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Research article

Is landscape connectivity a dependent or independent variable?

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Abstract

With growing interest in landscape connectivity, it is timely to ask what research has been done and what remains to be done. I surveyed papers investigating landscape connectivity from 1985 to 2000. From these papers, I determined if connectivity had been treated as an independent or dependent variable, what connectivity metrics were used, and if the study took an empirical or modeling approach to studying connectivity. Most studies treated connectivity as an independent variable, despite how little we know about how landscape structure and organism movement behaviour interact to determine landscape connectivity. Structural measures of connectivity were more common than functional measures, particularly if connectivity was treated as an independent variable. Though there was a good balance between modeling and empirical approaches overall – studies dealing with connectivity as a dependent, functional variable were mainly modeling studies. Based on the research achieved thus far, future landscape connectivity research should focus on: (1) elucidating the relationship between landscape structure, organism movement behaviour, and landscape connectivity (e.g., treating connectivity as a dependent variable), (2) determining the relationships between different measures of connectivity, particularly structural and functional measures, and (3) empirically testing model predictions regarding landscape connectivity.

Introduction

Merriam (1984) recognized that landscape structure and organism movement are inter-related and referred to the landscape property caused by that interaction as "connectivity". Early research into landscape connectivity focused on the presence and arrangement of movement corridors. Both modelling and empirical studies suggested that changing landscape connectivity by manipulating corridors (both presence/absence and corridor quality) led to changes in regional population size and persistence (Fahrig and Merriam 1985; Lefkovitch and Fahrig 1985; Burel 1989; Henein and Merriam 1990). An increasing appreciation of organism movements through non-habitat or matrix elements (Reddingius and den Boer 1970; Wegner and Merriam 1979; Liro and Szacki 1987; Potter 1990; Szacki and Liro 1991; Johnson et al. 1992) led to questioning the necessity of corridors for interpatch movement (Merriam 1991; Hobbs 1992). Subsequently, the concept of connectivity grew to encompass the influence of the entire landscape and "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993). In part due to this history, landscape connectivity is currently viewed either structurally, where connectivity is entirely based on landscape structure (usually habitat contiguity), or functionally, where behavioural responses to the landscape elements (patches and edges) are considered along with the spatial structure of the landscape (Tischendorf and Fahrig 2000b).

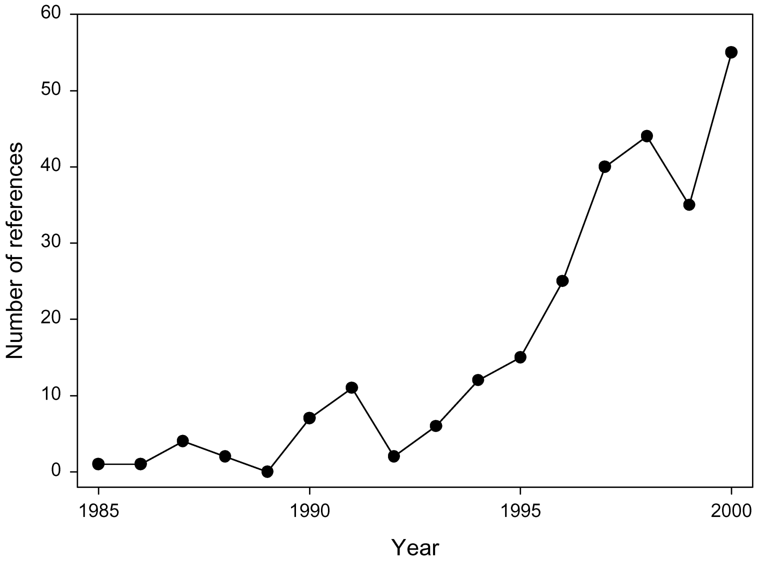

Figure 1. Number of published papers addressing landscape connectivity (up to and including 2000) determined by a search of the Biosys database using the criteria "connectivity and (landscape or habitat or patch)" in the keywords, title, or abstract. Appropriateness of papers was determined by scanning the title.

Landscape connectivity can affect individuals and populations in heterogeneous landscapes. A landscape's connectivity can determine foraging success when organisms forage over multiple patches (Kozakiewicz 1995) and dispersal success (Merriam 1994; Gustafson and Gardner 1996; Schumaker 1996; Schippers et al. 1996; Berggren et al. 2001). In turn, dispersal success can influence local population dynamics and metapopulation stability via immigration rates (Brown and Kodric-Brown 1977; Hanski and Gilpin 1997; Hanski 1999). Thus, to understand populations in heterogeneous landscapes it is essential to understand how organism movement behaviour and landscape structure interact to determine landscape connectivity.

The potential for landscape connectivity to impact populations in heterogeneous landscapes, and the obvious implications for conservation biology, has led to an increasing interest in landscape connectivity (Figure 1) and a proliferation of connectivity measures (Tischendorf and Fahrig 2000b). Given this increasing interest, it is timely to reflect on previous trends in connectivity research. Specifically, has research focused on understanding how landscape structure and movement behaviour interact to determine landscape connectivity (connectivity as a dependent variable) or how landscape connectivity might impact other ecological process (connectivity as an independent variable)? What measures of connectivity are being used? How many studies take an empirical versus a modeling approach? Such reflections will also point toward future research needs.

Methods

I searched the literature from 1985 to 2000 for papers with keywords "connectivity" and either "landscape" or "patch" or "habitat" presenting original research on landscape connectivity (as opposed to review papers). From the papers, I determined: 1) whether connectivity was treated as an independent or dependent variable, 2) the approach used to investigate landscape connectivity (empirical or modeling), and 3) the measure of connectivity used. Measures of connectivity were broadly classified as either structural or functional. The measures where also classified into ten types: 1) measures based on the presence or absence of corridors; 2) measures based on distances, sometimes weighted by some measure of dispersal ability, between habitat patches; 3) measures based on the amount of habitat in the landscape; 4) measures based on contagion or percolation; 5) measures based on dispersal success; 6) measures based on graph theory; 7) measures based on the probability of moving between patches; 8) measures based on the amount of time spent searching for a new habitat patch; 9) measures based on the rate of reobservation of displaced individuals; and 10) measures based on immigration rates.

Results

I found 63 papers investigating connectivity (Table 1). The papers covered a broad range of landscape types but studies using animals were much more prevalent than studies using plants (42 animal studies, 4 plant studies, and 17 modeling studies without a specific organism, Table 1). Approximately three quarters of the papers used landscape connectivity as an independent variable to explain some other ecological processes (77.8%, Figure 2). At the individual level, landscape connectivity was related to movement behaviour (Arnold et al. 1993; Lecomte and Clobert 1996; Wiens et al. 1997; Farmer and Parent 1997; Browne et al. 1999; With et al. 1999), spatial distributions (With and Crist 1995; Andreassen et al. 1998; Bjørnstad et al. 1998), and dispersal success (Demers et al. 1995; Bjørnstad et al. 1998; Rosenberg et al. 1998; Brooker et al. 1999; With and King 1999). At the population level, landscape connectivity was related to species occurrence (Laan and Verboom 1990; Clergeau and Burel 1997; Grashof-Bokdam 1997), population levels (Fahrig and Merriam 1985; Lefkovitch and Fahrig 1985; Henein and Merriam 1990; Paillat and Butet 1996; Fitzgibbon 1997; Schmigelow et al. 1997; Gonzalez et al. 1998; Henein et al. 1998; Zabel and Tscharntke 1998; Petit and Burel 1998a; Petit and Burel 1998b), population persistence (Lefkovitch and Fahrig 1985; Adler and Nuernberger 1994; Hjermann and Ims 1996; Swart and Lawes 1996; Hess 1996a; Hess 1996b; Henein et al. 1998; Root 1998), and population spread (Lavorel et al. 1995; Hutchinson and Vankat 1998). Finally, at the community level, landscape connectivity was related to community structure (Grashof-Bokdam 1997; Le Coeur et al. 1997; Schmigelow et al. 1997; Ault and Johnson 1998; Collinge and Forman 1998), pollinator efficacy (Steffan-Dewenter and Tscharntke 1999), and species richness/diversity (Laan and Verboom 1990; Metzger 1997; Zabel and Tscharntke 1998). Almost all the studies using landscape connectivity as an independent variable measured connectivity structurally (47 of 48 studies, Figure 2). Of those studies (independent, structural) three quarters were empirical (35 of 47 studies, Figure 2). The lone study using a functional measure of connectivity as an independent variable was a modeling study. Studies using connectivity as a dependent variable were evenly split between structural and functional measures of connectivity (8 studies each, Figure 2). When connectivity was a dependent variable, studies using structural measures were evenly split between empirical and modeling approaches (4 studies each, Figure 2) while studies using functional measures where dominated by modeling approaches (6 of 8 studies, Figure 2).

Many different measures of connectivity have been used in landscape connectivity research. Connectivity measures based on organism movement (e.g., dispersal success, immigration rate, search time) were more common in studies that used connectivity as a dependent variable while measures based on landscape structure (e.g., corridors, distance, amount of habitat) were more common in studies that used connectivity as an independent variable (Figure 3a). Studies tended to use different connectivity metrics depending on whether they took a structural or functional view of landscape connectivity (Figure 3b). Studies that used connectivity metrics based on landscape structure had a good balance between modeling and empirical approaches while studies that used connectivity metrics based on organism movements tended to use modeling approaches (Figure 3c). With very few exceptions, studies investigated a single measure of connectivity (only 8 of the studies in Table 1 considered multiple measures of landscape connectivity).

Discussion

Landscape connectivity arises from complex interactions between landscape structure and movement behaviour (Merriam 1984; Taylor et al. 1993). Accordingly, landscape connectivity should be treated as a dependent variable. Landscape connectivity has the potential to influence many ecological processes in heterogeneous landscapes, such as population persistence or the distribution of individuals in a landscape. Accordingly, landscape connectivity should be treated as an independent variable. These approaches need not be exclusive (though they often are). In fact, both approaches are necessary for a broad understanding of landscape connectivity.

Relatively few researchers treat landscape connectivity as a dependent variable. Yet the question of how landscape spatial structure and movement behaviour interact to determine landscape connectivity is crucial

Table 1. Summary of connectivity studies. The organism moving is identified (na indicates a species free modeling study), type of landscape described, and measure of connectivity described. The use column reports whether connectivity was used as an independent (I) or dependent (D) variable. The measure column reports whether connectivity was measured structurally (S) or functionally (F). The approach column reports the approach taken in studying connectivity (E = empirical or M = conceptual, simulation or mathematical model).

Study	Organism	Landscape	Measure of Connectivity	Use	Measure	Approach
(Adler and Nuernberger 1994)	na	virtual habitat patches in unsuitable matrix	isolation (distance)	I	S	M
(Andreassen et al. 1996a)	root vole (*Microtus oeconomus*)	mown meadow fragments	movement through corridors	D	F	E
(Andreassen et al. 1996b)	root vole (*Microtus oeconomus*)	mown meadow fragments	quality of corridors	D	S	E
(Andreassen et al. 1998)	root vole (*Microtus oeconomus*)	mown meadow fragments	presence/absence of corridors	I	S	E
(Arnold et al. 1993)	kangaroo (*Macropus robustus*)	native vegetation in agricultural matrix	presence/absence of corridors and stepping stones	I	S	E
(Ault and Johnson 1998)	reef fish	small coral reefs	size of and distance to nearest neighbour	I	S	E
(Bjørnstad et al. 1998)	root vole (*Microtus oeconomus*)	mown meadow fragments	presence/absence of corridors	I	S	E
(Brooker et al. 1999)	Blue-breasted Fairy-wren (*Malurus pulcherrimus*), White-browed Babbler (*Pomatostomus superciliosus*)	native vegetation in agricultural matrix	presence/absence of corridors and gap widths	I	S	M, E
(Browne et al. 1999)	hispid cotton rat (*Sigmodon hispidus*)	clear cut patches in forest matrix	presence/absence of corridors	I	S	E
(Bunn et al. 2000)	American mink (*Mustela vison*), prothonotary warbler (*Protonaria citrea*)	wetlands in forest matrix	graph operations (spanning trees, traversibility)	I	S	E
(Collinge and Forman 1998)	insect community	mown grassland	“straight line crossing” (Forman 1995)	I, D	S	E
(Collinge 2000)	insect community	mown grassland	presence/absence of corridors	I	S	E
(Danielson and Hubbard 2000)	old-field mice (*Peromyscus polionotus*), cotton rats (*Sigmodon hispidus*), cotton mice (*Peromyscus gossypinus*)	clear cut patches and corridors in loblolly pine forest	presence/absence of corridors	I	S	E
(Demers et al. 1995)	na	woodlots and fencerows in agricultural matrix	presence/absence of corridors and amount of habitat	I	S	M
(Doak et al. 1992)	na	virtual habitat patches in unsuitable matrix	search time	D	F	M
(Fahrig and Merriam 1985)	white-footed mouse (*Peromyscus leucopus*)	woodlots and fencerows in agricultural matrix	presence/absence of corridors	I	S	M, E
(Farmer and Parent 1997)	Pectoral sandpipers (*Calidris melanotos*)	wetlands in agricultural matrix	inter-patch distance, amount of habitat	I	S	E
(Fitzgibbon 1997)	wood mice (*Apodemus sylvaticus*), bank voles (*Clethrionomys glareolus*)	small woods in agricultural matrix	inter-patch distance	I	S	E
(Gonzalez et al. 1998)	microarthropod community	moss patches on bare rock	presence/absence of corridors	I	S	E
(Grashof-Bokdam 1997)	forest plants	forest patches in agricultural matrix	amount of forest in three zones around patch	I	S	E
(Green 1994)	na	grid with habitat/nonhabitat cells	percolation thresholds	D	S	M

Table 1. Continued.

Study	Organism	Landscape	Measure of Connectivity	Use	Measure	Approach
(Haddad 2000)	butterfly (*Junonia coenia*)	clear cut patches and corridors in loblolly pine forest	presence/absence of corridors	I	S	E
(Hanski 1999)	na	patch network	weighted isolation	I	S	M
(Henein and Merriam 1990)	white-footed mouse (*Peromyscus leucopus*)	woodlots and fencerows in agricultural matrix	presence/absence and quality of corridors	I	S	M
(Henein et al. 1998)	eastern chipmunk (*Tamias striatus*), white-footed mouse (*Peromyscus leucopus*)	woodlots and fencerows in agricultural matrix	presence/absence and quality of corridors	I	S	M
(Hess 1996a)	na	virtual habitat patches and corridors	arrangement of connections	I	S	M
(Hess 1996b)	na	virtual habitat patches	ability to move between patches	I	S	M
(Hjermann and Ims 1996)	wart bitter (*Detticus verrucivorus*)	un-grazed grassland in agricultural matrix	distance/area index	I	S	E
(Hof and Flather 1996)	na	virtual habitat patches in unsuitable matrix	probability of moving between patches	D	S	M
(Hof and Raphael 1997)	Northern spotted owl (*Strix occidentalis caurina*)	old-growth forest patches	probability of moving between patches	I	F	M
(Hutchinson and Vankat 1998)	Amur honeysuckle (*Lonicera maackii*)	forest patches in agricultural matrix	contagion	I	S	E
(Keitt et al. 1997)	na	forest patches	percolation cluster size	D	S	E
(Laan and Verboom 1990)	amphibians	pools	distance, presence of woods	I	S	E
(Lavorel et al. 1995)	plant community	hedgerow network	presence/absence of corridors	I	S	E
(Lavorel et al. 1995)	na	grid with habitat/nonhabitat cells	percolation threshold	I	S	M
(Le Coeur et al. 1997)	Short-toed tree creeper (*Certhia brachydactyla*)	native vegetation in agricultural matrix	presence/absence of corridors	I	S	E
(Lecomte and Clobert 1996)	lizard (*Lacerta vivipara*)	enclosures with connecting corridors	presence/absence of corridors	I	S	E
(Lefkovitch and Fahrig 1985)	white-footed mouse (*Peromyscus leucopus*)	woodlots and fencerows in agricultural matrix	presence/absence and arrangement of corridors	I	S	M
(Metzger 1997)	tropical tree community	forest fragments	presence/absence of corridors and stepping-stones	I	S	E
(Paillat and Butet 1996)	bank vole (*Clethrionomys glareolus*)	woody patches in agricultural matrix	length of hedges within a 0.5 km radius	I	S	E
(Petit and Burel 1998a)	forest carabid (*Abax parallelepipedus*)	woodland patches and a hedgerow network	Euclidean, network, and resistance weighted distances	I	S	E
(Petit and Burel 1998b)	forest carabid (*Abax parallelepipedus*)	woodland patches and a hedgerow network	resistance weighted distance	I	S	E
(Pither and Taylor 1998)	damselflies (*Calopteryx aequabilis and maculata*)	forest and pasture	reobservation after displacement	D	F	E
(Reunanen et al. 2000)	flying squirrel (*Pteromys volans*)	deciduous forest patches within coniferous matrix	largest patch size	I	S	E
(Root 1998)	Florida scrub jay (*Aphelocoursa coerulescens*)	scrub patches	nearest neighbour distance	I	S	M
(Rosenberg et al. 1998)	salamander (*Ensatina eschscholtzii*)	habitat patches and corridors	presence/absence of corridors	I	S	E

Table 1. Continued.

Study	Organism	Landscape	Measure of Connectivity	Use	Measure	Approach
(Ruckelshaus et al. 1997)	na	virtual habitat patches in unsuitable matrix	dispersal success	D	F	M
(Schiegg 2000)	saproxylic insects	dead wood on forest floor	distance, amount	I	S	E
(Schippers et al. 1996)	badger (*Meles meles*)	central Netherlands	fraction of dispersers arriving at a patch	D	F	M
(Schmigelow et al. 1997)	breeding bird community	Boreal forest patches in clear cut matrix	presence/absence of corridors	I	S	E
(Schumaker 1996)	na	old growth forest patches	dispersal success	D	F	M
(Spetich et al. 1997)	na	old growth forest patches	proximity index	D	S	E
(Steffan-Dewenter and Tscharntke 1999)	pollinator community	potted plants in agricultural matrix	distance to source	I	S	E
(Swart and Lawes 1996)	samango monkey (*Cercopithecus mitis*)	forest patches	presence/absence of corridors	I	S	M
(Tiebout and Anderson 1997)	na	grid with habitat/nonhabitat cells	contagion	D	S	M
(Tischendorf and Fahrig 2000a)	na	grid with habitat and two types of matrix cells	dispersal success, search time, cell immigration	D	F	M
(van Langevelde 2000)	nuthatch (*Sitta europara*)	forest patches in agricultural matrix	graph theory	I	S	E
(Wiens et al. 1997)	tenebrionid beetle (*Eleodes obsoleta*)	grass and sand mosaics	percolation threshold	I	S	E
(With and Crist 1995)	two grasshoppers (*Xanthippus corallipes* and *Psoloessa delicatula*)	shortgrass prairie	percolation threshold	I	S	M, E
(With and King 1999)	na	grid with habitat/nonhabitat cells	dispersal success	D	F	M
(With et al. 1997)	na	grid with three cell types	percolation thresholds	D	S	M
(With et al. 1999)	cricket (*Acheta domestica*)	grass and sand mosaics	percolation thresholds	I	S	M, E
(Zabel and Tscharntke 1998)	insect community	stinging nettle (Urtica dioica) patches in agricultural matrix	inter-patch distance	I	S	E

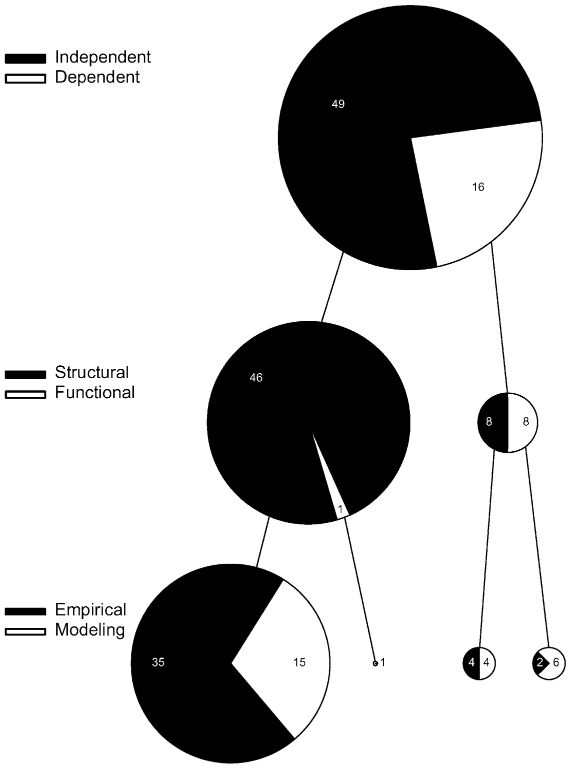

Figure 2. A hierarchical decomposition of studies of landscape connectivity that used connectivity as an independent or dependent variable (top level), took a structural or functional view of connectivity (middle level), and used modeling or empirical approaches (bottom level). The size of each pie indicates the number of studies. Studies fitting into two categories (e.g., used both modeling and empirical approaches) were counted in each of those categories. The number of studies in each category is indicated.

for understanding landscape connectivity. Many landscape indices depend, often non-linearly, upon either landscape state (e.g., habitat amount, fragmentation; Gustafson and Parker 1992; Hargis et al. 1998) or sampling scale (Turner et al. 1989; Plotnick et al. 1993; Cain et al. 1997). Modeling work has found similar complex interactions between landscape structure and some landscape connectivity metrics (Tischendorf 2001; Goodwin and Fahrig 2002b). Furthermore, since a particular landscape index quantifies a single aspect of the overall landscape structure (Gustafson 1998) and different aspects of landscape structure may influence landscape connectivity more or less strongly some landscape indices may be more or less strongly related to landscape connectivity. The relationship between landscape structure and landscape connectivity is unclear. Any effect of landscape structure on landscape connectivity will depend on the details of movement behaviour within and between the different landscape elements. Most animals move differently in non-habitat patches than in habitat patches (e.g., Baars 1979; Rijnsdorp 1980; Wallin and Ekbom 1988; Hansson 1991; Johnson et al. 1992; Matter 1996; Andreassen et al. 1996b; Charrier et al. 1997; Collins and Barrett 1997). Edge crossing behaviour (Mauremooto et al. 1995; Mills 1995; Schultz and Crone 2001), perceptual ability (Yeomans 1995; Zollner and Lima 1997), and density effects (Herzig 1995; Rhainds and Gries 1997; Andreassen and Ims 2001) have all been demonstrated to influence movement. Tischendorf (Tischendorf and Fahrig 2000a; Tischendorf 2001) modeled movement within landscapes using four generalized movement patterns (e.g., habitat specialist, habitat generalist) and found movement behaviour to influence landscape connectivity. Research that elucidates how movement behaviour and landscape spatial structure interact to set landscape connectivity is therefore essential for understanding landscape connectivity, yet research using connectivity as a dependent variable is relatively rare.

Studies using connectivity as a dependent variable tend to take modeling approaches. Modeling has two advantages: 1) it is possible to completely manipulate landscape structure in the model, which is not true in the field, and 2) it is much easier to track movement in simulations than in the field. Though well suited to investigating landscape connectivity, simulations only produce predictions and potential insight into natural systems, which should be held up to empirical scrutiny. However, simulation predictions are rarely tested empirically (but see Fahrig and Merriam 1985; With and Crist 1995; Brooker et al. 1999; With and King 1999) and empirical studies are rarely designed to test specific model predictions (but see Wiens et al. 1997). The propensity for models to rely on unrealistic movement behaviour may explain the paucity of empirical tests of model predictions. Many connectivity simulations model movement as random walks (Doak et al. 1992; Schumaker 1996; Schippers et al. 1996; With et al. 1997; Ruckelshaus et al. 1997; With and King 1999), which tend to ignore many of the complexities of movement behaviour in landscapes (Travis and French 2000). Furthermore, simulations use a variety of schema, including patch models (Hof and Flather 1996; Hess 1996b), cellular automata (Green 1994), grid based movements (Schumaker 1996; Schippers et al. 1996; With et al. 1997; Henein et al. 1998; With and King 1999), and vector based

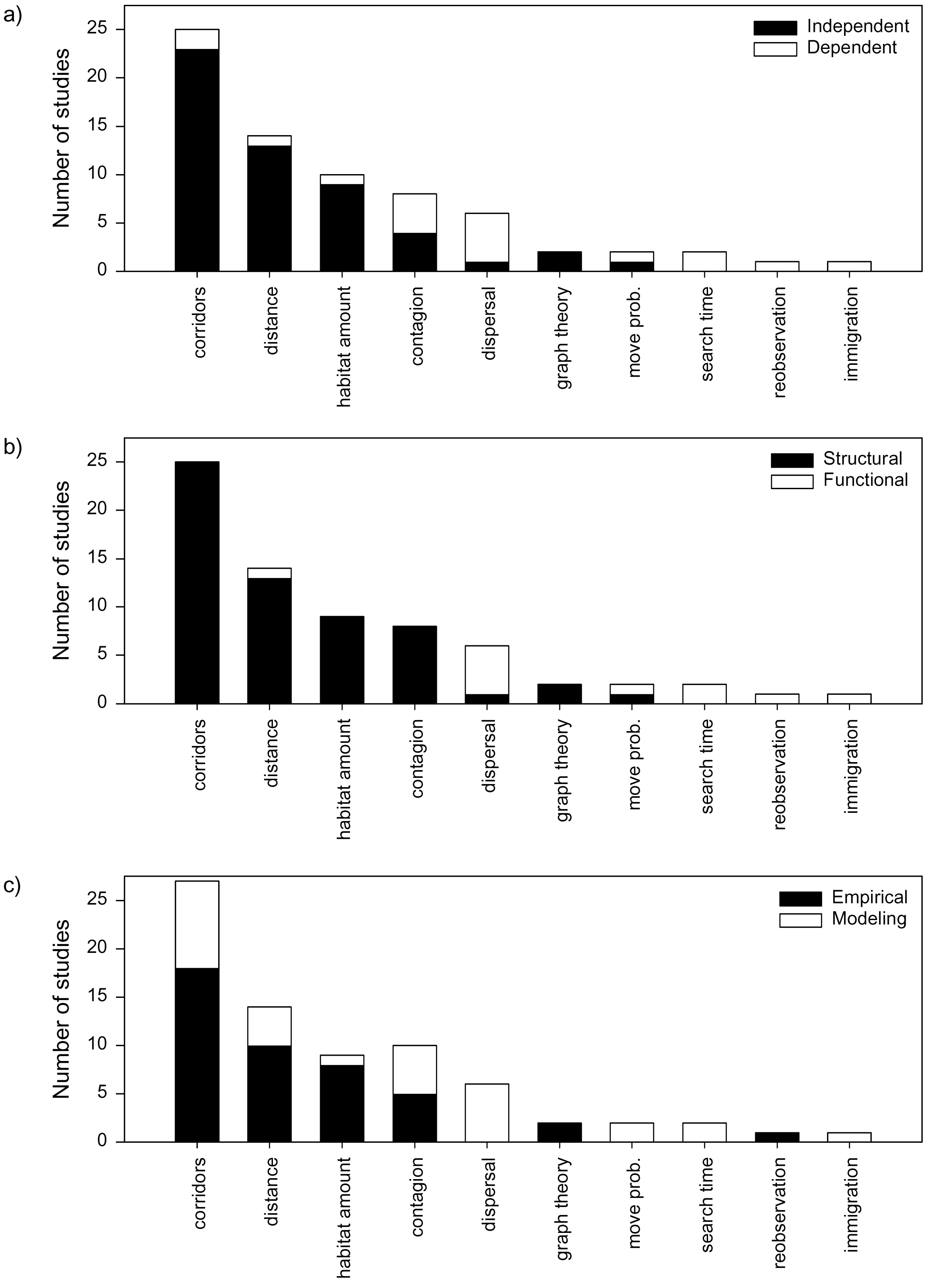

Figure 3. The distribution of different metrics of landscape connectivity by (a) connectivity used as an independent vs. dependent variable, (b) structural vs. functional measures of connectivity, and (c) empirical vs. modeling approaches. If a paper presented both categories (e.g., used both modeling and empirical approaches) it was counted twice, thus the number of papers for any one connectivity metric can change from pane to pane.

movements (Tischendorf and Fahrig 2000a) to model movement. Cellular automata and grid based movement models may not model movement very realistically and the grain of the landscape constrains, possibly inappropriately, the scale at which movements are simulated (Tischendorf 1997). Patch models often model movements as patch transition probabilities that are, unrealistically, independent of the intervening landscape (Hof and Flather 1996; Hess 1996b). Similarly, models might inappropriately use the same movement rules in both habitat and matrix elements (Schumaker 1996). Vector based movement models seem the most appropriate approach as they need not be constrained by the approach and scale taken to model the landscape (Tischendorf 1997). Also, empirical measures of movement are usually based on a vector description of movement trails (Turchin et al. 1991; Goodwin and Fahrig 2002a). Even so, simulations may lack an important nuance of movement behaviour (such as edge-crossing behaviour) critical to determining landscape connectivity. Thus the need for empirical tests of landscape connectivity simulations, even well designed ones. Unfortunately, simulation and empirical studies tend to use different measures of connectivity. Simulation studies have used dispersal success (Schumaker 1996; Schippers et al. 1996; Ruckelshaus et al. 1997; Tischendorf and Fahrig 2000a), search time (Doak et al. 1992; Tischendorf and Fahrig 2000a), and cell immigration (Tischendorf and Fahrig 2000a) while empirical studies have used dispersal success (Andreassen et al. 1996a) and re-observation frequency (Pither and Taylor 1998). This discrepancy impedes our ability to assess the validity of simulation results.

More commonly, researchers treat landscape connectivity as an independent variable and ask how landscape connectivity impacts some other ecological process such as species distribution or population dynamics. Such studies are important as they indicate the potential impact of landscape connectivity on individuals, populations, and communities in heterogeneous landscapes. However, they assume that the measure of connectivity employed accurately represents landscape connectivity for the organism in question. This might explain the almost exclusive use of structural measures of landscape connectivity when analyzing connectivity as an independent variable – structural measures avoid the potential complications of movement behaviour thereby seeming more accurate. In addition, studies using landscape connectivity as an independent variable tend to be empirical, making structural measures attractive since landscape structure is relatively easy to quantify and many metrics have been developed (Gustafson 1998). However, structural measures of connectivity may not be ecologically meaningful, that is they may not reflect the ability of the organism to move through the landscape if critical aspects of movement behaviour are not incorporated in the metric of landscape structure. For example, if individuals move between habitat patches exclusively via corridors then the degree to which habitat patches are interconnected by corridors will be a good measure of landscape connectivity. If animals avoid corridors or move between habitat patches without using corridors then the presence of corridors will overestimate or underestimate, respectively, landscape connectivity. Another structural measure, percolation theory, tends to focus on the presence of spanning clusters (Green 1994; With and Crist 1995; With et al. 1997; Metzger and Décamps 1997; Tiebout and Anderson 1997), habitat patches that cross from one side of the landscape to another (Gardner et al. 1989). Spanning clusters may have no bearing on an organism's ability to move between habitat patches in the landscape (compare to the definition of connectivity in Taylor et al. 1993). More subtly, the use of structural connectivity measures may colour a researcher's assumptions about movement. For example, structural measures of connectivity tend to divide the landscape into habitat and an impenetrable matrix element (With et al. 1997; Metzger and Décamps 1997; Tiebout and Anderson 1997), which is unrealistic for most species. In these cases, if animals truly are restricted to habitat then structural measures of connectivity will accurately estimate landscape connectivity but as the likelihood of movement into and through the matrix increases structural measures connectivity will increasingly underestimate landscape connectivity. Functional measures of connectivity, while more likely to be ecologically meaningful, are more difficult to attain than structural measures of connectivity, especially if care is taken to study movements at the appropriate spatial scale for the organism. Juvenile dispersal and migratory movements can cover very large distances making the movements difficult to study in any detail, though studying the movements of smaller organisms in an experimental model system (Wiens et al. 1993) can circumvent some of the logistical problems. Given the relative ease of assessing landscape structure, it is fruitful to ask if there is a predictable link between landscape structure and functional connectivity. This is still an open question.

Studies using a connectivity metric to explain another ecological process without understanding how that metric is influenced by the state of the landscape or the details of organism movement will lack generality. While a study might find a strong effect of connectivity for a particular organism in a particular landscape, those findings may not hold in other situations, possibly even the same organism in landscapes with different structure. It is necessary, therefore, to quantify the effects of landscape structure and movement behaviour on a connectivity metric (treat that metric as a dependent variable) before using that metric to explain other ecological processes. Any measure of connectivity used as an independent variable must be thoroughly investigated as a dependent variable first. With little overlap between the connectivity measures used as dependent and independent variables, such comparisons are presently impossible. Furthermore, modeling has illustrated the possibility of complex relationships between different connectivity metrics ranging from metrics being uncorrelated to complex non-linear relationships that change as the state of the landscape changes (Tischendorf and Fahrig 2000a; Goodwin and Fahrig 2002b). This implies that different connectivity metrics may not be directly comparable, making comparisons of studies using different metrics difficult or impossible. Since there are many connectivity metrics in the literature and most studies use a single metric, there will be many issues of comparing studies and generating generality for some time to come. These difficulties hinder any general understanding of landscape connectivity.

Studies of landscape connectivity are divided between those that seek to understand how landscape structure and movement behaviour interact to dictate connectivity and those that seek to evaluate the impact of connectivity on other ecological processes. At present, the two different approaches are isolated due to the use of different connectivity metrics. Studies are biased toward using connectivity as an independent variable. To fully understand landscape connectivity and evaluate its importance for other ecological processes both independent and dependent approaches are required, it is not enough to do one without the other. To this end, we need to bolster research, particularly empirical research, using connectivity as a dependent variable. This will require more research on how landscape structure influences landscape connectivity, how movement behaviour can impact connectivity and how functional measures of connectivity can be related to landscape structure. In particular, models should incorporate more realistic movement behaviour to determine which aspects of behaviour have a large effect on landscape connectivity. This, in turn, will require empirical research into the movement responses of organisms to landscape structure (e.g., landscape elements and edge types). Finally, we need more research interrelating various connectivity metrics. There are many measures of connectivity yet few studies to date have compared multiple measures of connectivity. What little work has been done comparing multiple connectivity metrics suggests that metrics may only be weakly correlated and difficult to relate one to the other.

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