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MINI-REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

On the usage and measurement of landscape connectivity

Lutz Tischendorf and Lenore Fahrig

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This paper examines the usage and measurement of "landscape connectivity" in 33 recent studies. Connectivity is defined as the degree to which a landscape facilitates or impedes movement of organisms among resource patches. However, connectivity is actually used in a variety of ways in the literature. This has led to confusion and lack of clarity related to (1) function vs structure, (2) patch isolation vs landscape connectivity and, (3) corridors vs connectivity. We suggest the term connectivity should be reserved for its original purpose. We highlight nine studies; these include modeling studies that actually measured connectivity in accordance with the definition, and empirical studies that measured key components of connectivity. We found that measurements of connectivity provide results that can be interpreted as recommending habitat fragmentation to enhance landscape connectivity. We discuss reasons for this misleading conclusion, and suggest a new way of quantifying connectivity, which avoids this problem. We also recommend a method for reducing sampling intensity in landscape-scale empirical studies of connectivity.

L. Tischendorf and L. Fahrig, Ottawa-Carleton Inst. of Biology, Carleton Univ., Ottawa, ON, Canada K1S 5B6 (present address of LT: Busestrasse 76, D-28213 Bremen, Germany [tischendorf@clavis-bremen.de]).

What is landscape connectivity?

The effects of spatial structure (patchiness) on population dynamics were first examined in patch-based population models beginning in the early 1970s (e.g., Levins 1969, Reddingius and den Boer 1970, Levin 1974, 1976, Roff 1974). Further modeling studies showed that assumptions about movement among habitat patches greatly influence the predictions of such models (e.g., Lefkovitch and Fahrig 1985, Fahrig 1988, 1990, Fahrig and Paloheimo 1988, Henein and Merriam 1990, Adler and Nuernberger 1994, Lindenmayer and Lacy 1995, Lindenmayer and Possingham 1996, Frank and Wissel 1998, Henein et al. 1998). Movement among habitat patches is, however, not simply a function of an organism itself, but also depends on the landscape through which it must move. To emphasize the interaction between species' attributes and landscape structure in determining movement of organisms among habitat patches, Merriam (1984) introduced the concept of "landscape connectivity".

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Taylor et al. (1993) defined landscape connectivity as "the degree to which the landscape facilitates or impedes movement among resource patches". Similarly, With et al. (1997) defined landscape connectivity as "the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure". These definitions accentuate the dependence of movement on landscape structure, which suggests that connectivity is species- and landscape-specific. One must therefore describe landscape structure from a species' point of view (Wiens and Milne 1989). This starts with defining the species' habitat. The next step is to determine the scale at which the species responds to landscape structure, through its fine-scale (grain) and large-scale (extent) movement (Wiens 1997). This determines the scale of habitat pattern as perceived by the organism. Finally, one must determine how the species responds to the different elements of a landscape. This comprises the species movement pattern and mortality risk on landscape elements (patches) as well as reactions at boundaries. Note that all of these behavioral facets contribute toward facilitating or impeding movement among resource patches.

In summary, landscape connectivity encapsulates the combined effects of (1) landscape structure and (2) the species' use, ability to move and risk of mortality in the various landscape elements, on the movement rate among habitat patches in the landscape.

Objective and approach

We reviewed the literature covered by the Agriculture, Biology & Environmental Sciences Edition of the Current Contents database (CC 1998), from May 1993 to November 1998. We searched article titles and key words for the term *connectivity* in combination with *landscape* or *patch* or *habitat*. The search resulted in 49 papers. However, 17 of these papers did not use connectivity at all. We omitted these from the review, and included one other paper (Doak et al. 1992) leaving 33 papers, which are assembled in descending chronological and alphabetical order in Table 1, and classified in Fig. 1.

Our objective was to examine the current usage and measurement of landscape connectivity. We start with a critical discussion of the diverse usage of connectivity, followed by a description of modeling and empirical studies that actually attempted to quantify connectivity or key components of it. We then discuss crucial modeling assumptions and reveal the deceptive paradox of patch-based connectivity measurements, and its potential for misleading conclusions. We end by suggesting ways to streamline and focus research on landscape connectivity.

Current usage of connectivity

Structure or function?

The literature review revealed that the term connectivity is sometimes used as a functional concept and other times in a structural way. Structural connectivity is equated with habitat contiguity and is measured by analyzing landscape structure, independent of any attributes of the organism(s) of interest (Collinge and Forman 1998).

The functional concept of connectivity explicitly considers the behavioral responses of an organism to the various landscape elements (patches and boundaries). Consequently, functional connectivity covers situations where organisms venture into non-habitat (matrix), where they may (1) face higher mortality risks (e.g., Lidicker 1975, Gaines and McGlenaghan 1980, Krohne and Burgin 1987, Henein and Merriam 1990, Schippers et al. 1996, Charrier et al. 1997, Poole 1997, Sakai and Noon 1997), (2) express different movement patterns (e.g., Baars 1979, Rijnsdorp 1980, Wallin and Ekbom 1988, Wegner and Merriam 1990, Hansson 1991, Johnson et al. 1992a, Andreassen et al. 1996b, Matter 1996, Charrier et al. 1997, Collins and Barrett 1997), and (3) cross boundaries (e.g., Mader 1984, Wiens et al. 1985, Bakowski and Kozakiewicz 1988, Merriam et al. 1989, Duelli et al. 1990, Mader et al. 1990, Frampton et al. 1995, Mauremooto et al. 1995, Charrier et al. 1997, Sakai and Noon 1997).

Depending on the movement attributes of the organism, structural and functional connectivity can be synonymous. This occurs when the organism's movement is confined to its preferred habitat, i.e., individuals do not cross the habitat/matrix boundary, and the organism moves freely within the preferred habitat (e.g., Bascompte and Solé 1996). This is the assumption behind most percolation-based connectivity measures (Gardner et al. 1987, Gardner and O'Neill 1991, Green 1994).

The fact that structural connectivity is relatively easy to measure could lead to the conclusion that connectivity is a generalized feature of a landscape. This would be erroneous. In fact, the same landscape will have different connectivities for different organisms. Structurally connected habitat patches still may not be functionally connected and even non-contiguous habitat patches may be functionally connected, depending on the species (With 1997). For example, if the only two habitat patches in a landscape are structurally connected by an inappropriate corridor for the species in question (too narrow or too long), structural connectivity would exist without successful movement (functional response) from one patch to the other. Likewise, non-contiguous habitat patches may functionally be connected if the species can cross the non-habitat area (matrix) successfully and move between habitat

Table 1. Chronological and alphabetical assemblage of the 33 reviewed connectivity studies.

No.	Study	Measurement/usage of connectivity	Comments/study target	Spatial scale	Study type and duration
1	Andreassen et al. 1998	presence/absence of corridors	effects on movement frequencies	landscape	experiment, radio-tracking, 13 wk, 3 generations
2	Ault and Johnson 1998	summed influence of size and spatial arrangement of neighboring patches	effect of structural patch isolation on community structure and population density	patch	observational, 2 yr
3	Bjornstad et al. 1998	presence/absence of corridors	effect on dispersal distances and spatial aggregation	landscape	experiment, live-trapping, 13 wk, 3 generation
4	Collinge and Forman 1998	percent of equally spaced straight lines covering habitat within a landscape	effect of structural connectivity measurement on insect density, richness, and community structure	landscape, 10 m × 10 m	experiment
5	Davidson 1998	structural patch isolation	rationale on the quantification of landscape fragmentation	landscape	discussion
6	Haig et al. 1998	movement of waterbirds among habitat patches	rationale on the importance of functional connectivity for waterbird conservation	landscape	discussion
7	Henein et al. 1998	presence, absence and quality of fencerows in simulated landscape	effects on population survival	landscape	spatially explicit simulation model, 25 yr
8	Petit and Burel 1998b	distances (euclidian, along hedgerows and, weighted by movement intensity and mortality in different habitat types) between sample sites	effect of structural and functional connectivity on species' local abundance	landscape	experiment, one season
9	Petit and Burel 1998a	"functional distance" (weighted by movement intensity and mortality in different habitat types)	effect of functional connectivity on species' local abundance	landscape	experiment, one season
10	Pither and Taylor 1998	movement ability of damselflies through different habitat types	effects of landscape structure on movement frequencies	landscape	manipulative mark-recapture experiment, one season
11	Root 1998	nearest neighbor distance (combined with dispersal frequency distribution) between habitat patches	effect of structural connectivity on (meta)population size	landscape	GIS based population dynamics model (RAMAS)
12	Grashofbokdam 1997	amount of forest habitat around patches within three zones up to 1000 m	effect of structural patch isolation on zoochorous and anemochorous plant species	patch	vegetation survey
13	Hof and Raphael 1997	population abundance relationship between adjacent cells in a grid model	connectivity measure assumed to be spatial limitation factor	landscape	static optimization and simulation model
14	Metzger and Décamps 1997	connectivity components: a) degree of habitat percolation, b) corridor and stepping stone networks, c) matrix permeability	rationale on the effect of connectivity on biodiversity	landscape	conceptual model, discussion
15	Schmiegelow et al. 1997	corridors (riparian buffer strips) between forest fragments	effect on local bird community (species abundances)	patch	experiment, 1 yr
16	Spetich et al. 1997	proximity index-summarized (patch area/distance to focal patch) relationship for all patches located within rectangular buffer zone around focal patch	effects of simulated landscape changes on structural patch isolation (proximity)	patch	quantification of spatial pattern in GIS maps
17	Tiebout and Anderson 1997	intrinsic (juxtaposition of similar habitat) and extrinsic (corridor) connectivity	estimation of effects on specialist colonizing ability	landscape	conceptual model
18	With et al. 1997	average distance between two sites of a grid belonging to the same (percolation) cluster, populations' spatial distribution	effect of landscape spatial structure on percolation threshold and populations' spatial distribution	landscape	random walk simulation model on neutral (random and fractal) landscape maps

Table 1. (Continued)

No.	Study	Measurement/usage of connectivity	Comments/study target	Spatial scale	Study type and duration
19	Andreassen et al. 1996b	structural discontinuities in corridors	effects on movement rates	patch (corridor)	experiment, 3 mo
20	Andreassen et al. 1996a	width of corridors	effects on movement rates	patch (corridor)	experiment, 3 mo
21	Hess 1996	physical connection between patches (corridors)	effect on recolonization and extinction rate	landscape	metapopulation model
22	Hjermann and Ims 1996	habitat isolation based on dispersal distance distributions and negative exponential dispersal function	effect of functional patch isolation on species patch occupancy	patch	observational, 2 yr
23	Hof and Flather 1996	between-patch movement probability dependent on a) species dispersal capability, b) harshness of inter-patch environment, c) inter-patch distance	effect on population means and variances	patch	optimization model
24	Lecomte and Clobert 1996	simulated presence/absence of corridors in an experimental landscape	effects on inter-patch dispersal	patch	experiment, 1 yr
25	Paillat and Butet 1996	total length of hedges in a 0.5-km radius around a sampling plot (patch)	effect of structural patch isolation on species abundance and fluctuations	patch	observational, 1 yr
26	Schippers et al. 1996	movement probabilities between all pairs of habitat patches	effect of real landscape structure on functional connectivity	landscape	GIS-related random walk simulation model
27	Schumaker 1996	dispersal success rate, fraction of individuals that located new territories	effect of landscape structure on functional connectivity	landscape	GIS-related random walk simulation model
28	Swart and Lawes 1996	presence/absence of corridors in metapopulation model	effect on metapopulation persistence	landscape	model
29	Demers et al. 1995	dispersal (colonization) success	effect of real landscape structure on functional connectivity	landscape	GIS-related random walk and population dynamics simulation model
30	Arnold et al. 1993	presence/absence of corridors and/or stepping stones	effect on movement rates and distances	landscape	observational, 3 yr
31	Hof and Joyce 1993	probabilistic, distance dependent isolation of a cell in a grid model	optimization of habitat placement	landscape	static optimization model
32	Taylor et al. 1993	degree to which the landscape facilitates or impedes movement among resource patches	definition of functional connectivity	landscape	conceptual discussion
33	Doak et al. 1992	search time-number of movement steps required to find a new habitat patch	effect of scale of clustering on functional connectivity	landscape	random walk simulation model on hierarchical, neutral landscape maps

patches. Research is needed to determine what, if any, simple measures of landscape structure can be used as measures of landscape connectivity.

Patch isolation or landscape connectivity?

Patch isolation is determined by the rate of immigration into the patch; 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). Since (1) and (3) are landscape structural features and (4) and (5) are the organisms' responses to landscape structure, patch isolation depends on "the degree to which the landscape facilitates or impedes movement..." (Taylor et al. 1993). Patch isolation is therefore imbedded within the concept of landscape connectivity. In fact, landscape connectivity is essentially equivalent to the inverse of the average degree of patch isolation over the landscape; a landscape including mostly patches with a high degree of isolation will be less connected than vice versa.

Five of the 33 studies we reviewed equated patch isolation with connectivity (Hjermann and Ims 1996, Paillat and Butet 1996, Grashofbokdam 1997, Spetich et al. 1997, Ault and Johnson 1998). Even though patch isolation is clearly part of landscape connectivity (above), none of these studies estimated immigration rates into patches. Rather, they related a species' abundance or presence/absence in a patch to structural attributes of the surrounding landscape, such as distance to the nearest occupied patch, or amount of habitat in a circle surrounding the patch. Such studies may reveal the relative importance of local patch vs surrounding landscape effects. However, they do not directly contribute to determining landscape connectivity, because they do not actually determine rates of movement among patches.

Corridors or connectivity?

Corridors are narrow, continuous strips of habitat that structurally connect two otherwise non-contiguous habitat patches. The corridor concept (e.g., Forman 1983, Bennett 1990, Merriam 1991, Saunders and Hobbs 1991, Lindenmayer and Nix 1993, Merriam and Saunders 1993, Bonner 1994, Dawson 1994, Rosenberg et al. 1997, Tischendorf 1997a) originated from the generalized assumption that organisms do not venture into non-habitat. Under this assumption, addition of any habitat to a landscape increases the ability of organisms to move. Corridors in a landscape may therefore be a component of its connectivity if they promote movement among habitat patches, but they do not determine its connectivity. The degree to which corridors contribute to landscape connectivity depends on the nature of the corridors, the nature of the matrix and the response of the organism to both (Rosenberg et al. 1997, Beier and Noss 1998).

Six of the reviewed studies equated the term connectivity with the presence/absence of corridors (Hess 1996, Lecomte and Clobert 1996, Swart and Lawes 1996, Schmiegelow et al. 1997, Andreassen et al. 1998, Bjornstad et al. 1998), and two studies associated connectivity with corridor width (Andreassen et al. 1996a) or corridor continuity (Andreassen et al. 1996b). The studies investigated (1) what features of a corridor

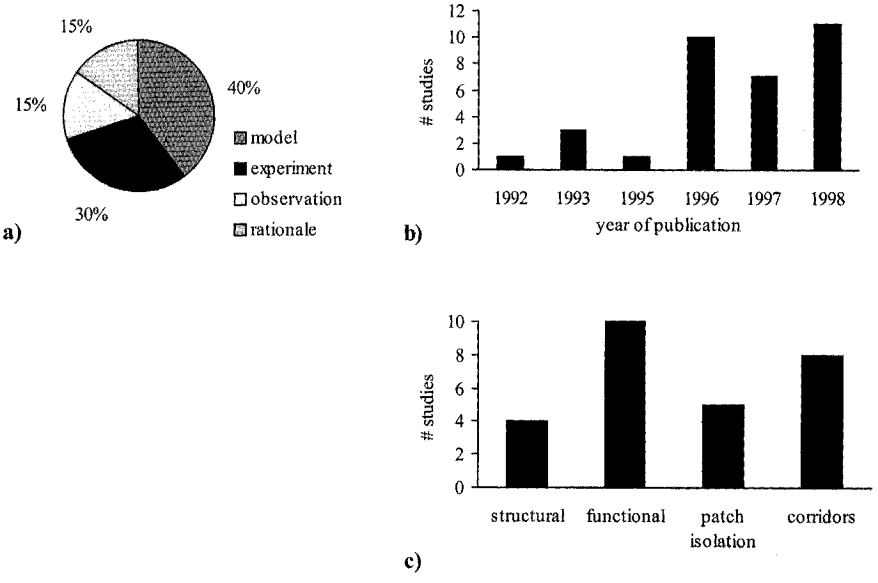

Fig. 1. Classification of the 33 reviewed studies according to study type (a), year of publication (b), and usage of the term connectivity (c).

determine its use by the organism, (2) space-use of organisms as a function of corridor presence/absence, and (3) population or community responses to corridors, e.g., species richness, diversity or abundance. None of the studies explicitly recognized that corridors are only a component of the concept of landscape connectivity; they actually equated the connecting function of corridors with connectivity.

Measurements of connectivity

In this section we review studies that quantified connectivity or key components of it. Recall that connectivity is defined as the degree to which the landscape facilitates or impedes movement among resource patches. Only four of the studies (Doak et al. 1992, Demers et al. 1995, Schippers et al. 1996, Schumaker 1996) measured movements among resource patches over the entire landscape and actually quantified connectivity in accordance with its definition. All of these were modeling studies and were based on simulated movements across heterogeneous landscapes. We also review five other studies which we think made an important contribution toward the concept of landscape connectivity (as explained below), even though they did not measure movement among resource patches directly (Arnold et al. 1993, With et al. 1997, Petit and Burel 1998a, b, Pither and Taylor 1998).

Modeling studies

Dispersal success

Dispersal success is usually defined as the proportion of individuals that successfully immigrate into a new habitat patch during the course of a simulation run. Three of the modeling studies quantified connectivity using dispersal success.

Schippers et al. (1996) (no. 26 in Table 1) simulated the badger's (*Meles meles*) response (movement probability and mortality risk) to landscape structure using a classified GIS grid map and empirical expertise. Movement probabilities between cells were derived by comparing the quality (for badger use) of adjacent cells. Higher quality cells attracted moving individuals. Mortality rates were higher in low-quality cells. The number of simulated movement steps corresponded to an estimated actual time of badger movement within a four-year period. The authors produced inter-patch transition probabilities and movement frequency maps (visits per grid cell), based on dispersal success.

Schumaker (1996) (no. 27 in Table 1) analyzed the potential of indices of landscape structure to predict dispersal success. He created landscape models in two ways: (1) sample landscapes were randomly drawn from a GIS data set to cover a range of different landscape configurations; (2) artificial landscape grids were created by randomly designating habitat cells. Cells of the grid represented territories. An individual-based correlated random walk model was used to simulate movements across the landscape. Individuals were released in a randomly selected 50% of habitat territories, and were allowed to settle in any unoccupied territory, which then became unavailable to subsequent immigrants. Landscape boundaries reflected approaching individuals. Connectivity was measured as the mean fraction (over several runs) of individuals that successfully dispersed into new territories during the course of a simulation. The results revealed correlations between each of ten indices of landscape structure and dispersal success (connectivity).

Demers et al. (1995) (no. 29 in Table 1) investigated the relationship between colonization success of edge-preferring organisms, and the amount and change of edge habitat, in real agricultural landscapes. A vector-based GIS data set containing fencerow and forest-edge coverages was used as a model landscape. Individuals were allowed to move only in suitable habitat after being dropped at random points across the landscape. Individuals could cross inhospitable habitat (matrix) up to a maximum distance, after any edge habitat in the landscape was successfully colonized. Occupied habitat could not be colonized by subsequent dispersers. The authors measured connectivity as the "total length and area of hedgerow and forest edge colonized by the offspring of each successful virtual organism". The results showed higher connectivity in landscapes with more and longer overall edge habitat.

Search time

One paper (Doak et al. 1992) (no. 33 in Table 1) used search time to quantify connectivity. Search time is the number of movement steps individuals require to find a new habitat patch.

Doak et al. (1992) examined the effect of spatial scale on the success of dispersing individuals. An artificial landscape was modeled by a hierarchical grid of three layers (spatial scales). Clusters of habitat cells were created on different spatial scales. Virtual individuals were released in the habitat and followed a random walk until a new habitat patch (different from the origin) was found. Landscape boundaries acted as reflecting borders. For each individual the number of movement steps required to find a new habitat patch (search time) was recorded. The mean and standard deviation over all individual search times were calculated and related to the scale of clustering. Large-scale clustering (few large patches) induced longer search times than small-scale clustering (more smaller patches) (see also Ruckelshaus et al. 1997).

Population spatial distribution

With et al. (1997) (no. 18 in Table 1) investigated the effects of landscape spatial structure on (1) the probabil-

ity of habitat contiguity (percolation), and (2) a population's spatial distribution. These are not direct measures of landscape connectivity but are components of landscape and population structure (respectively) that the authors assumed to be related to connectivity. Artificial landscape grid maps represented either random (spatially independent) or fractal (spatially dependent) distributions of three different habitat types. Virtual individuals followed a random walk, starting from random locations within the modeled landscape. Habitat type-specific residence probabilities controlled the movement probabilities at each simulation step. Habitat abundance, scale (for fractal maps), and the spatial arrangement of habitat (random vs fractal) turned out to be important for a population's spatial aggregation.

Empirical studies

Functional distances

Petit and Burel (1998a, b) (nos 8, 9 in Table 1) introduced functional distance as a way to extrapolate an organism's known responses to landscape elements. The functional distance between two points in a landscape was calculated as the sum of weighted distances. The weight or "cost of displacement" of each landscape element was a function of movement intensity and mortality rate for that element, which were quantified based on preliminary radio-tracking. High movement intensity and low mortality decreased the cost of displacement for a landscape element. The authors found functional distance to be a good predictor of local abundance of the forest carabid *Abax parallelepipedus*. Although functional distance is not landscape connectivity, in principle it could be integrated over all pairs of points in the landscape to give a measure of landscape connectivity.

Measuring movement

Pither and Taylor (1998) (no. 10 in Table 1) performed a manipulative mark-recapture experiment on two sympatric species of damselfly. Observations were made in five replicates of two different landscape types. Each landscape had a single type of habitat (either forest or pasture) between the release point of marked individuals and a stream. The number of individuals re-observed at the stream was equated with the movement abilities of the species through each habitat type. The authors found that the forest species moved significantly more readily through pasture habitat, while the open habitat species moved equally well through pasture and forest.

Arnold et al. (1993) (no. 30 in Table 1) radio-tracked movements of kangaroos in a fragmented landscape. They recorded longer movement distances across farmlands containing patches of trees or fencelines with native vegetation. They concluded that short-term refuges, such as stepping stones, may be important for landscape connectivity (see also Schultz 1998).

Although these movement studies did not actually measure landscape connectivity, they measured the response of movement to changes in landscape structure. These studies therefore demonstrate the dependence of connectivity on both landscape structure and movement attributes of the organism.

Assumptions and methods of connectivity models

Here we discuss critical modeling assumptions for measuring connectivity. We emphasize the importance of compatibility between model parameters and empirical data, and we discuss the potential for misleading conclusions from connectivity measures.

Landscape representation

In the reviewed modeling studies, landscapes were represented either by GIS data sets or by artificial habitat distribution maps. The advantage of artificial maps is that the simulated spatial pattern is adjustable, which allows for a systematic investigation of the effect of spatial pattern on connectivity (With and King 1997).

Two studies (Schumaker 1996, With et al. 1997) conducted comparisons between landscape representations. Schumaker (1996) concluded that the "study of simulated habitat pattern may provide little insight into the extent to which habitat fragmentation actually alters connectivity". However, we disagree with this conclusion. Schumaker showed that his landscape index, "patch cohesion", responded differently to habitat amount for maps of real vs artificial landscapes (see also Gustafson 1998). However, he did not actually examine dispersal success in the artificial maps. Therefore, Schumaker did not demonstrate a difference in structure–connectivity relationships for real vs artificial landscape representations.

With et al. (1997) found that a population's distribution was determined mainly by the spatial arrangement of habitat in random maps, and was scale-dependent in fractal maps. This is supported by Doak et al. (1992), who found the "scale of clustering to be the most important feature in determining disperser performance". In these studies the scale of clustering of the habitat was changed without adjusting the scale at which the organism responds to landscape structure (Wiens 1997), so the results reflect the fact that the range of scales at which clusters are created may exceed the organism's scale (extent) of response to landscape structure.

Movement description

Movement was usually modeled as a simple or correlated random walk based on probabilistic jumps into the adjacent cells of a grid. The rules differed greatly among the modeling studies and were only once supported with empirical expertise (Schippers et al. 1996; see also With and Crist 1995). The diversity of approaches to modeling movement impedes cross-comparisons between simulation results. We therefore argue for more consistency in describing movement in connectivity-related models.

To be compatible with empirical measures of movement (Kareiva and Shigesada 1983, Turchin et al. 1991), models should use vector-based movement rules (e.g., Tischendorf 1997a, b, Fahrig and Johsen 1998, Tischendorf et al. 1998). Length and direction of the movement steps determine the grain of the simulated organism's response to the landscape. In addition, the relationship between the extent of movement and the scale of landscape pattern (e.g., inter-patch distance relative to dispersal distance; see Fahrig (1992)) must always be addressed when examining landscape connectivity.

As has frequently been stated (Turchin 1991, Johnson et al. 1992a, Tischendorf 1997a, Wiens et al. 1997), movement rules need to be specific to landscape elements (e.g., Baars 1979, Rijnsdorp 1980, Wallin and Ekbom 1988, Hansson 1991, Johnson et al. 1992b, Andreassen et al. 1996b, Matter 1996, Charrier et al. 1997, Collins and Barrett 1997). In addition, mortality en route may influence the inter-patch movement success and should be taken into account when investigating landscape connectivity (e.g., Lidicker 1975, Gaines and McGlenaghan 1980, Krohne and Burgin 1987, Henein and Merriam 1990, Schippers et al. 1996, Charrier et al. 1997, Poole 1997, Ruckelshaus et al. 1997, Sakai and Noon 1997).

Measurements of connectivity

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. Thus, conclusions drawn from these measurements indirectly advocate fragmentation to enhance connectivity. This would have negative consequences for conservation. The problem with these measurements of connectivity is that they only count inter-patch movements (which become increasingly successful the more patches there are). They completely ignore within-patch movements (which should contribute to connectivity). Below we discuss an alternative way to measure connectivity that avoids this problem.

Another source for misleading conclusions is disregard of the effect of mortality on the success of movement across a landscape (Krohne and Dubbs 1984, Krohne and Burgin 1987). Dispersal success has recently been shown to be highly sensitive to mortality en route (Ruckelshaus et al. 1997). Consequently, ignoring mortality in modeling studies or interpreting empirical findings without the potential effects of mortality can lead to false results and misleading recommendations. Two examples should clarify this. First, mean search time, i.e., the average number of movement steps required to find a new habitat patch, can not reflect mortality-induced changes in the number of successful immigrations. This measure is solely based on counting time steps instead of individuals, so individuals that die would not contribute to a lack of connectivity, even though they should. Second, empirical studies (e.g., Baars 1979, Rijnsdorp 1980, Liro and Szacki 1987, Garrett and Franklin 1988, Wallin and Ekbom 1988, Kozakiewicz 1993, Charrier et al. 1997, Collins and Barrett 1997, Wiens et al. 1997, Pither and Taylor 1998) reveal movement rates or distances to be higher through inhospitable than through hospitable habitat (but see Wolff et al. (1997) for the opposite effect). This increased movement rate may result from a perceived increase in predation risk. Studies that assume higher movement, but do not include higher mortality in matrix, can lead to the erroneous conclusion that removal or fragmentation of habitat may enhance interactions among local populations at broad spatial scales. Such conclusions ignore the crucial tradeoff between movement and mortality and may be fatal for species that face higher mortality risks outside their habitat.

The future of connectivity research

The role of models and empiricism

The effort required to measure connectivity empirically likely exceeds any feasible project. In fact, we cannot rely on independent data sets on which to verify connectivity models. For this reason, the traditional evaluation of model predictions against empirical data becomes difficult, if not impossible. Therefore, empirical studies and models must complement each other.

Models should focus on revealing the relative importance of parameters and assumptions in determining connectivity. This information can be used to direct empirical research if model parameters are compatible with empirical data. For example, a model could indicate high relative importance of a particular movement parameter to connectivity, implying that it would be useful to collect this type of movement information in empirical studies.

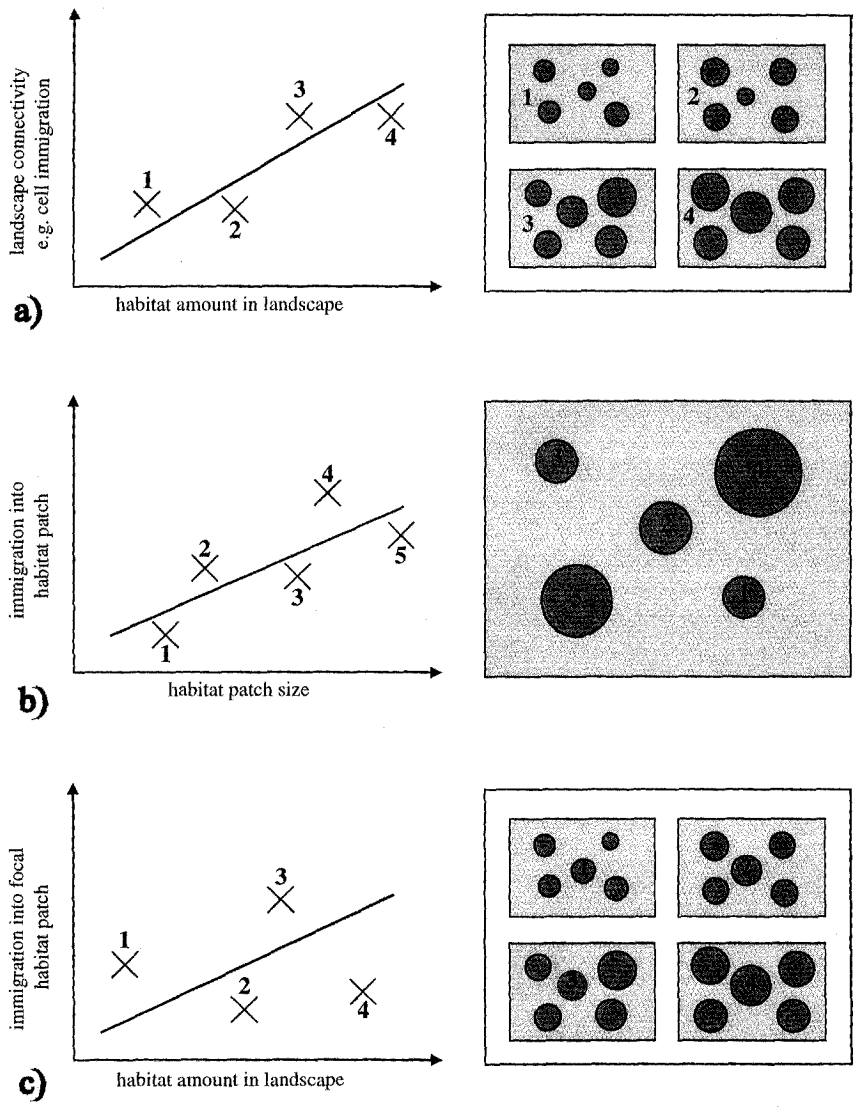

Fig. 2. Principal data – source relationships for studies replicated at the landscape scale (a), patch-scale studies in single landscapes (b), and hybrid patch-scale landscape-scale studies (c).

Empirical studies should provide data that either reinforce or question our modeling assumptions. For example, the observation that many organisms move more in inhospitable habitat than hospitable habitat should be included in models of connectivity.

Immigration into equal-sized areas

We suggest that measurement of connectivity should be based on immigration rates into equal-sized areas (territories in some cases), to eliminate the counter-intuitive conclusion, based on patch-based measures of connectivity, that habitat fragmentation is predicted to increase connectivity (as described above). This could be done by superimposing a grid of equal-sized cells on the landscape and measuring immigration into habitat cells (see Schumaker (1996) for a similar approach). This measurement would not depend on the number of patches in the landscape, which would prevent misleading conclusions. Using grid cells as the basis of immigration may also provide grounds for determining under which conditions the simplified structural viewpoint can substitute for actual connectivity.

Note that this approach is different from the measurement of connectivity based on percolation theory. Although both methods represent the landscape as a grid of cells, in the percolation approach connectivity is defined as the probability of the presence/absence of a percolating cluster of habitat cells on the landscape (Gardner et al. 1987, Gardner and O'Neill 1991, Green 1994). Using our proposed method, connectivity can have a range of values, depending on the rate of successful immigration into cells. Our method does not assume that contiguous cells are always functionally connected, as is assumed in percolation models.

In applying a cell-based measurement of connectivity it is important to note that the resolution of the superimposed grid implies an artificial scale of observation. The grid scale is likely to affect the value of connectivity calculated. Therefore in comparing connectivities of different landscapes for a particular species, the same grid scale should be used for all landscapes.

Hybrid patch-landscape scale empirical studies

Landscape connectivity is, by definition, an attribute of an entire landscape, where the scale of the landscape is determined by the movement scales of the species of interest (Goodwin and Fahrig 1998). Empirical studies investigating key components of connectivity must therefore be replicated at the landscape scale, i.e., each single data point in the study must be obtained from a separate landscape (Fig. 2a). However, studies that use the landscape as the unit of observation are generally rare (e.g., McGarigal and McComb 1995, Pedlar et al. 1997, Pither and Taylor 1998, Trzcinski et al. 1999).

In contrast, patch-scale studies, in which many patches within a single landscape are compared, are common (e.g., Opdam et al. 1985, van Dorp and Opdam 1987, Laan and Verboom 1990, van Apeldoorn et al. 1992, Fitzgibbon 1993, 1997, Dunning et al. 1995, Vos and Stumpel 1995, Kinnunen et al. 1996, Luiselli and Capicci 1997, Fahrig and Jonsen 1998, Delin and Andrén 1999, Hokit et al. 1999). In a patch-scale study each patch in the landscape represents an individual data point (Fig. 2b). Patch-scale studies can only produce a single measure of connectivity for the single landscape of the study. Therefore, such studies are unreplicated with respect to landscape connectivity.

We suggest a hybrid approach between patch-scale and landscape-scale studies. In such studies, sampling would be conducted in single patches (or equal-sized areas) in the centers of non-overlapping landscapes (Fig. 2c). The structure of the landscape surrounding the patches would be measured and related to the rates of immigration into the focal patches. Rate of immigration into the focal patches would be used as an indicator of connectivity for the whole landscape surrounding the patch. Such a study design allows for sampling in multiple landscapes, but only a single patch is sampled within each landscape, thus reducing sampling intensity. Note that for any one landscape, immigration to the selected patch may not be representative of connectivity for this landscape. However, a simulation study (Tischendorf and Fahrig unpubl.) suggests that this approach should generally work well for multi-landscape comparisons.

Conclusions

From our review of the current usage and measurement of the term connectivity, we conclude that the field currently lacks focus. The issue is not just semantics; erroneous conclusions and recommendations are made due to inconsistent usage and paradoxical measurement of connectivity. We suggest the following to streamline future connectivity research:

1. The term landscape connectivity should be reserved for its original meaning, i.e., the degree to which the landscape facilitates or impedes movement among resource patches.

2. Any measure of connectivity must be based on movement of an organism through a landscape. Measures of landscape structure as well as demographic indicators, such as species abundance and distribution, while potentially related to connectivity, are not measures of connectivity.

3. Relationships between measures of landscape structure and connectivity need to be examined.

4. We recommend measuring connectivity using immigration into equal-sized territories or grid cells, rather than variable-sized patches. This resolves the paradox of zero connectivity in single-patch landscapes, and avoids the problematic conclusion that habitat fragmentation increases landscape connectivity.

5. For field studies on connectivity we recommend the hybrid patch-landscape scale approach in which non-overlapping landscapes are the study units, but in each study unit only a single patch or sample area (at the center of the landscape) is sampled. Immigration to that patch or area is used as an index of connectivity for the surrounding landscape.

6. A consistent framework for modeling assumptions regarding movement, mortality and boundary reactions is necessary to allow cross-comparisons of simulation and empirical results. For example, to be compatible with empirical measures of movement, models should use vector-based movement rules.

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