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RESEARCH ARTICLE

Two measures of landscape-graph connectivity: assessment across gradients in area and configuration

Joseph R. Ferrari · Todd R. Lookingbill · Maile C. Neel

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Abstract Landscape connectivity is critical to species persistence in the face of habitat loss and fragmentation. Graph theory is a well-defined method for quantifying connectivity that has tremendous potential for ecology, but its application has been limited to a small number of conservation scenarios, each with a fixed proportion of habitat. Because it is important to distinguish changes in habitat configuration from changes in habitat area in assessing the potential impacts of fragmentation, we investigated two metrics that measure these different influences on connectivity. The first metric, graph diameter, has been advocated as a useful measure of habitat configuration. We propose a second area-based metric that combines information on the amount of connected habitat and the amount of habitat in the largest patch. We calculated each metric across gradients in habitat area and configuration using multifractal neutral landscapes. The results identify critical connectivity thresholds as a function of the level of fragmentation and a parallel is drawn between the behavior of graph theory metrics and those of percolation theory. The combination of the two metrics provides a means for targeting sites most at risk of suffering low potential connectivity as a result of habitat fragmentation.

J. R. Ferrari (✉) · T. R. Lookingbill
Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg, MD 21532, USA
e-mail: jferrari@al.umces.edu

M. C. Neel
Department of Plant Science and Landscape Architecture and Department of Entomology, University of Maryland, College Park, MD 20742, USA

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Introduction

Habitat destruction often results in physical fragmentation of the remaining habitat, simultaneously decreasing patch size and increasing distances among patches. The combined effects of habitat loss and fragmentation are considered to be the greatest threats to biological diversity worldwide (e.g. Pimm and Askins 1995; Rapport et al. 1985; Saunders et al. 1991; Wilcove et al. 1998). Whereas small, isolated populations may become locally extirpated, sufficient movement of individuals among populations can allow an entire network to persist (e.g.Lande 1987; Levins 1969, 1970). Because habitat fragmentation can have profound impacts on a species' ability to move among habitat patches, it affects probabilities of persistence on a landscape (e.g. Fahrig & Merriam 1985; Fahrig & Paloheimo 1988; Levins 1969, 1970). Understanding connectivity across fragmented landscapes is required to guide management decisions that will not compound the negative effects of habitat loss (Fagan et al. 2001; Moffatt 1994).

The importance of landscape connectivity has led to development of multiple approaches for assessing whether a structurally fragmented landscape (i.e. one in which a habitat type of interest exists in discrete, spatially isolated patches) is functionally fragmented for particular organisms. Calabrese and Fagan (2004) grouped connectivity measures used in ecological research into three categories along a continuum of increasing data requirements and complexity. Metrics that measure *structural connectivity* quantify the arrangement of habitat and characterize landscape pattern without requiring reference to particular species traits (e.g. Hargis et al. 1998; McGarigal et al. 2002; Neel et al. 2004). Methods such as graph theory (e.g. Urban and Keitt 2001) and spatially explicit metapopulation models (e.g. Bascompte and Sole 1996) that combine the physical attributes of the landscape with limited species information provide a measure of *potential connectivity*. *Actual connectivity* is determined from observations of organism movement among patches in the landscape (e.g. Gillis and Krebs 1999). It is questionable whether structural connectivity metrics are useful for inferring connectivity in fragmented landscapes (Bender et al. 2003; Moilanen and Nieminen 2002; Winfree et al. 2005). Spatially explicit metapopulation models can be data and calculation intensive, limiting their applicability across broad geographic regions or for a large number of taxa (e.g. Calabrese and Fagan 2004; Urban 2005). Actual connectivity is also not practical to determine for many situations due to the labor intensive nature of data collection. Graph theory has been identified as possessing the greatest ''benefit to effort ratio'' for examining connectivity at the broad spatial scales typical of conservation management (Calabrese and Fagan 2004).

Graph theory has a rich history in the fields of geography, computer science and information technology (e.g. Gross and Yellen 1999; Hayes 2000a,b) where it is used to determine optimal flow patterns or connectivity in networks. For landscape applications, graph-theoretic measures combine spatially explicit habitat data with information on the gap-crossing ability or dispersal biology of a species. Graph theory has been used to quantify landscape connectivity for specific organisms in individual landscapes (e.g. Bunn et al. 2000; Keitt et al. 1997; D'Eon et al. 2002; Urban and Keitt 2001;van Langevelde 2000). Comparability of the results from such case studies requires a thorough understanding of the behavior of the methods across parameter space (Pascual-Hortal and Saura 2006).

The mathematical graph is constructed by comparing the pair-wise distances among patches to a threshold distance, d_t, which represents the maximum distance an organism is expected to travel through non-habitat (Bunn et al. 2000; Keitt et al. 1997;Urban and Keitt 2001). If the distance between two patches is less than d_t, the two patches are considered connected. When two or more patches are connected they form a cluster. Generally, a landscape with one large cluster is considered very well connected while a landscape with multiple smaller clusters is considered less well connected. Metrics used to quantify graph connectivity include those derived from percolation theory, such as the correlation length (e.g. Keitt et al. 1997), as well as well-developed metrics specific to graph analysis, such as the graph diameter (e.g. Bunn et al. 2000; Urban and Keitt 2001).

A well connected landscape may result from extensive contiguous habitat, spatial proximity of discrete patches that allows inter-patch movement, or a combination of both factors. Our primary goal was to investigate the utility of two graph metrics at quantifying these different aspects of connectivity across a broad range of habitat proportion and configuration to isolate their characteristic behavior, similar to the approach used by Neel et al. (2004). Landscape-graph connectivity is often defined as some measure of the size and extensiveness of the largest cluster on a landscape (Bunn et al. 2000; D'Eon et al. 2002; Urban and Keitt 2001;), which can be defined in a number of ways. For example, the radius of gyration is interpreted as the average distance an organism could move within a cluster before encountering the cluster edge (Keitt et al. 1997). The correlation length is an area-weighted mean radius of gyration of all clusters in a landscape and is equal to the radius of gyration when there is one large cluster (Rothley and Rae 2005). Both of these metrics simultaneously incorporate configuration and area-based aspects of fragmentation, although it is desirable to distinguish between the two (Fahrig 2001, 2003). Therefore the graph metrics we analyzed were selected on their ability to assess one or the other of these facets of fragmentation.

The first metric, graph diameter, $d(G)$ (Bunn et al. 2000; Urban and Keitt 2001), measures the ''longest shortest path'' between the two most distant patches in a network (Urban and Keitt 2001) and can be interpreted as the total inter-patch distance an organism would have to traverse to span the largest cluster. If no connections form or if only one patch exists in the landscape, $d(G) = 0.0$. This assignment forces $d(G) = 0.0$ at the extreme conditions when only 1 pixel is considered habitat ($p \cong 0.0$) and when $p = 1.0$. Because graph diameter uses only distances among patches, its magnitude is influenced only by habitat configuration and total area of habitat and it does not include information regarding the size of individual patches in the network.

We propose a second, area-based metric, F, to measure the proportion of habitat in the largest contiguous patch relative to the proportion of habitat found in the largest cluster. This metric quantifies a different aspect of potential connectivity than does graph diameter, which measures extensiveness of the patch network. The area metric is defined as follows:

$$F = \frac{A_{LP}}{A_{LC}} \quad (1)$$

where A_{LP} is the proportion of habitat in the largest patch and A_{LC} is the proportion of habitat in the largest cluster. Both A_{LP} and A_{LC} range from 0.0 to 1.0. We define the largest cluster as that with the largest aggregate area, whereas most previous definitions are based on the cluster with the largest number of patches (e.g. Bunn et al. 2000; Urban and Keitt 2001). In most cases the two definitions yield identical clusters, but on occasion the patch-based definition may identify largest clusters of numerous small patches that have a far smaller aggregate area than the largest patch (Ferrari 2005). By our definition $A_{LC} \geq A_{LP}$. The area-based metric has the following features:

1) If no connections form on a landscape, $A_{LC} = A_{LP}$ and $F = 1.0$.
2) If all habitat is connected into one large cluster, $A_{LC} = 1.0$ and $F = A_{LP}$.
3) For any intermediate level of connectivity, $A_{LP} < F < 1.0$; therefore, the range of possible F values decreases with increasing A_{LP}.

A well connected cluster should have as much contiguous habitat as possible. This condition is met as F approaches 1.0. As a structurally fragmented landscape becomes fully connected by potential inter-patch movements, it would be ideal to have as much contiguous area as possible, which can be gauged by $F = A_{LP}$. The meaning of A_{LP} in this sense is not synonymous with simply assessing A_{LP} using GIS methods, rather $F = A_{LP}$ represents the proportion of the largest cluster that is found in a single large patch. Determination of whether or not such a cluster exists requires assessment of inter-patch connectivity, which is performed using graph analysis.

Used together, the metrics $d(G)$ and F can discriminate between different habitat configurations with the same p and similar correlation length (Fig. 1). In this example, it is assumed all patches are connected into one cluster. Two configurations with similar graph diameter (Figs. 1A and B) require an equivalent matrix traversal to span the cluster. However, these landscapes are not equivalent in terms of their connectivity, as indicated by the larger value of F for Fig. 1A. Many connectivity indices, including $d(G)$, would imply a landscape with a single patch is not well connected, even though all habitat is inherently connected (contiguous). The area metric F increases as the proportion of contiguous habitat (represented by A_{LP}) increases relative to the total cluster area (A_{LC}) and is therefore a measure of the departure of habitat from its most connected state (i.e. contiguous habitat).

Two configurations can also have equivalent F and differ in terms of the aspect of fragmentation associated with patch isolation (Figs. 1C and D). For these situations a smaller graph diameter (Fig. 1D) indicates a more compact (and easily traversable) configuration. To explore a broad range of possible habitat amounts and configurations, we systematically evaluated the behavior of $d(G)$ and F across gradients in area and aggregation using a series of multifractal neutral landscapes.

Our second goal was to determine whether graph diameter behavior across gradients in habitat proportion and configuration can be used to identify critical, percolation-type thresholds. Specification of a gap crossing ability, d_t, in graph analysis is synonymous with assignment of an extended

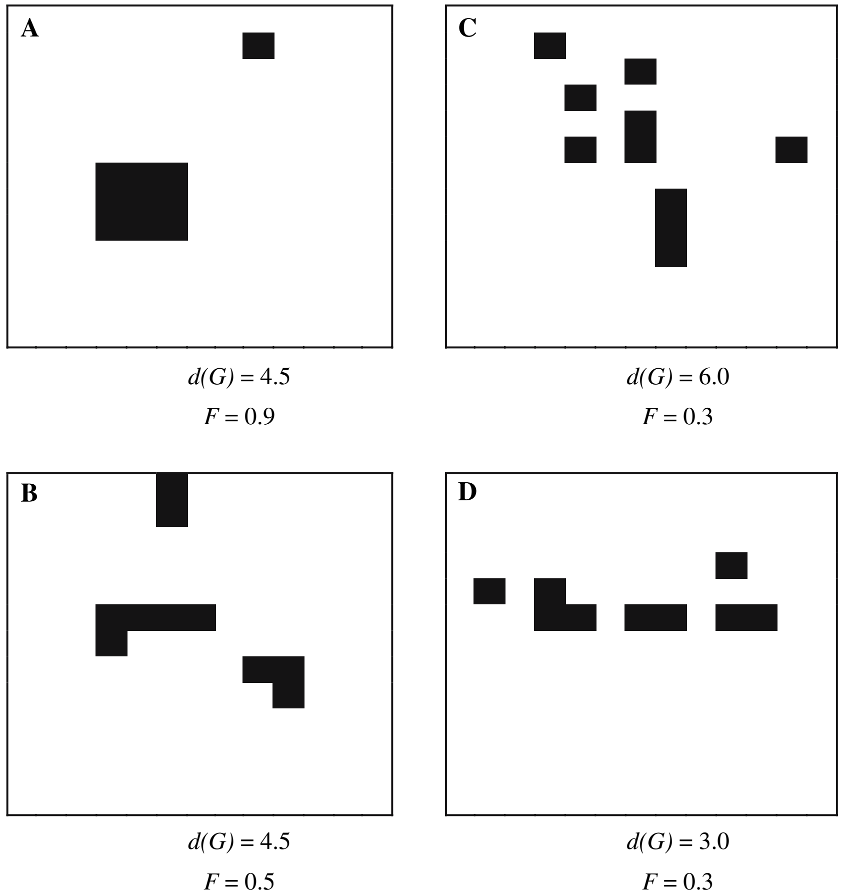

Fig. 1 Graph diameter, $d(G)$ (units of pixels) and area metric F for four configurations, each with equivalent proportion of habitat, p. Gap crossing ability set such that in each panel all patches are connected into a single cluster. All four arrangements have equivalent radius of gyration. Panels (**A**) and (**B**) have equivalent $d(G)$, but F is largest for panel A, indicating a cluster better connected by contiguous habitat. Panels (**C**) and (**D**) have equivalent F, but panel (**D**) has a smaller $d(G)$, indicating less matrix traversal required to span the cluster

neighborhood rule in percolation analysis. Graph diameter has been previously shown to be maximized at a threshold gap-crossing ability, d_{crit}, for landscapes with fixed habitat proportion and configuration (Bunn et al. 2000; Urban and Keitt 2001). Similarly, $d(G)$ should be maximized at the percolation threshold, p_c, for landscapes with a variable p and fixed d_t. The ability of graph-based methods to identify these thresholds in p was quantified and compared to measures derived from a more traditional percolation-based method. We discuss the differences and similarities between graph and percolation thresholds and offer guidance as to which would be most appropriate for specific ecological applications. In addition, we discuss how graph methods can be used to identify region and organism specific thresholds without reliance on neutral models or more complex metapopulation models.

Methods

Evaluation of graph metrics across gradients in p and H

We generated a series of binary neutral multifractal landscapes using the program RULE (Gardner 1999). Landscape size was 256×256 pixels and we assigned 30 m size to grid cells. Habitat proportion varied from $0.025 \leq p \leq 0.8$ in increments of $p = 0.025$. Configuration was controlled by the parameter H ($0.0 \leq H \leq 1.0$ in increments of $H = 0.25$), which set the level of aggregation among habitat cells. Large values of H yield aggregated (clumped) patch distributions (see With 1997). Patches were defined using the eight-neighbor rule. Fifty replicate landscapes were generated for each $H \times p$ combination.

Graph metrics were calculated for the maps using the LANDGRAPHS software package (Urban 2003), which uses Dijkstra's algorithm (Dijkstra 1959) to compute graph diameter. The original FORTRAN77 code was modified for calculation of the area metric and graph diameter using the new definition of the largest cluster as that with the largest aggregate area. Clusters were defined using d_t = 150 m based on Euclidean closest edge distances. Mean values of $d(G)$ and F from the 50 replicate landscapes were plotted against H and p for visual assessment of trends similar to the approach used by Neel et al. (2004). The proportions used to calculate the area ratio (A_{LP} and A_{LC}) could have been determined using GIS software. We chose to bundle calculation of the area ratio into the graph-theoretic software to maintain continuity of data structures within the generic graph analysis framework.

Similarities between graph and percolation theory

Percolation analyses were performed for the H and p gradients using the program RULE (Gardner 1999) with clusters defined by an approximately circular window with 112 cells (equivalent to graph-defined clusters with d_t = 150 m edge-edge). Percolation-based p_c was defined for each H as the first p at which mean percolation frequency, *pf*, exceeded a pre-defined cutoff level. Mean percolation frequency was calculated as the number of replicates of every $H \times p$ combination that percolated relative to the total (50). In percolation analysis, mean *pf* jumps from 0.0 to 1.0 across p_c for infinite random maps (Stauffer and Aharony 1992). Finite maps and maps with non-random structure typically have less sharply defined increases in *pf*. Accordingly, it is common practice to specify a user-defined cutoff for *pf* (Stauffer and Aharony 1992). A cutoff of *pf* = 0.5 has been used in landscape analysis (e.g. With 1999), while the strict definition from percolation theory is a value of 1.0 (O'Neill et al. 1988). We evaluated two cutoff values of *pf*, 0.5 and 1.0, to explore the sensitivity of percolation-based p_c to choice of *pf*. The graph-defined threshold was identified for each H as that habitat proportion at which maximum mean values of $d(G)$ occurred. These graph-based p_c values were compared to the percolation-based p_c values with the expectation that they should be very similar.

Results

Evaluation of graph metrics across gradients in p and H

Graph diameter, $d(G)$, was unimodally distributed as a function of habitat proportion, p, with a greater amplitude of response for landscapes with $H \leq 0.5$ (Fig. 2). As p approached 0.8, a single patch dominated the landscape and graph diameter tended towards 0.0, regardless of H. At lower p, clusters of habitat patches formed, with a consequent increase in graph diameter. Graph diameter peaked at different p values depending on the degree of clumping (H), with a maximum value occurring at $p = 0.175$ for $H = 0.0$. As habitat proportion fell below the value at which graph diameter peaked, a larger number of distances among remaining patches increased beyond the 150 m threshold distance, the largest cluster decreased in size and the sum of distances comprising the shortest path between the most distant patches ($d(G)$) decreased.

For fixed p, graph diameter monotonically increased as a function of decreasing H with a maximum value when $H = 0.0$ (Fig. 2). At high H, landscapes were highly ''clumped'' with a large proportion of habitat in the largest patch and a few

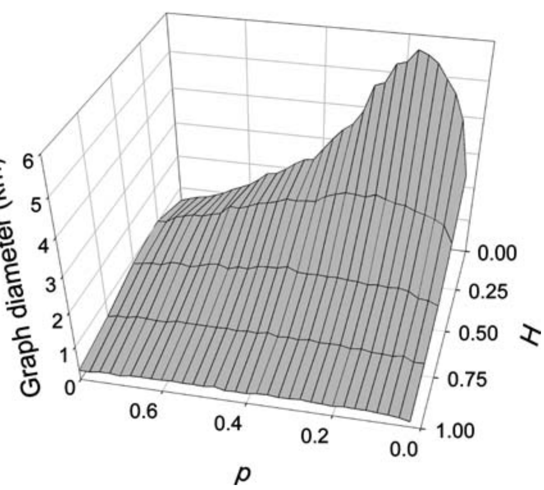

Fig. 2 Graph diameter $d(G)$ as a function of the proportion of habitat, p and aggregation factor H. Each value represents the mean $d(G)$ from 50 replicate simulations for each value of p and H tested

small patches in close proximity. Under these conditions, only a small amount of matrix need be traversed to span the largest cluster and $d(G)$, a measure of inter-patch distance, was small. At low H, habitat was distributed among a larger number of patches that were dispersed across the landscape. This configuration allowed for a larger number of connections among patches and consequently larger values for $d(G)$.

The area ratio F Eq. 1 decreased monotonically with decreasing H and p (Fig. 3). For relatively intact (high p) or highly aggregated (i.e. high H) landscapes, a single large patch dominated the largest cluster and F approached 1.0 with very little variance (SD in F for H = 1.0 for the thirty-two p values ranged from 0.002 to 0.12, median 0.04). For example, in landscapes with $H > 0.5$, the total proportion of habitat in the landscape that is in the single largest patch, A_{LP}, was greater than 0.6, which greatly limited the range of possible F values. In landscapes with $H = 0.0$, values of A_{LP} ranged from 0.09 to 0.99, which allowed for broader expression of F values (Fig. 3). The smallest values of F occurred for $H = 0.0$ and $p = 0.025$, indicating that although clusters formed, the largest contiguous patch represented at most 25% of the aggregate area within those clusters. The variance in F values was also greater for these maps (SD in F for $H = 0.0$ for the thirty-two p values ranged from 0.006 for $p = 0.8$ to 0.2 for $p = 0.025$ with a median of 0.13).

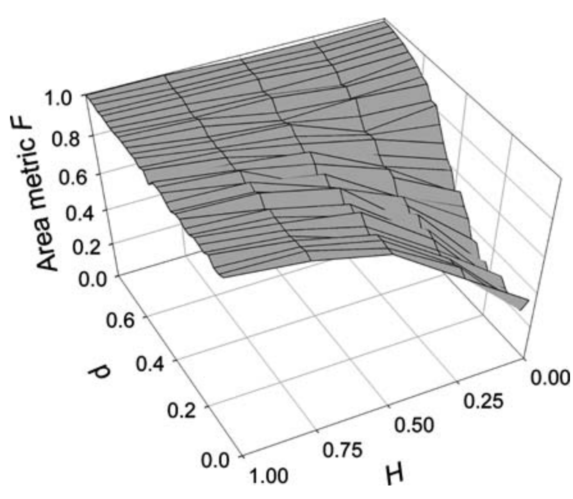

Fig. 3 Area ratio F as a function of the proportion of habitat, p and aggregation factor H. Each value represents the mean of F from 50 replicate simulations for each value of p and H tested

Similarities between graph and percolation theory, critical thresholds

For landscapes with a fixed-level of aggregation (fixed H), the values of p at which graph diameter was maximized were within the range predicted by percolation theory (Table 1). The percolation-based p_c values varied considerably depending on the value of pf. For example, for $H = 0.5$, p_c ranged from 0.4 to 0.75 for $pf = 0.5$ and $pf = 1.0$, respectively. The graph-based p_c values were similar to threshold values for $pf = 0.5$ (e.g. graph-based $p_c = 0.4$ for $H = 0.5$).

Discussion

We systematically evaluated two landscape graph metrics across gradients in habitat proportion, p, and configuration, H, using multifractal neutral landscapes. The first metric, graph diameter, $d(G)$, measures the amount of matrix an organism would have to traverse to span the largest cluster. This metric can simultaneously be interpreted as a measure of risk associated with movement outside of preferred habitat (Urban and Keitt 2001) and the degree to which a structurally patchy landscape is potentially traversable. As such, a large graph diameter can either be positive or negative and needs to be interpreted with caution. Additional caution is warranted because small values of $d(G)$ can occur for several reasons, and thus the metric does not provide a straightforward way to quantify landscape connectivity. For example, graph diameter approaches 0.0 as the proportion of habitat in the largest patch (A_{LP}) approaches 1.0, which occurs as p approaches 1.0 (all H) and across all values of p for highly clumped

Table 1 Critical thresholds of proportion of habitat area defined by cutoff percolation frequencies (pf) of 0.5 and 1.0, and by peak graph diameter, $d(G)$

H	Percolation-based p_c Cutoff $pf = 0.5$	Percolation-based p_c Cutoff $pf = 1.0$	p_c defined by maximum $d(G)$
0.0	0.15	0.3	0.175
0.25	0.25	0.4	0.225
0.5	0.4	0.75	0.4
0.75	0.45	0.7	0.4
1.0	0.5	0.7	0.5

landscapes ($H > 0.5$). However, $d(G)$ also approaches 0.0 for landscapes in which all patches are isolated beyond the threshold distance. Therefore, inferences about landscape connectivity based on $d(G)$ require additional information on habitat amount and the degree of habitat aggregation into patches and clusters.

The area metric F quantifies the proportion of the largest connected network that is composed of the largest patch. As such, it provides a measure of the proportion of habitat available without requiring matrix traversal. This metric can be useful for discriminating between both poor and well connected landscapes with similar graph diameter. In previous work, large $d(G)$ values were interpreted to imply a high level of connectivity (Bunn et al. 2000, Urban and Keitt 2001). Our analysis clarifies that large $d(G)$ values indicate only inter-patch connectivity. The metric F provides a complementary measure that indicates how well habitat in a network is connected by virtue of domination by a large patch of contiguous habitat independent of graph diameter.

The relative lack of sensitivity of both metrics to changes in p for clumped landscapes (high p and high H, Figs. 2 and 3) can be directly linked to the large values of A_{LP} for these landscapes. In essence, landscapes with large A_{LP} have not been subjected to substantial fragmentation, regardless of the amount of habitat loss represented by p. We suggest that before performing a detailed connectivity analysis, landscape managers should quantify the proportion of habitat in the largest patch, A_{LP}. Values of A_{LP} approaching 1.0 indicate dominance of the largest patch. If the largest patch is of sufficient size to maintain a viable population of the organism of interest, maintenance of the largest patch should be a management priority and issues of among-patch connectivity should be avoided by preventing creation of structurally isolated patches. Detailed connectivity analyses that assign importance of values to specific patches relative to the network (e.g. Bunn et al. 2000;Pascual-Hortal and Saura 2006; Urban and Keitt 2001) are generally unnecessary in these instances because they would identify the largest patch as being the most important regardless of network configuration. In contrast, connectivity analyses performed on landscapes with small A_{LP} values would be more likely to identify ''stepping-stone'' patches whose removal would isolate patches in a single large cluster into multiple clusters, each with an aggregate area much smaller than the original configuration. In general, the proportion of habitat in the largest patch is a better gauge of the effects of fragmentation on connectivity than is the number of patches or p.

Graph and percolation thresholds

Threshold analysis is a key research priority for conservation management (Groffman et al. 2006; Lindenmayer and Luck 2005), and we have shown that peaks in graph diameter across multifractal maps occur at points along the p gradient that are predicted to be thresholds in percolation analysis. Because a range of percolation-based critical p_c values are possible when analyzing thresholds, based on user-defined cutoff frequency, we feel that graph diameter maxima are a more direct way of quantifying thresholds. However, our findings highlight a practical problem in application of neutral model derived critical thresholds in p to conservation management. Real landscapes are not defined by random or multifractal patterns of habitat loss. Both percolation-based and graph-based p_c values were highly dependent on H in our analyses. Unfortunately, it is not clear that values of H can be calculated for real landscapes that are consistent with the definition of H used to generate multifractal landscapes. If land managers would like to use the concept of critical thresholds to identify landscapes most at risk of structural or functional fragmentation, we follow the recommendation of Muradian (2001) and suggest that decisions be based not on neutral map analysis, but on determination of thresholds that are specific to the region of interest. Region-specific thresholds will require graph analysis of a large number of sample landscapes taken from the region (e.g. Ferrari 2005), but these calculations can be accomplished relatively quickly using computationally efficient graph algorithms.

Furthermore, from a percolation theory perspective, map-spanning is the criteria for establishment of connectivity thresholds. Therefore percolation thresholds would be of greatest interest for scenarios in which the focal landscape is embedded in a larger extent, and issues of map-spanning are a concern (e.g. spread of fire, invasive species). Our landscapes were treated as closed systems, and map spanning was not required to define thresholds based on graph diameter maxima. These thresholds represent connectivity internal to the landscape maps. For fixed gap-crossing ability, d_t, the values indicate the critical proportion of habitat at which a majority of habitat is connected as part of one large cluster, irrespective of map spanning ability. These findings have strong parallels with case studies in which graph diameter maxima, calculated for a fixed p and varying d_t, were used to identify a threshold distance, or specific gap-crossing ability, below which functional fragmentation was observed (e.g. Bunn et al. 2000; Urban and Keitt 2001).

Conclusions

Our exploration of the behavior of two metrics across systematic gradients in habitat proportion, p, and configuration indicates that although graph diameter is a useful index of inter-patch movement associated with traversal of the largest cluster, it alone is not an acceptable gauge of connectivity. The proposed area metric F indicates the degree to which a cluster departs from the ideal state (no fragmentation, all contiguous habitat) and thus attains maximum values when matrix traversal is not required at all. We found that the combination of metrics can be used to discriminate between landscape configurations that yield similar values for metrics that blend both the area and configuration aspects of connectivity, such as the correlation length. Both metrics, $d(G)$ and F, showed regions of weak response across the $H \times p$ gradients in regions of high p ($p > 0.5$) and high H ($H > 0.5$), which were characterized by large patches containing more than 60% of available habitat ($A_{LP} > 0.6$). We conclude that connectivity analysis would not be very informative for landscapes with $A_{LP} > 0.6$, regardless of p, given the scale and parameters (e.g., $d_t = 150$ m) of our sample landscapes.

Our analysis also relates graph and percolation theories and provides justification for using trends in graph diameter, $d(G)$, as an indicator of the connectivity thresholds previously associated with percolation theory. The area metric F can be used as an additional criteria to identify landscapes that are more accurately classified as having undergone pure habitat loss, without substantial fragmentation. Inter-patch connectivity analyses are of limited value to such landscapes. Our analyses used theoretical landscapes, but the lessons learned can be extended to analysis of real landscapes. Our findings suggest a method for prioritizing landscapes in terms of their potential connectivity, for a specific organism with known gap-crossing ability. Landscapes with large proportion of habitat in a single patch (A_{LP} approaching 1.0) are not suitable for connectivity analyses regardless of p. Where A_{LP} is reasonably small, landscapes can be categorized across the p gradient into two classes relative to a region-specific threshold, p_c: (1) potentially ''connected'', $p > p_c$ and (2) potentially ''functionally fragmented'', $p < p_c$. This classification would provide a heuristic guide to land managers interested in identifying landscapes most at risk of functional fragmentation for which further analysis of connectivity is warranted.

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