Landscape Ecol (2008) 23:879–890
DOI 10.1007/s10980-008-9245-4

Connectivity measures: a review

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Received: 26 September 2007 / Accepted: 1 July 2008 / Published online: 31 July 2008

Abstract One of the central problems in contemporary ecology and conservation biology is the drastic change of landscapes induced by anthropogenic activities, resulting in habitat loss and fragmentation. For many wild living species, local extinctions of fragmented populations are common and recolonization is critical for regional survival. Successful recolonization depends on the availability of dispersing individuals and the degree of landscape connectivity. The obvious implications of landscape connectivity for conservation biology have led to a proliferation of connectivity measures. However, general relationships between landscape connectivity and landscape structure are lacking, and so are the relationships between different connectivity metrics. Consequently, there is a need to develop landscape metrics that more accurately characterize the landscape with an emphasis on the underlying processes. Here we review various definitions of landscape connectivity, explain their mathematical connotations, and make some unifying conclusions and suggestions for future research.

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Keywords Conservation biology · Habitat fragmentation · Landscape connectivity · Measures · Species extinction

Introduction

One of the central problems in ecology and contemporary conservation biology is the drastic change of landscapes due to anthropogenic pressures, which entails habitat loss and fragmentation for many wild living species (Benton et al. 2003). For such species, local extinctions of fragmented populations are common (Fahrig and Merriam 1994) and recolonization is critical for regional survival (Levin 1974; Hastings 1980; Fahrig and Merriam 1994; Hanski 1999a). This means that the species are likely to survive only within networks of patches that are sufficiently connected by dispersing individuals (Fahrig and Merriam 1985; Adler and Nuernberger 1994; Hanski 1999a; Bowne and Bowers 2004). Whether or not patches can be recolonized depends on the availability of dispersing individuals and the ease with which these individuals can move about within the landscape. The latter is usually called "landscape connectivity" (Merriam 1984) and is therefore considered to be of paramount importance for species survival (Fahrig and Merriam 1994; Moilanen and Hanski 1998; Pain et al. 2000; Ricketts 2001; Briers 2002).

Habitat loss tends to increase habitat inter-patch distances and decrease habitat patch sizes (Turner and Ruscher 1988; Saunders et al. 1993). Both effects will tend to decrease landscape connectivity, as greater inter-patch distances are harder to cross (Laan and Verboom 1990; Vos and Stumpel 1995) and smaller habitat patches are harder to find (Kareiva 1985). The rest of landscape after exclusion of habitat patches is usually called "matrix". The matrix thus consists of patches of non-habitat elements and its composition can also influence movement behavior (Baars 1979; Johnson et al. 1992a, b; Matthysen et al. 1995; Pither and Taylor 1998; Jonsen and Taylor 2000; Goodwin and Fahrig 2002a) and movement risk (Sakai and Noon 1997; Zollner and Lima 1999; Hanski et al. 2000). Landscapes dominated by matrix patches that facilitate movement will have high connectivity while landscapes dominated by matrix patches that impede movement will have low connectivity. Similarly, certain configurations of matrix patches might reduce landscape connectivity (e.g., when impassable patches encircle all habitat patches) or increase landscape connectivity (e.g., when impassable patches are clumped and far from habitat).

The potential for landscape connectivity to impact populations in heterogeneous landscapes, and the obvious implications for conservation biology, have led to an increasing interest in landscape connectivity (Goodwin 2003) and a proliferation of connectivity measures (Tischendorf and Fahrig 2000a, b). However, general relationships between landscape connectivity and landscape structure, necessary for predicting the impact of landscape change on its connectivity, are lacking, and so are the relationships between different connectivity metrics which in turn would allow the results from different studies of landscape connectivity to be compared. Moilanen and Hanski (2001) conclude that the connection between connectivity measures and the fundamental processes determining species distributions often seems unclear. Some connectivity measure is necessary for assessing the capacity of fragmented landscapes to support viable populations (Moilanen and Hanski 2001). Consequently, there is a need to develop landscape metrics that can adequately characterize the landscape with relevance to the underlying processes. Here we review various definitions of landscape connectivity, provide mathematical explanations of these definitions, and make some unifying conclusions and suggestions for future research.

From intuitive definitions to basic categorization

The way authors define the term "connectivity" is often vague (e.g., Brotons et al. 2003; Thies et al. 2003). Connectivity has been described as "*the degree to which landscape facilitates or impedes movement of organisms among patches*" (Taylor et al. 1993; Tischendorf and Fahrig 2000b; Schooley and Wiens 2003; "*the functional relationship among habitat patches due to their spatial distribution and the movement of organisms in response to landscape structure*" (Taylor et al. 1993; With et al. 1997); or "*the ease with which these individuals can move about within the landscape*" (this study). However, in order to compare results of different studies and to make quantitative predictions, we need more precise definitions.

Two basic groups of definitions can be distinguished: *structural* connectivity where connectivity is based entirely on landscape structure (e.g., Green 1994; With et al. 1997; Metzger and Décamps 1997; Tiebout and Anderson 1997; Girvetz and Greco 2007), with no direct link to any behavioral attributes of organisms (Green 1994; With et al. 1997; Metzger and Décamps 1997; Collinge and Forman 1998; Collinge 2000), and *functional* connectivity which considers organisms' behavioral responses to individual landscape elements (patches and edges) and the spatial configuration of the entire landscape (Doak et al. 1992; Demers et al. 1995; Gustafson and Gardner 1996; Schumaker 1996; Ruckelshaus et al. 1997; Pither and Taylor 1998; Tischendorf and Fahrig 2000b; Sweeney et al. 2007). Consequently, functional connectivity covers situations where organisms venture into non-habitat (matrix), where they may (1) face higher mortality risks (e.g., Gaines and McGlenaghan 1980; Henein and Merriam 1990; Poole 1997; Sakai and Noon 1997), (2) express different movement patterns (e.g., Baars 1979; Wallin and Ekbom 1988; Wegner and Merriam 1990; Hansson 1991; Johnson et al. 1992a; Andreassen et al. 1996b; FitzGibbon et al. 2007), and (3) cross boundaries (e.g., Mader 1984; Wiens et al. 1985; Duelli et al. 1990; Mader et al. 1990; Mauremooto et al. 1995; Sakai and Noon 1997;

Walker et al. 2007). Goodwin (2003) subdivides these two basic groups further into 10 subcategories, which are: presence or absence of corridors, distances, amount of habitat, contagion or percolation, dispersal success, graph theory, movement probability, searching time for a new habitat, re-observation of displaced individuals, immigration rate. Calabrese and Fagan (2004) subdivide functional connectivity measures into two: the potential type with limited information about dispersal ability and the actual type related to the observation of individuals moving in or out focal patches. This permits the differentiation of functional measures that are empirically based from those that combine field data with modeling. These two types correspond to what we call here structural and functional connectivity, as we define connectivity as a measure of easiness of movement.

The recent debate between landscape ecologists and metapopulation biologists (Tischendorf and Fahrig 2000b; Moilanen and Hanski 2001; Tischendorf and Fahrig 2001) seems to suggest that it is advisable to distinguish between "*landscape connectivity*", in which connectivity is seen as a property of an entire landscape, and "*patch connectivity*", which identifies connectivity as an attribute of a patch and is typically used in metapopulation ecology (Tischendorf and Fahrig 2001).

Structural definitions

Measures based on presence, absence, or configuration of corridors and stepping-stones

Corridors are narrow, continuous strips of habitat that structurally connect two otherwise non-contiguous habitat patches. The corridor concept (e.g., Forman 1983; Merriam 1991; Saunders and Hobbs 1991; Lindenmayer and Nix 1993; Merriam and Saunders 1993; Noss 1993; Bennett et al. 1994; Bonner 1994; Dawson 1994; Rosenberg et al. 1997; Tischendorf 1997; Haddad 1999; Brooker et al. 1999; Graves et al. 2007; Ockinger and Smith 2007) originated from the generalized assumption that organisms do not venture into non-habitat.

Some authors equate connectivity to the presence and absence of corridors between small fragments (e.g., Hess 1996; Swart and Lawes 1996; Anderson and Danielson 1997; Ims and Andreassen 1999; Danielson and Hubbard 2000; Hunter 2002), with corridor width (Andreassen et al. 1996a), length (Haddad 2000) or corridor continuity (Andreassen et al. 1996b). Thus no assumption is made about a particular animal, only the percentage of corridors between patches out of the possible number of corridors is considered as a measure of connectivity.

Measures based on distances

Structural connectivity is often measured by means of Euclidean shortest distance measures, starting from simple measures such as nearest-neighbor-distance, to more complex ones where all surrounding patches within dispersal distance of a patch contribute to its connectivity (Moilanen and Hanski 2001; Moilanen and Nieminen 2002). These include fractal dimension, patch contagion, or patch isolation (Turner 1989; Wiens et al. 1993; Schumaker 1996; Gustafson 1998; Hargis et al. 1998). Such approaches do not incorporate the characteristics of the landscape between the patches (Hof and Flather 1996; Hess 1996), and therefore might inappropriately use the same movement rules in both habitat and matrix elements (Schumaker 1996; Gustafson 1998). Most of these measures are based on the formula

$$S = \sum_{i=1}^{n} A_i^c \sum_{j \neq i} D(d_{ij}, \alpha) A_j^b$$

(Moilanen and Hanski 2001), where A_i is the area of patch i (=1, 2,…, n); parameters b and c scale area, patch i being the target and patch j being the source of migration; $D(d_{ij}, \alpha)$ scales the effect of distance on migration rate; d_{ij} is the distance between patches i and j and α is a vector of species-specific parameters describing the dispersal ability of the species.

This formula is used in many modifications, like ESLI (ecologically scaled landscape indices) by Vos et al. (2001), buffer-connectivity index by Cabeza (2003), IFM-connectivity index (Incidence Function Model) by Moilanen and Nieminen (2002). Topography is also sometimes considered (Swanson et al. 1998; Turner 1989; Dorner et al. 2002).

Measures based on graph theory

Graph theory is sometimes used to describe connectivity (e.g., Bunn 2000; Bunn et al. 2000; van Langevelde 2000; Ferrari et al. 2007; Jordan et al. 2007; Treml et al. 2007) and presents a combination of the previous two categories. Two commonly used connectivity measures include *area-weighted dispersal flux* and *traversability*:

$$F = \sum_{i}^{n} \sum_{j,i \neq j}^{n} p_{ij} s_i$$

$$p_{ij} = -e^{(\theta \cdot d_{ij})}$$

where s_i is the size of node i, $\theta > 0$ is an extinction coefficient, and d_{ij} are the functional distances between patches i and j.

If a graph's diameter, d(G), is defined as the longest path between any two nodes in the graph, where the path length between those nodes is itself the shortest possible length, then *traversability* is calculated as the average diameter of the largest component in the graph formed by the removal of one randomly chosen patch: $\mathrm{T} = \mathrm{d}(\mathrm{G}')$, where G' is the largest component of G.

Measures based on the amount of habitat in the landscape

In some studies, the *area of specific linear elements within a buffer around the patch*, for example the length or area of hedgerows closer to the habitat patch in question than some predefined distance, was used as a measure of connectivity (e.g., Verboom and Van Apeldoorn 1990; Vos and Chardon 1998). Another measure is the "*ring statistic*" (Wiegand et al. 1999). Its basic idea is to place rings with radius *r* around each cell of a given habitat type 1 (e.g., cells with good-quality habitat) and calculate the mean density of cells within these rings that are of habitat type 2 (e.g., cells with bad habitat). This statistic is supposed to characterize spatial structure as a function of the animal's perception of habitat types located at a critical distance from the animal's current location.

Measures based on contagion or percolation

In this approach, the landscape is again considered to be a two-dimensional grid, in which the grid cells are classified as either habitat or matrix cells. Landscape connectivity is then understood as the spatial contagion of habitat. This means that habitat is understood as connected, if each habitat cell is joined with a neighboring habitat cell along at least one horizontal or vertical edge. Thus any organism capable of using the habitat should be able to traverse across this landscape (With and Crist 1995). As the habitat becomes dissected into smaller and smaller parcels, such landscape connectivity may abruptly become disrupted. Thus landscapes may exhibit critical thresholds in this type of connectivity, often with serious ecological consequences (Gardner et al. 1987; Krummel et al. 1987; O'Neill et al. 1988). Percolation theory (Orbach 1986; Stauffer and Aharony 1991) has recently been used to predict where these critical thresholds occur and thus how landscape structure might affect ecological processes (Gardner et al. 1987; O'Neill et al. 1988).

Functional definitions

Functional definitions consider the behavioral responses of organisms to landscape pattern. Let us first introduce the variables used in the formulas in this section:

n_p, n_c, and n_b, number of patches, cells, or individuals in the landscape;

p^p_{ij}, the probability of moving from patch i to patch;

p^c_{ij}, the probability of moving from cell i to cell j;

v^p_i and v^c_i, the number of patches or cells visited by individual i;

m^p_i and m^c_i, the number of immigrants into patch i or cell i.

Measures based on the probability of moving between patches

Connectivity based on organism movements has been measured as *mean probability of moving between pairs of patches*, also referred to as emigration or dispersal success (Andreassen et al. 1996a; Gustafson and Gardner 1996; Schumaker 1996; Ruckelshaus et al. 1997; Tischendorf and Fahrig 2000a; Tischendorf 2001). It can be calculated as patch transition probability,

$$\frac{\sum_{i=1}^{n_p}\sum_{j=1}^{n_p} p_{ij}^{p}}{n_p(n_p-1)},\ i \neq j$$

or cell transition probability:

$$\frac{\sum_{i=1}^{n_c}\sum_{j=1}^{n_c} p_{ij}^{c}}{n_c(n_c-1)},\ i \neq j$$

Another aspect is represented by the multi-state models (Nichols and Kendall 1995; White and Burnham 1999).

Measures based on the amount of time spent searching for a new habitat patch

Search time is the average number of movement steps necessary for a randomly placed individual to reach a habitat patch. The average is usually calculated over all successful movements of all individuals between any two different habitat patches (Doak et al. 1992; Tischendorf and Fahrig 2000a; Tischendorf 2001).

Measures based on the rate of re-observation of displaced individuals

Connectivity based on organism movements has been measured as re-observation after displacement (Pither and Taylor 1998; Castellón and Sieving 2006).

Measures based on immigration rates

Dispersal success is the total number of immigration events into all habitat patches in the landscape, divided by the initial number of individuals. Usually only the first time an individual entered a habitat patch is counted as an immigration event for that individual (Demers et al. 1995; Schumaker 1996; Tischendorf and Fahrig 2000a; Tischendorf 2001): the lower the immigration rate, the more isolated is the patch. Immigration rate depends on (1) the amount of occupied habitat surrounding the focal patch, (2) the number of emigrants leaving the surrounding habitat, (3) the nature of the intervening matrix, (4) the movement and perceptual abilities of the organism, and (5) the mortality risk of dispersers (Wiens et al. 1993). Some studies equate patch isolation with connectivity (Hjermann and Ims 1996; Grashof-Bokdam 1997; Ault and Johnson 1998). Measures of dispersal success include:
Patch immigration:

$$\frac{\sum_{i=1}^{n_p} m_i^{p}}{n_p}$$

Cell immigration:

$$\frac{\sum_{i=1}^{n_c} m_i^{c}}{n_c}$$

Patch visits:

$$\frac{\sum_{i=1}^{n_b} \upsilon_i^{p}}{n_b}$$

Cell visits:

$$\frac{\sum_{i=1}^{n_b} \upsilon_i^{c}}{n_b}$$

Measures based on matrix permeability

One of the main determinants for movement behavior of the species under question is the resistance of the landscape matrix: land use types can hinder (roads, bare soil) or enhance (hedgerows—Gelling et al. 2007; Michel et al. 2007) movement (Dawson 1994; Debinski and Holt 2000). Thus Moilanen and Hanski (1998) used species-specific migration coefficients for the different land use types in the matrix between patches. They define connectivity of patch i as $C_i = \sum_j p_j e^{-\alpha d_{ij}} A_j^b$, where $p_\mathrm{j} > 0$, $\alpha > 0$, $0 < b \leq 1$ are parameters, A_j is area of patch j and d_{ij} is distance between patches i and j. Ricketts (2001) introduced another measure of permeability: If T_{jk} is the number of individuals transferring from site k to site j, D_{ijk} is the distance of the route across habitat i, and a and z are fitted constants, then resistance parameters, r_1, r_2,…, for habitats 1, 2,… can be fitted from the equation $T_{jk} = \frac{a}{\left(\sum_i r_i D_{ijk}\right)^z}$.

Baudry et al. consider a realistic assumption that movement is differentially difficult in different types of habitat. Chardon et al. (2003) compared the cost-distance measure that incorporates the resistance of the landscape matrix to movement with the Euclidean distance and show that the former is better. Species-specific dispersal capacity may also depend on habitatspecific mortality, food availability, and edge permeability among different types of habitat (Hein et al. 2003).

Dynamical landscapes

Landscape spatial structure is not constant but changes over time. Temporal heterogeneity (habitat life span) is variability over time in the extent and/or quality of the habitat. Rapidly changing landscape structure can result in increased distance and rate of dispersal. If the rate of change in dispersal is not as fast as the rate of change in the landscape, the regional population will not survive (Fahrig and Merriam 1994). Thus if patch lifetime becomes too small, metapopulation extinction becomes inevitable. Therefore, for a given life history, a threshold for metapopulation extinction exists not only for the amount of suitable habitat, but also for patch turnover (Keymer et al. 2000; Fischer 2001). Thus the higher the rate of landscape change, the lower the probability of regional population survival.

By focusing on temporal components of landscape structure, Marquet and Velasco-Hernández (1997) and Brachet et al. (1999) studied the effects of landscape dynamics upon metapopulation persistence. These studies agree about the importance of dynamic properties of the landscape in determining metapopulation persistence. Fahrig (1992) compared the relative effects of temporal and spatial scales upon metapopulation persistence of a single species. She found that the effect of temporal scale far outweighed the effect of spatial scale on population persistence. Generally, if habitat is very ephemeral, particulars about spatial parameters, such as dispersal distance and inter-patch distance, may be ignored (Fahrig 1992). Travis and Dytham (1999) show how higher dispersal rates evolve in ephemeral habitats in response to fluctuating habitat availability.

Relationship between different measures of landscape connectivity

Goodwin and Fahrig (2002b) compared patch transition probability, cell transition probability, patch immigration, cell immigration, patch visits and cell visits. Their simulations revealed that all of them were influenced by different aspects of landscape structure, suggesting that: (1) landscape connectivity is a poorly defined concept, and (2) the same landscape may have different landscape connectivity values when different measures of landscape connectivity are used. There were two general predictions that held over all measures of landscape connectivity: (1) increasing inter-patch distance significantly decreased landscape connectivity and (2) the influence of matrix elements on landscape connectivity was small in comparison to the influence of habitat elements.

Metapopulation models have been criticized for ignoring the characteristics of the non-habitat (“matrix”) portion of the landscape (Tischendorf and Fahrig 2001). In contrast, landscape models often assume that movement through matrix depends on attributes of the matrix, which may influence dispersal mortality and/or movement direction (e.g., Tischendorf and Fahrig 2000a). Therefore, in metapopulation ecology, movement between patches depends only on the distance between patches and the inherent “dispersal ability” of the organism (as captured in the colonization rate parameter). In landscape models, movement through the landscape is assumed to depend on the interaction between characteristics of the matrix and the movement behavior of the organism (Tischendorf and Fahrig 2001). There is a recent trend toward including population size and matrix effects in metapopulation models (e.g., Heino and Hanski 2001; Moilanen and Hanski 2001; Moilanen and Nieminen 2002), however. Spatially explicit models of metapopulations, on the other hand, have shown that landscape structure and patch dynamics can affect metapopulation dynamics and persistence (Bascompte and Solé 1996; Bevers and Flather 1999), and the outcome of species interaction (Tilman et al. 1997; Dytham 1995; Huxel and Hastings 1998; Klausmeier 1998).

Measuring connectivity based on patch immigration leads to the counter-intuitive result that connectivity is zero (no successful dispersal, or infinite search time) when there is only one habitat patch in a landscape. This goes counter to the assumption that a landscape containing a single contiguous habitat patch should have higher connectivity than a landscape with the same amount of habitat occurring in many disjoint patches (Tischendorf and Fahrig 2000b). This is sometimes attributed to the fact that these measures completely ignore within-patch movements (Tischendorf and Fahrig 2000b). However, if the patch-level connectivity measure takes into account the expected number of migrants, which in the simplest case scales linearly with patch area, increasing fragmentation does not necessarily increase patch connectivity (Moilanen and Hanski 2001).

Modeling approaches

Random pixel-to-pixel movement

Many models simulate movement as random walks (Doak et al. 1992; Schumaker 1996; With et al. 1997; Ruckelshaus et al. 1997; With and King 1999). In this approach, the step length (length of movement during one step) is usually chosen from a negative exponential distribution with a defined average. The direction of movement is usually chosen from the uniform or normal probability distribution, for a random and directed walk, respectively (Schumaker 1996; Tischendorf et al. 1998; Goodwin and Fahrig 2002b). This, however, tends to ignore many of the complexities of movement behavior in landscapes (Travis and French 2000). Thus differential mortality in different environments (e.g., habitat, hospitable matrix, inhospitable matrix), and/or differential permeability of boundaries can also be assumed (Tischendorf et al. 1998; Tischendorf and Fahrig 2000a).

Landscape submodel

A landscape is either randomly created or obtained from GIS, usually consisting of habitat, hospitable matrix and an inhospitable matrix (Tischendorf and Fahrig 2000a, b). One way to create a random landscape is as follows: Three-dimensional surfaces with different degrees of topographic "ruggedness" (i.e., spatial autocorrelation in elevational displacement) are created by superposing two-dimensional Gaussian functions

$$\mathrm{f}(\vec{x}) = h\frac{1}{\sqrt{2\pi\sigma}}\exp\left(\frac{1}{2}\frac{|\vec{x}-\vec{x}_0|^2}{\sigma^2}\right),$$

where $\vec{x}_0$ denotes random locations, and h and σ are real numbers. Placing horizontal planes at two (one positive and one negative) elevations along the elevational gradient within the three-dimensional maps produces three elevational zones in the landscape: high, intermediate, and low. High elevations are then associated with one type of habitat (e.g., good habitat), low elevations with another type of habitat, and intermediate elevations with the matrix (Wiegand et al. 1999).

Connectivity calculation

A set of individuals is randomly distributed in the landscape and let to move according to the defined rules. The rules differ greatly among modeling studies and therefore Tischendorf and Fahrig (2000b) argue for more consistency in describing movement in connectivity-related models. Various connectivity measures can then be calculated. One advantage of simulation models is that functional connectivity can be explicitly modeled.

Discussion

What is the way forward for landscape connectivity research? Because there are many connectivity metrics in the literature and because most studies use only a single metric, there is an urgent need for comparing and generalizing studies of landscape connectivity. Models should incorporate more realistic movement behavior to determine which aspects of behavior have a large effect on landscape connectivity (Goodwin 2003). We also need more research interrelating various connectivity metrics. Few studies to date have compared multiple measures of connectivity, suggesting that relating such metrics to one another may be difficult (Goodwin 2003). Because present measures of structural connectivity are not suitable for incorporating the role of the matrix, new measures are needed that adopt a more functional approach (Knaapen et al. 1992; Gustafson and Gardner 1996; Hanski 1999b).

Whether it is possible to extrapolate information about organism's movement behavior on small scales toward larger scales in space and time by movement modeling is a crucial question in landscape ecology. This observation is not new. The need to insert more animal behavior into landscape ecology was suggested by Lima and Zollner (1996), echoed by

Haddad (1999), and discussed in depth by Bélisle (2005). Experimental studies of trapping or tracing organisms are restricted in different ways. First, such experiments are constrained by space and time. Second, tracing studies, which provide the best insight into the movement behavior of individual organisms are protracted and labor intensive and therefore limited to a small number of organisms. Finally, field studies are carried out in one specific landscape configuration, yet conservation plans need information about the consequences of changing landscape structures on movements and their outcomes. Thus, modeling movement behaviors within heterogeneous landscapes could build a bridge between experimental studies and management decisions. So far, however, only few modeling attempts have been made towards this goal (Kareiva and Shigesada 1983; McCulloch and Cain 1989; Johnson et al. 1992a; Wiens et al. 1997). Spatially explicit models require fine-scale data on movement and demography. Acquiring these data depends on the dispersal distance (as capture-recapture methods and radio-tracking methods are difficult to use for long distance dispersers), mobility type, and body size of organisms of interest.

We should abandon the common belief that each landscape is associated with a certain connectivity value. It is not. Connectivity has two dimensions: landscape and the organism considered. Only a combination of these two will yield a meaningful value of connectivity. Thus, different landscapes may have different degrees of connectivity for the same species, and the same landscape may have different degrees of connectivity for different species or even for the same species at different times. Landscape connectivity also changes with the choice of measures. For example, connectivity measures based on distances may be appropriate for birds as the matrix and corridors may not be of great importance in this case. Measures based on the amount of corridors in the landscape may be appropriate for small mammals (e.g., carabid beetles) whose movement is affected by matrix permeability. Evidently, each of these measures will give us a different connectivity for the same landscape.

Thus, we should move from the idea of "Connectivity $= f(\text{landscape})$" to the approach of "Connectivity $= f(\text{landscape, organism})$". To achieve this goal, more functional connectivity measures need to be developed to reflect broad categories of organisms and their biological traits. In other words, a major challenge in connectivity research today is to develop functional connectivity measures that incorporate both species-specific movement behavior and landscape structure, and that are relatively simple to calculate.

Acknowledgements This research was supported by the Grant no. A6087301 of the GA AV CR and No. LC06073 of the MSMT.

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