



## Landscape Pattern Metrics and Regional Assessment

Robert V. O'Neill,\* K.H. Riitters,† J.D. Wickham,‡ and K. Bruce Jones§

\*Environmental Sciences, Oak Ridge National Laboratory, Oak Ridge, Tennessee;

†U.S. Geological Survey, North Carolina State University, Raleigh, North Carolina;

‡U.S. Environmental Protection Agency, Research Triangle Park, North Carolina;

§U.S. Environmental Protection Agency, Las Vegas, Nevada

---

### ABSTRACT

The combination of remote imagery data, geographic information systems software, and landscape ecology theory provides a unique basis for monitoring and assessing large-scale ecological systems. The unique feature of the work has been the need to develop and interpret quantitative measures of spatial pattern—the landscape indices. This article reviews what is known about the statistical properties of these pattern metrics

and suggests some additional metrics based on island biogeography, percolation theory, hierarchy theory, and economic geography. Assessment applications of this approach have required interpreting the pattern metrics in terms of specific environmental endpoints, such as wildlife and water quality, and research into how to represent synergistic effects of many overlapping sources of stress.

---

### INTRODUCTION

Analyses at large spatial scales can never replace the need to understand structure and function at the ecosystem level of organization. However, spatial changes, such as deforestation and urbanization, can place important constraints on ecosystem rate processes (O'Neill *et al.* 1986). For example, fragmentation can alter ecosystem recovery rates by impeding the dispersal of pioneer species (Gardner *et al.* 1993). Because of such constraints, considerable research has focused on changes in spatial pattern at larger scales (O'Neill *et al.* 1994).

The emphasis on larger scales has been made feasible by the availability of remotely sensed data. Satellite imagery can be interpreted for land cover and provides an economical approach to studying large areas (O'Neill *et al.* 1992). This ap-

proach has already proven invaluable, for example in support of global change studies (Roughgarden 1991). The development of geographic information systems (GIS) technology provides the means for handling the large spatial data sets. The technical capabilities of satellite imagery coupled with GIS technology offers an ideal combination for monitoring and assessing landscape condition.

Landscapes, in turn, provide the spatial context for ecosystem dynamics (O'Neill 1999) and may enhance or disrupt ecosystem integrity (O'Neill *et al.* 1997). Many of the proposed indicators of ecosystem health, including surrogates for productivity and organization (Mageau *et al.* 1995) are amenable to monitoring by remotely sensed data (Rapport *et al.* 1996; Jones *et al.* 1997). In addition, landscape metrics can directly estimate some aspects of terrestrial and aquatic ecosystem health, such as habitat integrity (Riitters *et al.* 1997) and water quality (Hunsaker *et al.* 1992). As ecological theory advances, we can anticipate the synthesis

Address correspondence to: R.V. O'Neill, Bldg. 1505 MS-4036, Environmental Sciences, Oak Ridge National Laboratory, Oak Ridge, TN 37831-4036; E-mail rvo@ornl.gov.

of landscape and ecosystem dynamics (Turner *et al.* 1995). As ecological assessment advances, we can anticipate a continued integration of landscape and ecosystem viewpoints (Graham *et al.* 1991).

Finally, the emergence of landscape ecology provided a theoretical framework (O'Neill *et al.* 1995) and developed some metrics of spatial pattern. Following an initial effort (O'Neill *et al.* 1988a), a large number of candidate indices have been proposed from landscape ecology (Baker & Cai 1992) and from traditional image processing (Gonzalez & Woods 1992). Helpful reviews are available for measures based on diversity and information theory (Magurran 1988), fractal geometry (Milne 1991), and image textural methods (Musick & Grover 1991).

The goal of the research presented here was to test and refine the existing suite of landscape pattern metrics and to propose several new indices capable of monitoring additional aspects of pattern change and ecosystem constraint.

## PROPERTIES OF THE LANDSCAPE INDICES

Pattern indices were a new approach to data analysis and assessment. Ecologists have experimented with novel metrics in the past, such as biodiversity, that created difficult statistical problems (Pielou 1977). It was clear, therefore, that routine application of landscape indices would require a firm statistical foundation. Key issues included (1) whether the metrics were orthogonal, i.e., whether the indices captured different, independent aspects of pattern, (2) whether they were sensitive to ecological change and errors in the data, and (3) how they changed with the scale of the data, both resolution (data grain) and range (data extent).

Many of the pattern metrics are correlated with each other. We performed a factor analysis on approximately 50 indices taken from the literature. The indices were averaged over all cover types in the image. This large suite of metrics actually measures, at most, a half-dozen independent aspects of pattern (Riitters *et al.* 1995). The first five factors all have eigenvalues greater than 1.0 and explain about 83% of the variance. The analysis was valid for land cover maps from different geographic regions and at scales (pixel size, number of attribute classes, analysis unit, etc.) likely to be encountered in regional assessments (Cain *et al.* 1997). Therefore, at present, land-

scape pattern can be represented as a point in a multidimensional ( $\sim 5$ ) "state space" of indices (O'Neill *et al.* 1996; Wickham *et al.* 1996).

Each factor is composed of several indicators and some subjective judgment is required to choose a single metric from each group. Based on the ease of calculation and interpretation, the following indices are recommended:

1. Average patch perimeter-area ratio:

$$P = \frac{1}{m} \sum_{k=1}^m \frac{E_k}{A_k}$$

where there are a total of  $m$  patches and  $E_k$  is the perimeter of the  $k$ 'th patch and  $A_k$  is the area.

2. Contagion:

$$C = 1 + \frac{1}{2\ln(n)} \sum_{i=1}^n \sum_{j=1}^n p_{ij} \ln(p_{ij})$$

where there are a total of  $n$  land cover types and  $p_{ij}$  is the probability of type  $i$  being adjacent to type  $j$ .

3. Relative patch area: (average ratio of patch area to the area of an enclosing circle)

$$R = \frac{1}{m} \sum_{k=1}^m \frac{A_k}{\pi L_k^2}$$

where  $L_k$  is one half of the longest straight line that can be drawn within the patch and the denominator is the area of a circle, with  $L_k$  as the radius.

4. Fractal Dimension:

$$F = 2B$$

where  $B$  is the slope from the regression of  $\ln(E_k)$  on  $\ln(A_k)$  for all patches greater than 3 pixels that do not touch the edge of the map.

Very small patches and those with a straight edge along the map boundary tend to distort the estimated slope in the regression (Krummel *et al.* 1987). A number of other measures of fractal dimension have been proposed (Milne 1991). Some appear to have properties that make them superior for specific applications (Loehle *et al.* 1996). However, factor analysis of these measures (Riitters *et al.* 1995; Cain *et al.* 1997) indicated they are usually correlated with contagion or with perimeter-area ratio. Therefore, at present, it seems prudent to recommend the fractal dimension given above which has proven to be orthogonal to other landscape indices.

5. Cover Types: (The total number of different land cover types on the map).

This final measure plays no role in describing the pattern of patches on a single landscape, but becomes important in comparing pattern across a number of different maps.

These five metrics provide relatively independent measures of spatial pattern. They are based on empirical analysis of 85 landscapes scattered across the United States (Riitters *et al.* 1995) and should be valid for most applications, at least in temperate zones around the world.

Most of the variance among indices (not among maps) is associated with overall image “texture” or contagion (eqn. 2) and considerable attention has focused on this metric (Li & Reynolds 1993; Riitters *et al.* 1996). Texture was originally calculated from raster data, i.e., land cover represented by discrete pixels. A vector-based method was also developed (Wickham *et al.* 1996) because geographic data may also be in a format that specifies the perimeter drawn around distinguishable patches. Computer algorithms to calculate texture can differ by orders-of-magnitude based on how the data is tabulated (Riitters *et al.* 1996). Much of this problem can be eliminated by adopting a simpler measure of texture (Wickham & Riitters 1995).

Experience with applying the indices to landscape analysis has suggested some rules of thumb for scale (O’Neill *et al.* 1996). Grain size should be 2–5 times smaller than the patch or other spatial feature of interest. The landscape size or extent should be 2–5 times larger. In practice, both of these requirements are easily met in regional assessments using 30–100 m satellite data.

We have explored the effects of scale on habitat assessment by using a sliding window algorithm (Riitters *et al.* 1997). The algorithm specifies a square window and asks whether all habitat requirements are fulfilled within the window. The window is then moved, pixel by pixel, to all positions on the map. This procedure permits one to visualize the landscape as a surface of habitats as perceived by organisms of increasing size and mobility. Thus, by changing window size, habitat suitability at several scales can be examined.

To compare maps at different scales, it would be convenient if the indices were insensitive to changes in scale. However, preliminary examination suggested that the indices are very sensitive to scale (grain, extent, number of attributes, etc.). At extreme values of scale, of course, this must be true since the pattern itself is distorted at the ex-

tremes. Therefore, the practical issue is not addressed by comparing the metrics at extreme scales, e.g., 10 m resolution maps with 10,000 m resolution maps. The issue is the sensitivity of pattern metrics to scale changes over a range of scales likely to be encountered in real-world satellite data, e.g., 10–100 m (SPOT/TM/MSS). Over this reduced range, indicators are relatively insensitive to pixel size, but results will vary depending on actual pattern and the specific indicator (Wickham & Riitters 1995).

There is a conundrum of sorts when thinking about the sensitivity of metrics. On one hand, the indicators must be sensitive to pattern change. That is the purpose for indices. But, on the other hand, we want those same metrics to be insensitive to scale change and data errors. The puzzler is, how do you have an index that both is and is not sensitive to pattern differences? Clearly, any indicator is limited to detecting change that is significantly greater than data errors.

The dilemma requires some attention to the nature of data errors in satellite imagery. The most important source of error is misclassification, i.e., a pixel is assigned to an incorrect land cover category. Unfortunately, available metrics depend heavily on patch perimeters and both misclassification and real change tend to occur along the perimeter. Simulations demonstrated that errors in the metrics were no greater than the data error itself (Wickham *et al.* 1997), i.e., the metrics do not artificially amplify the errors. Furthermore, applications to real landscapes indicates that actual pattern changes are quite large compared to the noise arising from misclassification (Wickham *et al.* 1997). Nevertheless, caution is required in ascribing significance to a very small change in pattern unless the data error is also very small. And in all cases, it will be necessary to know the misclassification error.

The metrics are also sensitive to scale in the sense of data grain or pixel size. This sensitivity makes it difficult to compare indices computed from different satellite sensors. Fortunately, these changes are systematic and can be described by the fractal dimension of the landscape (Krummel *et al.* 1987; Milne 1991). This approach is reliable over scales where the fractal dimension itself does not change (O’Neill *et al.* 1991). The logarithm of the index changes linearly with the logarithm of the grain size, with a slope related to the fractal dimension. Recent work by Plotnick & Gardner (1993) applies another parameter of scaling, lacunarity, for a similar purpose.

## NEW LANDSCAPE INDICES

The early emphasis on measuring pattern required easily measured parameters and resulted in indices that rely heavily on patch size and perimeter. But there are other possibilities that are now being explored.

## OTHER MAP MEASUREMENTS

Classic GIS overlay techniques provide access to additional aspects of landscape pattern. Based on combinations of land-cover, stream, and digital elevation data, these measures are likely to be orthogonal to the suite of pattern metrics discussed above. For example, riparian forest cover can be approximated by counting forest pixels adjacent to streams. Peterjohn & Correll (1984) have shown the importance of riparian forests for filtering agricultural runoff. Riparian forests are also important habitat for many species (Wharton *et al.* 1982).

The Universal Soil Loss Equation (USLE) (Renard *et al.* 1997) provides a conceptual source for estimating erosion and sediment transport. The index combines agriculture on steeply sloping land, patches of excessive soil erosion, and distance of erosion patches from recipient streams. Jones *et al.* (1997) demonstrated how pattern indices can be combined with GIS-derived measures to provide an integrated environmental assessment of the mid-Atlantic states.

**ISLAND BIOGEOGRAPHY.** One potential source of new indices is the Island Biogeography Theory of MacArthur & Wilson (1967; MacArthur 1972). The theory states that, at equilibrium, the number of species on a patch will be constant because immigration of new species will balance extinction. Immigration is expressed as a function of distance from the "source" community and extinction is a function of island size. An index that captures the key features of the landscape might be

$$\sum_{j=1}^n \sum_{i=1}^n \frac{A_i}{A_j D_{ij}^2}$$

where  $A_i$  is the area of the source patch and  $A_j$  is the area of the recipient patch, and  $D_{ij}^2$  is the distance between the patches. Note that  $A_i > A_j$ .

The index assumes that the dispersal relationship between two patches is proportional to the ratio of the areas and inversely proportional to the square of the distance between them. Insofar as dispersal between habitat patches follows Metapo-

pulation Theory (Hanski 1983) and experimental results dating back to Huffaker (1958), the index should be related to the stability of consumer populations operating on the landscape.

**PERCOLATION THEORY.** Percolation theory (Stauffer 1985) deals with the connectedness of a landscape (Gardner & O'Neill 1991). Consider a landscape with cover type A, distributed randomly with probability  $P_A$ . For very large, random maps, there exists a critical threshold for  $P_A$ . We assume that the landscape is represented by a square lattice with pixels connected in the cardinal directions and that the landscape is represented by only two cover types: A = habitat, and B = nonhabitat. When  $P_A > 0.5928$ . . . the pixels of A form a single patch.

The threshold,  $P_A$ , can be expressed in more meaningful ecological terms by considering how wildlife moves across the landscape (Gardner *et al.* 1989). A consumer must adjust the scale of its movements to reach sufficient resources. Let us assume that the consumer can move  $n$  spatial units per unit time. When  $P_A > 0.6$  and  $n = 1$ , the consumer should be able to find a unit of resource at each step in time. But if  $P_A << 0.6$ , then the resource is not continuously connected and the consumer will have to take multiple steps to find a unit of resource during each unit of time. We can define:

$$n = \frac{-0.89845}{\ln(1 - P_A)}$$

This Resource Utilization Scale (O'Neill *et al.* 1988b) simply rescales the map so that the percolation threshold is reached. If the consumer takes  $n$  steps, the resource will appear to be connected throughout the landscape.

The concept of Resource Utilization Scale can be extended to landscapes that show some degree of pattern. Consider, for example, that A occurs in patches characterized by  $Q$ , the probability of finding an adjacent unit of A, given that one is standing on a unit of A. Then

$$n^* = \frac{-0.89845 - 2 \ln(1 - P_A) + \ln(1 - 2P_A + QP_A)}{\ln(1 - 2P_A + QP_A) - \ln(1 - P_A)}$$

If  $P_A = 0.5928$ ,  $n^* = 1$  irrespective of the value of  $Q$ . As  $Q$  approaches 1.0 and the resource is all clumped in one place, the denominator approaches 0.0 and  $n^*$  approaches infinity. Since the resource is all in one place, it becomes impossible to locate additional resources by moving around on the land-

scape. When  $Q = P_A$ , the resource is randomly scattered and  $n' = n$ .

Percolation theory also predicts the largest patch size (Plotnick *et al.* 1993). As long as  $P_A > 0.6$ , the largest patch will occupy  $P_A$  of the landscape. This aspect of percolation theory was used to examine the relationship between the size of largest forest patch and the amount of anthropogenic cover (nonhabitat) across 120 watersheds in the U.S. mid-Atlantic region (Wickham *et al.*, 1999). The size of the largest forest patch began to decrease at an increasing rate, well before the percolation threshold. A similar nonlinear relationship was found by Vogelmann (1995) in a forest fragmentation study in New England.

The clumped nature of the fragmentation pattern suggests a strategy for restoration. By carefully selecting reforestation sites, it should be possible to reconnect existing fragments into larger, continuous patches. By examining a subset of the 120 watersheds (Wickham *et al.*, 1999), it was found that the size of the largest forest patch could be increased quite close to  $P_A$ . The conceptual approach represents a multiscale targeting for ecosystem restoration.

**HIERARCHY THEORY.** Hierarchy theory (Allen & Starr 1982; O'Neill *et al.* 1986) predicts that ecosystem processes are not uniformly distributed over spatial and temporal scales. Dynamics and spatial pattern tend to be lumped into discrete scales of interaction (Rowe 1961; Simon 1962).

The simplest way to measure spatial hierarchies (Levin & Buttel 1986) plots variance as a function of scale. Variance is inversely proportional to sample size  $n$ , the number of samples or the spatial size of the sample. If  $\ln S^2$  is plotted as a function of  $\ln n$ , we expect a straight line with a slope of  $-1$ . However, if the spatial data is organized into levels, then immediately adjacent points within a level will be correlated and the slope will lie between  $-1$  and  $0$ . If there are several hierarchical levels, we would expect to show slopes of  $-1.0$  (no correlation = no level) alternating with slopes much closer to  $0.0$  (high correlation = distinct level). The resulting graph would look like a staircase and the number of "steps" would be an indicator of the number of hierarchical levels. The number of hierarchical levels could then be used as the indicator of landscape pattern.

Several applications indicate that the approach is practical. O'Neill *et al.* (1991) used the analysis on two grassland and four forest landscapes. The expected "staircase" pattern appeared

on all landscapes. Multiple scales appeared on four of the landscapes and a single scale was evident on the two landscapes dominated by urban development. This approach was also applied by Palmer (1988) to spatial patterns in plant communities.

**ECONOMIC GEOGRAPHY THEORY.** Geographers have long been concerned with the physical location of economic activity (Thoman *et al.* 1962; Healey & Ilbery 1990). A significant body of theory has been developed including: location theory (e.g., Hall 1966; Friedrich 1929), market area analysis (e.g., Losch 1954), and central place theory (e.g., Berry & Pred 1961). These theories provide idealized projections of where activities "ought" to be located. Location theory, for example, considers the value of various products and the cost of transporting them to a central market (Jones & O'Neill 1993; 1994). The theory then predicts which product will be grown close to the market and which can be profitably grown at greater distances (Jones & O'Neill 1995). The theory has been used to model land use change and deforestation in Brazil (Southworth *et al.* 1991; Dale *et al.* 1993)

The simple theories do not provide realistic predictions but can be used in the sense of a "neutral model" (Gardner *et al.* 1987). The approach would be similar to applications of percolation theory (Gardner *et al.* 1989), which gives properties of a totally randomized landscape. Deviations from the expectation, then, can be used to analyze nonrandom or structured properties. We don't expect the model to fit, we want to analyze the residuals.

In the case of economic geography theories, deviations from the "ideal" picture might be a measure of the "tension for change" in the region. For example, changes in the transportation system might alter the economic viability of patches in traditional crops, increasing the probability of the patches disappearing or relocating. The region could then be characterized as spatially "stable" or "transitional" depending on the deviation from the ideal location theory.

## ASSESSMENT APPLICATIONS

Following the National Environmental Policy Act (NEPA) in 1970 (Shoemaker 1994), assessment largely focused on identifiable "point sources" of stress. The emphasis shifted away from large re-

gional scales, though it was clear from the beginning that individual assessments would provide baseline information against which larger scaled impacts could be evaluated (see Fabos 1985).

One of the motivations for the landscape approach was the need to link changes in land cover to “nonpoint-source” environmental stresses in a region (Mankin *et al.* 1981; Graham *et al.* 1991). The use of metrics based on land-cover data covering large spatial scales provided the opportunity to conduct environmental assessments at the same scale (O’Neill *et al.* 1997). The landscape approach has made feasible a regional approach to assessment (Klopatek *et al.* 1983), and the preliminary evaluation of large regions, such as the mid-Atlantic states (Jones *et al.* 1997).

The best developed areas of regional assessment deal with wildlife and water quality. The wildlife connection is based on the established relationships between habitat fragmentation and biodiversity (Dale *et al.* 1994; Gustafson 1998; Hargis *et al.* 1998). Thus, one can go directly from a change in spatial patterning of habitat on the landscape to impact on a valued resource, e.g., biodiversity (Offerman *et al.* 1995; Pearson *et al.* 1996). The water quality connection is based on the established relationship between watershed land cover and concentrations of nitrogen, phosphorus, and silt (Hunsaker *et al.* 1990). Thus, one can go directly from measures of agriculture on steep slopes, riparian vegetation, road crossing streams, etc. to an impact on a second valued resource, such as water quality (Hunsaker *et al.* 1992).

As the scale of environmental assessments increased, recognition grew that impacts could be cumulative (Odum 1982). For example, two or more disturbances may overlap in space and time. Each would produce an effect by itself, but if acting together at the same place and time, there is also the possibility of synergistic effects. Accounting for interactions of many stress factors provides a framework for making integrated environmental assessments. At present, integrated environmental assessments that are regional in scope depend heavily on landscape metrics for practical applications (Wickham *et al.* 1999).

## FUTURE RESEARCH

Future possibilities include the increased use of covariates to improve statistical analysis and interpretation of landscape change. Although initial research focused on measures of land cover, experience has demonstrated that other nonpattern

covariates (e.g., erosion, biodiversity, productivity, roads, etc.) are needed to relate pattern to ecological endpoints. Ecological models, such as individual-based models of animal movement, are needed to relate pattern change to potential impacts on ecosystem function. Output from such models forms another class of covariates.

Such covariates have only received a modicum of analytical treatment and form but one of the continuing statistical challenges. There will be need to optimize data collection and indices for specific purposes. There is also need for better characterization of data quality, beyond simple estimates of per-pixel error rates. There is need, for example, for variance estimation including error propagation with a dozen sources of error. Characterization of the errors will be critical before we have the ability to make statements about the significance of changes in land-cover time series. We also need to develop methods for automated pattern recognition as opposed to simple pattern description. And with the availability of time-series of large regional maps, we will need the development of data management and visualization techniques.

Finally, there is the need to translate the complex multistaged assessment process into a “risk assessment” framework (O’Neill *et al.* 1982). The fundamental difference in the risk approach is that assessments needs to be conservative, even though they cannot be completely accurate. Consider the difference between our inability to predict tomorrow’s weather and the need to issue “severe winter storm watches.” In the case of storms, it is permissible to be inaccurate if the storm does *not* occur. An inaccurate storm watch causes inconvenience, but no real loss. But the analysis needs to be conservative because it is not permissible to miss any storms and have them occur without any warning. If no warning is issued of a severe winter storm, the losses can be tremendous. Translated into the assessment context, we want to identify large scale, synergistic stresses that *might* endanger the environment. At one level, additional detailed monitoring might be called for, a sort of a storm “watch.” At another level, policy or legal action might be called for, a sort of a storm “warning.”

## ACKNOWLEDGMENTS

This research was supported by the U.S. Environmental Protection Agency under Intergency Agreement 42W106601. Oak Ridge National Laboratory

is operated by Lockheed Martin Energy Research, Inc. under subcontract DE-AC05-96OR22464 with the U.S. Department of Energy.

## REFERENCES

- Allen, T.F.H. & Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago.
- Baker, W.L. & Cai, Y. (1992) The role programs for multiscala analysis of landscape structure using the GRASS geographical information system. *Landscape Ecology* **7**, 291–302.
- Berry, B.J.L. & Pred, A. (1961) *Central place studies: A bibliography*. Regional Studies Research Institute, University of Pennsylvania, Philadelphia, PA.
- Cain, D.H., Riitters, K., Orvis, K. (1997) A multi-scale analysis of landscape statistics. *Landscape Ecology* **12**, 199–212.
- Dale, V.H., O'Neill, R.V., Pedlowski, M., Southworth, F. (1993) Causes and effects of land use change in central Rondonia, Brazil. *Photogrammetric Engineering and Remote Sensing* **59**, 997–1005.
- Dale, V.H., Pearson, S.M., Offerman, H.L., O'Neill, R.V. (1994) Relating patterns of land-use change to faunal biodiversity in the central amazon. *Conservation Biology* **8**, 1027–1036.
- Fabos, J.G. (1985) *Land Use Planning: From Local to Global Challenges*. Chapman & Hall, New York.
- Friedrich, C.J. (1929) *Alfred Weber's Theory of the Location of Industries*. University of Chicago Press, Chicago.
- Gardner, R.H. & O'Neill, R.V. (1991) Pattern, process and predictability: The use of neutral models for landscape analysis. In: Turner, M.G. & Gardner, R.H. (eds) *Quantitative Methods in Landscape Ecology*. pp. 289–307. Springer-Verlag, New York.
- Gardner, R.H., Milne, B.T., Turner, M.G., O'Neill, R.V. (1987) Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* **1**, 19–28.
- Gardner, R.H., O'Neill, R.V., Turner, M.G. (1993) Ecological implications of landscape fragmentation. In: McDonnell, M.J. & Pickett, S.T.A. (eds) *Humans as Components of Ecosystems*. pp. 208–226. Springer-Verlag, New York.
- Gardner, R.H., O'Neill, R.V., Turner, M.G., Dale, V.H. (1989) Quantifying scale dependent effects with simple percolation models. *Landscape Ecology* **3**, 217–227.
- Gonzalez, R.C. & Woods, R.E. (1992) *Digital Image Processing*. Addison-Wesley, Reading, MA.
- Graham, R.L., Hunsaker, C.T., O'Neill, R.V., Jackson, B.L. (1991) Ecological risk assessment at the regional scale. *Ecological Applications* **1**, 196–206.
- Gustafson, E.J. (1998) Quantifying landscape spatial patterns: What is the state of the art? *Ecosystems* **1**, 143–156.
- Hall, P. (ed.) (1966) *Von Thunen's Isolated State*. Pergamon Press, Oxford, U.K.
- Hanski, I. (1983) Coexistence of competitors in patchy environments. *Ecology* **64**, 493–500.
- Hargis, C.D., Bissonette, J.A., David, J.L. (1998) The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology* **13**, 167–186.
- Healey, M.J. & Ilbery, B.W. (1990) *Location and Change; Perspectives on Economic Geography*. Oxford University Press, Oxford, U.K.
- Huffaker, C.B. (1958) Experimental studies on predation: Dispersion factors and predator-prey oscillations. *Hilgardia* **27**, 343–383.
- Hunsaker, C.T., Graham, R.L., Suter, G.W., O'Neill, R.V., Barnthouse, L.W., Gardner, R.H. (1990) Assessing ecological risk on a regional scale. *Environmental Management* **14**, 325–332.
- Hunsaker, C.T., Levine, D.A., Timmins, S.P., Jackson, B.L., O'Neill, R.V. (1992) Landscape characterization for assessing regional water quality. In: McKenzie, D.H., Hyatt, D.E., McDonald, V.J. (eds) *Ecological Indicators*. pp. 997–1006. Elsevier, New York.
- Jones, D.W. & O'Neill, R.V. (1993) Human-environmental influences and interactions in shifting agriculture when farmers form expectations rationally. *Environment and Planning A* **25**, 121–136.
- Jones, D.W. & O'Neill, R.V. (1994) Development policies, rural land use, and tropical deforestation. *Regional Science and Urban Economics* **24**, 753–771.
- Jones, D.W. & O'Neill, R.V. (1995) Development policies, urban unemployment and deforestation: The role of infrastructure and tax policy in a 2-sector model. *Journal of Regional Science* **35**, 135–153.
- Jones, K.B., Riitters, K.H., Wickham, J.D., Tankersley, R.D., O'Neill, R.V., Chaloud, D.J., Smith, E.R., Neale, A.C. (1997) *An Ecological Atlas of the U.S. Mid-Atlantic Region: A Landscape Atlas*. EPA/600/R-97/130, Office of Research and Development. U.S. Environmental Protection Agency, Washington, D.C.
- Klopatek, J.M., Krummel, J.R., Mankin, J.B., O'Neill, R.V. (1983) A theoretical approach to regional environmental conflicts. *Journal of Environmental Management* **16**, 1–15.
- Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V., Coleman, P.R. (1987) Landscape patterns in a disturbed environment. *Oikos* **48**, 321–324.
- Levin, S.A. & Buttel, L. (1986) *Measures of patchiness in ecological systems*. Ecosystem Research Center Report ERC-130. Cornell University, Ithaca, NY.
- Li, H. & Reynolds, J.F. (1993) A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology* **8**, 155–162.
- Loehle, C., Li, B.-L., Sundell, R.C. (1996) Forest spread and phase transitions at forest-prairie ecotones in Kansas U.S.A. *Landscape Ecology* **11**, 225–235.
- Losch, A. (1954) *The Economics of Location*. Yale University Press, New Haven, CT.

- MacArthur, R., & Wilson, E.O. (1967) *Island Biogeography*. Princeton University Press, Princeton, NJ.
- MacArthur, R.H. (1972) *Geographical Ecology*. Harper & Row, New York.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- Mankin, J.B., Klopatek, J.M., O'Neill, R.V., Krummel, J.R. (1981) A regional modeling approach to an energy-environment conflict. In: Mitsch, W.J., Bosserman, R.W., Klopatek, J.M. (eds) *Energy and Ecological Modeling*. pp. 535–542. Elsevier, Amsterdam.
- Mageau, M.T., Costanza, R., Ulanowicz, R.E. (1995) The development and initial testing of a quantitative assessment of ecosystem health. *Ecosystem Health* **1**, 201–213.
- Milne, B.T. (1991) Lessons from applying fractal models to landscape patterns. In: Turner, M.G. & Gardner, R.H. (eds) *Quantitative Methods in Landscape Ecology*. pp. 199–235. Springer-Verlag, New York.
- Musick, H.B. & Grover, H.D. (1991) Image textural measures as indices of landscape pattern. In: Turner, M.G. & Gardner, R.H. (eds) *Quantitative Methods in Landscape Ecology*. Springer-Verlag, New York.
- O'Neill, R.V. (1999) Ecosystems on the landscape: The role of space in ecosystem theory. In: Jorgensen, S. (ed) *Handbook of Ecosystem Modeling*, in press.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B., Allen, T.F.H. (1986) *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, NJ.
- O'Neill, R.V., Gardner, R.H., Barnthouse, L.W., Suter, G.W., Hildebrand, S.G., Gehrs, C.W. (1982) Ecosystem risk analysis: A new methodology. *Journal of Environmental Toxicological Chemistry* **1**, 167–177.
- O'Neill, R.V., Hunsaker, C.T., Jones, D., Klopatek, J.M., Dale, V.H., Turner, M.G., Gardner, R.H., Graham, R. (1995) Sustainability at landscape and regional scales. In: Munasinghe, M. & Shearer, W. (eds) *Defining and Measuring Sustainability*. pp. 137–143. World Bank, Washington, D.C.
- O'Neill, R.V., Hunsaker, C.T., Jones, K.B., Riitters, K.H., Wickham, J.D., Schwarz, P., Goodman, I.A., Jackson, B., Baillargeon, W.S. (1997) Monitoring environmental quality at the landscape scale. *Bioscience* **47**, 513–519.
- O'Neill, R.V., Hunsaker, C., Levine, D. (1992) Monitoring challenges and innovative ideas. In: McKenzie, D.H., Hyatt, D.E., McDonald, V.J. (eds) *Ecological Indicators*. pp. 1443–1460. Elsevier, New York.
- O'Neill, R.V., Hunsaker, C.T., Timmins, S.P., Jackson, B.L., Jones, K.B., Riitters, K.H., Wickham, J.D. (1996) Scale problems in reporting landscape pattern at the regional scale. *Landscape Ecology* **11**, 169–180.
- O'Neill, R.V., Jones, K.B., Riitters, K.H., Wickham, J., Goodman, I.A. (1994) Landscape Monitoring and Assessment Research Plan EPA-620/R-94-009. 53pp.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S., Dale, V.H., Graham, R.L. (1988a) Indices of landscape pattern. *Landscape Ecology* **1**, 153–162.
- O'Neill, R.V., Milne, B.T., Turner, M.G., Gardner, R.H. (1988b) Resource utilization scales and landscape pattern. *Landscape Ecology* **2**, 63–69.
- O'Neill, R.V., Turner, S.J., Cullinan, V.I., Coffin, D.P., Cook, T., Conley, W., Brunt, J., Thomas, J.M., Conley, M.R., Gosz, J. (1991) Multiple landscape scales: An intersite comparison. *Landscape Ecology* **5**, 137–144.
- Odum, W.E. (1982) Environmental degradation and the tyranny of small decisions. *Bioscience* **32**, 728–729.
- Offerman, H., Dale, V., Pearson, S., Bierregaard, R.O., O'Neill, R.V. (1995) Effects of forest fragmentation on neotropical fauna: Current research and data availability. *Environmental Reviews* **3**, 191–211.
- Palmer, M.W. (1988) Fractal geometry: A tool for describing spatial patterns of plant communities. *Vegetatio* **75**, 91–102.
- Pearson, S.M., Turner, M.G., Gardner, R.H., O'Neill, R.V. (1996) An organism-based perspective of habitat fragmentation. In: Szaro, R.C. & Johnston, D.W. (eds) *Biodiversity in Managed Landscapes: Theory and Practice*. pp. 77–95. Oxford University Press, New York.
- Peterjohn, W.T. & Correll, D.L. (1984) Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. *Ecology* **65**, 1466–1475.
- Pielou, E.C. (1977) *Mathematical Ecology*. John Wiley and Sons, New York.
- Plotnick, R.E., Gardner, R.H., O'Neill, R.V. (1993) Lacunarity indices as measures of landscape texture. *Landscape Ecology* **8**, 201–212.
- Rapport, D.J., Whitford, W.G., Groothusen, R.M. (1996) The Central Rio Grande Valley: Organizing and interpreting ecosystem health assessment data. *GIS World* **9**, 60–62.
- Renard, K.G., Foster, G.R., Weesies, G.A., McCool, D.K., Yoder, D.C. (1997) *Predicting Soil Erosion by Water: A Guide to Conservation Planning with the Revised Universal Soil Loss Equation (RUSLE)*. U.S. Department of Agriculture, Agriculture Handbook no. 703.
- Riitters, K.H., O'Neill, R.V., Jones, K.B. (1997) Assessing habitat suitability at multiple scales: A landscape-level approach. *Biological Conservation* **1997**, 191–202.
- Riitters, K.H., O'Neill, R.V., Wickham, J.D., Jones, K.B. (1996) A note on contagion indices for landscape analysis. *Landscape Ecology* **11**, 197–202.
- Riitters, K.H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B., Jackson, B.L. (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* **10**, 23–39.
- Roughgarden, J. (1991) What does remote sensing do for ecology? *Ecology* **72**, 1918–1922.
- Rowe, J.S. (1961) The level-of-integration concept and ecology. *Ecology* **42**, 420–427.

- Shoemaker, D.J. (1994) *Cumulative Environmental Assessment*. Department of Geography Publication Series, Number 42. University of Waterloo, Ontario, Canada.
- Simon, H.A. (1962) The architecture of complexity. *Proceedings of the American Philosophical Society* **106**, 467–482.
- Southworth, F., Dale, V.H., O'Neill, R.V. (1991) Contrasting patterns of land use in Rondonia, Brazil: Simulating the effects on carbon release. *International Social Science Journal* **43**, 681–698.
- Stauffer, D. (1985) *Introduction to Percolation Theory*. Taylor and Francis, London, U.K.
- Thoman, R.S., Conkling, E.C., Yeates, M.H. (1962) *The Geography of Economic Activity*. McGraw-Hill, New York.
- Turner, M.G., Gardner, R.H., O'Neill, R.V. (1995) Ecological dynamics at broad scales: Ecosystems and landscapes. *Bioscience Supplement: Science and Biodiversity Policy* S29–S35.
- Vogelmann, J.E. (1995) Assessment of forest fragmentation in southern New England using remote sensing and geographic information system technology. *Conservation Biology* **9**, 439–449.
- Wharton, C.H., Kitchens, W.M., Pendelton, E.C., Sipe, T.W. (1982) *The ecology of bottomland hardwood swamps of the southeast: A community profile*. FWS/OBS-81/37. U.S. Fish and Wildlife Service. Biological Services Program, Washington, D.C.
- Wickham, J.D. & Riitters, K.H. (1995) Sensitivity of landscape metrics to pixel size. *International Journal of Remote Sensing* **16**, 3585–3594.
- Wickham, J.D., Jones, K.B., Riitters, K.H., O'Neill, R.V., Tankersley, R.D., Smith, E.R., Neale, A.C., Chaloud, D.J. (1999) An integrated assessment of the U.S. Mid-Atlantic Region. *Environmental Management* **24**, 553–560.
- Wickham, J.D., Jones, K.B., Riitters, K.H., Wade, T.G., O'Neill, R.V. (1999) Transitions in forest fragmentation: Implications for restoration opportunities at regional scales. *Landscape Ecology* (in press).
- Wickham, J.D., O'Neill, R.V., Riitters, K.H., Wade, T.G., Jones, K.B. (1997) Sensitivity of landscape pattern metrics to land cover misclassification and differences in land-cover composition. *Photogrammetric Engineering and Remote Sensing* **63**, 397–402.
- Wickham, J.D., Riitters, K.H., O'Neill, R.V., Jones, K.B., Wade, T.G. (1996) Landscape contagion in raster and vector environments. *International Journal of Geographical Information Systems* **10**, 891–899.