



Landscape Metrics

Landscape Metrics for Categorical Map Patterns

Instructor: K. McGarigal

Assigned Reading: Turner et al. 2001 (Chapter 5); McGarigal (Lecture notes)

Objective: Provide an overview of common landscape metrics and insights into their use and interpretation. Highlight importance of selecting the “right” metric for the “right” problem.

Topics covered:

1. Introduction and overview: distribution statistics
2. Area & edge metrics
3. Shape metrics
4. Core area metrics
5. Contrast metrics
6. Aggregation metrics
7. Diversity metrics
8. General considerations

Insights on Metrics...*taxonomy of metrics*

Metrics can be grouped loosely according to the level of heterogeneity (patch, class, landscape) and the aspect of landscape pattern represented, but any taxonomy is somewhat arbitrary



Level of Heterogeneity:

- Patch
- Class
- Landscape

Aspect of Pattern:

- Area & edge
- Shape
- Core area
- Contrast
- Aggregation
- Subdivision
- Isolation
- Diversity

1. Taxonomy of metrics

Landscape metrics exist at the patch, class (patch type) and landscape level. At the class and landscape level, some of the metrics quantify landscape composition, while others quantify landscape configuration. Landscape composition and configuration can affect ecological processes independently and interactively. Thus, it is especially important to understand for each metric what aspect of landscape pattern is being quantified. In addition, many of the metrics are partially or completely redundant; that is, they quantify a similar or identical aspect of landscape pattern. In most cases, redundant metrics will be very highly or even perfectly correlated. For example, at the landscape level, *patch density* (PD) and *mean patch size* (MPS) will be perfectly correlated because they represent the same information. These redundant metrics are alternative ways of representing the same information; they are available as metrics because the preferred form of representing a particular aspect of landscape pattern will differ among applications and users. It behooves the user to understand these redundancies, because in most applications only 1 of each set of redundant metrics should be employed. It is important to note that in a particular application, some metrics may be empirically redundant as well; not because they measure the same aspect of landscape pattern, but because for the particular landscapes under investigation, different aspects of landscape pattern are statistically correlated. The distinction between this form of redundancy and the former is important, because little can be learned by interpreting metrics that are inherently redundant, but much can be learned about landscapes by interpreting

metrics that are empirically redundant.

Many of the patch metrics have counterparts at the class and landscape levels. For example, many of the class metrics (e.g., mean shape index) represent the same basic information as the corresponding patch metrics (e.g., patch shape index), but instead of considering a single patch, they consider all patches of a particular type simultaneously. Likewise, many of the landscape metrics are derived from patch or class characteristics. Consequently, many of the class and landscape metrics are computed from patch and class statistics by summing or averaging over all patches or classes. Even though many of the class and landscape metrics represent the same fundamental information, naturally the algorithms differ slightly. Class metrics represent the spatial distribution and pattern within a landscape of a single patch type; whereas, landscape metrics represent the spatial pattern of the entire landscape mosaic, considering all patch types simultaneously. Thus, even though many of the metrics have counterparts at the class and landscape levels, their interpretations may be somewhat different. Most of the class metrics can be interpreted as fragmentation indices because they measure the configuration of a particular patch type; whereas, most of the landscape metrics can be interpreted more broadly as landscape heterogeneity indices because they measure the overall landscape pattern. Hence, it is important to interpret each metric in a manner appropriate to its scale (patch, class, or landscape).

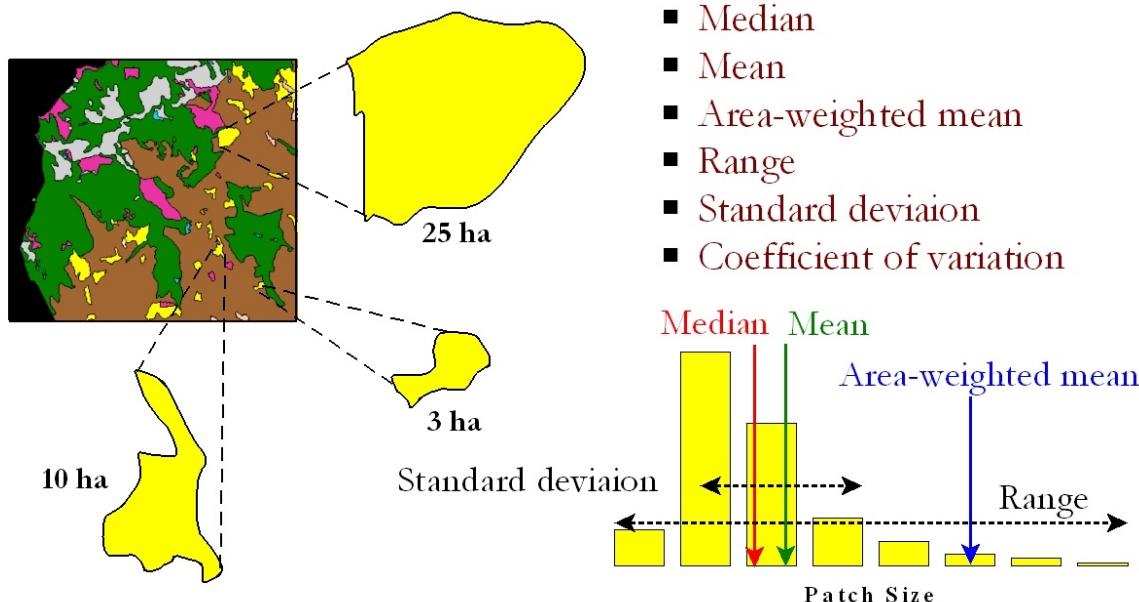
Landscape metrics are typically grouped loosely according to the aspect of landscape pattern measured – but note that these groupings are done for mostly for convenience as these are not independent aspects of landscape pattern and most metrics can fall into more than one group – as follows:

- Area & edge metrics
- Shape metrics
- Core area metrics
- Contrast metrics
- Aggregation metrics
- Subdivision metrics
- Isolation metrics
- Diversity metrics

Within each of these groups, metrics are further grouped into patch, class, and landscape metrics.

Insights on Metrics... *distribution statistics*

Patch metrics can be summarized for a single class or the entire landscape using a variety of *distribution* statistics



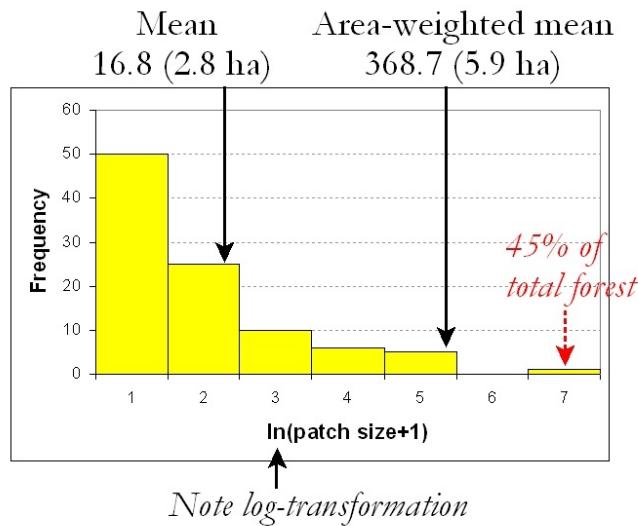
2. Distribution Statistics

Patch metrics can be summarized at the class and landscape levels using a variety of distribution statistics that provide first- and second-order statistical summaries of the patch metrics for the focal class or the entire landscape, such as: (1) mean, (2) area-weighted mean, (3) median, (4) range, (5) standard deviation, and (6) coefficient of variation. The difference between the mean and the area-weighted mean in this context is especially important as discussed below.

Metrics applied to categorical patch mosaics (under the “landscape mosaic model” of landscape structure) fundamentally represent the structure of the landscape as defined by its *patch* structure. Clearly, patches are the basic building blocks of categorical patch mosaics and, as such, most metrics derive from the spatial character and distribution of the patches themselves. However, most patch-based metrics can be summarized at the class and landscape levels to reflect the character and distribution of individual patches over a broad extent. Indeed, in most applications, the objective involves characterizing the patch structure for a single focal class or for the entire patch mosaic across the full extent of the landscape, rather than focusing on individual patches. Despite the common objective of characterizing the class or landscape structure, metrics differ in whether they offer a “patch-based” or “landscape-based” perspective of landscape structure. This is perhaps best illustrated by the difference between class and/or landscape distribution metrics based on the simple arithmetic mean or the area-weighted mean.

Insights on Metrics... *distribution statistics*

The mean versus area-weighted mean distinguishes a *patch-centric* from *landscape-centric* interpretation

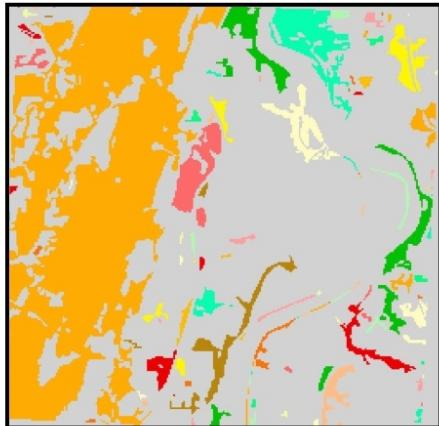


Mean versus area-weighted mean

Metrics based on the *mean* patch characteristic, such as mean patch size (AREA_MN) or mean patch shape index (SHAPE_MN), provide a measure of central tendency in the corresponding patch characteristic across the entire landscape, but nevertheless describe the patch structure of the landscape as that of the average patch characteristic. Thus, each patch regardless of its size is considered equally (i.e., given equal weight) in describing the landscape structure. Consequently, metrics based on the mean patch characteristic offer a fundamentally patch-based perspective of the landscape structure. They do not describe the conditions, for example, that an animal dropped at random on the landscape would experience, because that depends on the probability of landing in a particular patch, which is dependent on patch size.

Insights on Metrics... *distribution statistics*

The mean versus area-weighted mean distinguishes a *patch-centric* from *landscape-centric* interpretation



- *Mean*...average patch characteristic for a *patch* selected at random (patch-centric)
- *Area-weighted mean*...average patch characteristic for a *cell* selected at random (landscape centric)

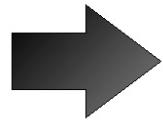
Conversely, metrics based on the *area-weighted mean* patch characteristic, such as the area-weighted mean patch size (AREA_AM) and area-weighted mean patch shape index (SHAPE_AM), while still derived from patch characteristics, provide a landscape-based perspective of landscape structure because they reflect the average conditions of a pixel chosen at random or the conditions that an animal dropped at random on the landscape would experience. This is in fact the basis for the subdivision metrics of Jaeger (2000) described later.

Insights on Metrics... *distribution statistics*

All patch metrics can be summarized at the class or landscape level using the mean and the area-weighted mean; the choice depends on the perspective sought

Patch-centric metrics

- AREA_MN
- GYRATE_MN
- SHAPE_MN
- CORE_MN
- ECON_MN
- Etc.



Landscape-centric metrics

- AREA_AM
- GYRATE_AM (CL)
- SHAPE_AM
- CORE_AM
- ECON_AM
- Etc.

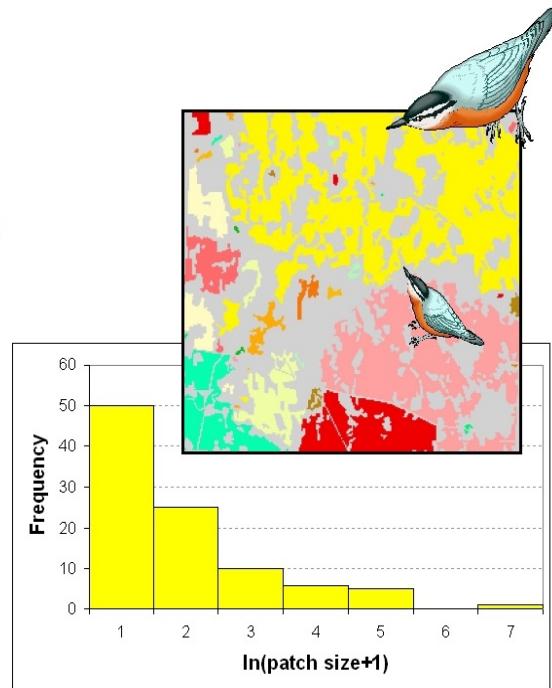
All patch metrics can be summarized at the class or landscape level using the mean and the area-weighted mean; the choice of formulation depends on the perspective sought: *patch-centric* or *landscape-centric*. In most applications, the landscape-centric perspective is the one sought and thus the area-weighted mean is the proper formulation. However, there are some special cases involving the isolation metrics (proximity index, similarity index, and nearest neighbor distance) where the area-weighted mean patch characteristic can provide misleading results. The isolation metrics describe the spatial context of individual patches, and they can be summarized at the class or landscape level to characterize the entire landscape. Consider the proximity index (PROX). The proximity index operates at the patch level. For each patch, the size and distance to all neighboring patches of the same type (within some specified search distance) are enumerated to provide an index of patch isolation. A patch with lots of other large patches in close proximity will have a large index value (i.e., low isolation). Both the mean and area-weighted mean proximity index can be calculated at the class and landscape levels. A potential problem in interpretation lies in cases involving widely varying patch sizes. Consider the special case involving 10 patches of the focal class, in which 9 of the 10 patches are equal in size and quite small (say 1 ha each). The ninth patch, however, is quite large (say 1,000 ha). Let's assume that all the small patches are close to the large patch (within the search distance). The proximity index for each of the 9 small patches will be quite large, because the single large patch will be enumerated in the index. The proximity index for the single large patch will be quite small, because the only neighboring patches are quite small (1 ha each). Consequently, the mean proximity index will be much larger than the area-weighted mean proximity index, connoting

very different levels of patch isolation. Which is correct? It is difficult to say. From a purely patch-based perspective, the mean would appear to capture the structure best, since the average “patch” is not very isolated. However, the average “organism” would be found in the single large patch, since it represents >99% of the focal habitat area, so it seems logical that the area-weighted mean would provide a better measure. In this case, the area-weighted mean proximity index will be quite small, connoting high isolation, when in fact the single large patch represents the matrix of the landscape. In this case, it is not clear whether either the mean or area-weighted mean proximity index provides a useful measure of isolation. The important point here is that for some metrics, namely the isolation metrics, under some conditions, namely extreme patch size distributions, the mean and area-weighted mean can provide different and potentially misleading results.

Insights on Metrics... *distribution statistics*

Recommendations:

- Carefully consider the relevant perspective... in most cases the landscape perspective is more relevant; hence, use area-weighted means generally
- Examine the patch distribution... right-skewed distributions will exhibit the greatest differences between mean and area-weighted mean

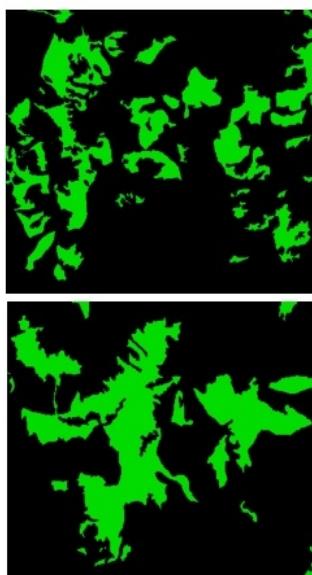


Recommendations

Given these important differences between the mean and area-weighted mean, careful consideration should be given to the choice of metrics in any particular application. Despite the preponderance of use of the mean in practice, in most applications, it is likely that the area-weighted mean provides a more meaningful perspective on landscape structure, although for the isolation metrics one needs to take great care to ensure that the interpretation is meaningful given the landscape structure.

Insights on Metrics...*area & edge metrics*

Collection of basic metrics describing the spatial “grain” of the landscape



Finer
grain

Coarser
grain

- Patch area (ha)
- Patch radius of gyration (m)
- Class area (ha) or percentage of landscape (%)
- Total edge (m) or edge density (m/ha)
- Largest patch index (%)

2. Area & Edge Metrics

This group represents a loose collection of metrics that deal with the size of patches and the amount of edge created by these patches. These metrics variously refer to the spatial “grain” of the landscape. Although these metrics could easily be subdivided into separate groups or assigned to other already recognized groups, there is enough similarity in the patterns assessed by these metrics to include them under one umbrella. Some of the common metrics in this group include the following:

- *Patch area (AREA)* – area (ha) of each patch.
- *Patch radius of gyration (GYRATE)* – extent (m) of each patch; i.e., how far across the landscape a patch extends its reach, given by the mean distance between cells in a patch. All other things equal, the larger the patch, the larger the radius of gyration. Similarly, holding area constant, the more extensive the patch (i.e., elongated and less compact), the greater the radius of gyration. The radius of gyration can be considered a measure of the average distance an organism can move within a patch before encountering the patch boundary from a random starting point.
- *Class area (CA) or percentage of landscape (PLAND)* – area (ha) of each patch type (class)

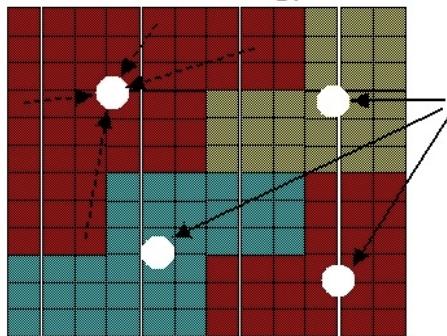
or the percentage of the landscape comprised of a particular patch type.

- *Total edge* (TE) or *edge density* (ED) – total length (m) or density (m/ha) of edge of a particular patch type (class level) or of all patch types (landscape level).
- *Largest patch index* (LPI) – percentage of the landscape comprised of the single largest patch (at the class or landscape level).

Insights on Metrics...area & edge metrics

- Area-weighted mean radius of gyration (m)
(correlation length)

Patch radius of gyration



Patch
“cluster”
centroid

Correlation Length

$$\sum_{i=1}^m R_i P_i$$

Landscape level

R = patch “radius of gyration”

P = proportion of landscape

Correlation length (m) gives the distance that one might expect to traverse the map while staying in a particular patch type, from a random starting point and moving in a random direction

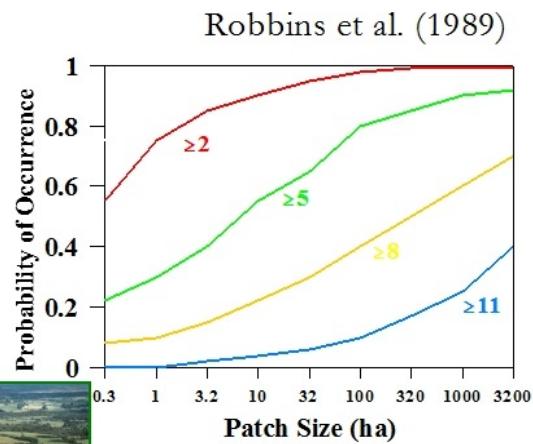
Correlation length

- *Area-weighted mean radius of gyration (GYRATE_AM)* – otherwise known as “correlation length” is the mean patch radius of gyration at the class or landscape level where each patch is weighted by its area. Correlation length (m) gives the distance that one might expect to traverse the map while staying in a particular patch, from a random starting point and moving in a random direction. As such, correlation length is often interpreted as a measure of the physical connectedness of the landscape.

Insights on Metrics...area & edge metrics

Why does area and edge matter?

- Minimum area requirements of species and ecosystems
- Edge effects and implications for interior-sensitive species and ecosystem integrity
- Disruption of landscape continuity and connectivity

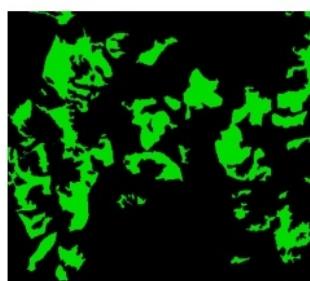


Why does area & edge matter?

- The area of each patch comprising a landscape mosaic is perhaps the single most important and useful piece of information contained in the landscape. Not only is this information the basis for many of the patch, class, and landscape metrics, but patch area has a great deal of ecological utility itself. For example, there is considerable evidence that species richness and the occurrence and abundance of some species are strongly correlated with patch size.
- The total amount of edge in a landscape is important to many ecological phenomena. Indeed, in many landscape ecological investigations, much of the presumed importance of spatial pattern is related to edge effects. For example, one of the most dramatic and well-studied consequences of habitat fragmentation is an increase in the proportional abundance of edge-influenced habitat and its adverse impacts on interior sensitive species.
- Lastly, area, density and edge metrics represent in various ways the physical continuity of the landscape and thus either directly or indirectly deal with the issue of landscape connectivity.

Insights on Metrics...*shape metrics*

Collection of unitless metrics describing the geometric complexity and/or compactness of patch shapes



Complex
geometry



Simple
geometry

- Perimeter/area ratio
- Shape index
- Fractal dimension index
- Perimeter-area fractal dimension
- Circumscribing circle index
- Contiguity index

3. Shape Metrics

This group of metrics represents a collection of unitless metrics that describe the geometric complexity and/or compactness of patch shapes and quantify landscape configuration in terms of geometric complexity at the patch, class, and landscape levels. Most of these shape metrics are based on perimeter-area relationships. Some of the common metrics in this group include the following:

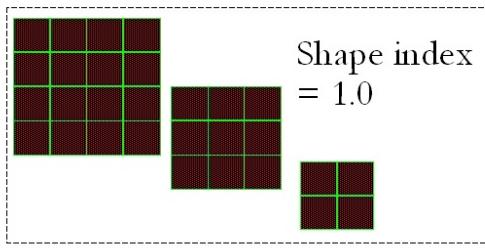
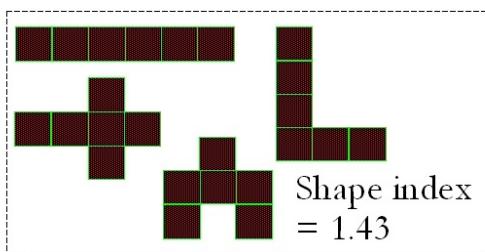
- *Perimeter-area ratio* (PARA) – simple ratio of patch perimeter to area, in which patch shape is confounded with patch size; holding shape constant, an increase in patch size will cause a decrease in the perimeter-area ratio.
- *Shape index* (SHAPE) – normalized ratio of patch perimeter to area in which the complexity of patch shape is compared to a standard shape (square) of the same size, thereby alleviating the size dependency problem of PARA.
- *Fractal dimension index* (FRAC) – another normalized shape index based on perimeter-area relationships in which the perimeter and area are log transformed (see below).
- *Perimeter-area fractal dimension* (PAFRAC) – a similar index to FRAC, but applied to a

collection of patches at the class or landscape level (see below).

- *Related circumscribing circle* (CIRCLE) – another method of assessing shape based on the ratio of patch area to the area of the smallest circumscribing circle; providing a measure of overall patch elongation. A highly convoluted but narrow patch will have a relatively low related circumscribing circle index due to the relative compactness of the patch. Conversely, a narrow and elongated patch will have a relatively high circumscribing circle index. This index may be particularly useful for distinguishing patches that are both linear (narrow) and elongated.
- *Contiguity index* (CONTIG) – another method of assessing patch shape based on the spatial connectedness or contiguity of cells within a patch; large contiguous patches will result in larger contiguity index values.

Insights on Metrics... *shape metrics*

- Shape index (unitless)



Shape Index

$$\frac{P_{ij}}{m \cdot n} \rightarrow p_{ij}$$

$1 \leq \text{SHAPE}$, without limit

Shape index is measure of patch geometric complexity based on a standardized perimeter to area ratio; i.e., >1 equals increasing departure from square shape

Shape index

The *shape index* (SHAPE) was initially proposed by Patton (1975) as a diversity index based on shape for quantifying habitat edge for wildlife species and as a means for comparing alternative habitat improvement efforts (e.g., wildlife clearings). The shape index measures the complexity of patch shape compared to a standard shape (square) of the same size, and therefore alleviates the size dependency problem of the perimeter-area ratio (PARA). Specifically, the shape index is given as the patch perimeter (m) divided by the patch perimeter (m) for a patch square patch of the same size. Thus, the index equals 1 for square patches of any size and increases without limit as the patch becomes increasingly non-square (i.e., more geometrically complex).

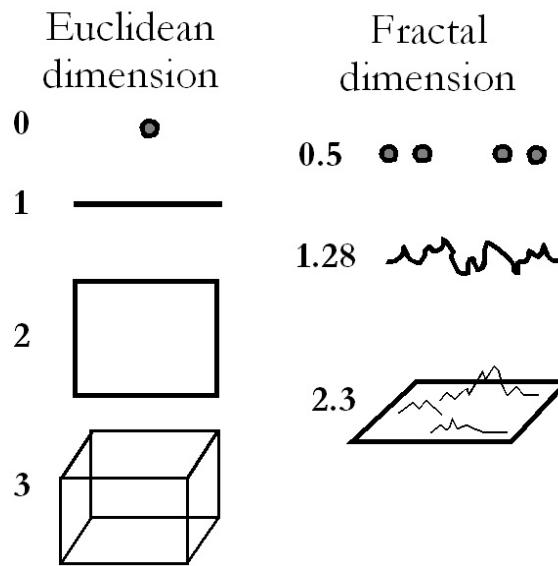
Insights on Metrics... *shape metrics*

■ Fractal dimension (unitless)

A “*dimension*” specifies how to relate a small part of something to the whole.

Fractals are subsets of the geometrical space within which they reside.

By virtue of occupying a small portion of a larger geometrical space, fractals have “*fractal dimensions*” that are less than or equal to the Euclidean dimension of the space they occupy.



Fractal dimension

A “*dimension*” specifies how to relate a small part of something to the whole. Fractals are subsets of the geometrical space within which they reside. By virtue of occupying a small portion of a larger geometrical space, fractals have “*fractal dimensions*” that are less than or equal to the Euclidean dimension of the space they occupy. Thus, in Euclidean space a point has no dimensionality, a straight line is one dimensional, a plane is two dimensional, and a cube is three dimensional. A series of points along a line has a fractal dimension greater than zero (that of a single point) and less than one (that of a line), because it occupies more space than a single point, but less than that of a entire line. Similarly, a squiggly line has a fractal dimension greater than one (that of a straight line) and less than two (that of a plane), because it occupies more space than a straight line but does not occupy that of a full plane. Likewise, a rough surface has a fractal dimension greater than two (that of a plane) and less than three (that of a cube), because it occupies more space than a plane but does not occupy that of a full cube. The more like a Euclidean object a fractal object is, the closer its fractal dimension is to the corresponding Euclidean dimension. We can use this property to measure the geometric complexity of an object. For example, the more geometrically complex the perimeter of a patch is, the more plane-filling it becomes, and the closer its fractal dimension is to the Euclidean dimension of a plane – two.

Insights on Metrics... *shape metrics*

- Fractal dimension (unitless)
- The noninteger values exhibited by fractal dimensions stem from the general scaling law, in which a quantity **Q** varies as a power of the length scale **L** and **k** is a constant. The exponent **D** is the fractal dimension of the quantity. Quantities that obey this scaling law are fractal.
- Fractal models represent exponential changes in measured quantities with changes in length scale.
 - A fractal dimension is generally constant within a finite range of length scales.

General Scaling Law

$$\begin{array}{c} Q = kL^{D_q} \\ \downarrow \\ \ln(Q) = \ln(k) + D_q \ln(L) \\ \downarrow \\ y = b_0 + b_1x \end{array}$$

The noninteger values exhibited by fractal dimensions stem from the general scaling law, in which a quantity **Q** varies as a power of the length scale **L** and **k** is a constant:

$$Q = kL^D$$

The exponent **D** is the fractal dimension of the quantity, and quantities that obey this scaling law are fractal. Thus, fractal models represent exponential changes in measured quantities with change in length scale. Note, the power equation can be transformed into a simple linear equation by log transforming both sides of the equation:

$$\ln(Q) = \ln(k) + D_q \ln(L)$$

which can be seen as a simple linear equation of the form:

$$y = b_0 + b_1x$$

Thus, the fractal dimension of an object is often determined analytically by estimating the slope of the log-log transformed equation.

Insights on Metrics...*shape metrics*

- Fractal dimension (unitless)

- The measured length of the coastline is a function of the caliper width (i.e., resolution).

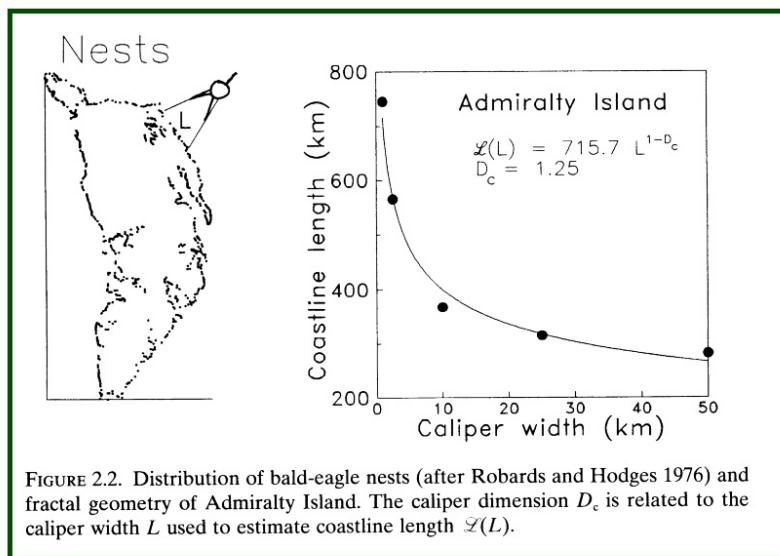
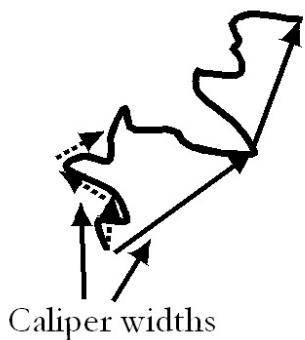
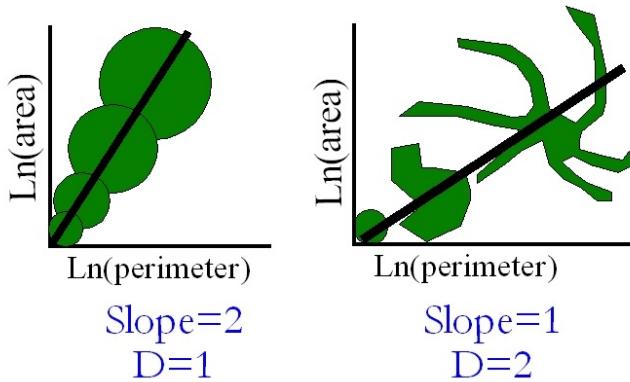


FIGURE 2.2. Distribution of bald-eagle nests (after Robards and Hodges 1976) and fractal geometry of Admiralty Island. The caliper dimension D_c is related to the caliper width L used to estimate coastline length $\mathcal{L}(L)$.

The classic example of using fractal dimension to describe the geometric structure of landscapes is that of estimating the length of coastlines, where the measured length of the coastline is a function of the caliper width (i.e., resolution). In the example shown here, Robards and Hodges (1976) used fractal dimension to describe the coastline of Admiralty Island in relation to the distribution of bald eagle nests. Here, caliper (fractal) dimension D_c is related to the caliper width L used to estimate coastline length. As the caliper width increases, the measured coastline gets shorter and shorter, because it increasingly misses the small bays and inlets, and in fact it gets shorter by a fractal dimension of 1.25. Thus, coastline length depends on the caliper width, or more generally the resolution at which it is measured. By computing the fractal dimension, we can index the complexity of the coastline without having to choose a single scale.

Insights on Metrics... *shape metrics*

- Fractal dimension (unitless)
- Perimeter-area fractal dimension



- Measures irregularity of patch configurations at all scales

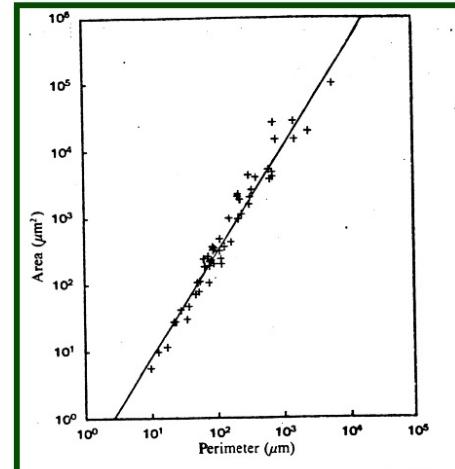


Fig. 1 Fractal area-perimeter relationship for slit islands. 300-Grade Maraging steel. Ruler = 1.5625 μm ; fractal dimensional increment = 1.28.

Mandelbrot (1977, 1982) introduced the concept of fractal, a geometric form that exhibits structure at all spatial scales, and proposed a perimeter-area method to calculate the fractal dimension of natural planar shapes. The perimeter-area method quantifies the degree of complexity of the planar shapes. The degree of complexity of a polygon is characterized by the fractal dimension (D), such that the perimeter (P) of a patch is related to the area (A) of the same patch by $P \approx \sqrt{A^D}$ (i.e., $\log P \approx \frac{1}{2}D \log A$). For simple Euclidean shapes (e.g., circles and rectangles), $P \approx \sqrt{A}$ and $D = 1$ (the dimension of a line). As the polygons become more complex, the perimeter becomes increasingly plane-filling and $P \approx A$ with $D \rightarrow 2$. The appeal of fractal analysis is that it can be applied to spatial features over a wide variety of scales.

The *perimeter-area fractal dimension* (PAFRAC) is similar to the above, but applied to a collection of patches at the class or landscape level using the perimeter-area relationship $A = k P^{2/D}$, where k is a constant. If sufficient data are available, the slope of the line obtained by regressing $\log(P)$ on $\log(A)$ is equal to $2/D$. Note, fractal dimension computed in this manner, where A is the quantity of interest (left-hand side of the power equation) and P is the length scale (right-hand side of the equation), is equal to 2 divided by the slope. Because this index employs regression analysis, it is subject to spurious results when sample sizes are small. In landscapes with only a few patches, it is not unusual to get values that greatly exceed the theoretical limits of this index. Thus, this index is probably only useful if sample sizes are large (e.g., $n > 20$). The perimeter-area fractal dimension of a patch mosaic provides an index of patch shape

complexity across a wide range of spatial scales (i.e., patch sizes). Specifically, it describes the power relationship between patch area and perimeter, and thus describes how patch perimeter increases per unit increase in patch area. If, for example, small and large patches alike have simple geometric shapes, then PAFRAC will be relatively low, indicating that patch perimeter increases relatively slowly as patch area increases. Conversely, if small and large patches have complex shapes, then PAFRAC will be much higher, indicating that patch perimeter increases more rapidly as patch area increases—reflecting a consistency of complex patch shapes across spatial scales.

The fractal dimension of patch shapes, therefore, is suggestive of a common ecological process or anthropogenic influence affecting patches across a wide range of scales, and differences between landscapes can suggest differences in the underlying pattern-generating process.

Krummel et al. (1987) used this principle to investigate the processes structuring flood-plain forests of the Mississippi River, where he computed the perimeter-area fractal dimension of deciduous forest patches. Fractal dimension values as determined by successive regressions of the log of perimeter (P) on log of area (A) for a moving window subset of patches in rank order size from smallest to largest. Fractal dimension remained relatively low (~1.2) until the patch size exceeded 13.5 m^2 on the log scale, after which the fractal dimension increased abruptly and remained relatively high (~1.4).

Insights on Metrics... *shape metrics*

- Fractal dimension (unitless)

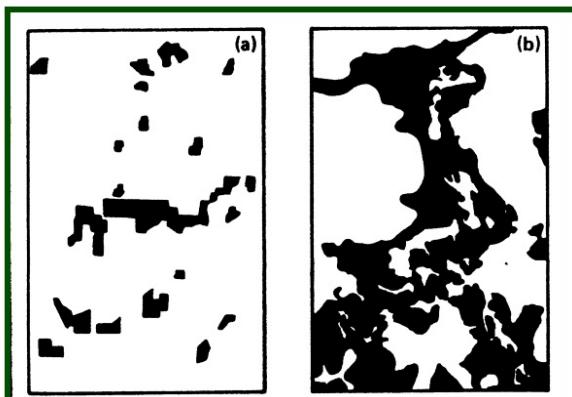


Fig. 2. Computer plots (both at same scale) of deciduous forest in two different areas of the Natchez Quadrangle that illustrate the differences in shape complexity between small forest patches in the Mississippi flood-plain (a) and a larger forested area on the eastern edge of the floodplain (b).

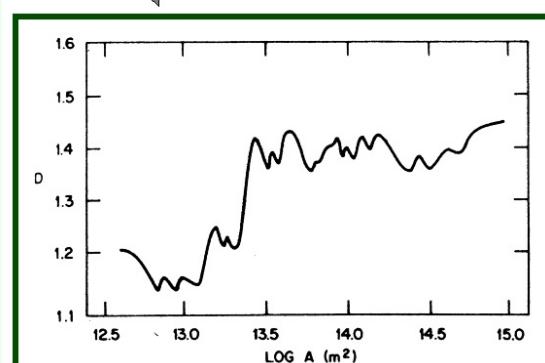


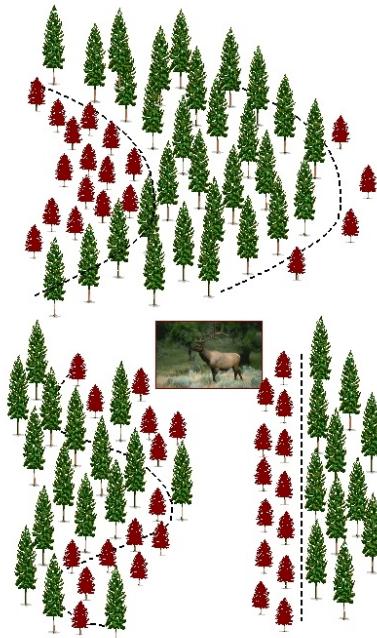
Fig. 1. Changes in fractal dimension (D) values as the log of area (A) increases; as determined by successive regressions of the log of perimeter (P) on log of A .

Krummel et al. 1987

Insights on Metrics... *shape metrics*

Why does shape matter?

- Plant establishment and growth
- Transboundary movements and implications for landscape connectivity
- Edge effects and implications for interior-sensitive species and ecosystem integrity



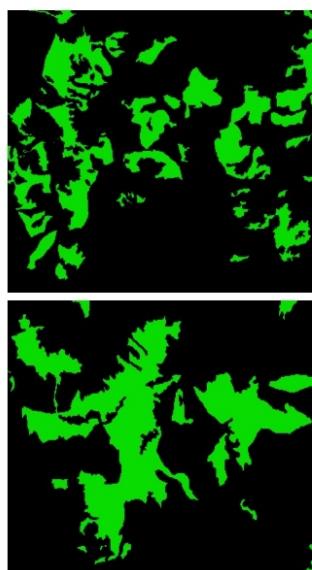
Why does shape matter?

The interaction of patch shape and size can influence a number of important ecological processes:

- Patch shape can influence woody plant colonization and growth in some systems (Hardt and Forman 1989), whereby concave boundaries promote seedling establishment and growth.
- Patch shape can influence transboundary or inter-patch movements such as small mammal migration (Buechner 1989) and ungulate foraging strategies (Forman and Godron 1986), which has implications for landscape connectivity.
- However, the primary ecological consequence of shape seems to be related to ‘edge effects’, which has implications for interior-sensitive species and ecosystem integrity.

Insights on Metrics... *core area metrics*

Collection of metrics describing the patch interior (core) area after accounting for depth-of-edge effects



Less
core area

More
core area

- Patch core area (ha)
- Core area index (%)
- Total core area (ha) or
Core area percent of
landscape (%)
- Number of disjunct core
areas (#) or
Disjunct core area density
(#/ha)

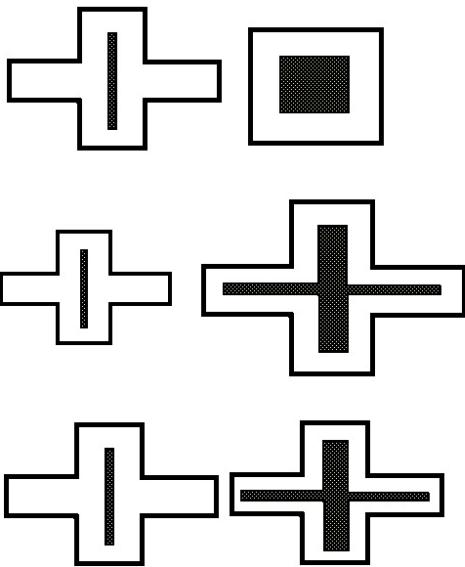
4. Core Area Metrics

This group represents a collection of metrics that describe the patch interior (i.e., core) area after accounting for depth-of-edge effects defined by the user. These metrics are counterparts of most of the area/density metrics in which the size and number of patches is computed after removing the depth-of-edge effect along the boundary of each patch. Some of the common metrics in this group include the following:

- *Patch core area* (CORE) – the area (ha) of the patch that is comprised of core area.
- *Core area index* (CAI) – the percentage of the patch that is comprised of core area (see below).
- *Total core area* (TCA) or *core area percent of landscape* (CPLAND) – total core area (ha) or the percentage of the landscape comprised of core area at the class or landscape level.
- *Number of disjunct core areas* (NCORE) or *disjunct core area density* (DCAD) – number (#) or density (#/ha) of disjunct core areas at the patch, class or landscape levels. Note, if core area is deemed more important than total area, then these indices may be more applicable than their counterparts.

Insights on Metrics... *core area metrics*

Core area is a compound measure of shape, area and edge depth; i.e., all three components effect core area



- *Shape effect...* increasing shape complexity decreases core area
- *Area effect...* increasing patch area increases core area
- *Edge depth effect...* increasing depth-of-edge effect decreases core area

Core area

Core area is a compound measure of shape, area and edge depth. In other words, core area is effected by all three of these components simultaneously (i.e., they are confounded). All other things held constant, increasing shape complexity decreases core area. Similarly, all other things held constant, increasing patch area increases cores area. And lastly, all other things held constant, increasing the depth-of-edge effect decreases core area. Thus, core area metrics confound these three effects: the shape effect, the area effect, and the edge depth effect. This can be viewed as an advantage, because it is an integrative measure of functional relevance, and as a disadvantage, because it confounds multiple effects.

Insights on Metrics... *core area metrics*

■ Core area index (%)

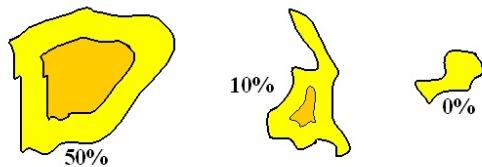


Edge depth... based on user-specified distance

Core Area Index

$$\frac{a_{ij}^c}{a_{ij}} (100)$$

Patch level



Core area index (%) gives the percentage of the patch comprised of interior area (core) based on user-specified depth-of-edge effects, and can be summarized at the class or landscape levels

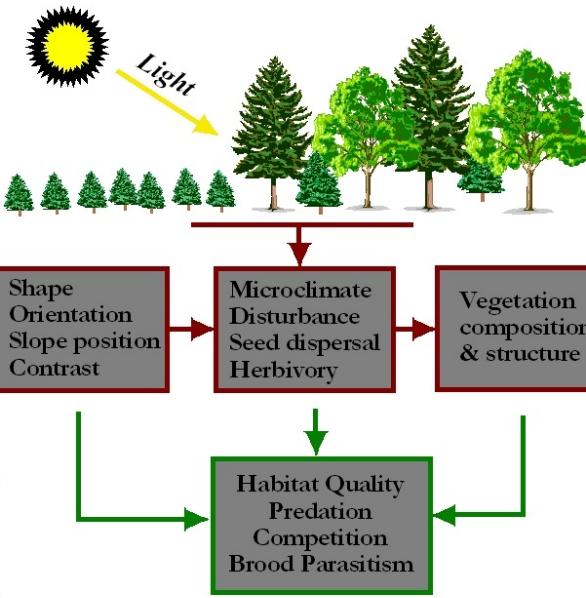
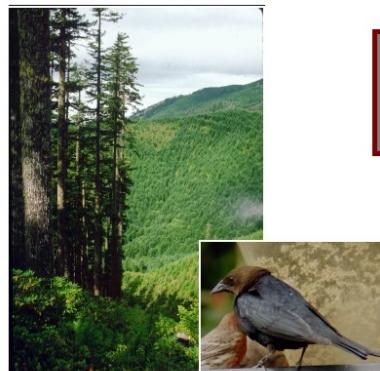
Core area index

The core area index measures the percentage of the patch that is comprised of core area, and it can be computed at the patch level and summarized at the class or landscape level. For example, the *total core area index* gives the percentage of the class or landscape that is comprised of core area. The core area index is basically an edge-to-interior ratio like many of the shape indices (see Shape Metrics), the main difference being that the core area index treats edge as an area of varying width and not as a line (perimeter) around each patch. In addition, the core area index is a relative measure; it does not reflect patch size, class area, or total landscape area; it merely quantifies the percentage of available area, regardless of whether it is 10 ha or 1,000 ha, comprised of core. Consequently, this index does not confound area and configuration like the other core area metrics; rather, it isolates the configuration effect. For this reason, the core area index is probably best interpreted in conjunction with total area at the corresponding scale. For example, in conjunction with total class area, this index could serve as an effective fragmentation index for a particular class.

Insights on Metrics... *core area metrics*

Why does core area matter?

- Edge effects and implications for interior-sensitive species and ecosystem integrity



Why does core area matter?

Like patch shape, the primary significance of core area in determining the character and function of patches in a landscape appears to be related to the ‘edge effect’. Edge effects result from a combination of biotic and abiotic factors that alter environmental conditions along patch edges compared to patch interiors. The nature of the edge effect differs among organisms and ecological processes (Hansen and di Castri 1992). For example, some bird species are adversely affected by predation, competition, brood parasitism, and perhaps other factors along forest edges. Core area has been found to be a much better predictor of habitat quality than patch area for these forest interior specialists (Temple 1986). Unlike patch area, core area is affected by patch shape. Thus, while a patch may be large enough to support a given species, it still may not contain enough suitable core area to support the species. In some cases, it seems likely that edge effects would vary in relation to the type and nature of the edge (e.g., the degree of floristic and structural contrast and orientation). Thus, the user often specifies edge effect distances for every pairwise combination of patch types.

Insights on Metrics... *contrast metrics*

Collection of metrics describing the magnitude of contrast (difference) along patch edges



Less
contrast

- Edge contrast index (%)
- Contrast-weighted edge density (m/ha)



More
contrast



Low
contrast



High
contrast

5. Contrast Metrics

This group represents a collection of metrics that describe the magnitude of contrast (difference) along patch edges, where contrast refers to the magnitude of difference between adjacent patch types with respect to one or more ecological attributes at a given scale that are relevant to the organism or process under consideration as defined by the user. Some of the common metrics in this group include the following:

- *Edge contrast index* (ECON) – percentage of maximum contrast along an edge between two patches, summarized as the patch, class or landscape levels (see below).
- *Contrast-weighted edge density* (CWED) – contrast-weighted density of edge (m/ha) at the class or landscape level, which is equal to the density of edge after weighting each edge segment proportionate to the degree of contrast along that edge, which is equivalent to the maximum-contrast edge density.

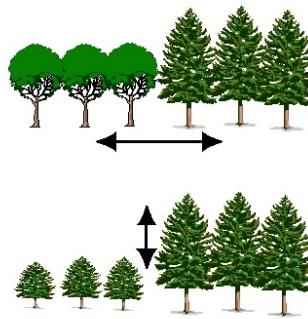
Insights on Metrics... *contrast metrics*

- Total edge contrast index (%)

Total Edge Contrast Index

$$\frac{\sum_{i=1}^m \sum_{k=i+1}^m (e_{ik} \cdot d_{ik})}{E} (100)$$

Landscape level



Floristic Contrast

Structural Contrast

d_{ik} = user-specified edge contrast weight (0-1)

Total edge contrast index (%) gives the magnitude of edge contrast as a percentage of the maximum for the average unit of edge, based on user-specified edge contrast weights

Total edge contrast index

As noted above, in the edge contrast index each segment of edge is weighted by the degree of contrast between adjacent patches, where weights range from 0-1. Thus, at the patch level, the total patch perimeter is reduced proportionate to the degree of contrast in the perimeter and reported as a percentage of the total perimeter. Thus, a patch with a 10% edge contrast index has very little contrast with its neighborhood; it has the equivalent of 10% of its perimeter in maximum-contrast edge. Conversely, a patch with a 90% edge contrast index has high contrast with its neighborhood. Note that this index is a relative measure. Given any amount of edge, it measures the degree of contrast in that edge. In other words, high values of ECON mean that the edge present, regardless of whether it is 10 m or 1,000 m, is of high contrast, and vice versa. The edge contrast index can be summarized at the class and landscape levels as well. For example, the *total edge contrast index* (TECI) quantifies edge contrast as a percentage of maximum possible for the landscape as a whole.

Insights on Metrics... *contrast metrics*

Establishing Contrast Weights

In this example, a community (patch type) contrast key is established base on four factors: 1) vegetation structure, 2) floristics, 3) wetness, and 4) hydrology

Community contrast key:

value	Structure (short)	Floristics (deciduous)	Wetness (dry)	Hydrology (still)	value
1	unvegetated	pure deciduous	xeric	stagnant	1
2	lichen or moss			still	2
3	herbaceous		mesic		3
4				slow flow	4
5	shrub	mixed	temporarily saturated		5
6					6
7	tree: open canopy		temporarily flooded	moderate flow	7
8					8
9			permanently flooded		9
10	tree: closed canopy	pure coniferous	deepwater	fast flow	10
	(tall)	(coniferous)	(wet)	(fast)	

Establishing edge contrast weights

Clearly, edge contrast can assume a variety of meanings for different ecological processes. Therefore, contrast can be defined in a variety of ways, but it always reflects the magnitude of difference between patches with respect to one or more ecological attributes at a given scale that are important to the phenomenon under investigation. Weights must range between 0 (no contrast) and 1 (maximum contrast). Under most circumstances, it is probably not valid to assume that all edges function similarly. Often there will not be a strong empirical basis for establishing a weighting scheme, but a reasoned guess based on a theoretical understanding of the phenomenon is probably better than assuming all edges are alike. For example, from an avian habitat use standpoint, we might weight edges somewhat subjectively according to the degree of structural and floristic contrast between adjacent patches, because a number of studies have shown these features to be important to many bird species. In the example shown here, first a community (patch type) contrast key was established based on four ecological factors: 1) vegetation structure, 2) floristics, 3) wetness, and 4) hydrology. Next, each patch type was assigned a score (1-10) for each factors, where appropriate. Finally, the contrast between each pair of patch types was computed empirically based on the weighted Euclidean distance among the factors, using only the factors evaluated for both patch types. The end result was a square symmetrical matrix showing the contrast between each pair of patch types.

Insights on Metrics... *contrast metrics*

Establishing Contrast Weights

Next, each patch type is assigned a score (1-10) for each of four factors (vegetation structure, floristics, wetness, and hydrology), where appropriate

Code	Natural Community	Weight:	Structure	Floristics	Wetness	Hydro.
			4	1	3	1
100	FORESTS	8	*	2	*	*
110	Deciduous forest	8	2	2	*	
111						
120	Mixed forest	8	5	2	*	
121						
130	Coniferous forest	9	8	2	*	
131						
190	Forested wetland	7	*	7	1	
191						
200	NONFORESTED UPLANDS	3	*	1	*	
210	Shrubland	5	5	1	*	
211	Powerline shrubland	4	*	*	*	
212	Old field	5	*	*	*	
220	Grasslands	3	*	2	*	
221	Cultural grassland					
230	Cliffs & steep slopes	2	*	1	*	
231						

Insights on Metrics... *contrast metrics*

Establishing Contrast Weights

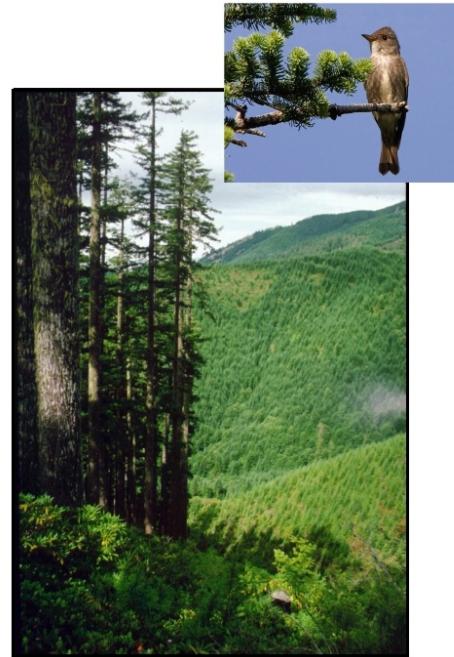
Finally, the contrast between each pair of patch types is computed empirically based on the weighted Euclidean distance among the vegetation and hydrography factors

	High-intensity	Low-intensity	High-density	Low-density	Agriculture	Dam (large)	Dam (medium)	Dam (small)	Dam (non-j)	Expressway
Deciduous forest	0.62	0.62	0.62	0.09	0.44	0.62	0.62	0.62	0.62	0.62
Mixed forest	0.62	0.62	0.62	0.09	0.44	0.62	0.62	0.62	0.62	0.62
Coniferous forest	0.71	0.71	0.71	0.18	0.53	0.71	0.71	0.71	0.71	0.71
Forested wetland	0.66	0.63	0.63	0.33	0.48	0.66	0.66	0.66	0.66	0.66
Powerline shrubland	0.38	0.38	0.38	0.38	0.13	0.38	0.38	0.38	0.38	0.38
Old field	0.50	0.50	0.50	0.25	0.25	0.50	0.50	0.50	0.50	0.50
Cultural grassland	0.19	0.18	0.18	0.35	0.00	0.19	0.19	0.19	0.19	0.19
Cliff and steep slope	0.09	0.11	0.11	0.45	0.11	0.09	0.09	0.09	0.09	0.09
Shrub swamp	0.58	0.53	0.53	0.44	0.44	0.58	0.58	0.58	0.58	0.58
Emergent marsh	0.56	0.50	0.50	0.58	0.46	0.56	0.56	0.56	0.56	0.56
Pond	0.60	0.53	0.53	0.75	0.56	0.60	0.60	0.60	0.60	0.60
Vernal pool	0.62	0.62	0.62	0.09	0.44	0.62	0.62	0.62	0.62	0.62
Lake	0.60	0.53	0.53	0.75	0.56	0.60	0.60	0.60	0.60	0.60
First order flatwater	0.75	0.66	0.66	0.66	0.66	0.75	0.75	0.75	0.75	0.75
First order pool-riffle	0.75	0.66	0.66	0.66	0.66	0.75	0.75	0.75	0.75	0.75
First order plane-bed	0.75	0.66	0.66	0.66	0.66	0.75	0.75	0.75	0.75	0.75
First order step-pool	0.75	0.66	0.66	0.66	0.66	0.75	0.75	0.75	0.75	0.75
First order cascade	0.75	0.66	0.66	0.66	0.66	0.75	0.75	0.75	0.75	0.75

Insights on Metrics... *contrast metrics*

Why does contrast matter?

- Transboundary movements and implications for landscape connectivity
- Negative edge effects and implications for interior-sensitive species
- Positive edge/juxtaposition effects and implications for edge-loving species (e.g., high contrast edge specialists)



Why does contrast matter?

The contrast between a patch and its neighborhood can influence a number of important ecological processes (Forman and Godron 1986).

- The degree of contrast along an edge may influence transboundary movements, as some organisms may be reluctant to move across hard edges, with implications for landscape connectivity. Accordingly, patch isolation may be a function of the contrast between a patch and its ecological neighborhood. Similarly, an organism's ability to use the resources in adjacent patches, as in the process of landscape supplementation (Dunning et al. 1992), may depend on the nature of the boundary between the patches. The boundary between patches can function as a barrier to movement, a differentially-permeable membrane that facilitates some ecological flows but impedes others, or as a semipermeable membrane that partially impairs flows (Wiens et al. 1985, Hansen and di Castri 1992). The contrast along an edge may influence its function in this regard. For example, high-contrast edges may prohibit or inhibit some organisms from seeking supplementary resources in surrounding patches.
- Negative 'edge effects', described elsewhere, may be influenced by the degree of contrast between patches. Microclimatic changes (e.g., wind, light intensity and quality, etc.) are likely to extend farther into a patch along an edge with high structural contrast than along an edge with low structural contrast (Ranney et al. 1981). Similarly, the adverse affects of

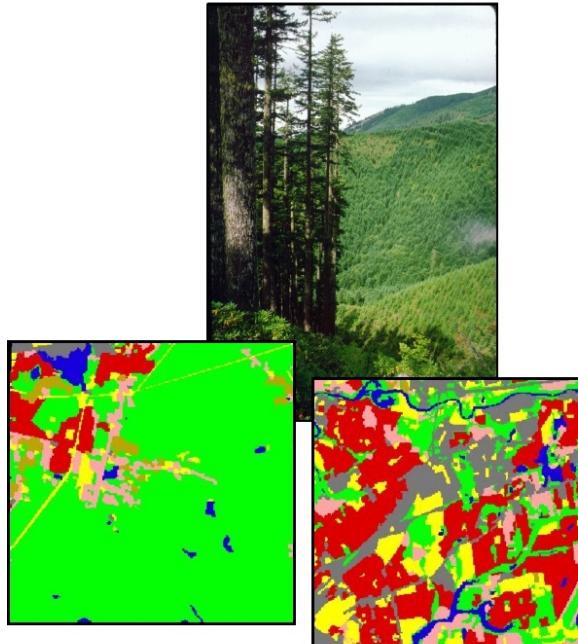
brown-headed cowbird nest parasitism on some forest-dwelling neotropical migratory bird species are likely to be greatest along high-contrast forest edges (e.g., between mature forest patches and grassland), because cowbirds prefer to forage in early-seral habitats and parasitize nests in late-seral habitats (Brittingham and Temple 1983).

- Conversely, some species (e.g., great horned owl, *Bubo virginianus*) seem to prefer the juxtaposition of patch types with high contrast, as in the process of landscape complementation (Dunning et al. 1992).

Insights on Metrics... *core vs contrast*

Recomendations:

- Ask the right question:
 - ▶ Is the focus on the edges (boundaries) themselves (e.g., boundary crossing)
 - ▶ Is the focus on adverse penetrating edge effects
- Absolute (CORE, CWED) or relative (CAI, ECON) effects



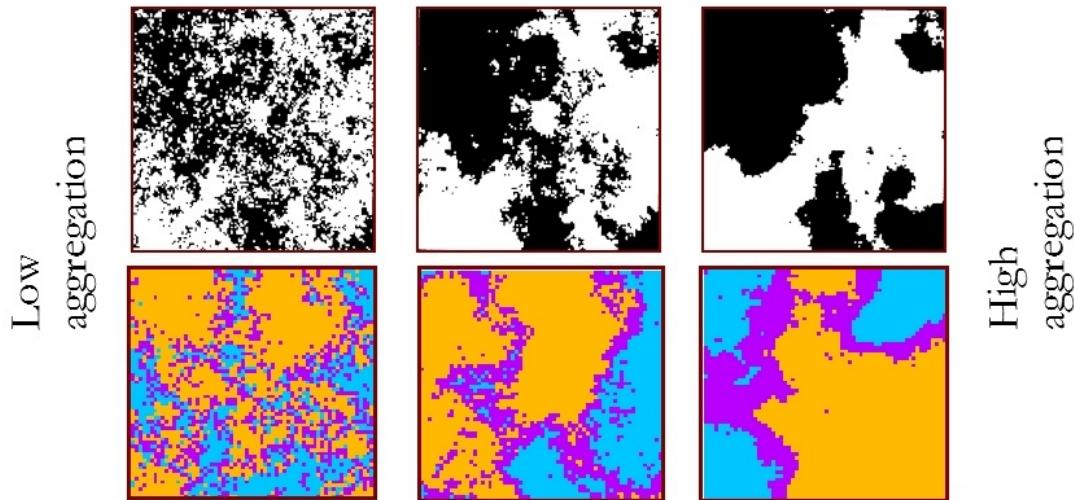
Recommendations

One of the common dilemmas in choosing edge metrics is determining whether to select core area metrics or contrast metrics. Both groups are edge metrics, but the former focus on the penetrating adverse effects of edges, whereas the latter focuses on the edges themselves as boundaries and potential impediments to movement. If the focus is on how edges influence landscape connectivity, then the contrast metrics are more likely to be appropriate, as they focus on how the boundaries between patches function. On the other hand, if the focus is on how the patchiness caused by edges reduces the interior or core environment for organisms sensitive to adverse edge effects, then the core area metrics are more likely to be appropriate.

Another dilemma involves the choice between absolute measures of core area and contrast (e.g., total core area, contrast-weighted edge density) and relative measures (e.g., core area index, edge contrast index). The former measure the total amount of core area or edge (weighted by contrast), whereas the latter measure the relative amount as a percentage of the maximum. For example, the edge contrast index measures the average contrast of the edge, regardless of how much total edge is present. Thus, the difference between the absolute and relative measures can be profound. If landscapes under comparison differ in size, then the relative measures will likely be more appropriate.

Insights on Metrics...*aggregation metrics*

Umbrella concept (also referred to as landscape texture) referring to several closely related concepts and a large collection of metrics dealing variously with the *dispersion*, *interspersion*, *subdivision* and *isolation* of patch types

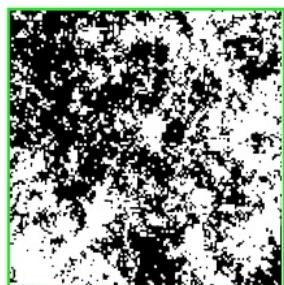


6. Aggregation Metrics

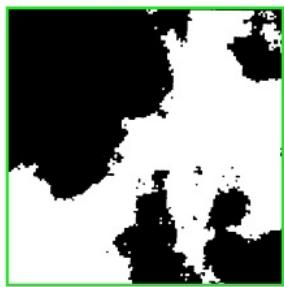
Aggregation refers to the tendency of patch types to be spatially aggregated; that is, to occur in large, aggregated or "contagious" distributions. This property is also often referred to as landscape texture. We use the term "aggregation" as an umbrella term to describe several closely related concepts: 1) dispersion, 2) interspersion, 3) subdivision, and 4) isolation. Each of these concepts relates to the broader concept of aggregation, but is distinct from the others in subtle but important ways, as discussed below.—

Insights on Metrics... *dispersion & interspersion*

Collection of metrics describing the degree of dispersion and/or interspersion of patch types



Low
aggregation



High
aggregation

- Contagion (%)
- Interspersion & Juxtaposition index (%)
- Percentage of like adjacencies (%)
- Aggregation index (%)
- Clumpiness index
- Patch cohesion index
- Landscape shape index
- Normalized landscape shape index

6.1. Dispersion and Interspersion Metrics

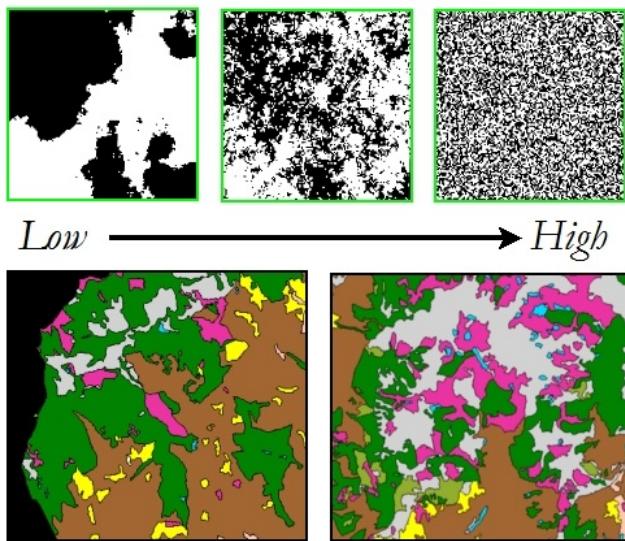
This group represents a collection of metrics that describe the degree of dispersion and/or interspersion of patch types. The common metrics in this group include the following:

- *Contagion index* (CONTAG) – extent to which patch types are aggregated or clumped as a percentage of the maximum possible; higher values of contagion may result from landscapes with a few large, contiguous patches characterized by poor dispersion and interspersion of patch types, whereas lower values generally characterize landscapes with many small patches characterized by high dispersion and interspersion (see below).
- *Interspersion and juxtaposition index* (IJI) – extent to which patch types are interspersed (not necessarily dispersed, see below) as a percentage of the maximum possible; higher values result from landscapes in which the patch types are well interspersed (i.e., equally adjacent to each other), whereas lower values characterize landscapes in which the patch types are poorly interspersed (i.e., disproportionate distribution of patch type adjacencies).
- *Percentage of like adjacencies* (PLADJ) – percentage of cell adjacencies involving the corresponding patch type that are like adjacencies (i.e., cells bordering cells of the same patch type); increasing percentage of like adjacencies implies greater aggregation of the patch type.

- *Aggregation index* (AI) – the ratio of the observed number of like adjacencies to the maximum possible number of like adjacencies given the proportion of the landscape comprised of each patch type, given as a percentage (see below).
- *Clumpiness index* (CLUMPY) – normalized index depicting the deviation from a random distribution; i.e., distinguishing distributions more uniform than random and more aggregated (or clumped) than random (see below).
- *Patch cohesion index* (COHESION) – proportional to the area-weighted mean perimeter-area ratio divided by the area-weighted mean patch shape index (i.e., standardized perimeter-area ratio); essentially, it is an area-weighted mean perimeter-area ratio, similar to PLADJ, but it is invariant to changes in the cell size and is bounded 0-1 which makes it easier to interpret and robust to changes in the grain; has the interesting property of increasing monotonically until an asymptote is reached near the critical percolation threshold, and as such has been used as a measure of continuity (Shumaker 1996).
- *Landscape shape index* (LSI) – normalized ratio of edge (i.e., patch perimeters) to area (class or landscape) in which the total length of edge is compared to a landscape with a standard shape (square) of the same size and without any internal edge; values greater than one indicate increasing levels of internal edge and corresponding decreasing aggregation of patch types.
- *normalized Landscape shape index* (LSI) – normalized version of LSI that scales the metric to range 0-1 between the theoretical minimum and maximum index values; values approaching one indicate increasing levels of internal edge and corresponding decreasing aggregation of patch types.

Insights on Metrics... *dispersion & interspersion*

Some aggregation metrics deal with the spatial property of dispersion, interspersion or both



- *Dispersion*...spatial distribution of a patch type (class)
- *Interspersion*...spatial intermixing of different patch types (classes)

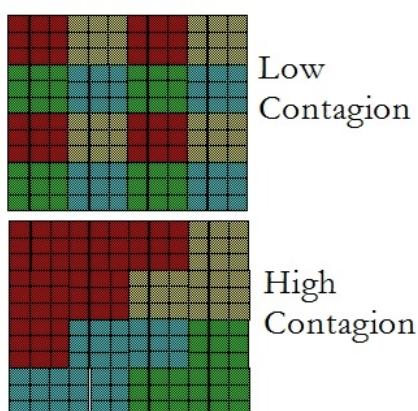
Dispersion versus Interspersion

Some aggregation metrics deal with the spatial property of dispersion or interspersion or both, and thus it is important to distinguish between these distinct components.

- *Dispersion* – refers to the spatial distribution of a patch type (class) without explicit reference to any other patch types. Dispersion deals with how spread or dispersed a patch type is. Percent like adjacencies (PLADJ), aggregation index (AI), clumpiness index (CLUMPY), patch cohesion index (COHESION), and landscape shape index (LSI and nLSI) all deal exclusively with dispersion.
- *Interspersion* – refers to the spatial intermixing of different patch types (classes) without explicit reference to the dispersion of any patch type. Interspersion deals solely with how often each patch type is adjacent to each other patch type and not by the size, contiguity or dispersion of patches. The interspersion and juxtaposition index (IJI) deals exclusively with interspersion. The contagion index (CONTAG) deals with both dispersion and interspersion.

Insights on Metrics... *dispersion & interspersion*

- Contagion (%)



Contagion Index

$$1 + \frac{\sum_{i=1}^m \sum_{k=1}^m \left\{ P_i \left(\frac{g_{ik}}{\sum_{k=1}^m g_{ik}} \right) \right\} \cdot \left\{ \ln(P_i) \left(\frac{g_{ik}}{\sum_{k=1}^m g_{ik}} \right) \right\}}{2 \ln(m)} \quad (100)$$

Landscape level

g_{ik} = # cell adjacencies between patch type i and k

Contagion index (%) gives the magnitude of landscape clumping as a percentage of the maximum; high contagion equals poorly dispersed and poorly interspersed patch types

Contagion

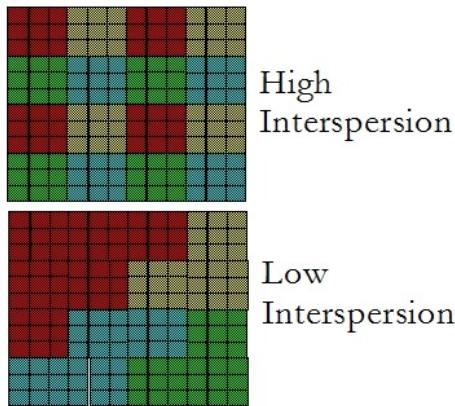
The contagion index gives the magnitude of landscape clumping as a percentage of the maximum; high contagion equals highly aggregated and poorly interspersed patch types. Contagion is based on the probability of finding a cell of type i next to a cell of type j . This index was proposed first by O'Neill et al. (1988) and subsequently it has been widely used (Turner and Ruscher 1988, Turner 1989, Turner et al. 1989, Turner 1990a and b, Graham et al. 1991, Gustafson and Parker 1992). The typical formula for contagion, based on Li and Reynolds (1993), is based on raster "cell" adjacencies, not "patch" adjacencies, and consists of the sum, over patch types, of the product of 2 probabilities: (1) the probability that a randomly chosen cell belongs to patch type i (estimated by the proportional abundance of patch type i), and (2) the conditional probability that given a cell is of patch type i , one of its neighboring cells belongs to patch type j (estimated by the proportional abundance of patch type i adjacencies involving patch type j). The product of these probabilities equals the probability that 2 randomly chosen adjacent cells belong to patch type i and j . This contagion index is appealing because of the straightforward and intuitive interpretation of this probability.

The contagion index has been widely used in landscape ecology because it seems to be an effective summary of overall clumpiness on categorical maps (Turner 1989). In addition, in many landscapes, it is highly correlated with indices of patch type diversity and dominance (Ritters et al. 1995) and thus may be an effective surrogate for those important components of pattern

(O'Neill et al. 1996). Contagion measures both patch type interspersion (i.e., the intermixing of units of different patch types) as well as patch dispersion (i.e., the spatial distribution of a patch type) at the landscape level. All other things being equal, a landscape in which the patch types are well interspersed will have lower contagion than a landscape in which patch types are poorly interspersed. Contagion measures the extent to which patch types are aggregated or clumped; higher values of contagion may result from landscapes with a few large, contiguous patches, whereas lower values generally characterize landscapes with many small and dispersed patches. Thus, holding interspersion constant, a landscape in which the patch types are aggregated into larger, contiguous patches will have greater contagion than a landscape in which the patch types are fragmented into many small patches. Contagion measures dispersion in addition to patch type interspersion because cells, not patches, are evaluated for adjacency. Landscapes consisting of large, contiguous patches have a majority of internal cells with like adjacencies. In this case, contagion is high because the proportion of total cell adjacencies comprised of like adjacencies is very large and the distribution of adjacencies among edge types is very uneven.

Insights on Metrics...*interspersion metrics*

- Interspersion & Juxtaposition index (%)



IJI Index

$$IJI = \frac{-\sum_{i=1}^m \sum_{k=i+1}^m \left[\left(\frac{e_{ik}}{E} \right) \cdot \ln \left(\frac{e_{ik}}{E} \right) \right]}{\ln(0.5[m(m - 1)])} (100)$$

Landscape level

e_{ik} = # cell adjacencies between patch type $i \neq k$

Interspersion & Juxtaposition index (%) gives the magnitude of interspersion of patch types as a percentage of the maximum given the number of patch types, independent of the area of each patch type

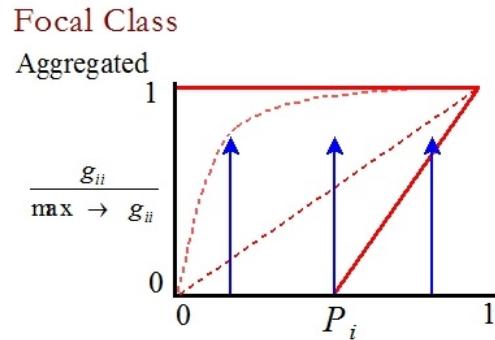
Interspersion & Juxtaposition index

The Interspersion & Juxtaposition index (%) gives the magnitude of interspersion of patch types as a percentage of the maximum given the number of patch types, independent of the area of each patch type. Note, IJI isolates the interspersion component of aggregation by focusing solely on the edges or patch perimeters (i.e., unlike cell adjacencies) and asking: “how evenly distributed are the edges among the available patch types”. Consequently, IJI is not sensitive to the spatial resolution (i.e., cell size) of the landscape, as is contagion and all the dispersion metrics based on like cell adjacencies (below).

Insights on Metrics... *dispersion metrics*

- Aggregation index (%)

$$AI = \left[\frac{g_{ii}}{\max \rightarrow g_{ii}} \right] (100)$$



Adjacency matrix

Class ID	8	5	6	7	3	9	4	background	total
8	87684	3126	2118	365	1323	1478	1224	498	97816
5	3126	33386	728	219	510	111	582	242	38904
6	2118	728	19506	161	855	216	1091	117	24792
7	365	219	161	2724	19	11	19	18	3536
3	1323	510	855	19	25370	729	1045	61	29912
9	1478	111	216	11	729	18350	68	61	21024
4	1224	582	1091	19	1045	68	42068	75	46172

Aggregation index

Like the contagion index, the aggregation index (AI) is computed from the cell adjacency matrix, in which the adjacency of patch types is first summarized in an adjacency or co-occurrence matrix, which shows the frequency with which different pairs of patch types (including like adjacencies between the same patch type) appear side-by-side on the map. The maximum number of like adjacencies is achieved when the class is clumped into a single compact patch, which does not have to be a square. The trick here is in determining the maximum value of g_{ii} for any P_i (proportion of the landscape in patch type i). The index ranges from 0 when there is no like adjacencies (i.e., when the class is maximally dissaggregated) to 1 when g_{ii} reaches the maximum (i.e., when the class is maximally aggregated).

The difficulty in interpreting the aggregation index arises from the fact that the minimum number of like adjacencies varies as a function of P_i . When $P_i < 0.5$, the minimum number or proportion of like adjacencies is 0 – when the landscape has a checkerboard like distribution. However, when $P_i > 0.5$, the minimum number or proportion of like adjacencies increases and linearly approaches the maximum number or proportion of like adjacencies with $P_i = 1$. Consequently the ability to distinguish deviations from random decrease as P_i increases beyond 0.5, making interpretation difficult. For example, an AI=0.8 could be more clumped than random or more uniform than random depending on P_i .

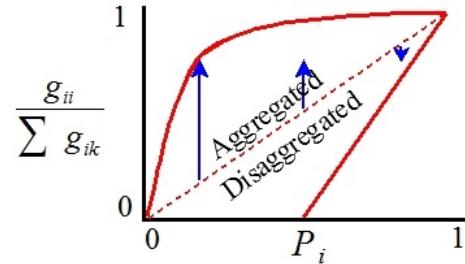
Insights on Metrics... *dispersion metrics*

- Clumpiness index (unitless)

Focal Class

$$Given \quad G_i = \left(\frac{g_{ii}}{\sum_{k=1}^m g_{ik}} \right)$$

$$CLUMPY = \begin{cases} \frac{G_i - P_i}{P_i} & \text{for } G_i < P_i \& P_i < 5; \text{ else} \\ \frac{G_i - P_i}{1 - P_i} & \end{cases}$$



Adjacency matrix

Class ID	8	5	6	7	3	9	4	background	total
8	87684	3126	2118	365	1323	1478	1224	498	97816
5	3126	33386	728	219	510	111	582	242	38904
6	2118	728	19506	161	855	216	1091	117	24792
7	365	219	161	2724	19	11	19	18	3536
3	1323	510	855	19	25370	729	1045	61	29912
9	1478	111	216	11	729	18350	68	61	21024
4	1224	582	1091	19	1045	68	42068	75	46172

Clumpiness index

The clumpiness index is also computed from the adjacency matrix, but it is computed to represent the deviation from a random distribution. Clumpiness index ranges from -1 when the patch type is maximally disaggregated to 1 when the patch type is maximally clumped. It returns a value of zero for a random distribution, regardless of P_i . Values less than zero indicate greater dispersion (or disaggregation) than expected under a spatially random distribution, and values greater than zero indicate greater contagion. Hence, this index provides a measure of class-specific contagion that effectively isolates the configuration component from the area component and, as such, provides an effective index of fragmentation of the focal class that is not confounded by changes in class area.

Insights on Metrics... *dispersion metrics*

Recommendations:



- **PLADJ** – strongly confounded with P
(not recommended)
- **COHESION** – similar to PLADJ but normalized for changes in cell size
- **LSI** – strongly confounded with P in nonlinear manner *(not recommended)*
- **nLSI** – independent of P *(percent aggregation within theoretical range given P)*
- **AI** – partially confounded with P
(percent of maximum aggregation given P)
- **CLUMPY** – independent of P *(deviation from random aggregation)*

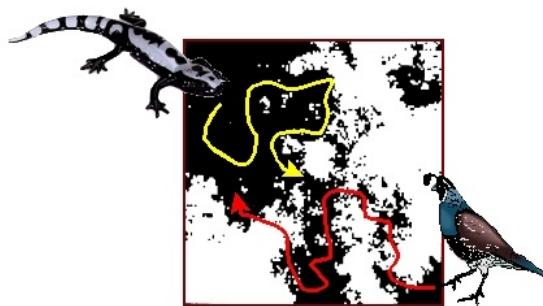
Recommendations

The choice among the metrics in this group that deal solely with the dispersion component will ultimately depend on the question and specific application. However, percentage of like adjacencies (PLADJ) confounds aggregation with the landscape composition; specifically, the percentage of the landscape comprised of the focal patch type at the class level (P) or of all patch types at the landscape level. Thus, in most applications this metric cannot be recommended. The landscape shape index (LSI) suffers from a similar confounding, but the confounding is nonlinear making interpretation even more difficult. The normalized landscape shape index (nLSI) isolates the aggregation effect from the landscape composition effect by attempting to scale LSI between the theoretical minimum and maximum values for any given level of P, but it can be biased when P is quite large (e.g., $P >> .5$) and when the landscape shape is not rectangular. The patch cohesion index (COHESION) is similar to the perimeter-to-area ratio metric (PARA, see Shape metrics) and thus is also confounded with P (like PLADJ), but it is invariant to changes in the cell size and is bounded 0-1, which makes it easier to interpret and robust to changes in the grain. The aggregation index (AI) is similarly confounded, but its formulation accounts for the expected maximum aggregation given the abundance of a patch type, making it a useful index when it is meaningful to measure the deviation from maximum clumping. The clumpiness index (CLUMPY) is the only aggregation index that isolates the aggregation effect from the landscape composition effect and is unaffected by the shape of the landscape, and thus it offers a useful index of aggregation independent of patch type abundance.

Insights on Metrics... *dispersion & interspersion*

Why do dispersion & interspersion matter?

- Population subdivision and implications for metapopulation dynamics
- Edge effects and implications for interior-sensitive species and ecosystem integrity
- Juxtaposition effects and implications for multi-habitat species
- Landscape continuity and implications for spread of disturbances



Dispersion is a fundamental property of the landscape and is central to the study of habitat fragmentation

Why does dispersion and interspersion matter?

The dispersion and/or interspersion of a landscape is a fundamental aspect of landscape pattern and is important in many ecological processes.

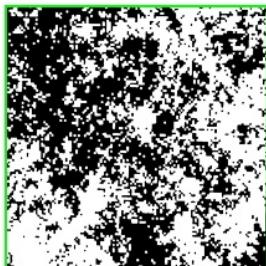
- The disaggregation of a patch type plays a crucial role in the process of habitat fragmentation. Specifically, habitat fragmentation involves the disaggregation and subdivision of contiguous habitat into disaggregated and/or disjunct patches. As habitat fragmentation proceeds, habitat contagion decreases, habitat disaggregation increases, and eventually ecological function is impaired (Saunders et al. 1991). Specifically, the subdivision and isolation of populations caused by this fragmentation can lead to reduced dispersal success and patch colonization rates which may result in a decline in the persistence of individual populations and an enhanced probability of regional extinction for entire populations across the landscape (e.g., Lande 1987; With and King 1999a,b; With 1999).
- One of the primary ecological consequences of aggregation seems to be related to ‘edge effects’, which has implications for interior-sensitive species, edge species, and ecosystem integrity.
- Interspersion is presumed to affect the quality of habitat for many species that require different patch types to meet different life history requisites, as in the process of landscape

complementation (Dunning et al. 1992). Indeed, the notion of habitat interspersion has had a preeminent role in wildlife management during the past century. Wildlife management efforts are often focused on maximizing habitat interspersion because it is believed that the juxtaposition of different habitats will increase species diversity (Leopold 1933).

- Lastly, the dispersion and interspersion of patch types may affect the propagation of disturbances across a landscape (Franklin and Forman 1987). Specifically, a patch type that is highly disaggregated and/or subdivided may be more resistant to the propagation of some disturbances (e.g., disease, fire, etc.), and thus more likely to persist in a landscape than a patch type that is highly aggregated and/or contiguous. Conversely, highly disaggregated and/or subdivided patch types may suffer higher rates of disturbance for some disturbance types (e.g. windthrow) than more aggregated and /or contiguous distributions.

Insights on Metrics...*subdivision metrics*

Collection of metrics describing the degree of subdivision of the class or landscape



High subdivision



Low subdivision

- Number of patches (#) or patch density (#/ha)
- Landscape division index
- Splitting index
- Effective mesh size (ha)

Based on the notion that two animals, placed randomly in different areas somewhere in a region, will have a certain likelihood of being in the same patch

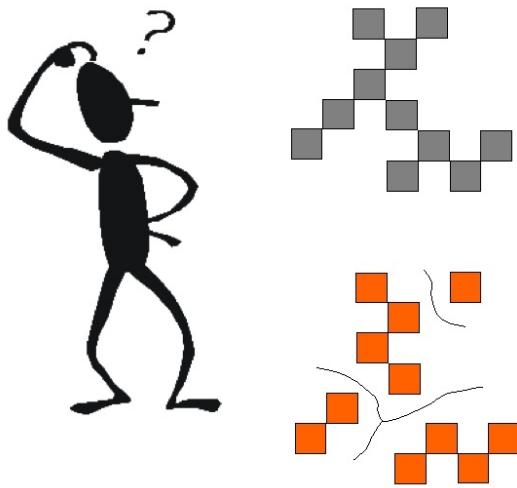
6.2. Subdivision Metrics

This group represents a collection of metrics closely allied to the aggregation metrics that describe the degree of subdivision of the class or landscape. Most of the metrics in this group are based on the notion that two animals, placed randomly in different areas somewhere in a region, will have a certain likelihood of being in the same patch, which is a function of the degree of subdivision of the landscape (Jaeger 2000). The metrics in this group include the following:

- *Number of patches* (NP) or *patch density* (PD) – number (#) or density (#/ha) of patches at the class or landscape level.
- *Landscape division index* (DIVISION) – probability that two randomly chosen places in the landscape are not situated in the same patch (see below).
- *Splitting index* (SPLIT) – number of patches one gets when dividing the total landscape into patches of equal size in such a way that this new configuration leads to the same degree of landscape division as obtained for the observed cumulative area distribution; in other words, the number of patches obtained with subdividing the landscape into equal-sized patches based on the effective mesh size (below).
- *Effective mesh size* (MESH) – size (ha) of the patch that can be accessed from a random cell without leaving the patch; in other words, the area-weighted mean patch size.

Insights on Metrics... *subdivision metrics*

Subdivision and aggregation are closely related but different concepts



These two configurations have the same level of *aggregation* based on all of the cell adjacency metrics (which consider only orthogonal neighbors), but clearly have a different degree of *subdivision* per se

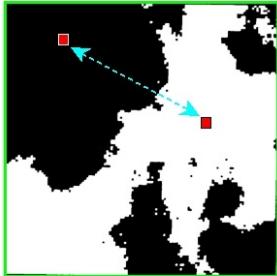
In most real-world landscapes, these components of pattern are highly correlated (confounded)

Subdivision versus aggregation

Subdivision and aggregation are very closely related concepts. Both refer to the aggregation of patch types, but subdivision deals explicitly with the degree to which patch types are broken up (i.e., subdivided) into separate patches (i.e., fragments), whereas the concept and measurement of aggregation does not honor patches per se. In most real-world landscapes, however, these components of pattern are highly correlated (and thus confounded).

Subdivision can be evaluated using a wide variety of metrics already described; for example, the number, density, and average size of patches and the degree of contagion all indirectly relate to subdivision. However, these metrics have been criticized for their insensitivity and inconsistent behavior across a wide range of subdivision patterns. Jaeger (2000) discussed the limitations of these metrics for evaluating habitat fragmentation and concluded that most of these metrics do not behave in a consistent and logical manner across all phases of the fragmentation process. He introduced a suite of metrics derived from the cumulative distribution of patch sizes that provide alternative and more explicit measures of subdivision. When applied at the class level, these metrics can be used to measure the degree of fragmentation of the focal patch type. Applied at the landscape level, these metrics measure the graininess of the landscape; i.e., the tendency of the landscape to exhibit a fine- versus coarse-grain texture.

Insights on Metrics... *subdivision metrics*

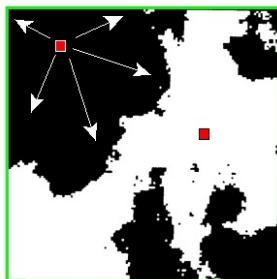


Landscape division index

$$1 - \sum_{j=1}^n \left(\frac{a_{ij}}{A} \right)^2$$

Class level

The *probability* that two randomly chosen pixels in the *landscape* are not situated in the same patch



Effective mesh size

$$\sum_{j=1}^n \frac{a_{ij}^2}{A}$$

Class level

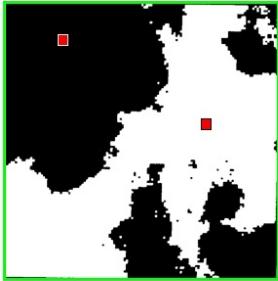
The contiguous patch *area* that can be accessed from a randomly chosen pixel (i.e., w/o leaving the patch)

Landscape division index versus effective mesh size

All of these metrics are based on the notion that two animals, placed randomly in different areas somewhere in a region, will have a certain likelihood of being in the same undissected area (i.e., the same patch), which is a function of the degree of subdivision of the landscape. The *landscape division index* (DIVISION) is based on the degree of coherence (C), which is defined as the probability that two animals placed in different areas somewhere in the region of investigation might find each other. Degree of coherence is based on the cumulative patch area distribution and is represented graphically as the area above the cumulative area distribution curve. Degree of coherence represents the probability that two animals, which have been able to move throughout the whole region before the landscape was subdivided, will be found in the same patch after the subdivision is in place. The degree of landscape division is simply the complement of coherence and is defined as the probability that two randomly chosen places in the landscape are not situated in the same undissected patch. Graphically, the degree of landscape division is equal to the area below the cumulative area distribution curve.

The *effective mesh size* (MESH) simply denotes the size of the patches when the landscape is divided into S areas (each of the same size) with the same degree of landscape division as obtained for the observed cumulative area distribution; in other words, the contiguous patch area that can be accessed from a randomly chosen cell without leaving the patch.

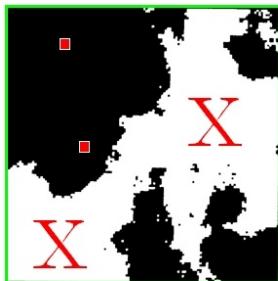
Insights on Metrics... *subdivision metrics*



Effective mesh size

$$\sum_{j=1}^n \frac{a_{ij}^2}{A}$$

Class level



Area-weighted mean patch size

$$\sum_{j=1}^n \left(\frac{a_{ij}^2}{\sum_{j=1}^n a_{ij}} \right)$$

Class level

Based on the *probability* that two randomly chosen pixels in the *landscape* are not situated in the same patch

Based on the *probability* that two randomly chosen pixels in the *class* are not situated in the same patch

Effective mesh size versus area-weighted mean patch size

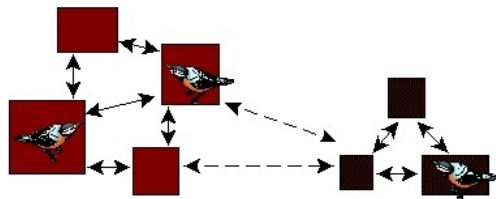
All three subdivision metrics are easily computed from the cumulative patch area distribution. These measures have the particular advantage over other conventional measures of subdivision (e.g., mean patch size, patch density) in that they are insensitive to the omission or addition of very small patches. In practice, this makes the results more reproducible as investigators do not always use the same lower limit of patch size. Jaeger (2000) argues that the most important and advantageous feature of these new measures is that effective mesh size is ‘area-proportionately additive’; that is, it characterizes the subdivision of a landscape independently of its size.

In fact, these three measures are closely related to the area-weighted mean patch size (AREA_AM) discussed previously, and under certain circumstances are perfectly redundant. At the landscape level, these two metrics are identical. At the class level, they differ in a subtle but important way. Effective mesh size is based on the probability that two randomly chosen pixels in the *landscape* are not in the same patch. Note, here the landscape includes the entire landscape, not just the focal patch type. Conversely, area-weighted mean patch size is based on the probability that two randomly chosen pixels in the focal patch type (class) are not situated in the same patch. Here, the probability is limited to the focal class. As a consequence, the two metrics have a different probabilistic interpretation.

Insights on Metrics...*subdivision metrics*

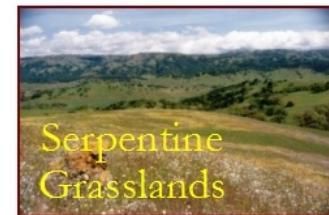
Why does subdivision matter?

- Population subdivision and implications for metapopulation dynamics
- Landscape continuity and implications for spread of disturbances



Subdivision is central to the study of habitat fragmentation

Bay Checkerspot Butterfly
(*Euphydryas editha bayensis*)

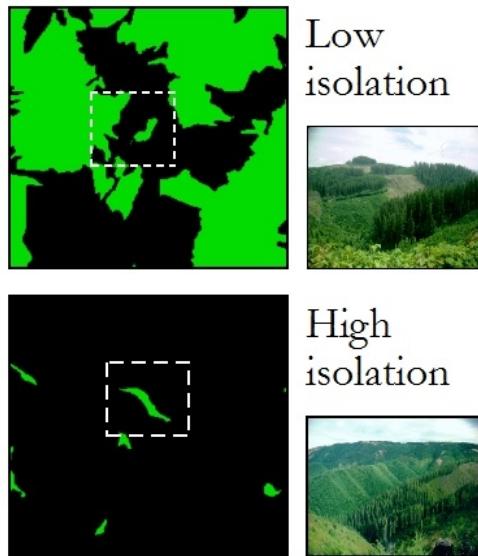


Why does subdivision matter?

Subdivision is important for the same reasons as aggregation, but here the importance is related more to the subdivision of populations (and implications for metapopulation dynamics) and the disruption of landscape continuity and connectivity with implication for population persistence, ecosystem integrity and the spread of disturbances. Note, subdivision is a central concept in the study of habitat fragmentation.

Insights on Metrics...*isolation metrics*

Collection of metrics describing the degree of spatial isolation of patches



- Euclidean nearest neighbor distance (m)
 - Connectance index (%)
 - Proximity index
 - Similarity index
-
- Similarity index
 - Connectedness
 - Traversability

Cell level metrics

6.3. Isolation Metrics

This group represents a collection of metrics closely allied to the subdivision (and thus aggregation) metrics that describe the degree of spatial isolation of patches. Some of the metrics in this group include the following:

- *Euclidean nearest neighbor distance* (ENN) – shortest straight-line distance (m) between a focal patch and its nearest neighbor of the same class, summarized at the patch, class or landscape levels.
- *Connectance index* (CONNECT) – number of functional joins between patches of the same type (class), where each pair of patches is either connected or not based on some criterion, as a percentage of the maximum possible number joins (see below).
- *Proximity index* (PROX) – sum, over all patches of the corresponding patch type whose edges are within the search radius of the focal patch, of each patch size divided by the square of its distance from the focal patch; quantifies the spatial context of a (habitat) patch in relation to its neighbors of the same class; specifically, the index distinguishes sparse distributions of small habitat patches from configurations where the habitat forms a complex cluster of larger patches.

- *Similarity index* (SIMI) – same as proximity index except considering the size, proximity and similarity of all patches within a specified search radius of the focal patch (see below).

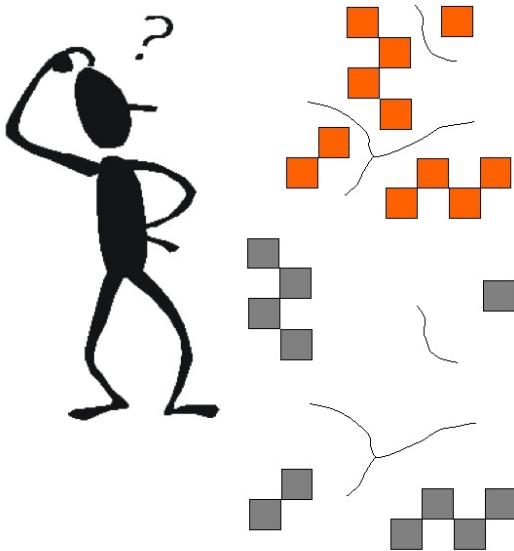
Cell-level metrics:

There are several useful cell-level isolation metrics that are distinct from the patch-based metrics above in that the algorithm is applied to each focal cell independent of patch membership per se, and thus each cell can take on a unique value.

- *Similarity index* (SIMILAR) – cell metric based on a standard kernel in which each neighboring cell is weighted by the kernel distance from the focal cell (according to the shape and width of the chosen kernel) multiplied by the similarity (0-1) between the focal cell and each neighboring cell; gives the similarity of the neighborhood of the each focal cell when access to the neighboring cells is not considered limiting; e.g., as in the case of highly vagile organisms that can easily cross non-habitat.
- *Connectedness index* (CONNECTED) – cell metric based on a resistance-weighted spread algorithm (i.e., resistant kernel); resistant kernel is built from each neighboring cell and multiplied by the similarity (0-1) between the focal cell and each neighboring cell (i.e., depressing the kernel surface by the magnitude of dissimilarity with the focal cell), and then summed across kernels at the focal cell; gives the magnitude of flow to the focal cell from neighboring cells similar to the focal cell.
- *Traversability index* (TRAVERSE) – cell metric based on a resistance-weighted spread algorithm (i.e., resistant kernel) to determine the area that can be reached from each cell, expressed as a proportion of the maximum dispersal area under conditions of minimum resistance.

Insights on Metrics...*isolation metrics*

Isolation and subdivision (and thus aggregation) are closely related but different concepts



These two configurations have the same level of *subdivision* based on the number of disjunct patches, but clearly have a different degree of patch *isolation*

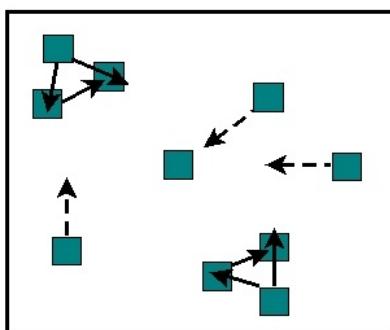
In most real-world landscapes, these components of pattern are highly correlated (confounded)

Isolation versus subdivision

Isolation and subdivision (and thus aggregation) are very closely related concepts. Both isolation and subdivision refer to the subdivision per se of patch types, but isolation deals explicitly with the degree to which patches are spatially isolated from each other, whereas subdivision doesn't address the distance between patches, only that they are disjunct. In most real-world landscapes, however, these components of pattern are highly correlated (and thus confounded).

Insights on Metrics...*isolation metrics*

- Connectance index (%)



Connectance Index

$$\frac{\sum_{i=1}^m c_{ij}}{N(N-1)} \quad \text{Class level}$$

Connectance index (%) gives the percentage of all possible inter-patch connections less than a specified threshold distance, where distance is either Euclidean or functional based on least cost path distance on a resistant surface

Connectance index

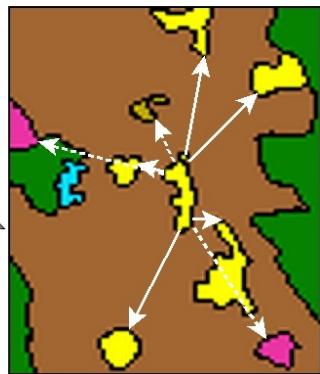
The connectance index measures the number of functional joins between patches of the same type (class), where each pair of patches is either connected or not based on a user-specified nearest neighbor distance criterion, as a percentage of the maximum number of possible joins. The threshold distance can be based on either Euclidean (straight line) distance or functional distance based on least cost paths on a resistant surface (currently not implemented in FRAGSTATS). The metric can be computed at the class or landscape level.

Insights on Metrics...*isolation metrics*

- Similarity index



User-specified neighborhood



Similarity Index

$$\frac{\sum_{j=1}^n \sum_{s=1}^n \frac{a_{ijs} \cdot d_{ik}}{h_{ijs}^2}}{n_i}$$

Class level

	$d_{11} = 1.0$
	$d_{12} = 0.5$
	$d_{13} = 0.2$

Similarity index (unitless) gives the cumulative area of neighboring patches weighted by degree of similarity and distance within a user-specified distance of each focal patch

Similarity index

The similarity index is a modification of the proximity index. The proximity index considers the size and proximity of all patches of the same class as the focal patch whose edges are within a specified search radius of the focal patch. The area of each patch of the same class as the focal patch whose nearest edge is within the user-specified radius of the focal patch is summed after weighting by the square of its distance. Thus, larger and closer patches contribute more to the value of the index than small and distant patches. The similarity index on the other hand considers the size and proximity of all patches, regardless of class, whose edges are within a specified search radius of the focal patch. Each neighboring patch is considered weighted by the user-defined similarity between patch types. Thus, a neighboring patch with a similarity weight of 1 is given full consideration, whereas a neighboring patch with a similarity weight of 0.2 is given only 20% consideration. In this manner, the similarity index quantifies the spatial context of a (habitat) patch in relation to its neighbors of the same or similar class; specifically, the index distinguishes sparse distributions of small and insular habitat patches from configurations where the habitat forms a complex cluster of larger, hospitable (i.e., similar) patches. All other things being equal, a patch located in a neighborhood (defined by the search radius) deemed more similar (i.e., containing greater area in patches with high similarity) than another patch will have a larger index value. Similarly, all other things being equal, a patch located in a neighborhood in which the similar patches are distributed in larger, more contiguous, and/or closer patches than another patch will have a larger index value.

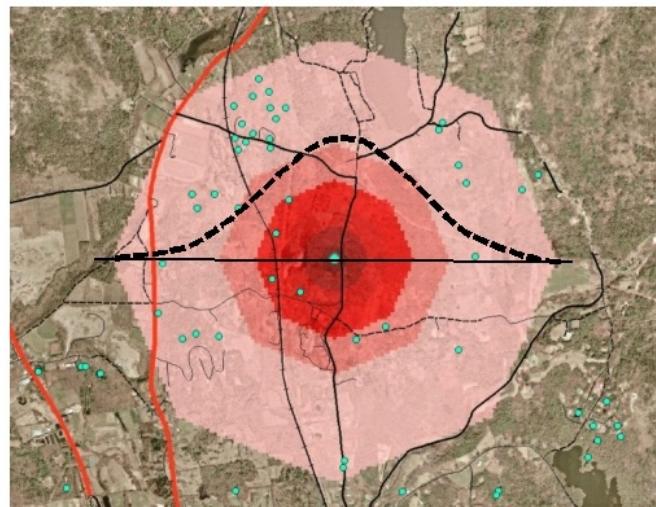
Insights on Metrics...*isolation metrics*

■ Similarity index (cell-level metric)

Based on a
standard kernel
algorithm

Similarity index (%) gives the proportional similarity of the ecological neighborhood of a focal cell, where neighboring cells are weighted by their kernel distance and by their similarity (0-1) to the focal cell

Standard Gaussian kernel

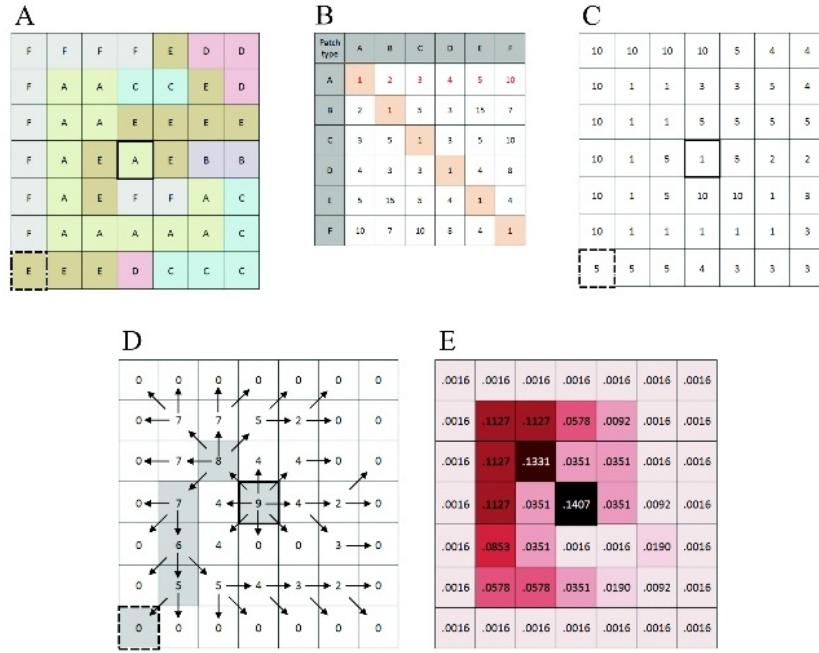


Similarity index (cell-level metric)

In the similarity index at the cell level, a standard kernel is superimposed over each focal cell; the kernel weights are multiplied by the user-defined degree of similarity (0-1) to the focal cell, and then summed across all cells in the kernel. The result is an index of similarity of the ecological neighborhood of the focal cell, whereby it approaches zero if the entire neighborhood is maximally dissimilar and reaches a maximum of one if the entire neighborhood is maximally similar. Note, this index uses a "standard kernel", which radiates outward from the focal cell according to the specified shape and width of the kernel, regardless of the character of the surrounding landscape. For example, a standard Gaussian kernel extends outward in all directions from the focal cell according to a normal function and produces a bell-shaped kernel over the focal cell, regardless of the composition of the neighboring cells. In this manner, it is assumed that every cell in the kernel is accessible to the organism or process under consideration and that accessibility varies solely as a function of the shape and width of the kernel. This makes sense for highly vagile organisms and processes where accessibility to the ecological neighborhood is not limited by landscape features. For example, some bird species might be able to easily cross inhospitable roads and other land cover features to access favorable habitat that is within a certain distance. In this case, the use of a standard kernel makes sense. However, for many organisms and processes, access to areas within their range of vagility may be more limiting and the use of a standard kernel may not be meaningful. In such cases, we can instead apply a "resistant kernel", as described next.

Insights on Metrics...*isolation metrics*

■ Connectedness index (cell-level metric)



Based on a
resistant kernel
algorithm

Connectedness index (cell-level metric)

Isolation can be measured at the cell level using a resistant kernel instead of a standard kernel. The resistant kernel estimator, introduced by Compton et al. (2007), is a hybrid between two existing approaches: the standard kernel estimator (described previously) and least-cost paths based on resistant surfaces. The resistant kernel estimator begins by placing a standard kernel over each sample point. Here, we can think of the standard kernel as estimating the ecological neighborhood of a focal cell (or sample point). Resistant surfaces (also referred to as cost surfaces) are being increasingly used in landscape ecology, replacing the binary habitat/nonhabitat classifications of island biogeography and classic metapopulation models with a more nuanced approach that represents variation in habitat quality (e.g., Ricketts 2001). In a patch mosaic, a resistance value (or cost) is assigned to each patch type, typically representing a divisor of the expected rate of ecological flow (e.g., dispersing or migrating animals) through a patch type. For example, a forest-dependent organism might have a high rate of flow (and thus low resistance) through forest, but a low rate of flow (and thus high resistance) through high-density development. In this case, the cost assigned to each patch type in the resistant surface may represent the willingness of the organism to cross the patch type, the physiological cost of moving through the patch type, the reduction in survival for the organism moving through the patch type, or an integration of all these factors. Empirical data on costs are often lacking, but can be derived from a variety of data sources, including location, movement and/or genetic data for the organism (or process) under consideration. Traditional least-cost path analysis finds the

shortest functional distance between two points based on the resistant surface. The cost distance (or functional distance) between two points along any particular pathway is equal to the cumulative cost of moving through the associated cells. Least-cost path analysis finds the path with the least total cost. This least-cost path approach can be extended to a multidirectional approach that measures the functional distance (or least-cost path distance) from a focal cell to every other cell in the landscape. In the resistant kernel estimator, the complement of least-cost path distance (a.k.a. functional proximity; see below) to each cell from the focal cell is multiplied by a weight reflecting the shape and width of the standard kernel. The result is a resistant kernel that depicts the functional ecological neighborhood of the focal cell. In essence, the standard kernel is an estimate of the fundamental ecological neighborhood and is appropriate when resistant to movement is irrelevant (e.g., highly vagile species), while the resistant kernel is an estimate of the realized ecological neighborhood when resistance to movement is relevant.

The resistant kernel is derived as follows, as shown in the figure:

1. First, given a patch mosaic (Fig. A), assign a cost to each patch type. Note, the cost matrix (Fig. B) represents the relative cost of moving through each patch type from an initial patch type, and it need not be symmetrical. For example, the cost matrix in figure B is read as follows. The row heading represents the "from" patch type, and the column heading represents the "to" patch type. Thus, the first row of the matrix is read as follows: from a focal cell of patch type A, the cost of moving through a cell of the same patch type (A) is one (the minimum cost); the cost of moving through a cell of patch type B is two (i.e., two times more costly than moving through a cell of patch type A); the cost of moving through a cell of patch type C is three (i.e., three times more costly than A), and so on. The costs are user-defined and can take on any values, as long as the minimum cost (and the cost of moving through a cell of the same patch type) is one. Thus, the diagonal elements of the matrix are always set to one, but the off-diagonals can take on any value greater than one.
2. Next, for a focal cell generate a resistant (or cost) surface by assigning the relevant cost to each cell based on the cost matrix (Fig. C). For example, the focal cell in figure C is of patch type A, so the costs assigned to each cell are based on the information in the first row of the cost matrix corresponding to "from" patch type A. Note, the resistant surface will change depending the patch type of the focal cell.
3. Next, assign to the focal cell a "bank account" based on the width of the standard kernel, and spread outward to adjacent cells iteratively, depleting the bank account at each step by the minimum cost of spreading to each cell (Fig. D). For illustrative purposes, let's say that the grid cell size in the figure is 10 m and we wish to create a resistant Gaussian kernel with a bandwidth h (equal to one standard deviation) of 30 m (three cells). Further, let's say that we want the Gaussian kernel to extend outward to no more three standard deviations ($3h$; 90 m or nine cells), since beyond that distance the landscape has only a trivial influence on the focal cell. Given these parameters, we start with a bank account of nine, since at the minimum cost of one of moving through a single cell, the kernel will extend outward nine cells. Starting with a bank account of nine in the focal cell, if we move to an adjacent cell of patch type F (cost of 10, Fig. B), we

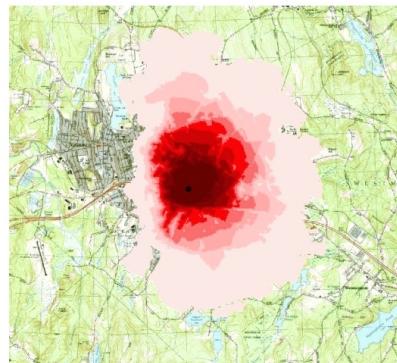
reduce the bank account by ten and assign a balance of zero (since negative accounts are not allowed) to that cell. This means that we use up our entire bank account if we attempt to move through a cell of patch type F and can spread no further from that cell. On the other hand, if we move to an adjacent cell of patch type A (cost of one; Fig. B), we reduce the bank account by one and assign a balance of eight to that cell. For simplicity in this illustration, diagonal paths are treated the same as orthogonal paths; in the model diagonal costs are multiplied by 1.4. Note, an artifact of weighting the diagonal neighbors in this manner and using a cellular automata approach (in which distance is measured in a zig-zag like manner instead of straight line) is an octagonal shaped standard kernel. This process is repeated iteratively, spreading outward in turn from each visited cell, each time finding the least cost of getting to that cell from any of its neighbors, until the balance reaches zero. This produces a functional proximity surface representing the proximity of every cell to the focal cell within a threshold proximity distance. Note the difference between functional proximity and least cost path distance. Functional proximity decreases as you move away from the focal cell, whereas least-cost path distance increases -- they are complementary measures of distance. In addition, note that the proximity surface has embedded within it the least cost path to each cell.

4. Next, multiply the cell values in the proximity surface by weights derived from the specified kernel function. This actually involves three steps. First, based on the specified kernel function, transform the proximity values into number of bandwidths from the focal cell. For example, for a Gaussian kernel, transform the proximity values into number of standard deviation units from the focal cell, such that in our example, a proximity value of nine (focal cell) is equal to zero and a proximity value of zero (cells at the periphery of the kernel) is equal to three. Second, based on the specified kernel function, compute the probability density for the value derived above. For example, for a Gaussian kernel, compute the probability density for each value based on a normal distribution with a mean of zero and standard deviation of one. Third, divide these values by a constant equal to the sum of the values above for a standard kernel (or resistant kernel in a non-resistant landscape). Note, the constant above ensures that the volume of a standard kernel (or resistant kernel in a non-resistant landscape) is equal to one. The resulting surface is the resistant kernel and its volume is always less than or equal to one (Fig. E).

Insights on Metrics...*isolation metrics*

- Connectedness index (cell-level metric)

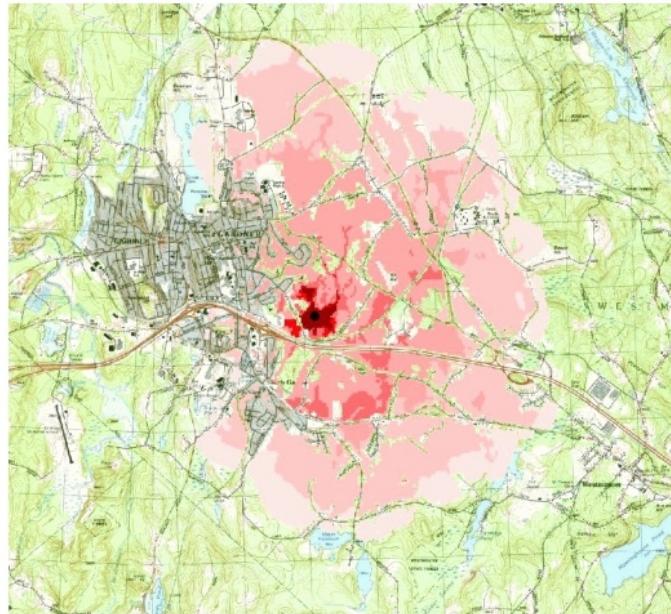
- ▶ For each focal cell, build a *resistant kernel*;
- ▶ multiply the kernel values by the similarity (0-1) between the focal cell and each neighboring cell;
- ▶ sum across the resulting values.



Insights on Metrics...*isolation metrics*

■ Connectedness index (cell-level metric)

- ▶ For each focal cell, build a *resistant kernel*;
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- ▶ sum across the resulting values.

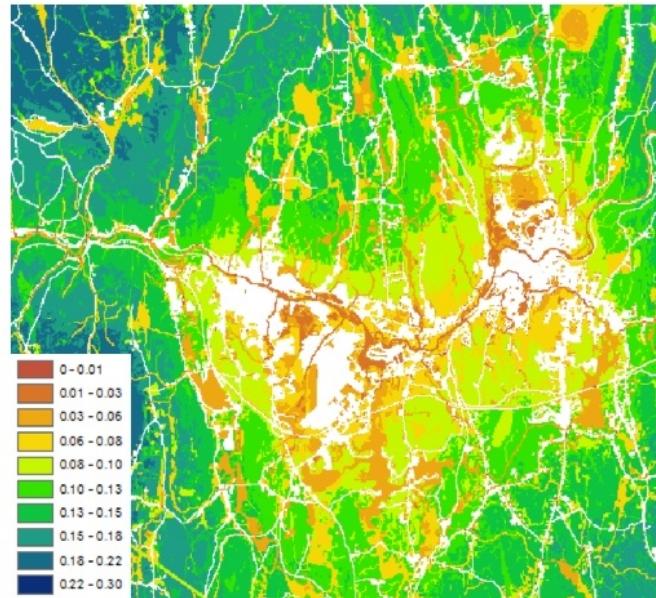


5. Next, multiply the resistant kernel values by the similarity (0-1) between the focal cell and each neighboring cell. Specifically, each neighboring cell is down-weighted by the degree of similarity with the focal cell. Thus, if the neighboring cell has a similarity weight of 1.0, it is given the full value of the resistant kernel. If, on other hand, the neighboring cell has a similarity weight of 0.2, it is given only 20% of the value of the resistant kernel. Ultimately, this step involves depressing the resistant kernel surface proportionate to the degree of similarity between each neighboring cell and the focal cell.

Insights on Metrics...*isolation metrics*

■ Connectedness index (cell-level metric)

- ▶ For each focal cell, build a *resistant kernel*;
- ▶ multiply the kernel values by the similarity (0-1) between the focal cell and each neighboring cell;
- ▶ sum across the resulting values.



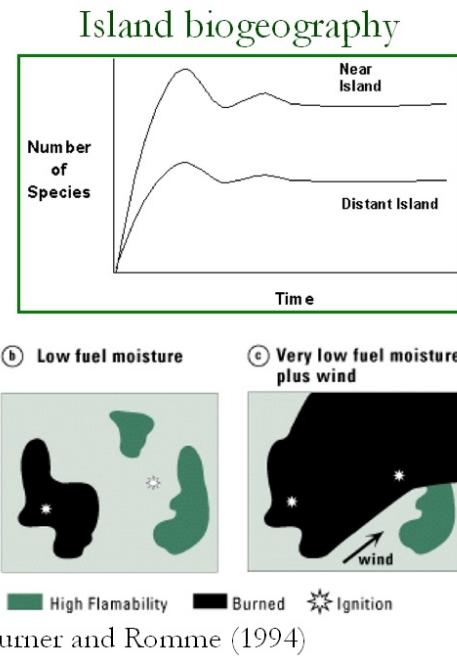
6. Lastly, at each focal cell, sum across the kernel surfaces derived above from all the neighboring cells. This represents the amount of flow to the focal cell from neighboring cells weighted by their ecological distance (as represented by the kernel shape and width) and their similarity (as represented by the similarity weights).

Note, the *connectedness index* is identical to the similarity index described above, except that it uses a resistant kernel instead of a standard kernel. As such, it seeks to distinguish neighborhoods that are both highly similar and accessible from those that are either highly dissimilar or highly similar but inaccessible. The difference between the similarity index and connectedness index is important and is based on the difference between a standard kernel and a resistant kernel. The former does not consider accessibility to neighboring cells, while the latter does. Consider two scenarios: a focal cell of forest surrounded by contiguous forest, and a focal cell adjacent to an expressway (of high resistance) with extensive forest on the other side. The similarity index for the focal cell would not differ significantly between scenarios because the majority of the neighborhood in both cases is forest. However, the connectedness index for the focal cell would differ significantly between scenarios because in the second scenario the forest on the other side of the expressway would be relatively inaccessible as expressed through the resistant kernel.

Insights on Metrics...*isolation metrics*

Why does isolation matter?

- Population isolation and implications for metapopulation dynamics
- Landscape continuity and implications for spread of disturbances



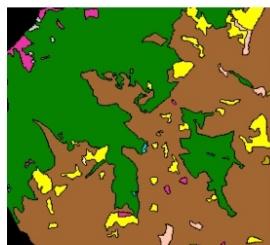
Why does isolation matter?

Isolation deals explicitly with the spatial (and ideally temporal) *context* of habitat patches, rather than the spatial character of the patches themselves, and is important in many ecological processes:

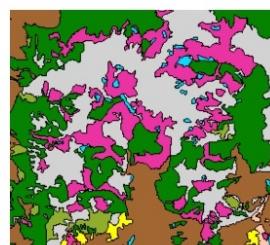
- Isolation of habitat patches is a critical factor in the dynamics of spatially structured populations (metapopulations) and community dynamics (e.g., predator-prey dynamics, island biogeography).
- Isolation is particularly important in the context of habitat fragmentation as it relates to the disruption of habitat continuity and connectivity which can vary in relation to species' life history.
- Isolation is important to the spread of disturbances across the landscape as it can disrupt the continuity of susceptible patches (e.g., host plants for an insect/pathogen, fuels for wildfire).

Insights on Metrics... *diversity metrics*

Collection of metrics describing the compositional makeup of the landscape



Low diversity



High diversity

- Richness
 - ▶ Patch richness (#)
 - ▶ Patch richness density (#/ha)
 - ▶ Relative patch richness (%)
- Evenness
 - ▶ Shannon's evenness index
 - ▶ Simpson's evenness index
- Diversity
 - ▶ Shannon's diversity index
 - ▶ Simpson's evenness index

7. Diversity Metrics

This group represents a collection of metrics that describe the compositional makeup of the landscape. These are entirely nonspatial measures of the landscape that deal with the number and area of patch types (classes) at the landscape level. Some of the metrics in this group include:

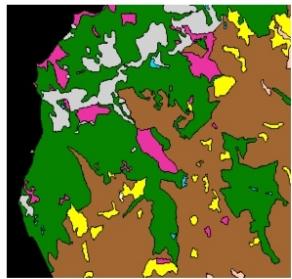
- Richness – refers to the number or variety of patch types present in a landscape, formulated in the following ways:
 - ▶ *Patch richness* (PR) – number (#) of patch types present.
 - ▶ *Patch richness density* (PRD) – standardizes richness to a per area basis (#/ha) that facilitates comparison among landscapes, although it does not fully correct for the species (patch type)-area relationship in which the number of species (patch types) increases nonlinearly with landscape area.
 - ▶ *Relative patch richness* (RPR) – percentage of the maximum potential richness given a user-specified number of patch types.
- Evenness – based on the distribution of area among patch types and typically given as the observed level of diversity (see below) divided by the maximum possible diversity given the patch richness, which equals one when the area is distributed evenly among patch types:
 - ▶ *Shannon's evenness index* (SHEI) – proportion of maximum Shannon's diversity index

(below).

- ▶ *Simpson's evenness index* (SIEI) – proportion of maximum Simpson's diversity index (below).
- Diversity – compound measure of landscape diversity based on the richness and evenness of patch types, and indexed by a variety of measures, including the following:
 - ▶ *Shannon's diversity index* (SHDI) – based on information theory; represents the amount of "information" per individual (or patch type, in this case); larger values indicate a greater number of patch types and/or greater evenness among patch types.
 - ▶ *Simpson's diversity index* (SIDI) – probability that any two cells selected at random would be different patch types; the larger the value the greater the likelihood that any 2 randomly drawn cells would be different patch types (see below).

Insights on Metrics... *diversity metrics*

■ Simpson's diversity index



Mixed Conifer	45%
Spruce-Fir	42%
Aspen	5%
Shrubland	4%
Nonforested	4%

Simpson's Diversity Index

$$1 - \sum_{i=1}^m P_i^2$$

Landscape level

Simpson's diversity index gives the probability that any two pixels drawn at random will be of different patch types (classes)

Simpson's diversity index

Simpson's diversity index is a popular diversity measure that is not based on information theory (Simpson 1949). Simpson's index is calculated as one minus the sum of the proportional areas of each patch type squared. Simpson's index is less sensitive to the presence of rare types and has an interpretation that is much more intuitive than Shannon's index. Specifically, the value of Simpson's index represents the probability that any two cells selected at random would be different patch types. Thus, the higher the value the greater the likelihood that any 2 randomly drawn cells would be different patch types. Because Simpson's index is a probability, it can be interpreted in both absolute and relative terms.

Insights on Metrics... *diversity metrics*

Why does diversity matter?

- Biodiversity is partly a function of gamma (landscape) diversity
- Resistance and resilience to disturbances, e.g., diseases and pathogens, and stressors, e.g., climate change



Why does diversity matter?

Diversity measures have been used extensively in a variety of ecological applications. While diversity expresses no information about the spatial configuration of the landscape, it expresses critical information about the landscape composition, but does so without taking into account the uniqueness or potential ecological, social, or economical importance of individual patch types. A landscape may have high diversity yet be comprised largely of common or undesirable patch types. Conversely, a landscape may have low diversity yet be comprised of especially unique, rare, or highly desired patch types. Despite these limitations, diversity is often viewed as a critical aspect of landscape structure:

- ▶ Biodiversity is generally considered to be partly a function of gamma or landscape diversity, as many organisms may be associated with a single patch type as defined.
- ▶ Landscape diversity is generally considered to be a factor contributing to landscape resilience or the ability to recover from disturbance (e.g., insect and pathogen outbreaks) and stressors (e.g., climate change).

Insights on Metrics...*general considerations*

Conceptual Similarity ≠ Behavioral Similarity

- | | | |
|---|--|--|
| <ul style="list-style-type: none">■ Area & Edge<ul style="list-style-type: none">▶ CA▶ PLAND▶ ED▶ LSI▶ LPI▶ nLSI▶ AREA▶ GYRATE
■ Shape<ul style="list-style-type: none">▶ PAFRAC▶ PARA▶ SHAPE▶ FRAC▶ COHESION
■ Aggregation<ul style="list-style-type: none">▶ PLADJ▶ CLUMPY▶ AI▶ IJI | <ul style="list-style-type: none">■ Contrast<ul style="list-style-type: none">▶ CWED▶ TECI▶ ECON
■ Subdivision<ul style="list-style-type: none">▶ NP/PD▶ DIVISION▶ SPLIT▶ MESH
■ Isolation<ul style="list-style-type: none">▶ PROX▶ SIMI▶ ENN | <ul style="list-style-type: none">■ Core area<ul style="list-style-type: none">TCACPLANDNDCADCADCOREDCORECAI |
|---|--|--|

8. Insights on the Use of Landscape Metrics

All landscape metrics suffer from limitations that restrict their use and/or interpretation in different contexts. Unfortunately, a comprehensive theoretical understanding of metric behavior under varying conditions does not exist. Moreover, given the varied landscape contexts in which metrics are applied in real-world landscapes, a comprehensive empirical understanding of metric behavior under the full range of conditions in which they may be applied is not possible. Consequently, the choice and interpretation of metrics in any particular application is often quite challenging. In addition to the many specific considerations and limitations of particular metrics or groups of metrics, a couple of additional general considerations regarding the overall use of metrics are warranted.

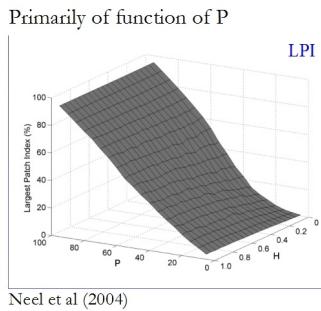
Conceptual similarity does not equal behavioral similarity

As noted in the introduction, landscape structure metrics have traditionally been organized conceptually according to the aspect of landscape composition or configuration they supposedly measure (as in the previous sections). It is common for practitioners to choose metrics from each of the conceptual classes in order to describe different aspects of a landscape (Ripple et al. 1991). Neel et al (2004) demonstrate that it is also important to consider behavioral groupings because a number of conceptually different metrics have similar behavior and thus are redundant. Similarly, metrics from the same conceptual group often exhibit widely varying behaviors indicating

differences in how they respond to attributes of landscape pattern. Unfortunately, given the range of conditions in real-world landscapes, it is not possible to assign metrics to behavioral groups that are guaranteed to be stable across the full range of real-world landscapes. The important point here is that conceptual similarity does not always equal behavioral similarity. Thus, in choosing a parsimonious suite of metrics for a particular application, don't simply used conceptual groups as the basis for metric choice.

Insights on Metrics...*general considerations*

Conceptual Similarity ≠ Behavioral Similarity

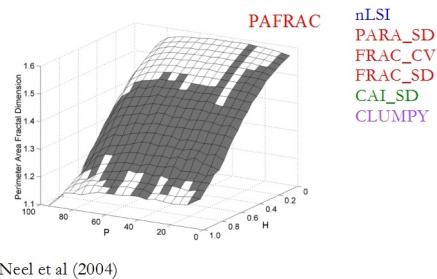


AREA_AM
AREA_SD
GYRATE_AM
GYRATE_SD
CORE_AM
CORE_SD
TCA
DCORE_AM
DCORE_SD
DIVISION
MESH
PROX_MN
PROX_CV
PROX_SD

Insights on Metrics...*general considerations*

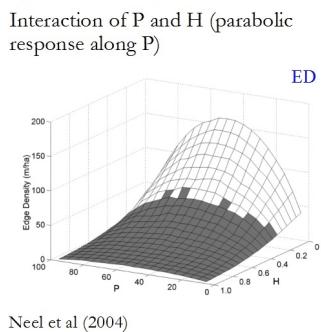
Conceptual Similarity ≠ Behavioral Similarity

Primarily of function of H



Insights on Metrics...*general considerations*

Conceptual Similarity ≠ Behavioral Similarity



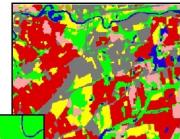
LSI
GYRATE_CV
FRAC_AM
SHAPE_AM
SHAPE_CV
SHAPE_SD
DCORE_CV
DCAD
PD
PROX_AM

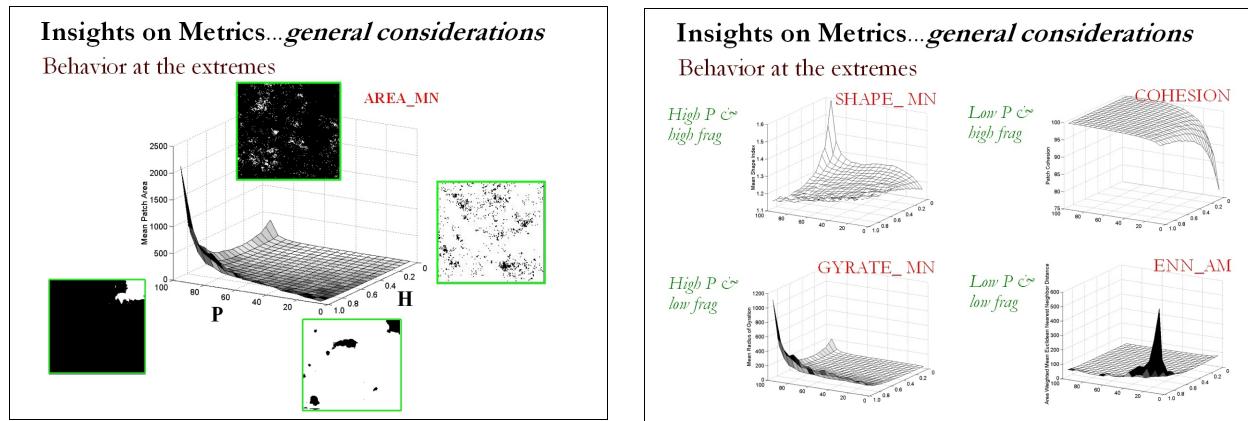
Insights on Metrics...*general considerations*

Conceptual Similarity ≠ Behavioral Similarity

Recomendations:

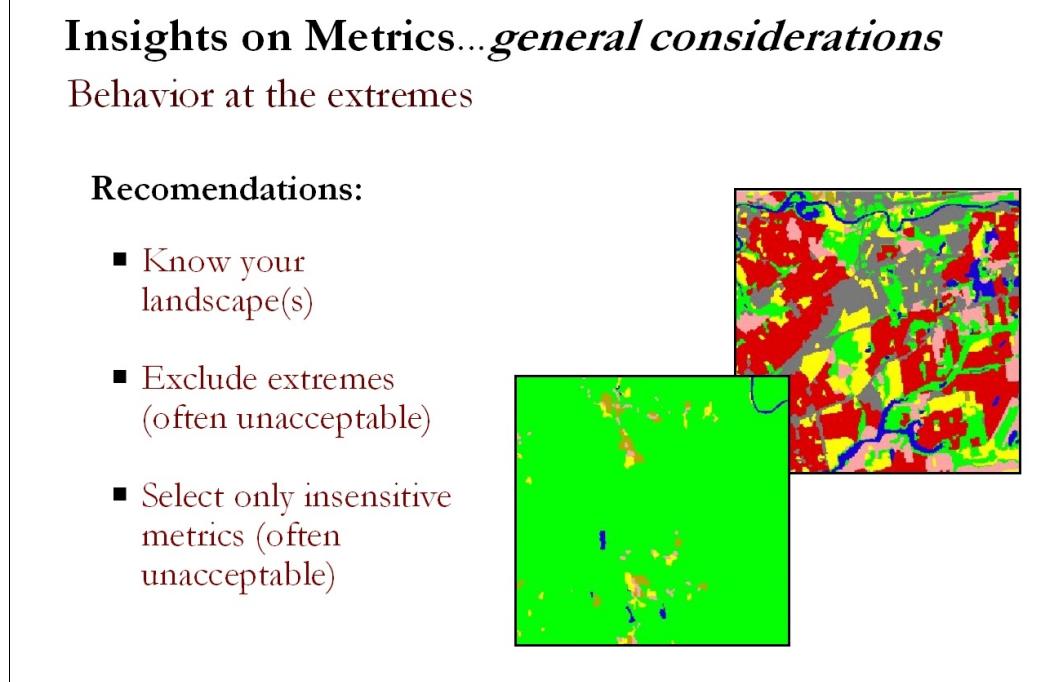
- Know your metrics
- Select metrics based on hypothesized relationships
- Conduct redundancy analysis, if practical





Behavior at the extremes

Finally, a number metrics exhibit erratic and/or unstable behavior at extreme conditions and demonstrate that landscape structure is difficult to characterize at the class level when the focal class is either dominant or extremely rare and at the landscape level when a single class is dominant (Neel et al. 2004). Fortunately, quantifying configuration may not be that relevant or interesting in such landscapes anyway. This instability is not necessarily a problem with the metrics per se, but rather accentuates the need to understand what the metrics are describing and to apply them intelligently. For example, when the focal class dominates the landscape and forms a matrix, it is not meaningful to measure landscape structure with patch-based metrics. Similarly, when the focal class is extremely rare, patch-based metrics do a poor job of distinguishing among levels of configuration.



LITERATURE CITED

- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? Bio-Science 33:31-35.
- Baker, W. L., and Y. Cai. 1992. The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. *Landscape Ecology* 7: 291-302.
- Bendell, P. R., and J. E. Gates. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). *J. Mammology* 68:243-255.
- Buechner, M. 1989. Are small-scale landscape features important factors for field studies of small mammal dispersal sinks? *Landscape Ecology* 2:191-199.
- Burrough, P. A. 1986. Principles of Geographical Information Systems for Land Resources Assessment. Clarendon Press, Oxford.
- Cain, D.H., K. Ritters, and K. Orvis. 1997. A multi-scale analysis of landscape statistics. *Landscape Ecology* 12:199-212.
- Chasko, G. G, J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildl. Monogr.* 82.
- Chen, J., and J. F. Franklin. 1990. Microclimatic pattern and basic biological responses at the clearcut edges of old-growth Douglas-fir stands. *Northwest Environ. J.* 6:424-425.
- Cifaldi, R.L, J.D. Allen, J.D. Duh, and D.G. Brown. 2004. Spatial patterns in land cover of exurbanizing watersheds in southeastern Michigan. *Landscape Urban Planning* 66:107-123.
- Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445-453.
- Compton BW, K McGarigal, SA Cushman, and LR Gamble. 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conservation Biology* 21(3):788-799.
- Dale, M. R. T. 2000. Lacunarity analysis of spatial pattern: a comparison. *Landscape Ecol.* 15:467-468.
- Dale, V. H., S. M. Pearson, H. L. Oferman, and R. V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. *Conservation Biology* 8:1027-1036.
- Dickman, C. R. 1987. Habitat fragmentation and vertebrate species richness in an urban environment. *J. Appl. Ecol.* 24:337-351.

- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169-175.
- Forman, R. T. T., A. E. Galli, and C. F. Leck. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. *Oecologia* 26:1-8.
- Forman, R. T. T., and M. Godron. 1986. *Landscape Ecology*. John Wiley & Sons, New York. 619 pp.
- Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. *Wildl. Monogr.* 87. 64 pp.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape pattern by forest cutting: ecological consequences and principles. *Landscape Ecology* 1:5-18.
- Gardner, R. H., B. T. Milne, M.G. Turner, and R.V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecol.* 1:19-28.
- Gardner, R. H., and R. V. O'Neill. 1991. Pattern, process, and predictability: the use of neutral models for landscape analysis. Pages 289-307 In M. G. Turner and R. H. Gardner, eds. *Quantitative Methods in Landscape Ecology*. Springer-Verlag, New York.
- Gilpin, M. E., and I. Hanski (eds). 1991. *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, San Diego. 336 pp.
- Graham, R. L., C. T. Hunsaker, R. V., O'Neill, and B. Jackson. 1991. Ecological risk assessment at the regional scale. *Ecol. Appl.* 1:196-206.
- Gratkowski, H. J. 1956. Windthrow around staggered settings in old-growth Douglas-fir. *For. Sci.* 2:60-74.
- Griffith, J.A., E.A. Marinko, and K.P. Price. 2000. Landscape structure analyses of Kansas in three scales. *Landscape Urban Planning* 52:45-61.
- Gustafson, E. J. 1998. Quantifying landscape spatial pattern: What is the state of the art. *Ecosystems*:143-156.
- Gustafson, E. J., and G. R. Parker. 1994. Using an index of habitat patch proximity for landscape design. *Landscape and Urban Planning* 29:117-30.
- Gustafson, E. J., G. R. Parker, and S. E. Backs. 1994. Evaluating spatial pattern of wildlife habitat: a case study of the wild turkey (*Meleagris gallopavo*). *Am. Midl. Nat.* 131:24-33.
- Gustafson, E. J., and G. R. Parker. 1992. Relationships between landcover proportion and indices

- of landscape spatial pattern. *Landscape Ecology* 7:101-110.
- Hansen, A., and F. di Castri (eds). 1992. *Landscape Boundaries*. Springer, New York.
- Hardt, R. A., and R. T. T. Forman. 1989. Boundary form effects on woody colonization of reclaimed surface mines. *Ecology* 70:1252-1260.
- Hargis, C. D., J. A. Bissonette, and J. L. David. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecol.* 13:167-186.
- Hayden, I. J., J. Faaborg, and R. L. Clawson. 1985. Estimates of minimum area requirements for Missouri forest birds. *Missouri Academy of Science* 19:11-22.
- He, H. S., B. E. DeZonia, and D. J. Mladenoff. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. *Landscape Ecology* 15:591-601.
- Helliwell, D. R. 1976. The effects of size and isolation on the conservation value of wooded sites in Britain. *J. Biogeogr.* 3:407-416.
- Iverson, L. R. 1989. Land use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. *Landscape Ecology* 2:45-61.
- Jaeger, J. A. G. 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecol.* 15:115-130.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Phil. Trans. R. Soc. Lond. B* 330:175-190.
- Keitt, T.H., D.L. Urban, and B.T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecol.* 1(1):4. (online)
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.
- Kremsater, L. and F. L. Bunnell. 1999. Edge effects: theory, evidence and implications to management of western North American forests.
- Kroodsma, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. *J. of Applied Ecology* 19:361-370.
- Krummel, J. R., R. H. Gardner, G. Sugihara, R. V. O'Neill, and P. R. Coleman. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321-324.
- Lamberson, R.H., R. McKelvey, B.R. Noon, and C. Voss. 1992. A dynamic analysis of northern

- spotted owl viability in a fragmented forest landscape. *Conservation Biology* 6(4):1-8.
- LaGro, J., Jr. 1991. Assessing patch shape in landscape mosaics. *Photogrammetric Eng. Remote Sens.* 57:285-93.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* 130:624-635.
- Lausch, A., and F. Herzog. 2002. Applicability of landscape metrics for the monitoring of landscape change: issues of scale, resolution and interpretability. *Ecol. Indicators* 2:3-15
- Lehmkuhl, J. F., and M. G. Raphael. 1993. Habitat pattern around northern spotted owl locations on the Olympic Peninsula, Washington. *J. Wildl. Manage.* 57:302-315.
- Leopold, A. 1933. Game Management. Charles Scribners, New York.
- Levins, R. 1970. Extinctions. Pages 77-107 In M. Gertenhaber, ed. *Some Mathematical Questions in Biology*, vol 2. Lectures on Mathematics in the Life Sciences. Amer. Math. Soc., Providence, Rhode Island.
- Li, H., and J. F. Reynolds. 1993. A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology* 8:155-162.
- Logan, W., E. R. Brown, D. Longrie, G. Herb, and R. A. Corthell. 1985. Edges. Pages 115-127 In E. R. Brown, tech. ed. *Management of wildlife and fish habitats in forests of western Oregon and Washington*. USDA For. Serv. Publ. No. R6-F&WL-192-1985.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton. 203 pp.
- Mandelbrot, B. B. 1982. *The Fractal Geometry of Nature*. W. H. Freeman and Co., New York.
- Mandelbrot, B. B. 1977. *Fractals, Form, Chance and Dimension*. W. H. Freeman and Co., New York.
- Mader, H-J. 1984. Animal habitat isolation by roads and agricultural fields. *Biological Conservation* 29:81-96.
- McKelvey, K., B.R. Noon, and R. Lamberson. 1992. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. Pages 338-357 In J. Kingsolver, P. Kareiva, and R. Hyey, eds. *Biotic interactions and global change*. Sinauer Associates, Sunderland, MA.
- Milne, B. T. 1988. Measuring the fractal geometry of landscapes. *Applied Mathematics and*

Computation 27:67-79.

Moore, N. W., and M. D. Hooper. 1975. On the number of bird species in British woods. Biol. Conserv. 8:239-250.

Morgan, K. A., and J. E. Gates. 1982. Bird population patterns in forest edge and strip vegetation at Remington Farms, Maryland. J. Wildl. Manage. 46:933-944.

Neel, M. C., K. McGarigal, and S. A. Cushman. 2004. Behavior of class-level landscape metrics across gradients of class aggregation and area. Landscape Ecology 19:435-455.

Noss, R. F. 1988. Effects of edge and internal patchiness on habitat use by birds in a Florida hardwood forest. Ph.D. Thesis. Univ. of Florida, Gainesville. 109 pp.

O'Neill , R. V., C. T. Hunsaker, S. P. Timmins, B. L. Jackson, K. B. Jones, K. H. Ritters, and J. D. Wickham.1996. Scale problems in reporting landscape pattern at the regional scale. Landscape Ecology 11:

O'Neill , R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and R. L. Graham. 1988. Indices of landscape pattern. Landscape Ecology 1:153-162.

Patton, D. R. 1975. A diversity index for quantifying habitat "edge". Wildl. Soc. Bull. 3:171-173.

Pearson, S. M., M. G. Turner, R. H. Gardner, and R. V. O'Neill. 1996. An organism-based perspective of habitat fragmentation. Pages 77-95 In R. C. Szaro and D. W. Johnston, eds. Biodiversity in Managed Landscapes: Theory and Practice. Oxford University Press, New York.

Pielou, E. C. 1975. Ecological Diversity. Wiley-Interscience, New York.

Plotnick, R. E., R. H. Gardner, and R.V. O'Neill. 1993. Lacunarity indices as measures of landscape texture. Landscape Ecol. 8:201-211.

Plotnick, R. E., R. H. Gardner, W. W. Hargrove, K. Pretegaard, and M. Perlmutter.1996. Lacunarity analysis: a general technique for the analysis of spatial patterns. Phys. Rev. E53:5461-5468.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-94 In R. L. Burgess and D. M. Sharpe, eds. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, New York.

Ripple, W. J., G. A. Bradshaw, and T. A. Spies. 1991. Measuring landscape pattern in the Cascade Range of Oregon, USA. Biological Conserv. 57:73-88.

Ritters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecol.* 10: 23-40.

Ritters, K. H., R. V. O'Neill, J. D. Wickham, and K. B. Jones. 1996. A note on contagion indices for landscape analysis. *Landscape Ecol.* 11:197-202.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildl. Monogr.* 103. 34 pp.

Rogers, C. A. 1993. Describing landscapes: indices of structure. M.S. Thesis, Simon Fraser University, Burnaby, British Columbia. 170 pp.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecol. Monogr.* 52:199-221.

Saunders, D., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5:18-32.

Scanes, H.M., and R.G.H. Bunce. 1997. Directions of landscape change (1741-1993) in Virestad, Sweden—characterised by multivariate analysis. *Landscape Urban Planning* 38:61-75.

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77:1210-25.

Shannon, C., and W. Weaver. 1949. The mathematical theory of communication. Univ. Illinois Press, Urbana.

Simpson, E. H. 1949. Measurement of diversity. *Nature* 163:688.

Stauffer, D. 1985. Introduction to Percolation Theory. Taylor and Francis, London.

Strelke, W. K., and J. G. Dickson. 1980. Effect of forest clearcut edge on breeding birds in Texas. *J. Wildl. Manage.* 44:559-567.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 73:43-48.

Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pages 301-304 In J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. Univ. of Wisconsin Press, Madison, WI.

Thomas, J. W., C. Maser, and J. E. Rodiek. 1979. Edges. Pages 48-59 In J. W. Thomas, tech. ed.

Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. USDA For. Serv. Handb. 553.

Thomas, J. W., C. Maser, and J. E. Rodiek. 1978. Edges--their interspersion, resulting diversity, and its measurement. Pages 91-100 In R. M. Degriff, tech. coord. Proceedings of the workshop on nongame bird habitat management in the coniferous forests of the western United States. Gen. Tech. Rep. PNW-64.

Tinker, D.B., C.A.C. Resor, G.P. Beauvais, K.F. Kipfmüller, C.I. Fernandes, and W.L. Baker. 1998. Watershed analysis of forest fragmentation by clearcuts and roads in a Wyoming forest. *Landscape Ecology* 13:149-165.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Ann. Rev. Ecol. Syst.* 20:171-197.

Turner, M. G. 1990a. Spatial and temporal analysis of landscape patterns. *Landscape Ecology* 4:21-30.

Turner, M. G. 1990b. Landscape changes in nine rural counties of Georgia. *Photogram. Engine. and Rem. Sens.* 56:379-386.

Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne. 1989. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* 3:153-162.

Turner, M. G., and C. L. Ruscher. 1988. Changes in the spatial patterns of lands use in Georgia. *Landscape Ecology* 1:241-251.

Voss, R. F. 1988. Fractals in nature: from characterization to simulation. Pages 21-70 In H.O. Petigen and D. Saupe, eds. *The Science of Fractal Images*. Springer-Verlag, New York.

Wegner, J. F., and H. G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. *J. Appl. Ecol.* 16:349-357.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 in R. L. Burgess and D. M. Sharpe, eds. *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag, New York.

Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45: 421-427.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.

With, K. A. 1999. Is landscape connectivity necessary and sufficient for wildlife management? Pages 97-115 in J. A. Rochelle, L. A. Lehmann, and J. Wisniewski, editors. Forest fragmentation: wildlife and management implications. Brill, The Netherlands.

With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76:2446-59.

With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:151-169.

With, K. A., and A.W. King. 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* 14:73-82.

With, K. A., and A.W. King. 1999b. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13:314-326.

Yahner, R. H. 1986. Spatial distribution of white-footed mice (*Peromyscus leucopus*) in fragmented forest stands. *Proceedings of the Pennsylvania Academy of Science* 60:165-166.

Yahner, R. H., and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. *J. Wildl. Manage.* 52:158-161.