Landscape connectivity: a return to the basics

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INTRODUCTION

In the decade or so since the concept was formalized in landscape ecology (Taylor *et al.* 1993) the meaning of the term "landscape connectivity" has become rather diffuse and ambiguous. Many researchers continue to ignore key elements of the original concept, which greatly diminishes its potential utility for land management and the conservation of biodiversity. As originally defined, *landscape connectivity* is "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor *et al.* 1993; see also With *et al.* 1997). This definition emphasizes that the types, amounts, and arrangement of habitat or land use on the landscape influence movement and, ultimately, population dynamics and community structure. Landscape connectivity thus combines a description of the physical structure of the landscape with an organism's response to that structure. In contrast, common usage generally emphasizes only the structural aspect, where landscape connectivity is simply equated with linear features of the landscape that promote dispersal, such as corridors. Moreover, most commonly employed measures of connectivity focus only on how patch area and inter-patch distances affect movement (e.g., Moilanen and Hanski Chapter 3); such measures ignore the rich complexity of how organisms interact with spatial heterogeneity that may ultimately affect dispersal and colonization success (e.g., interactions with patch boundaries, matrix heterogeneity: Wiens *et al.* 1993; Wiens 1997; Jonsen and Taylor 2000a). Our aim in this chapter is thus to refine the concepts inherent in the original definition of landscape connectivity, to outline why it is important to disentangle landscape connectivity from

other (equally important) landscape characteristics, and to advise how a return to the basics may aid land managers charged with managing landscape connectivity as a component of biodiversity.

JUST WHAT IS LANDSCAPE CONNECTIVITY, ANYWAY?!! ISSUES AND CONCEPTS

Landscape connectivity is an "emergent property" of species—landscape interactions, resulting from the interaction between a behavioral process (movement) and the physical structure of the landscape. It is therefore a dynamic property that is assessed at the scale of the landscape (with particular organisms or suites of organisms in mind) and is not simply an aggregate property of a set of patches within the landscape. We can broadly consider two kinds of landscape connectivity: structural and functional connectivity. Structural connectivity ignores the behavioral response of organisms to landscape structure and describes only physical relationships among habitat patches such as habitat corridors or inter-patch distances. It is readily measured with a variety of landscape metrics or spatial analytical approaches (e.g., Gustafson 1998; Moilanen and Nieminen 2002). When physical relationships between habitat patches are tightened, structural connectivity is increased. Functional connectivity, on the other hand, increases when some change in the landscape structure (including but not limited to changes in structural connectivity) increases the degree of movement or flow of organisms through the landscape. The original concept of landscape connectivity thus emphasizes the functional connectivity of landscapes.

This distinction between structural and functional connectivity is not a trivial one. First and foremost, habitat does not necessarily need to be structurally connected to be functionally connected. Some organisms, by virtue of their gap-crossing abilities, are capable of linking resources across an uninhabitable or partially inhabitable matrix (Dale *et al.* 1994; Desrochers *et al.* 1998; Pither and Taylor 1998; Hinsley 2000; Bélisle and Desrochers 2002). Conversely, structural connectivity does not provide functional connectivity if corridors are not used by target species (see also Crooks and Sanjayan Chapter 1; Fagan and Calabrese Chapter 12; Noss and Daly Chapter 23). Nevertheless, structural connectivity is still all-too-frequently equated with functional connectivity in the literature and, in our experience, by land managers.

It is generally not possible to simply extrapolate from measures of structural connectivity (such as distances between patches) to derive

a measure of overall landscape connectivity. That is because measures of structural connectivity ignore variability in the behavior of the organism(s) in response to the landscape structure, and ignore broader-scale influences of landscape structure on finer-scale movement decisions. Measures of landscape connectivity could be derived from inter-patch distances in situations where the matrix is invariant and ecologically neutral over the area of study, and where there are no effects of landscape structure on movement decisions at the scale of study, but such situations are likely quite rare.

Some recent work is paving the way to linking these two general frameworks. In particular, incidence function models were originally solely distance-based and so only measured structural connectivity. More recent derivations of these models contain coefficients that represent differential rates of movement of organisms through different habitats (e.g., Roland *et al.* 2000; Moilanen and Hanski Chapter 3). Such coefficients effectively represent the behavioral response of an organism to the physical structure of the landscape, so the models include a better metric of functional connectivity than measures based only on distance. The coefficients capture the ''effective isolation'' of patches (Ricketts 2001), in which movement may be reduced (or even avoided) in some cover types, and thus patches are effectively more isolated than Euclidean measures of distance would suggest.

ASSESSING LANDSCAPE CONNECTIVITY

Structural connectivity is usually easier to assess than functional connectivity, since the former can be computed using landscape metrics of spatial analyses of maps or within a geographic information system (GIS). This likely explains its prevalence in the literature (including some papers in this volume). However, the relative ease of calculating structural connectivity is not a sufficient reason for defaulting to its use. Using structural connectivity in place of landscape connectivity can (and does) lead to inappropriate land-management strategies, and obfuscates what might be key problems in managing a given landscape. We see this commonly when corridors are proposed as mitigative measures in forested landscapes slated for harvest. In forest landscapes, corridors probably do not improve access to small patches for mobile species, such as songbirds (Hannon and Schmiegelow 2000) and flying squirrels (Selonen and Hanski 2003), because movement among forest patches is actually a function of both gap-crossing abilities (Bélisle and Desrochers 2002)

and the successional stage of the intervening habitat (Robichaud *et al.* 2002). Thus, a land manager charged with protecting a given volume of timber within a landscape might be advised to use that allocation to protect areas that serve other functions (e.g., riparian zones) or to increase the sizes of protected areas. Furthermore, attention can then be placed on managing the intervening patches of non-habitat – ''managing the matrix'' – in such a way as to maximize the speed at which remnant resource patches can be re-accessed by target species. On the other hand, some species may benefit from habitat corridors that physically connect suitable habitat or resource patches (Tewksbury *et al.* 2002; Varkonyi *et al.* 2003). Thus, managing for structural connectivity may, for some taxa, in some situations, also improve functional connectivity.

Another difficulty in measuring functional connectivity is that the effect of a landcover type on movement can also vary depending on type of landscape in which the cover type is embedded. For example, Calopterygid damselflies inhabiting streams in Nova Scotia, Canada, readily cross stream/forest boundaries but move little through forest. When streams are embedded in landscapes that are partially forested, the animals also readily cross stream/pasture boundaries and move through pasture to access the forest resource. However, when forest is almost completely removed damselflies are unlikely to move into pasture (Jonsen and Taylor 2000a, 2000b). Therefore, for these damselflies, the effect of pasture on landscape connectivity depends on the amount of forest in the landscape at a broader spatial scale. Landscape context is thus important for evaluating how land-use change will affect landscape connectivity.

Assessing landscape connectivity requires a species-centered approach (Hansen and Urban 1992). It requires information on species' movement responses to landscape structure (e.g., movement rates through different landscape elements, dispersal range, mortality during dispersal, and boundary interactions) and how those responses differ as a function of broader-scale influences. Such information is typically quite difficult to obtain, but this is changing rapidly owing to advances in satellite-based tracking devices and new methods for analyzing movement data (Jonsen *et al.* 2003; Tracey Chapter 14). Many researchers are now exploiting these technological and analytical advances, which will lead to significant progress in our understanding of how organisms interact with landscape pattern.

Heterogeneity and asymmetrical landscape connectivity

In assessing the functional connectivity of a landscape, one needs to keep in mind that regions that facilitate movement need not be discrete features

of the landscape such as habitat corridors, but may occur where the juxtaposition of particular habitats or land uses act to funnel dispersers between habitat patches. Using an individual-based simulation model, Gustafson and Gardner (1996) demonstrated how the structure and heterogeneity of the matrix can affect the transfer of virtual organisms among forest fragments. Although patch size and relative isolation explained most of the variability in dispersal success, with closer and larger patches having the greatest exchange of individuals, the structure of the surrounding matrix also significantly altered transfers among patches. Roads, waterways, or land uses such as plowed fields may act as barriers to dispersal, encouraging dispersing individuals to move away from them. This can create asymmetries in the transfer probabilities among patches or regions of the landscape. There may be a lack of symmetry in the landscape pattern as well; emigrants from an isolated patch may succeed in reaching a neighboring patch, but if the neighboring patch is surrounded by a number of closer patches, then few of its dispersers will likely reach the isolated patch. Such asymmetrical landscape connectivity has been found for the Iberian lynx (*Lynx pardinus*) in southwestern Spain where suitable habitat surrounding one population tends to limit emigration but encourage immigration (Ferreras 2001). Less-suitable habitat can also function as an important conduit for dispersal in regions where landscape structure would otherwise limit structural connectivity among patches or populations (Milne *et al.* 1989). For example, Schultz (1998) suggested that dispersal of the Fender's blue butterfly (*Icaricia icarioides fenderi*) among lupine patches could be facilitated by creating small lupine "stepping stones" because butterflies moved more quickly through the matrix habitat, and were thus more likely to reach isolated patches of lupine in extensively fragmented landscape than if they moved along lupine corridors.

Directional connectivity among patches has also been documented in the case of the cactus bug (*Chelinidea vittiger*), which uses olfaction to locate its *Opuntia* cactus host (Schooley and Wiens 2003). In a release experiment, successful dispersal was determined by the size of the target patch and the structure of the intervening matrix, but there was a strong effect of prevailing wind direction on orientation behavior such that bugs were more likely to orient toward cactus patches located upwind. Similarly, the directionality of water currents may contribute to asymmetrical connectivity of populations in aquatic or marine systems (e.g., Man *et al.* 1995; DiBacco *et al.* Chapter 8; Pringle Chapter 10). Although this clearly complicates assessment of functional connectivity, these examples

illustrate why landscape connectivity cannot be captured simply by an index of landscape pattern, but must be determined based on the organisms' perception of, and interaction with, the structure and heterogeneity of the landscape.

Non-linear effects of landscape connectivity are possible

Theory predicts that landscapes will become disconnected abruptly, at a threshold level of habitat availability, which may have some surprising and unexpected consequences for the management of biodiversity. For example, neutral landscape models, derived from percolation theory, are model landscapes in which complex habitat patterns are generated using theoretical spatial distributions (e.g., random or spatially correlated habitat distributions: With 2002). Landscape connectivity is assessed by determining how organisms move and interact with the structural heterogeneity of the resulting landscapes (With and Crist 1995; With *et al.* 1997). Such models may exhibit critical thresholds in landscape connectivity (Gardner *et al.* 1987; With 1997). The specific threshold at which landscapes become disconnected (the *percolation threshold*) depends on both the distribution of habitat and the habitat-specific movement rates of the species (With 2002). *There is thus no single critical threshold value at which a particular landscape becomes disconnected for all species simultaneously*, and a given landscape could be perceived simultaneously as both connected and disconnected by two species that differ in dispersal characteristics (i.e., definitions of landscape connectivity are organism-centered: Pearson *et al.* 1996). Such thresholds have also been identified in other theoretical approaches that quantify connectivity (e.g., Hanski 1999; Urban and Keitt 2001).

It is tempting to assume that thresholds in landscape connectivity precipitate other ecological thresholds, such as in dispersal success, population persistence, species interactions, and community composition, and thus ultimately, system resilience. However, these ecological thresholds may not – and generally do not – coincide with thresholds in landscape connectivity. For example, thresholds in dispersal success were not found to coincide with percolation thresholds in landscape connectivity (With and King 1999a) probably because dispersal success is typically assessed at different spatial and temporal scales than landscape connectivity. It follows then that the critical level of habitat at which landscape connectivity becomes disrupted is generally not the same level as a species' extinction threshold (the minimum habitat area required for population persistence: With and King 1999b). What is important to realize is that

a connected landscape does not guarantee species persistence, just as a disruption of landscape connectivity may not result in the immediate extinction of a species. The latter could nevertheless set the stage for delayed extinctions that occur years or decades later (extinction debt: Tilman *et al.* 1994; Hanski and Ovaskainen 2002).

MISAPPLICATION OF CONNECTIVITY CONCEPTS ON THE LANDSCAPE

Land managers are understandably eager to incorporate scientifically based guidelines concerning the maintenance of landscape connectivity into management plans. Unfortunately, this can lead to the well-intentioned but misguided application of principles supposedly derived from theory.

A specific example illustrates this point. The Woodland Trust, the UK's leading conservation organization devoted to the protection of native woodland, had initially established targets for forest cover throughout the UK based on a "30% Rule" derived from random neutral landscape models (Peterken 2002; Woodland Trust 2002). Empirical support for this 30% Rule was also taken from literature that showed persistence thresholds for various species (birds, mammals) in this vicinity (Andrén 1994; Peterken 2002). The implication of the 30% Rule was that connectivity was presumably assured in landscapes with more than 30% forest cover. On the surface, advocating for 30% forest cover would appear to be a good idea, given that only 12% of the country is currently forested (Woodland Trust 2000). But real landscapes are not random; they contain barriers, detrimental matrix habitat, reproductive sinks, and predator pits, and thus simple random neutral landscape models are inappropriate as a basis for developing general guidelines for managing connectivity in these landscapes (although neutral landscapes with greater spatial contagion provided a better model: K. Watts, pers. comm.). Even if 30% woodland cover is above the connectivity threshold for a species of concern, it is not necessarily above its persistence threshold. Suggesting that a goal of 30% woodland cover is "not arbitrary" but is "based on [a] well-established mathematical model" (Woodland Trust 2002) is misleading, in that it lends an aura of scientific rigor and credibility that may not be defensible, even if does help to promote increased protection and restoration of woodlands (i.e., a worthy goal, but for the wrong reason). This is a significant concern when one considers that the concept of forest habitat networks has been incorporated into the current forestry

strategies of the Forestry Commission and other conservation organizations in the UK (Peterken 2002; Watts *et al.* 2005). Fortunately, the Woodland Trust is no longer using such simple landcover thresholds as a basis for conservation planning, and instead appears to be exploring alternatives that move beyond such structural-connectivity measures toward more of a functional-based approach that would entail managing the matrix to enhance connectivity among existing woodlands (K. Watts, pers. comm.). Nevertheless, their initial recommendation based on this 30% Rule was apparently so influential (and appealing) that other organizations within the UK, such as the South West Wildlife Trusts, are incorporating the 30% Rule in the development of their own action plans (e.g., the South West Nature Map: South West Wildlife Trusts 2004).

No matter how well-intentioned or advantageous the outcome, such recommendations based on the flawed application of connectivity concepts and theory will erode our credibility as scientists and practitioners. Even worse, we run the risk of mismanaging the lands we have been entrusted to protect. Instead, land managers should focus on the suite of ecological processes that maintain biodiversity in the landscape. Managing landscape connectivity is but a small part of that large task.

LESSONS LEARNED

We summarize this chapter with a set of key lessons that have emerged and should be considered by those studying or implementing concepts of landscape connectivity on the ground.

Landscape connectivity is species-specific

Different organisms interact with landscape structure at different scales and in a variety of ways. Landscape managers must deal with that explicitly. Note that this does not necessarily mean that detailed measures of landscape connectivity are needed for every particular species—landscape combination, but rather that we need to recognize that organisms will exhibit a diversity of responses to any given management intervention, and that we should attempt to manage for a range of responses, across a range of taxa and a range of spatial scales.

Manage the matrix!

Managing the matrix can offer an effective means of managing the landscape to preserve or restore functional connectivity. Recall that there

are three components to landscape connectivity (1) species movement patterns and behaviors, (2) the size and arrangement of resource patches, and (3) the matrix. Our ability to manipulate or manage these components varies considerably. We can redirect and manipulate the behavioral responses of species through the use of fences, roadway crossings, and other devices, but we generally cannot directly alter the inherent behavior of a species. It should however be observed that there is surprising plasticity of response to changes in landscape structure in some species. For example, Taylor and Merriam (1995) and Pither and Taylor (2000) showed that wing morphology of a calopterygid damselfly differed between individuals living in landscapes dominated by forest and those in landscapes dominated by pasture. Such responses should be looked for since the need for expensive mitigative measures may be alleviated if species can behaviorally adapt to a disruption in landscape connectivity.

With respect to the second component, there are times when it is possible to alter the size and arrangement of habitat on the landscape, but frequently, economic or social constraints preclude our ability to do so. For example, commercial forest enterprises are often structured such that they require access to fixed amounts of wood fiber on a continuous basis — these economic constraints may preclude some management options. As a further example, it can be costly to reclaim and revegetate landscapes that have already been converted to agricultural use. These examples are not excuses to ignore issues around habitat loss and exploitation, but simply a reflection that at times there is a limited ability for land managers to affect the extent of such human activities.

Managing the matrix is the third means through which we can manage landscape connectivity. The matrix is often more extensive than remaining patches of habitat, so a focus on managing it may make more sense in many circumstances. This is not a new idea but the fundamental relationship between managing the matrix and landscape connectivity is sometimes ignored. This may be partly because managing the matrix can require decisions with high political or economic costs. For example, improvements in landscape connectivity may be best accomplished through removing or moving roadways, restricting urban development, or limiting pesticide use on farmland. Opposition to such decisions by the stakeholders involved may preclude implementation. Conservation plans should nevertheless consider what actions are possible in the matrix along with habitat conservation and restoration.

Real landscapes are not random

Nor are they archipelagos. The use of simple mathematical models to provide guidance for the management of complex, heterogeneous landscape is not always appropriate for practical applications. Their utility lies in generating general expectations about properties of landscapes that may have importance for land management and the conservation of biodiversity (strategic application), rather than providing specific recommendations for the management of a given landscape (tactical application).

Landscape connectivity is a necessary but not sufficient condition for species conservation

Landscape connectivity is important because it influences access to resources and colonization of empty habitat. However, population persistence at the landscape scale ultimately depends on the balance between reproduction and mortality. A change in landscape connectivity can affect reproduction and mortality, for example, through allowing or limiting access to potential breeding sites. However, reproduction and mortality (and therefore population persistence) are mainly determined by the amount and quality of habitats available on the landscape (Fahrig 1997; With and King 1999b; Breininger and Carter 2003; Woodford and Meyer 2003). Note that habitat quality can include the effects of species inter-actions on reproduction or mortality; for example, forest edge may be low quality habitat if predation rate is higher in edges (Chalfoun *et al.* 2002). Therefore, in conservation, a focus on landscape connectivity to the exclusion of habitat amount and quality (e.g., Stith *et al.* 1996, Keitt *et al.* 1997) will not guarantee species persistence in the landscape.

In fact, landscape connectivity may be either positively or negatively related to population persistence. For example, an increase in habitat amount could lead to a decrease in landscape connectivity if the organism moves less when it is in habitat than when it is in non-habitat (Jonsen and Taylor 2000a; Goodwin and Fahrig 2002). If habitat amount has a large positive effect on population persistence, this behavior would translate into a negative relationship between landscape connectivity and persistence (Tischendorf and Fahrig 2000). Alternatively, human impacts in the matrix, such as roads and pesticide applications, reduce matrix quality and thereby reduce landscape connectivity (Johnson and Collinge 2004; Clevenger and Wierzchowski Chapter 20). Modeling studies suggest that dispersal mortality has a large effect on population persistence (Lindenmayer *et al.* 2000; Fahrig 2001; Cooper *et al.* 2002).

In this situation, the effect of lowering landscape connectivity is thus not only to reduce movement, but also to increase mortality in the population; an increase in landscape connectivity (e.g., through reduced pesticide use or roadway crossing structures) would thus have a positive effect on population persistence.

Our main point is that a focus on landscape connectivity to the exclusion of habitat amount and quality will not guarantee population persistence or maintenance of biodiversity. Landscape connectivity is not a panacea in conservation or land management, but needs to be considered as a component of the suite of interacting factors that influence the demography of a species.

Landscape connectivity is inherently neither good nor bad

Through its effects on ecological processes, connectivity may positively influence population persistence for some organisms in some situations, and negatively influence them in others. Therefore, if one is managing for connectivity in the landscape, one is not trying to "maximize" it in some way − rather, one is trying to understand how altering other elements of landscape structure will affect it, and then assess what the importance of those changes will be to critical ecological outcomes, such as population persistence.

Landscape connectivity is a dynamic concept

Landscape connectivity must be assessed, and therefore managed, in the context of human land-use change. It will change over both short and long timescales. As such, it is prudent to consider assessments of landscape connectivity (and its ultimate effects on population dynamics and persistence) as part of adaptive management and management for resilience (Gunderson and Holling 2000). In many landscapes, connectivity may initially decline with some types of land use (e.g., removal of forest for timber) but then return (for some species) as the matrix undergoes successional change (e.g., Sekercioglu *et al.* 2002). Landscape connectivity will play an increasingly important role in the persistence of many plant and animal populations in the face of global change and resultant shifts and restructuring of species distributions (e.g., Pitelka *et al.* 1997; Warren *et al.* 2001; Soulé *et al.* Chapter 25). Landscape connectivity will be related directly to species' abilities to track shifts in habitat, their abilities to adapt to changing matrix conditions, and their abilities to persist in the modified landscapes that they colonize. Although its role is important, it bears repeating that connectivity does not play an exclusive role in each of

these processes. Understanding for which species and under what conditions connectivity is important remains a considerable research challenge.

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