the case of lacunarity.[40] The lacunarity index was shown to be a good predictor of dispersal success for simulated organisms in fractal landscapes.[41]

Because functional connectivity is specific to the species or process of interest, it is necessary to know something about species' movement behavior to measure functional connectivity. Species may perceive and respond to landscape pattern differently according to their dispersal characteristics, their preferred habitat type, or other life history traits.[26] For example, seed-dispersing birds differ in their presence in remnant trees within the matrix based on their frugivory levels. Fruiting trees could represent stepping stones across the matrix for birds with a completely fruit-based

Table 2 A subset of metrics used to measure landscape connectivity

Metric	Scale	Connectivity type	References
Nearest-neighbor distance	Patch	Structural	2, 38
Buffer area	Patch	Structural	32
Incidence function models	Patch	Structural	27, 28
Lacunarity	Landscape	Structural	39, 40, 41
Network centrality metrics	Patch	Potential	59
Cohesion index	Landscape	Potential	44
Least-cost paths	Dispersal route	Potential	36
Multiple shortest paths	Dispersal route	Potential	67
Isolation by resistance	Dispersal route	Potential	65
Probability of connectivity (PC)	Landscape	Potential	63, 64
Cell or patch immigration	Patch or landscape	Actual	48
Animal homing time	Landscape	Actual	53

diet, but may not for birds with mixed diets.[42] Functional connectivity measures are usually considered to be superior to structural connectivity measures.

Depending on how it is measured, functional connectivity can be divided into *potential connectivity*, where information about the movement ability of the organisms is limited, and *actual connectivity*, where there is detailed movement data for the organism of interest.[14] Potential connectivity measures may be based on attributes such as body size of the animal or dispersal mechanism of the plant. At the patch level, measuring potential connectivity may be as simple as using an ecologically meaningful distance when counting nearest neighbors.[43] At the landscape level, potential connectivity can be measured using the cohesion index, for example. This index integrates habitat quality, amount and configuration of habitat, and permeability of the landscape matrix to indicate species persistence.[44] Potential connectivity of both patches and landscapes can be calculated based on resistance or cost surfaces, which represent the willingness of a focal organism to cross the environment between habitat patches.[45] This approach emphasizes the importance of the matrix to connectivity and is based on potential "costs" of movement (usually in terms of energetic expenditures or mortality risks) through different regions of the landscape. Cost surfaces have been used to identify potential conservation corridors for jaguars[46] and were shown to help predict patch occupancy for prairie dogs in Colorado, United States of America.[47] Dispersal routes connecting habitat patches can be identified using least-cost path tools. This estimates the route with the least resistance between two points; however, by identifying a single route, alternative paths with comparable resistance costs may be ignored. This approach has been extended to include multiple routes, with methods such as circuit theory or Multiple shortest paths (MSPs), which are described in greater detail at the end of this section.

Actual connectivity measures are based on empirical, often spatially explicit, information about the movement of a particular organism. At the patch level, actual connectivity can be measured as the number of immigrants into a patch.[48] At the landscape level, actual connectivity may be measured as the number of patches visited by an organism or movement rates across the landscape.[49,50] However, these approaches can present a paradox in that animals may move more frequently between patches in lower-quality habitat, counterintuitively resulting in higher connectivity indices in these less-desirable environments.[51] Another approach to measuring actual connectivity draws heavily from behavioral ecology. For instance, Bélisle[51] suggests several different experimental methods for determining the motivation underlying movement of individuals through the landscape, including translocations, playback experiments, and measuring giving-up densities. Playback and homing experiments have been used to study the effect of roads[52] and other barriers[53] on animal movement. More recently, playback techniques have been used to parameterize graph theory models (described below) to explain the occurrence pattern of an Atlantic rainforest bird.[54]

Functional connectivity can also be inferred from genetic information. Dispersal influences gene flow between subpopulations,[55,56] which results in genetic differences among organisms occupying different parts of the landscape. Landscape genetics is a rapidly growing field and will likely continue to make large contributions to measuring and understanding the consequences of landscape connectivity.[57]

Graph theory, also called network analysis, is a flexible method for measuring landscape connectivity that has gained traction over the last decade. A graph is a set of nodes connected by links, where a link between nodes indicates a connection between them. In landscape ecology, the nodes typically represent habitat patches, and links indicate dispersal between patches.[58] Commonly used

metrics from graph theory include various centrality measures, which determine the importance of individual nodes in the graph (i.e., patch-level connectivity). Some examples include degree centrality, which measures the number of links of a given node (akin to the number of neighboring patches), and betweenness centrality, which measures the number of shortest paths that pass through a given patch.[59] Graph theory can measure both potential and actual connectivity, at either the patch or the landscape level or a combination of both. To date, most applications of graph theory define links based on either an ecologically relevant measure of Euclidean distance[60,61] or a distance that incorporates cost or resistance to movement.[36,62]

Graph-based metrics have also been developed around the concept of measuring habitat availability or reachability at a landscape level. In this approach, movement between and within patches is combined in a single metric that describes the ability of species to reach resources across the landscape whether those resources come from the same patch (intrapatch connectivity), from connected neighboring patches (interpatch connectivity), or from a combination of both. Habitat availability metrics combine topological features with ecological characteristics of landscape elements, which has helped to place connectivity considerations in a broader and more informative context for conservation management alternatives.[63,64]

Some graph theory-based methods explicitly model multiple paths between two points of interest, extending the least-cost path approach described earlier. Circuit theory, which comes from the field of electrical engineering,[65] can be used to model the movement of individuals across a landscape based on the idea of isolation by resistance[65] and incorporates the effect of the matrix on movement across the landscape. In circuit theory, landscape "circuits" are a kind of graph with links defined in terms of resistances between nodes. Circuit theory techniques can be combined with genetic information, for example, to examine the influence of landscape composition and configuration on gene flow.[66] Additional graph theory methods that account for multiple paths across the landscape include calculating conditional minimum transit costs (CMTCs) and MSPs. Both methods have been used to enable visualization of multiple dispersal routes that, together, are assumed to form a corridor.[67]

RELEVANCE OF LANDSCAPE CONNECTIVITY TO CONSERVATION, RESTORATION, AND EXOTIC SPECIES MANAGEMENT

Habitat fragmentation and loss put many species at risk of local or regional extinction,[68] and persistence of many plant and animal populations depends on their ability to recolonize distant habitat patches.[6] One consequence of habitat fragmentation is that isolated populations tend to lose fitness though inbreeding depression and a loss of genetic diversity.[66] This reduces the ability of populations to adapt to environmental changes and could result in an increased risk of local extinction.[69–72] Habitat fragmentation may also prevent species from shifting their range in the case of climate change.[71] Recent studies have focused on how climate change will affect dispersal of individuals through the landscape and how populations will shift their distributions. For example, based on their movement capacities, it has been estimated that populations of many mammal species will be vulnerable following climate change.[73]

Many authors have suggested that increasing landscape connectivity is one of the best options for conservation in the face of habitat loss and climate change (reviewed in[74]). Corridors and stepping stones have been suggested as one way to increase connectivity[20, 75] and have been shown to direct the movement of a number of different species.[17,76,77] Designing strategic networks of patches and corridors that allow for dispersal between environmentally similar habitats[78] or between different climatic areas based on expected changes in climates[79] may help to counterbalance the effects of climate change on natural populations. Where habitat fragmentation is prevalent, restoring functional connectivity in the landscape can broaden species distributions, rescue genetically isolated populations, and assist in the conservation of animal and plant species.[17,19,20,80–82] Connectivity measures based on graph theory in particular have been used to assist with conservation planning for many species, including the European bison[83] and the gray wolf,[84] and have also been applied to freshwater[85] and marine[86] environments.

One concern about increasing landscape connectivity is the potential for also increasing the risk of invasion from exotic species and pathogens.[87,88] However, the degree to which landscape configuration constrains the spread of an exotic species may depend on dispersal characteristics of the focal species. For example, species considered to be "invasive" and species with frequent long-distance dispersal events are likely to spread across a landscape regardless of the configuration of landscape elements.[89,90] Fortunately, the methods described earlier may be useful for predicting and managing the spread of exotic species. For example, Minor and Gardner[89] used graph theory to identify critical points on the landscape where management could help contain the spread of invasive plants. Similarly, Wang et al.[91] identified particular types and spatial arrangements of land cover that were conducive to the spread of the invasive rice water weevil (*Lissorhoptrus oryzophilus*) in eastern China.

CONCLUSION

There is a large and expanding body of literature on the topic of landscape connectivity. Connectivity is known to be important for a number of ecological processes and

thus for long-term biological conservation. There are currently dozens of methods for measuring landscape connectivity and new methods are proposed on a regular basis. However, because movement is difficult to observe, and large-scale experiments are expensive and logistically challenging, the field has lagged behind on empirically testing the effect of landscape configuration on the movement of plants and animals. Therefore, much remains to be learned about how organisms move around the landscape, how these movements influence population processes and gene flow, and how we can improve connectivity for species of conservation concern while minimizing the movement of exotic species. Future research can help us to find the balance between "desirable" movement, like gene flow or seed and pollen dispersal of native species, with "undesirable" movement of invasive species and pathogens. In both cases, understanding how landscape connectivity influences population dynamics will allow us to identify better conservation strategies and management plans.

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