A comparison-shopper's guide to connectivity metrics

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Connectivity is an important but inconsistently defined concept in spatial ecology and conservation biology. Theoreticians from various subdisciplines of ecology argue over its definition and measurement, but no consensus has yet emerged. Despite this disagreement, measuring connectivity is an integral part of many resource management plans. A more practical approach to understanding the many connectivity metrics is needed. Instead of focusing on theoretical issues surrounding the concept of connectivity, we describe a data-dependent framework for classifying these metrics. This framework illustrates the data requirements, spatial scales, and information yields of a range of different connectivity measures. By highlighting the costs and benefits associated with using alternative metrics, this framework allows practitioners to make more informed decisions concerning connectivity measurement.

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Dispersal, the movement of individuals among populations, is a critical ecological process (Ims and Yoccoz 1997). It can maintain genetic diversity, rescue declining populations, and re-establish extirpated populations. Sufficient movement of individuals between isolated, extinction-prone populations can allow an entire network of populations to persist via metapopulation dynamics (Hanski 1991). As areas of natural habitat are reduced in size and continuity by human activities, the degree to which the remaining fragments are functionally linked by dispersal becomes increasingly important. The strength of those linkages is determined largely by a property known as "connectivity", which, despite its intuitive appeal, is inconsistently defined. At one extreme, metapopulation ecologists argue for a habitat patch-level definition, while at the other, landscape ecologists insist that connectivity is a landscape-scale property (Merriam 1984; Taylor *et al.* 1993; Tischendorf and Fahrig 2000; Moilanen and Hanski 2001; Tischendorf 2001a; Moilanen and Nieminen 2002). Differences in perspective notwithstanding, theoreticians do agree that connectivity has undeniable effects on many population processes (Wiens 1997; Moilanen and Hanski 2001).

In a nutshell:

- Measures of connectivity differ in their data requirements and informational yield
- The commonly used connectivity metrics can be classified according to their different strengths and weaknesses
- This framework can be used to decide which connectivity metrics to calculate, given particular datasets or, conversely, which type of data to collect, given a particular metric

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It is therefore desirable to quantify connectivity and use these measurements as a basis for decision making. Currently, many reserve design algorithms factor in some measure of connectivity when weighing alternative plans (Siitonen *et al.* 2002, 2003; Singleton *et al.* 2002; Cabeza 2003). Consideration of connectivity during the reserve design process could highlight situations where it really matters. For example, alternative reserve designs that are similar in other factors such as area, habitat quality, and cost may differ greatly in connectivity (Siitonen *et al.* 2002). This matters because the low-connectivity scenarios may not be able to support viable populations of certain species over long periods of time. Analyses of this sort could also redirect some project resources towards improving the connectivity of a reserve network by building movement corridors or acquiring small, otherwise undesirable habitat patches that act as links between larger patches (Keitt *et al.* 1997). Reserve designs could therefore include the demographic and genetic benefits of increased connectivity without substantially increasing the cost of the project (eg Siitonen *et al.* 2002).

If connectivity is to serve as a guide, at least in part, for conservation decision-making, it clearly matters how it is measured. Unfortunately, the ecological literature is awash with different connectivity metrics. How are land managers and decision makers to efficiently choose between these alternatives, when ecologists cannot even agree on a basic definition of connectivity, let alone how it is best measured? Aside from the theoretical perspectives to which they are tied, these metrics differ in two important regards: the type of data they require and the level of detail they provide. Here, we attempt to cut through some of the confusion surrounding connectivity by developing a classification scheme based on these key differences between metrics.

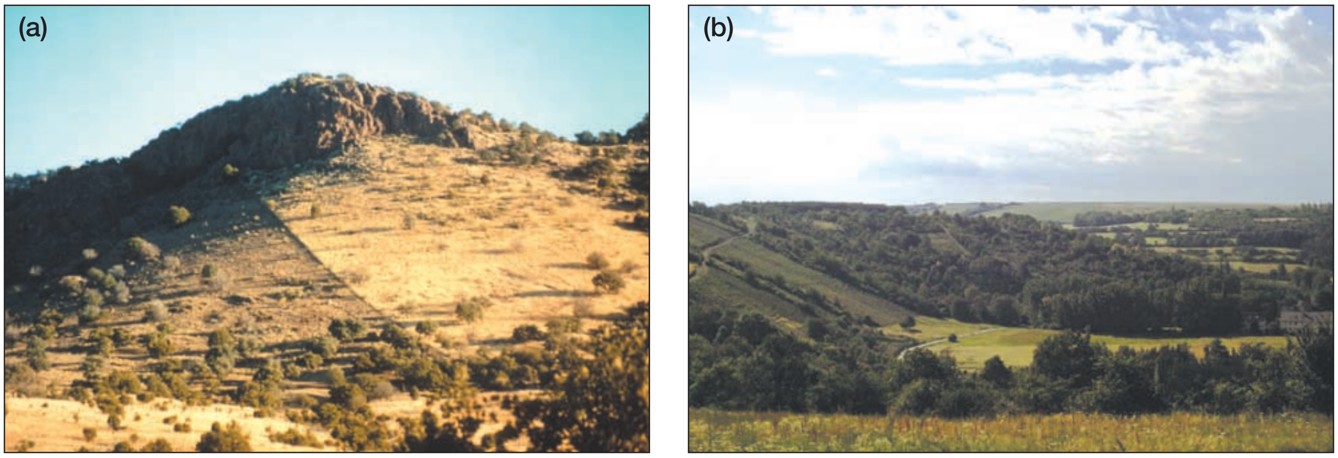

Figure 1. (a) A pronounced edge in semi-arid grassland habitat of the Chiricahua Mountains, Arizona, induced by different grazing practices. Habitat edges like this represent semi-permeable barriers, disrupting the dispersal behaviors of some species but not others. Interspecific differences in edge responses are one reason why ecologists need to be alert to the species-specific nature of connectivity metrics. (b) A more complex landscape near Würzburg, Germany. Different species may have different perceptions about which landscape elements are usable. For example, some may be restricted to the forest fragments while others will move freely through forest as well as vineyards.

Connectivity comes in multiple flavors

Connectivity depends on the interaction between particular species and the landscapes in which they occur (Schumaker 1996; Wiens 1997; Tischendorf and Fahrig 2000; Moilanen and Hanski 2001). Put another way, a single landscape or habitat patch will possess different degrees of connectivity, depending on the behaviors, habitat preferences, and dispersal abilities of the species being considered (Johnson and Gaines 1985; Figure 1). Strategies exist for developing multi-species connectivity metrics (Fagan and Calabrese in press), but here we stick to the standard, single species view. We distinguish three classes of connectivity metrics, based on interactions between focal species and the landscape. Listed in increasing order of detail, they are: structural, potential, and actual connectivity (Figure 2). Structural connectivity is derived from physical attributes of the landscape, such as size, shape, and location of habitat patches, but does not factor in dispersal ability (Figure 2a). Potential connectivity combines these physical attributes of the landscape with limited information about dispersal ability to predict how connected a given landscape or patch will be for a species (Figure 2b). Examples of limited dispersal information include estimates of mobility derived from body size or energy budgets (Cresswell *et al.* 2000; Porter *et al.* 2000), or measurements with little spatial detail, such as mean or maximum recapture distances from mark–recapture studies (Clark *et al.* 2001). Actual connectivity relates to the observation of individuals moving into or out of focal patches, or through a landscape, and thus provides a concrete estimate of the linkages between landscape elements or habitat patches (Figure 2c).

To facilitate classification of connectivity metrics according to their data-dependence, the various types of data used to estimate connectivity are simplified into six frequently encountered categories (see below). Within each data category, the spatial scales at which the metrics are usually calculated are simplified to four levels: point occurrences, individual habitat patches, landscape classes, and entire landscapes (Figure 3). Our approach here is to sketch the relationships between the three types of connectivity described above and the basic data requirements of the various connectivity metrics (Table 1). We also discuss the common modifications to many connectivity metrics and the scale-dependence of connectivity.

The data-dependent framework

Nearest neighbor distance: patch occupancy data and interpatch distance

Field surveys of a species' occupancy pattern in a habitat patch and measurements of the distance to the nearest occupied patch provide a simple, patch-level structural connectivity metric. Interpatch distance is, technically, a patch isolation measure, and connectivity is its inverse. Though simple to obtain, distance to the nearest occupied neighbor is a crude connectivity metric. Moilanen and Nieminen (2002) demonstrated the poor performance of this metric through a meta-analysis of published studies that quantified connectivity, and by using various connectivity metrics to predict colonization events in two detailed empirical butterfly metapopulation datasets. Overall, they found that nearest neighbor measures were less likely to detect a significant effect of connectivity and were more sensitive to sample size than were other, more complex connectivity metrics. Bender *et al.* (2003) obtained similar results using a computer-simulated dispersal process on both real – derived from a geographic information system (GIS) – and artificially generated landscapes. They found that nearest neighbor distance was consistently the worst or second worst performer of the four proximity indices they studied, and that it performed especially poorly when patch size and shape were varied (Bender *et al.* 2003).

The weak performance of nearest neighbor distance can be attributed to several factors. First, this metric counts only the contribution of the patch nearest to the focal patch, thus ignoring how all other patches affect the connectivity of the focal patch (Bender *et al.* 2003). Furthermore, in its most basic form, the nearest neighbor measure includes no information about the population size of the focal species in the nearest patch. Finally, no knowledge of the species' dispersal ability is incorporated into the metric. Despite these limitations, the nearest neighbor distance is one of the most commonly used connectivity metrics (Moilanen and Nieminen 2002; Bender *et al.* 2003). This is most likely due to its simplicity and modest data requirements. Unfortunately, these advantages do not adequately compensate for its limitations.

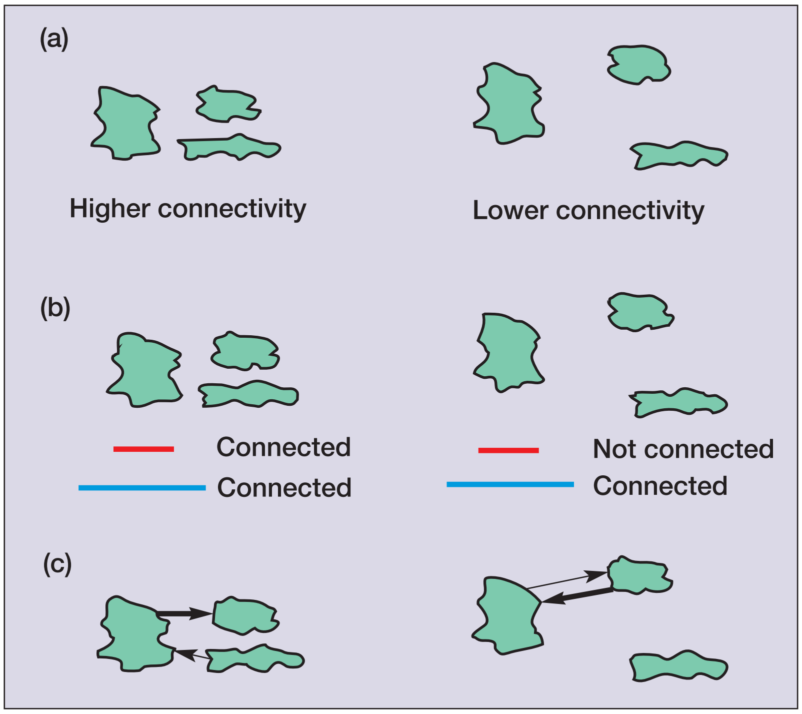

Figure 2. *Schematic representation of the three types of connectivity. (a) Structural connectivity depends mainly on physical attributes of landscape elements, such as spatial proximity. Therefore the elements in the left column have higher structural connectivity than those in the right column. (b) Potential connectivity depends on physical attributes, but also on the dispersal ability of focal species. The red and blue bars represent measures of dispersal ability for two hypothetical species. If the distance between patches is greater than this measure of dispersal ability, the patches are not connected. Thus, the landscape on the left is connected for both species while the landscape on the right is connected for the blue species but not for the red species. (c) Actual connectivity is based on observed movement pathways. While factors considered in the other two classes of connectivity metrics certainly influence actual connectivity, movement must be observed or quantified. The left and right columns represent different observed pathways that would not necessarily be predicted by the structural or potential connectivity approaches. Thicker arrows indicate higher movement rates, and thus, higher actual connectivity.*

Spatial pattern indices: spatially explicit habitat data

Spatially explicit habitat data are often remotely sensed, cover a large area, and are represented in either raster or vector form in a GIS. Spatial pattern indices quantify the number, size, extent, shape, or aspects of the spatial arrangement of landscape elements. The use of these indices as connectivity metrics relies on the assumption that the spatial patterns these indices quantify actually affect species' ability to move through the landscape. Examples of spatial pattern metrics include number of patches, patch area, core area, patch perimeter, contagion, perimeter–area ratio, shape index, fractal dimension, and patch cohesion (Haines-Young and Chopping 1996; Schumaker 1996). The increasing availability of this type of data and software packages such as Fragstats (McGarigal *et al.* 2002) make the metrics in this category relatively easy to calculate. Although spatial pattern indices are sometimes assumed to represent actual connectivity, we consider them estimators of structural connectivity because they do not incorporate dispersal data. The lack of dispersal data does not, however, preclude the possibility that these indices could show predictable relationships with actual connectivity. There has been little empirical research regarding this possibility, but several simulation modeling studies have explored the relationships between spatial pattern indices and dispersal success. For example, Schumaker (1996) demonstrated that shape index and patch cohesion were the best predictors of dispersal success, while fractal dimension, number of patches, patch area, core area, patch perimeter, contagion, and perimeter–area ratio were, at best, weakly correlated with dispersal success. Similarly, Tischendorf (2001b) found that, while some spatial pattern indices were strongly correlated with simulated dispersal success, 68% of the statistical relationships between the 26 metrics and three measures of dispersal success considered were inconsistent when landscape structure and dispersal behavior were varied. The simulation results therefore suggest that relationships between spatial pattern indices and dispersal success might not generalize well across landscapes or species.

A potential advantage of spatial pattern indices is that they could be used to quickly characterize connectivity for large areas. However, the weak or inconsistent relationships between spatial pattern indices and dispersal success suggest that further research is required before these indices can be relied upon to estimate actual connectivity. The lack of empirical work in this area only

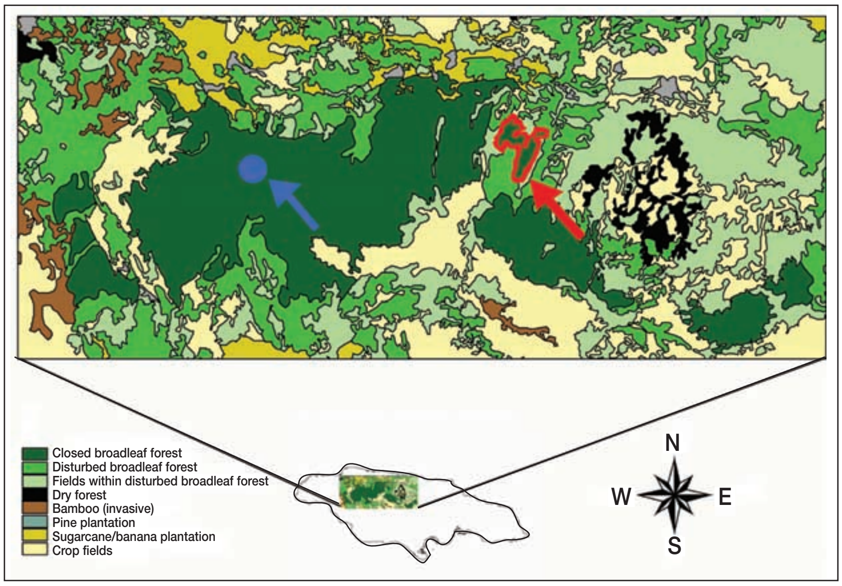

Figure 3. *A simplification of the spatial scales discussed in this paper, based on a recent landcover classification for Jamaica (Evelyn and Camirand 2003). The entire inset represents a 19 054.74-ha landscape scale. Eight landcover classes are represented within the landscape, as described by the legend. For example, closed broadleaf forest, in dark green, represents a single landcover class. An individual patch within the broadleaf forest class is outlined in red and highlighted with a red arrow. The blue dot highlighted by the blue arrow represents a hypothetical point occurrence of a focal species. Land classification provided by the Forestry Department of Jamaica.*

underscores this point. As several authors have noted (Schumaker 1996; Tischendorf 2001b; Fortin *et al.* 2003), focusing on the relationships between the spatial pattern that these metrics quantify and the underlying ecological processes that influence connectivity, such as demographics, dispersal, and behavior, may be the most effective way to develop these metrics further.

Scale–area slope: point- or grid-based occurrence data

Another approach to quantifying structural connectivity can be used when records of species' spatial occurrences are available, but the locations of actual habitat patches are unknown. Datasets fitting into this category include those assembled from museum records or long-term surveys of species presence or absence, where patch boundaries are not known or may have changed since the data were collected. This approach builds from individual occurrences of a species to a landscape-level connectivity metric known as the "scale–area slope". Both point data, where considerable spatial detail is available, and grid data, where spatial descriptions are less precise, can be used to estimate structural connectivity based on the slope of a scale–area curve (Kunin 1998; Fagan *et al.* 2002). Scale–area slopes are derived by dividing a landscape into a series of equal-sized grid cells at several map resolutions, with a fixed number of fine-resolution cells inside each coarser-resolution cell. Presence or absence of the focal species in each cell at each resolution is determined and the map area occupied by the species (assuming a cell with at least one incidence record is occupied) is plotted against grid cell size at each map resolution. Scale–area slope is then estimated via power–law regression. Steep scale–area slopes characterize species that have fragmented distributions, whereas shallow slopes identify species with less fragmented (ie more contiguous) spatial occurrences. A shallow (ie numerically small) scale–area

Table 1. A summary of the data-dependent classification framework for connectivity metrics

Connectivity metrics	*Type of connectivity/ level of detail*	*Habitat-level data*	*Species-level data*	*Methodology*
Nearest neighbor distance	Structural	Nearest neighbor distance	Patch occupancy	Patch-specific field surveys
Spatial pattern indices	Structural	Spatially explicit	None	GIS/remote sensing
Scale–area slope	Structural	None	Point- or grid-based occurrences	Occurrence databases, presence/absence sampling
Graph-theoretic	Potential	Spatially explicit	Dispersal ability	GIS/remote sensing + dispersal studies
Buffer radius, IFM	Potential	Spatially explicit, including patch area	Patch occupancy and dispersal ability	Multi-year, patch-specific field surveys or single-year, patch occupancy study with dispersal study
Observed emigration, immigration, or dispersal rates	Actual	Variable, depends on methodology	Movement pathways or location-specific dispersal ability	Track movement pathways (specific methods depend on study organism), mark–release–recapture studies

slope would therefore be associated with higher structural connectivity.

The use of the scale–area slope as a connectivity metric assumes that proximity is the major determinant of the connectivity among occurrences. Such an assumption is clearly justified in certain circumstances. For example, Fagan *et al.* (2002) demonstrated that for Sonoran Desert fishes, species that were historically distributed more compactly (ie species with shallow scale–area slopes) were at a distinct advantage when it came to weathering the ensuing decades of anthropogenic alterations to their habitats and landscape. In contrast, species with steep scale–area slopes, whose distributions were more fragmented historically, were at greater risk of local extinction. Despite this promising result, the relationships between scale–area slope and various measures of actual connectivity have not yet been established. Although scale–area approaches do not provide a direct linkage between connectivity and dispersal, the techniques can help to identify the spatial scales over which processes affecting connectivity are most important.

Graph-theoretic measures: spatially explicit habitat data with dispersal data

Graph-theoretic measures combine spatially explicit habitat data derived from a GIS with data acquired from independent studies on the dispersal biology of species. Inclusion of species-specific dispersal data represents a substantial increase in data requirements, but allows these metrics to go beyond structural connectivity and address potential connectivity. In their most basic form, graph-theoretic approaches entail making a mathematical "graph" of a network of habitat patches for a species that incorporates information on the spatial arrangement of patches as well as patch attributes (Cantwell and Forman 1993; Keitt *et al.* 1997; Bunn *et al.* 2000; Urban and Keitt 2001). The graph is simply a means of summarizing the spatial relationships between landscape elements in a concise way. Next, potential connections between all pairwise combinations of habitat patches are established by considering the dispersal ability of the focal species. If the distance between a given pair of patches is less than or equal to the measure of dispersal ability used, the patches are considered connected. Measures of dispersal ability typically include a fixed critical dispersal distance (Keitt *et al.* 1997; D'Eon *et al.* 2002) or a random draw from a dispersal kernel. A fixed critical distance represents the distance after which a species' probability of dispersal is assumed to decline rapidly (van Langvelde 2000), while a dispersal kernel is a function describing the relationship between dispersal distance and a species' probability of dispersal (eg Kot *et al.* 1996; Havel *et al.* 2002). These potential connections are depicted on the graph as lines ("edges" in the terminology of graph theory) drawn between each pair of connected patches.

After establishing pairwise connections, graph-theoretic approaches scale up to consider the connectivity of the entire patch network (landscape level), using metrics including correlation length, distance to cluster edge, number of graph components, and diameter of the largest graph component (Keitt *et al.* 1997; Urban and Keitt 2001; D'Eon *et al.* 2002). These metrics are different ways of quantifying how connected the graph is overall. For example, a graph that had one large cluster of interconnected patches would be considered to have higher connectivity than a graph that had several small, isolated clusters of interconnected patches. An advantage of these methods is that graph operations that simulate the destruction of habitat patches or dispersal corridors can be used to rank habitat patches by their contributions to landscape-level connectivity (Keitt *et al.* 1997). The graph-theoretic approach could therefore allow land managers to make decisions based on which patches are most critical to landscape connectivity.

Buffer radius and incidence function metrics: spatially explicit patch occupancy, patch area, and dispersal data

Spatially explicit patch occupancy data are usually obtained by directly sampling habitat patches for a species of interest and spatially referencing patch locations. With such data, one can calculate buffer radius or incidence function measures (see below) of patch-level, potential connectivity, depending on assumptions about the dispersal biology of the species in question. These metrics incorporate patch occupancy information, usually for a large number of patches. Such data allow the potential contribution of each patch to be assessed by its occupancy status as well as by proxies for population size, such as area, if it is occupied. The result of this extra information is that these indices can give a more detailed estimate of patch-level potential connectivity than other metrics.

For buffer radius measures, patch-occupancy data for all patches that lie within a fixed distance, or "buffer radius", of the focal patch are required. The connectivity of a patch is a function of the number and areas of all occupied patches that lie within the buffer radius. Though buffer radii are often arbitrarily selected, Moilanen and Nieminen (2002) have shown that the performance of these measures is sensitive to the buffer radius chosen, suggesting that incorporation of even the most basic dispersal information could substantially improve the performance of these metrics.

A similar set of connectivity metrics derive from the incidence function metapopulation model (IFM) (Hanski 1994; Hanski *et al.* 1996). These measures require spatially explicit patch-occupancy data for a large number of patches in a metapopulation, and also a dispersal kernel describing how the focal species' probability of dispersal decays with distance. The dispersal kernel can be parameterized either with independent data on the dispersal ability of the focal species, or by model fit to patch-occupancy data. If such data are used to estimate dispersal ability, it is desirable to have more than one year of data to obtain robust parameter estimates (Hanski 2001). The basic IFM connectivity measure essentially sums the potential contribution of all occupied patches in a metapopulation, weighted by area and distance, to the connectivity of a focal patch.

Buffer and IFM metrics can still be calculated in the absence of patch-occupancy data, but give a less detailed estimate of potential connectivity. This method, called the "connectivity of landscape elements" (Moilanen and Hanski 2001), is similar to the graph-theoretic approaches described above. When patch-occupancy data are available, buffer radius and IFM measures provide detailed descriptions of patch-level potential connectivity, but do not necessarily scale up to landscape levels. However, if sufficient data are available to parameterize a stochastic patch-occupancy metapopulation model (eg the IFM), one could then calculate the "metapopulation capacity" of the study system (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001). Although connectivity is not directly quantified by metapopulation capacity, it may be a more useful quantity than landscape-level connectivity per se because it quantifies a landscape's potential to maintain a viable metapopulation over time.

Observed emigration, immigration, or dispersal rates: individual movement data

Data on the individual movements of organisms provide the most direct estimate of actual connectivity. Many methods exist for obtaining such data (Ims and Yoccoz 1997), but often these types of studies are too labor intensive to be conducted at even moderately large, let alone landscape, scales. Depending on the taxa in question, detailed tracking of the movement pathways of individual animals via radiotelemetry or other methods (Gillis and Krebs 1999, 2000; Turchin 1998), mark–release–recapture studies (Southwood 1978; Sutherland 1996), or mass mark–recapture methods (where individuals do not have a unique marking) may be used. In addition, measurements of patch-level immigration or colonization rates for unmarked animals can, by themselves, serve as a connectivity metric (van Langevelde 2000). This approach is difficult in practice, however, because immigration or colonization rates must be sufficiently high that useful data can be collected over a reasonable period of time. Despite the difficulty, many techniques for the direct measurement of movement can be applied to a variety of taxa, and these methods provide direct information about short-term dispersal. Alternatively, to quantify the extent of past dispersal over long time scales, metrics based on genetic data (eg Andreassen and Ims 2001) could be used.

Although landscape-level estimates of actual connectivity are possible for wide-ranging species that can be radio tracked – eg Florida panthers (Meegan and Maehr 2002) – the data-intensive nature of direct measurement methods will generally limit the spatial scales to which they can be applied. Still, in situations where movement data are already available or only a few habitat patches are of interest, quantifying emigration, immigration, or dispersal rates provides a detailed estimate of how well particular patches are connected in a fragmented landscape.

■ Modifications

For many of the metrics discussed here, additional data, not included in the basic definition of the metric, can be incorporated to improve performance. The most common modification is weighting patch contributions to connectivity by area or some other proxy for population size. Such "area-informed" metrics generally perform better than those that lack area considerations (Moilanen and Nieminen 2002; Bender *et al.* 2003; Tischendorf *et al.* 2003). Additionally, parameters that scale patch emigration or immigration according to patch area or population size can be used to capture some aspects of the dispersal behavior of species (Moilanen and Nieminen 2002). For example, for a given habitat area or population size, individuals of different species may not be equally willing to leave or enter habitat patches (Haddad 1999). Another commonly modified component of many connectivity metrics is the definition of interpatch distance. While it is the simple Euclidean distance most often used, other distance measures, such as least-cost movement pathways, can be used when appropriate (Bunn *et al.* 2000). Alternate movement pathways may be especially important to assess connectivity when landscape features such as rivers or mountains force organisms to disperse along pathways not well described by Euclidean distances (Dunham and Rieman 1999; Fagan 2002). In addition to the quantity of data, the effects of data quality on metric performance should also be considered. Such a discussion is beyond the scope of this paper, but Ruckelshaus *et al.* (1997, 1999) and Moilanen (2002) provide effective starting points.

■ Scale dependence

Two issues of scale dependence arise when considering connectivity. First, on which scale should connectivity be defined? Though several papers have debated this point (Tischendorf and Fahrig 2000; Tischendorf 2001a; Moilanen and Hanski 2001), there is no evidence that connectivity should be limited to a particular spatial scale. This leads to the second issue: connectivity will change with spatial scale. How does one decide which scale is most appropriate for a particular problem? Clearly, the dispersal ability of the species imposes a relevant scale on the landscape (Wiens 1997), but dispersal ability is often unknown or poorly known. In such cases, explicitly calculating connectivity at a series of nested spatial scales and examining how connectivity changes as a function of scale is likely to provide a more robust picture of connectivity for the study area. Many of the approaches to connectivity detailed in this review have, at least to some degree, utilized this method. Tischendorf (2001b) showed that spatial pattern indices were generally better predictors of dispersal success when calculated at the landscape element (class) level than at the landscape level. The scale–area approach of Kunin (1998) and Fagan *et al.* (2002) is defined by a nested spatial scale methodology, scaling up from individual occurrences to the entire landscape. Similarly, graph theory naturally lends itself to such multi-scale analyses and allows the integration of patch-level and class- or landscape-level connectivity (Keitt *et al.* 1997; Urban and Keitt 2001). Though not purely a connectivity measure, metapopulation capacity accomplishes a similar scaling-up from patch to class or landscape levels by focusing on how landscape structure, which affects patch-level connectivity, influences population persistence for particular species (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001). Such multiscale methodologies could be used to look for connectivity thresholds (Keitt *et al.* 1997) or to assess the sensitivity of connectivity estimates to assumptions about the dispersal ability of the focal species.

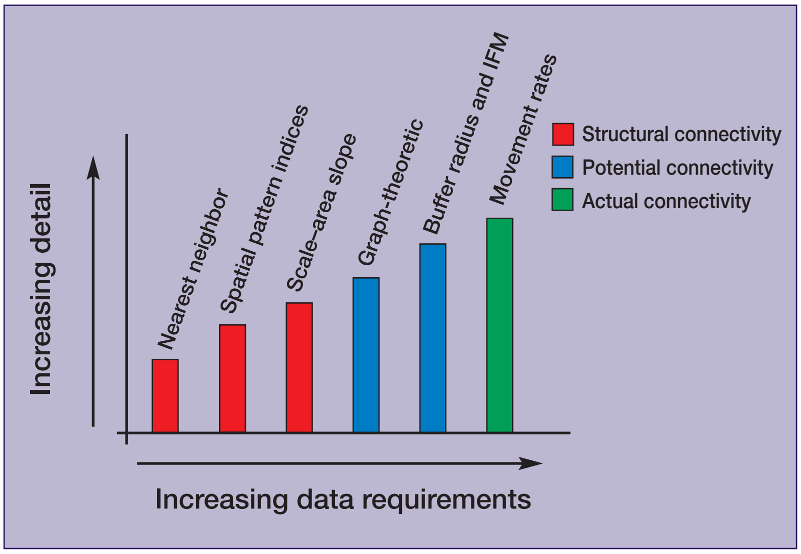

Figure 4. *Schematic representation of the tradeoff between information content and data requirements among connectivity metrics. Both information content and data requirements increase going from nearest neighbor measures to actual movement rates. The embellishments to the metrics mentioned in the "modifications" section may alter the position of various metrics in the hierarchy, but in general, the tradeoff between information content and data requirements holds.*

The tradeoff between data requirements and realism

Across the different connectivity metrics, a tradeoff exists between information content and data requirements (Figure 4). For example, the nearest neighbor measures and spatial pattern indices do not require extensive data to calculate, but provide only a crude estimate of structural connectivity. In contrast, buffer radius and IFM approaches provide very detailed estimates of potential connectivity at the individual patch level, but are extremely data-intensive. Likewise, the direct observation methods provide the only estimates of actual connectivity, but are, again, applicable mainly to small scales and are extremely data-intensive. Given the tradeoff between information content and data requirements, the graph-theoretic approaches may possess the greatest benefit to effort ratio for conservation problems that require characterization of connectivity at relatively large scales. These measures provide a reasonably detailed picture of potential connectivity, but have relatively modest data requirements. When habitat patches cannot be reliably delimited, the scale–area approach might be the only option. However, the relationship between scale–area slopes and actual connectivity needs to be better developed.

Unfortunately, no all-purpose method exists for choosing which of the many connectivity metrics to use in addressing real-world problems. Future research will undoubtedly illustrate which of these metrics perform best and which need to be left by the wayside. However, for many urgent conservation decisions, we do not have the luxury of waiting until a consensus is reached. Our goal in developing this classification system was to give non-theoreticians a starting point from which to choose appropriate connectivity metrics. Hopefully, knowledge of data requirements and informational detail, as well as the strengths and weaknesses of different approaches to connectivity, will allow practitioners to invest limited funds and efforts wisely when connectivity is used to evaluate alternative conservation strategies.

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References

Andreassen HP and Ims RA. 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. *Ecology* **82**: 2911–26.

Bender DJ, Tischendorf L, and Fahrig L. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecol* **1**: 17–39.

Bunn AG, Urban DL, and Keitt TH. 2000. Landscape connectivity: a conservation application of graph theory. *J Environ Manage* **59**: 265–78.

Cabeza M. 2003. Habitat loss and connectivity of reserve networks in probability approaches to reserve design. *Ecol Lett* **6**: 665–72.

Cantwell MD and Forman RTT. 1993. Landscape graphs: ecological modeling with graph theory to detect configurations common to diverse landscapes. *Landscape Ecol* **8**: 239–55.

Clark JS, Lewis M, and Horvath L. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *Am Nat* **157**: 537–54.

Cresswell JE, Osbourne JL, and Goulson D. 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecol Entomol* **25**: 249–55.

D'Eon RG, Glenn SM, Parfitt I, and Fortin M. 2002. Landscape connectivity as a function of scale and organism agility in a real forested landscape. *Conserv Ecol* **6**: Article 10.

Dunham JB and Rieman BE. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecol Appl* **9**: 624–55.

Evelyn OB and Camirand R. 2003. Forest cover and deforestation in Jamaica: an analysis of forest cover estimates over time. *Int Forest Rev* **5**: 354–63.

Fagan WF. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* **83**: 3243–49.

Fagan WF, Unmack PJ, Burgess C, and Minckley WC. 2002. Rarity, fragmentation, and extinction risk in desert fishes. *Ecology* **83**: 3250–56.

Fagan WF and Calabrese JM. Quantifying connectivity: balancing metric performance with data requirements. In: Crooks K and Sanjayan MA (Eds). Connectivity conservation. Cambridge, UK: Cambridge University Press. In press.

Fortin MJ, Boots B, Csillag F, and Remmel TK. 2003. On the role of spatial stochastic models in understanding landscape indices in ecology. *Oikos* **1**: 203–12.

Gillis EA and Krebs CJ. 1999. Natal dispersal of snowshoe hares during a cyclic population increase. *J Mammal* **80**: 933–39.

Gillis EA and Krebs CJ. 2000. Survival of dispersing versus philopatric juvenile snowshoe hares: do dispersers die? *Oikos* **90**: 343–46.

Haddad NM. 1999. Corridor use predicted from behaviors at habitat boundaries. *Am Nat* **152**: 215–27.

Haines-Young R and Chopping M. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Prog Phys Geog* **4**: 418–45

Hanski I. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biol J Linn Soc* **42**: 3–16.

Hanski I. 1994. A practical model of metapopulation dynamics. *J Anim Ecol* **63**: 151–62.

Hanski I. 2001. Spatially realistic theory of metapopulation ecology. *Naturwissenschaften* **88**: 372–81.

Hanski I, Moilanen A, Pakkala T, and Kuussaari M. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conserv Biol* **10**: 578–90.

Hanski I and Ovaskainen O. 2000. The metapopulation capacity of a fragmented landscape. *Nature* **404**: 755–58.

Havel JE, Shurin JB, and Jones JR. 2002. Estimating dispersal from patterns of spread: spatial and local control of lake invasions. *Ecology* **83**: 3306–18.

Ims RA and Yoccoz NG. 1997. Studying transfer processes in metapopulation: emigration, migration, and colonization. In: Hanski IA and Gilpin ME (Eds). Metapopulation biology: ecology, genetics, and evolution. San Diego, CA: Academic Press.

Johnson ML and Gaines MS. 1985. Selective basis for emigration of the prairie vole, *Microtus ochrogaster:* open field experiment. *J Anim Ecol* **54**: 399–410.

Keitt TH, Urban DL, and Milne BT. 1997. Detecting critical scales in fragmented landscapes. *Conserv Ecol* **11**: Article 4.

Kot M, Lewis MA, and van den Dreissche P. 1996. Dispersal data and the spread of invading organisms. *Ecology* **77**: 2027–42.

Kunin WE. 1998. Extrapolating species abundance across spatial scales. *Science* **281**: 1513–15.

McGarigal K, Cushman SA, Neel MC, and Ene E. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html. Viewed: 12 October 2004

Meegan RP and Maehr DS. 2002. Landscape conservation and regional planning for the Florida panther. *Southeast Nat* **1**: 217–32.

Merriam G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. In: Brandt J and Agger P (Eds). Proceedings of the first international seminar on methodology in landscape ecological research and planning. Roskilde, Denmark: Roskilde University.

Moilanen A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos* **96**: 516–30.

Moilanen A and Hanski I. 2001. On the use of connectivity measures in spatial ecology. *Oikos* **95**: 147–51.

Moilanen A and Nieminen M. 2002. Simple connectivity measures in spatial ecology. *Ecology* **83**: 1131–45.

Ovaskainen O and Hanski I. 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theor Popul Biol* **60**: 281–302.

Porter WP, Budaraju S, Stewart WE, and Ramankutty N. 2000. Physiology on a landscape scale: applications in ecological theory and conservation practice. *Am Zool* **40**: 1175–76.

Ruckelshaus M, Hartway C, and Kareiva P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conserv Biol* **11**: 1298–306.

Ruckelshaus M, Hartway C, and Kareiva P. 1999. Dispersal and landscape errors in spatially explicit population models: a reply. *Conserv Biol* **13**: 1223–24.

Schumaker NH. 1996. Using landscape indices to predict habitat connectivity. *Ecology* **77**: 1210–25.

Siitonen P, Tanskanen A, and Lehtinen A. 2002. Method for selection of old-forest reserves. *Conserv Biol* **16**: 1398–08.

Siitonen P, Tanskanen A, and Lehtinen A. 2003. Selecting forest reserves with a multiobjective spatial algorithm. *Environ Sci Policy* **6**: 301–09.

Singleton PH, Gaines WL, and Lehmkuhl JF. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. United States Department of Agriculture Forest Service Pacific Northwest Research Station Research Paper **549**: 1–89.

Southwood TRE. 1978. Ecological methods, 2nd edn. London: Chapman and Hall.

Sutherland WJ 1996. Predicting the consequences of habitat loss for migratory populations. *P Roy Soc Lon Ser B Bio* **263**: 1325–27.

Taylor PD, Fahrig L, Henein K, and Merriam G. 1993. Connectivity is a vital element of landscape structure. *Oikos* **68**: 571–73.

Tischendorf L. 2001a. On the use of connectivity measures in spatial ecology: a reply. *Oikos* **95**: 152–55.

Tishcendorf L. 2001b. Can landscape indices predict ecological processes consistently? *Landscape Ecol* **16**: 235–54.

Tischendorf L and Fahrig L. 2000. On the usage and measurement of landscape connectivity. *Oikos* **90**: 7–19.

Tischendorf L, Bender DJ and Fahrig L. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecol* **18**: 41–50.

Turchin P. 1998, Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sunderland, MA: Sinauer Associates, Inc.

Urban D and Keitt T. 2001. Landscape connectivity: a graph–theoretic perspective. *Ecology* **82**: 1205–18.

Van Langevelde F. 2000. Scale of habitat connectivity and colonization in fragmented nuthatch populations. *Ecography* **23**: 614–22.

Wiens JA. 1997. The emerging role of patchiness in conservation biology. In: Pickett STA, Ostfeld RS, Shachak M, and Likens GE (Eds). The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. New York: Chapman and Hall.