



## Dispersal success on fractal landscapes: a consequence of lacunarity thresholds

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### Abstract

Habitat fragmentation is expected to disrupt dispersal, and thus we explored how patch metrics of landscape structure, such as percolation thresholds used to define landscape connectivity, corresponded with dispersal success on neutral landscapes. We simulated dispersal as either a purely random process (random direction and random step lengths) or as an area-limited random walk (random direction, but movement limited to an adjacent cell at each dispersal step) and quantified dispersal success for 1000 individuals on random and fractal landscape maps across a range of habitat abundance and fragmentation. Dispersal success increased with the number of cells a disperser could search ( $m$ ), but poor dispersers ( $m < 5$ ) searching via area-limited dispersal on fractal landscapes were more successful at locating suitable habitat than random dispersers on either random or fractal landscapes. Dispersal success was enhanced on fractal landscapes relative to random ones because of the greater spatial contagion of habitat. Dispersal success decreased proportionate to habitat loss for poor dispersers ( $m = 1$ ) on random landscapes, but exhibited an abrupt threshold at low levels of habitat abundance ( $p < 0.1$ ) for area-limited dispersers ( $m < 10$ ) on fractal landscapes. Conventional metrics of patch structure, including percolation, did not exhibit threshold behavior in the region of the dispersal threshold. A lacunarity analysis of the gap structure of landscape patterns, however, revealed a strong threshold in the variability of gap sizes at low levels of habitat abundance ( $p < 0.1$ ) in fractal landscapes, the same region in which abrupt declines in dispersal success were observed. The interpatch distances or gaps across which dispersers must move in search of suitable habitat should influence dispersal success, and our results suggest that there is a critical gap-size structure to fractal landscapes that interferes with the ability of dispersers to locate suitable habitat when habitat is rare. We suggest that the gap structure of landscapes is a more important determinant of dispersal than patch structure, although both are ultimately required to predict the ecological consequences of habitat fragmentation.

### Introduction

Dispersal is a critical component of metapopulation dynamics and population persistence, and is the 'key to survival' for species in fragmented landscapes (Opdam 1990). Dispersal may be more important than demographics (e.g., reproductive rates) in determining the regional abundance and persistence of a species (e.g., Lande 1987; Fahrig and Paloheimo 1988). Patch structure (i.e. the number, size and distribution of

habitat or resource patches) affects almost every aspect of animal movement, from foraging behavior to the colonization of oceanic islands (e.g., see review of empirical studies on the responses of insects to environmental patchiness, Doak et al. 1992).

Because one of the more immediate consequences of habitat fragmentation should be a disruption in dispersal between patches, there has been considerable interest in using indices of patch structure to quantify or predict dispersal success in fragmented landscapes

(e.g., Gustafson and Gardner 1996; Schumaker 1996). A number of patch metrics and quantitative methods have been developed to quantify landscape structure (e.g., O'Neill et al. 1989; Turner and Gardner 1991). Indeed, this has been one of the major contributions of landscape ecology, a discipline concerned with the ecological consequences of landscape structure (Turner 1989; Pickett and Cadenasso 1995). What ultimately influences the success of individuals in locating suitable habitat, or some other patchily distributed resource, is the scale of movement relative to the scale of patchiness. Intuitively, dispersal or search success will decline if the distance between patches exceeds the abilities of the organism to either locate habitat or traverse gaps of unsuitable habitat. Habitat fragmentation thus may affect the scale at which organisms must operate to acquire resources (O'Neill et al. 1988) or find suitable habitat, interfere with their ability to traverse the landscape (Gardner et al. 1989), or disrupt movement behavior (Wiens et al. 1997). Unfortunately, many of the patch-based indices commonly employed to describe landscape structure appear to be poor predictors of dispersal success in fragmented landscapes (Schumaker 1996).

In this paper, we quantify the dispersal success for different types of dispersers on random and fractal landscapes across a gradient of fragmentation severity. Thresholds in dispersal success were found to occur at low levels of habitat abundance ( $p < 0.1$ ), but these do not relate to any of the patch-based metrics typically used to define landscape structure, including the percolation-based measure of landscape connectivity known to show threshold behavior. We present a previously unreported feature of landscape structure—lacunarity thresholds in the gap structure of landscape patterns. Lacunarity analysis (Plotnick et al. 1993, 1996) of landscape patterns provides information on the difficulty dispersers should have in locating suitable habitat (variability in gap sizes that must be traversed). The threshold in the lacunarity index coincides with abrupt declines in dispersal success on fractal landscapes. Subsequently, we suggest that landscape gap structure may be a more important determinant of dispersal success than patch structure.

## Methods

### *Neutral landscape maps*

We employed neutral landscape models (Gardner et al. 1987; Gardner and O'Neill 1991; With and King 1997) to produce theoretical distributions of habitat, which enabled us to explore in a general way how landscape structure affects dispersal success. We generated neutral landscapes (grids) of  $128 \times 128$  cells with either random or fractal distributions of habitat using RULE, a computer program for the generation and analysis of landscape patterns (Gardner 1998). The landscapes were binary maps of 'habitat' and 'non-habitat', in which a proportion,  $p$ , of grid cells were classified as habitat. Fractal landscapes were generated as segmented fractional Brownian surfaces based on the mid-point displacement algorithm (Saupe 1988; With et al. 1997; With 1997). Fractal landscape patterns enabled us to vary independently the amount of habitat ( $p$ ) and the spatial contagion or clumping of habitat ( $H$ ;  $D = 3 - H$ , where  $H$  is the Hurst exponent of the fractional Brownian motion and  $D$  is the fractal dimension of the surface) across a range of fragmentation severity, producing complex spatial patterns characteristic of natural landscapes (With et al. 1997; With 1997). Fractal landscapes with a high degree of spatial contagion ( $H = 1.0$ ) have extremely clumped habitat distributions, whereas fractal landscapes with low spatial contagion ( $H = 0.0$ ) are very patchy (Figure 1). We generated a series of fractal landscapes representing three levels of spatial contagion ( $H = 0.0, 0.5, 1.0$ ) and 13 levels of habitat abundance ( $p = 0.01, 0.05, 0.1, 0.2 \dots 0.9, 0.95, 0.99$ ), producing 39 different fractal landscapes. Random landscapes were generated at the same 13 levels of habitat abundance. Dispersal success as a function of landscape structure was thus assayed on a total of 52 different landscapes.

### *Analysis of landscape structure*

The patch structure of random and fractal landscapes was quantified using a variety of rule-based measures generated by RULE (Gardner 1998) such as: (1) size of the largest patch on the landscape, (2) total number of patches; (3) amount of edge habitat, the total number of non-habitat edges adjacent to individual habitat cells; (4) correlation length, the average distance between cells within a patch, which relates to the ability of individuals to move within habitat patches; and, (5) percolation frequency, a measure of overall landscape

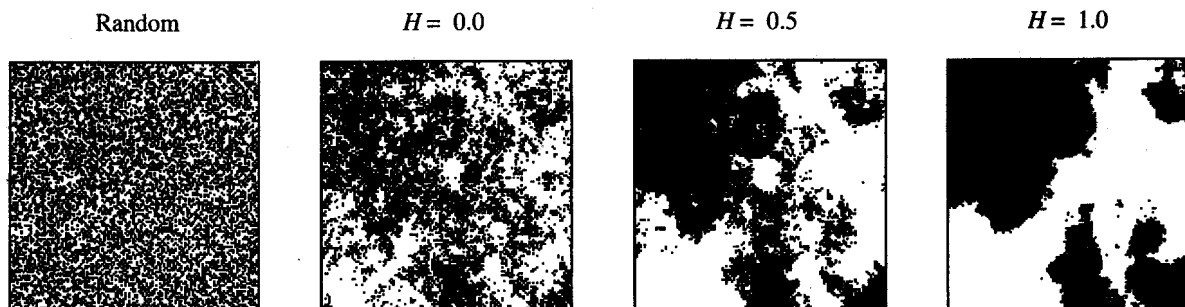


Figure 1. Examples of random and fractal neutral landscapes. Spatial contiguity ( $H$ ) can be varied in fractal landscapes to produce landscape maps that differ in fragmentation severity. Habitat abundance (shaded cells) in all maps is 50%.

connectivity based on the probability that a percolating cluster (a single patch of habitat that spans the entire landscape) occurs. Landscape connectivity provides a quantitative prediction of when the landscape becomes fragmented, which should affect the ability of organisms to traverse the landscape (Gardner et al. 1989; Gardner et al. 1993; With and Crist 1995; Pearson et al. 1996; With et al. 1997).

Because landscape structure is sensitive to the scale at which it is measured (Plotnick and Gardner 1993), we used two patch connectivity rules to derive these metrics. The first rule (Rule 1 or nearest-neighbor) defines patches as habitat cells that share at least one adjacent edge, excluding diagonals. This is the simplest rule of patch connectivity and describes the structural connectivity of landscapes (With and King 1997). This patch connectivity rule has been used to define how organisms constrained to move only through adjacent habitat cells might perceive landscape structure (Pearson et al. 1996). We also used a more extensive patch connectivity rule (Rule 3) in which habitat cells within a 12-cell neighborhood are considered to be connected. This rule of patch connectivity has been used to quantify the functional connectivity of landscapes, in which an organism capable of crossing gaps of unsuitable habitat might perceive patches as connected even if they are not adjacent (Pearson et al. 1996). Because dispersers in our model can move across unsuitable habitat (i.e., they are not constrained to move only within habitat, see below), patch metrics assessed at this scale (Rule 3) may provide a better descriptor of landscape structure for analysis of dispersal success in fragmented landscapes.

In addition to quantifying the patch structure of neutral landscapes, we also analyzed the gap structure. Lacunarity analysis has been presented as a means of

measuring the pattern and spatial scaling of gap sizes in a landscape (Plotnick et al. 1993, 1996). Whereas spatial distributions that differ in patch structure may give rise to the same fractal dimension, they may differ in gap structure and thus in their lacunarity index (e.g., see Figure 1 of Cantor dusts in Plotnick et al. 1993, or Plate 318 of Sierpinski carpets in Mandelbrot 1983). Landscapes in which the sizes of gaps are uniform at a particular spatial scale have a low lacunarity index ( $\Lambda = 1$ ); high lacunarity indices characterize landscapes in which gap sizes are extremely variable at a given scale. The lacunarity index is basically a variance-mean ratio of the number of non-habitat cells (gaps) per unit area at a particular scale ('box size'; see details in Plotnick et al. 1996). The lacunarity index is calculated within RULE using Allain and Cloitre's (1991) 'gliding box' algorithm, in which the frequency distribution of non-habitat cells is assayed at increasingly larger 'box sizes' or scales.

In a given landscape, lacunarity decreases as box size increases, because the variance among individual boxes at large scales is diminished (Plotnick et al. 1993, 1996). Lacunarity is also affected by the proportion of habitat ( $p$ ) on the landscape, such that landscapes in which habitat is rare have high lacunarity indices (i.e., the sizes of gaps between habitat patches are highly variable). Finally, lacunarity analysis is sensitive to the spatial patterning of habitat. Higher lacunarity indices are generated by clumped habitat distributions than by random or regular patterns for a given level of habitat abundance (Plotnick et al. 1993).

#### *Simulation of dispersal on neutral landscapes*

Many species undergo a dispersal phase in which offspring depart their natal patch or territory and move through the landscape in search of suitable habitat

in which to settle and eventually breed (e.g., Greenwood 1980; Greenwood and Harvey 1982; Hansson 1991). We simulated dispersal behavior on the random and fractal neutral landscapes as either a purely random search or as an area-limited random search. In each mode of dispersal, the individual left its natal site (which by definition is a suitable habitat cell) and searched up to  $m$  cells for suitable habitat (i.e. dispersal was obligate). While the effect of dispersal range ( $m = 1-50$ ) on success was explored in these simulations, a maximum dispersal range of  $m = 50$  was set because individuals generally succeeded in finding suitable habitat within this range (Figures 2-3). At most, then, an individual could interact with 0.3% of the landscape (50 cells/16384 cells in landscape). Landscape edges were treated as reflecting barriers.

For random dispersal, the individual moved a random direction and distance at each dispersal step. Any cell in the landscape could be reached in any dispersal step (i.e. step length, the number of cells crossed, was variable). The probability of successfully encountering suitable habitat with random dispersal is given by  $\text{Pr}(\text{success}) = 1 - u^m$ , where  $u = 1 - p$  is the proportion of unsuitable habitat in the landscape (see Lande 1987). Thus, there was no need to simulate random dispersal on neutral landscapes. Note that the underlying spatial distribution does not affect the probability of encountering suitable habitat for random search; only the abundance of habitat ( $p$ ) is important. Search success for a random disperser is thus equivalent on random and fractal landscapes (With and King in press).

In area-limited dispersal (referred to as nearest-neighbor dispersal in With and King in press), movement in a single dispersal step is limited to adjacent cells (habitat or non-habitat) sharing an edge; dispersers thus were not constrained to move only through habitat cells. The choice of cell is random with equal (25%) probability. Thus direction is random, but step length is fixed at a single cell. The probability of successful dispersal via area-limited dispersal may not have a closed-form solution (With and King in press). Dispersal success therefore was derived empirically by simulating dispersal for 1000 independent individuals per landscape and scoring each disperser's success or failure at finding suitable habitat within  $m$  steps. Again, the disperser could search up to  $m$  cells for a suitable habitat cell before dying if unsuccessful. On average, the area searched in  $m$  steps by a disperser following this nearest-neighbor random walk is less than the area searched by a random disperser in the

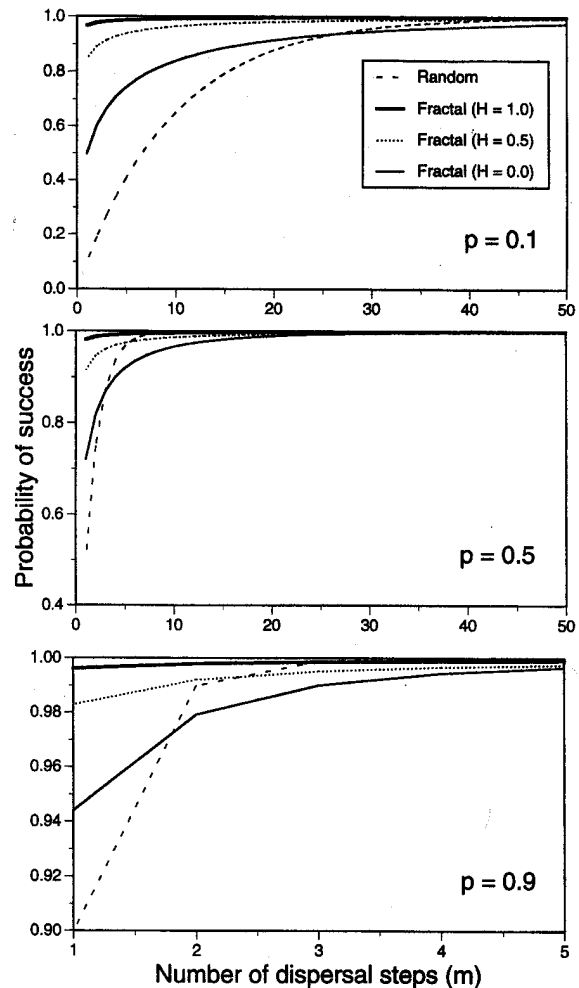


Figure 2. The probability of successfully encountering a suitable habitat cell as a function of dispersal ability ( $m$ , number of cells searched) for dispersers moving via area-limited dispersal in random or fractal landscapes at different levels of habitat abundance ( $p$ ). Dispersal success was quantified as the fraction of 1000 independent individuals that located habitat within  $m$  steps.

same  $m$  steps, and the search is relatively limited to the area surrounding the natal cell; hence, our designation of this dispersal behavior as area-limited dispersal.

## Results

Not surprisingly, dispersal success—the probability of finding a suitable habitat cell—increases with dispersal ability ( $m$ ). When habitat is rare ( $p = 0.1$ ), random dispersers have a 10% probability of finding habitat in one step ( $1 - u^m = 0.1$  for  $m = 1$ ), but dispersal success is 48% for area-limited dispersers ( $m = 1$ ) in

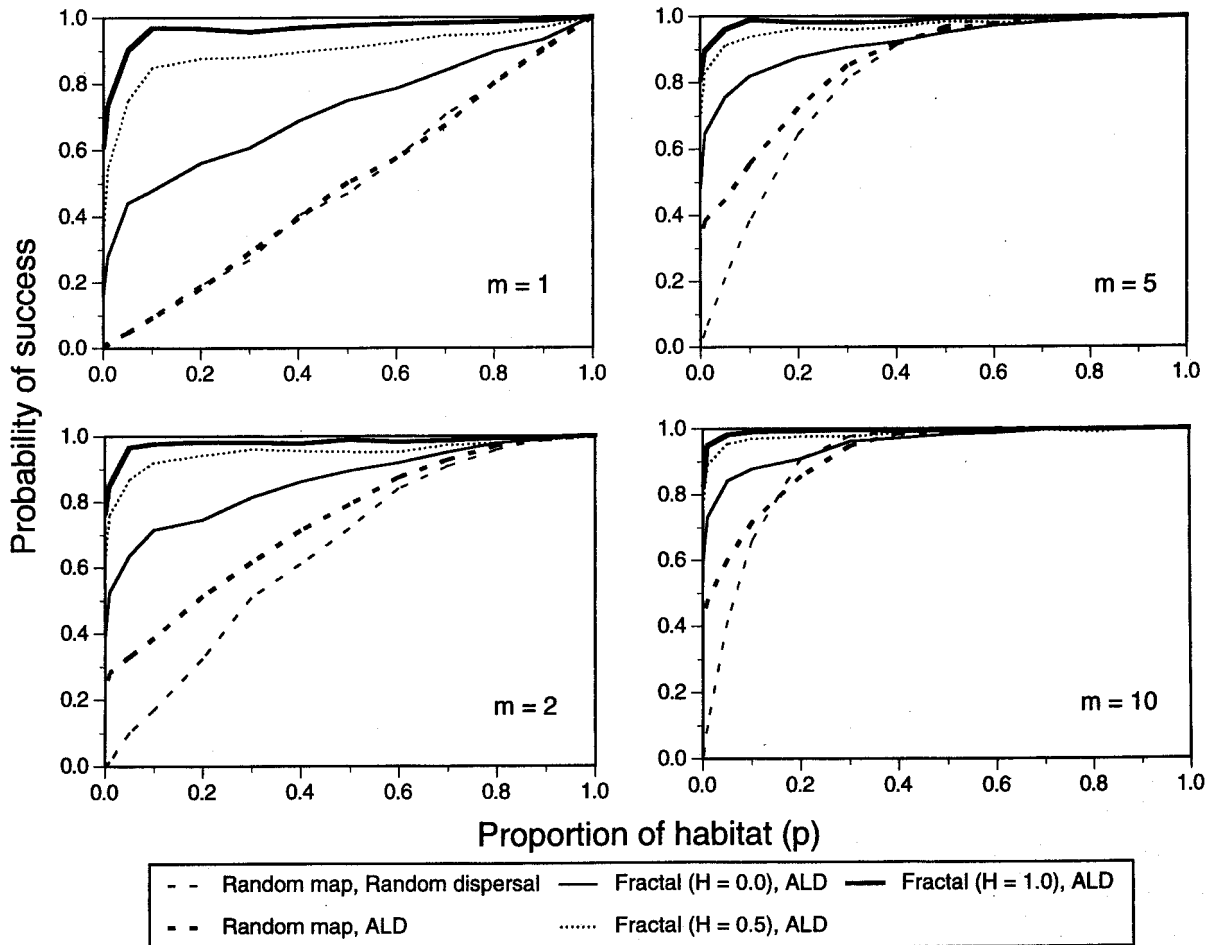


Figure 3. Dispersal success as a function of habitat abundance ( $p$ ) for species with different levels of dispersal ability ( $m$ , the number of cells that can be searched before disperser dies). Dispersal was simulated as either a random process (random direction and distance) on random landscapes, or as area-limited dispersal (ALD, random direction but steps limited to nearest-neighbor cells) on either random or fractal landscapes. Random search on fractal landscapes is identical to the curves for random search on random landscapes (With and King in press).

highly fragmented ( $H = 0.0$ ) fractal landscapes and is 97% in clumped ( $H = 1.0$ ) fractal landscapes (Figure 2). It takes nearly 10 and 35 steps, respectively, for a random disperser to achieve this level of success when habitat is rare. When half of the landscape is habitat ( $p = 0.5$ ), poor dispersers ( $m = 1$ ) adopting a random search have only a 50% probability of successfully encountering a suitable habitat cell, whereas area-limited dispersal produces a 70–100% success rate even for poor dispersers. A random disperser can achieve this level of success in 2–10 steps. Finally, when habitat is very abundant ( $p = 0.9$ ), all dispersal strategies result in a high level of success (90–100%) and dispersers are virtually guaranteed to find suitable habitat within 5 steps (Figure 2). Thus, spatial pattern-

ing does not affect dispersal success when habitat is very abundant.

Dispersal success decreases in direct proportion to habitat loss (declining  $p$ ) for poor dispersers ( $m = 1$ ) searching for suitable habitat on random landscapes either at random or by area-limited dispersal (Figure 3). The dispersal success of poor dispersers also decreases essentially linearly for area-limited dispersers on fractal landscapes when  $p > 0.1$ , but at a slower rate than for dispersers on random landscapes. The rate of decline with lower  $p$  decreases with increasing  $H$ . Note, however, that there is an abrupt decline in dispersal success at  $p \leq 0.1$  for area-limited dispersers in all fractal landscapes. The rapid decline or threshold persists even with increasing dispersal ability ( $m = 2, 5, \text{ and } 10$ ; Figure 3). Nonlinear

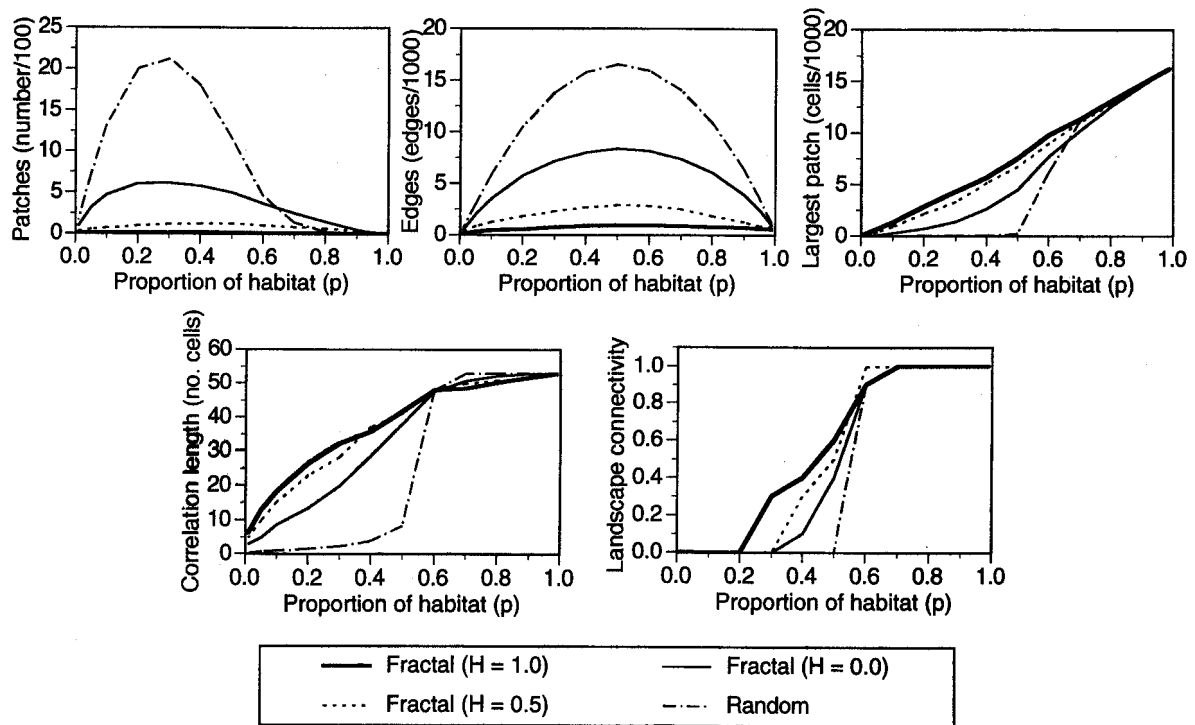


Figure 4. Patch-based metrics for random and fractal neutral landscapes as a function of habitat abundance ( $p$ ). 'Patch' is defined by the nearest-neighbor rule (Rule 1), as habitat cells that are adjacent along at least one edge. Curves represent the average statistic based on an analysis of 10 maps for each type of neutral landscape at each level of  $p$ .

declines in dispersal success also occur for  $m = 5, 10$  on random landscapes, but at higher levels of habitat abundance ( $p = 0.3$ ) than in fractal landscapes. Dispersal success was thus affected sooner by habitat loss in random landscapes than in fractal landscapes.

What aspects of landscape structure might account for the threshold in dispersal success observed at low habitat abundances in fractal landscapes? Percolation thresholds, defined as a  $\geq 50\%$  likelihood of having a spanning habitat cluster on the landscape, occur at higher levels of habitat abundance than these dispersal thresholds. The oft-reported percolation threshold,  $p_{\text{crit}} = 0.59$ , applies only to random neutral landscapes for Rule 1 (Figure 4), and the percolation threshold on random landscapes for Rule 3 is  $p_{\text{crit}} = 0.29$  (Figure 5; Plotnick and Gardner 1993). Fractal landscapes are inherently more connected than random landscapes because of their greater spatial contagion (Figure 1). Consequently, percolation thresholds occur at  $p_{\text{crit}} = 0.54$  for the highly fragmented ( $H = 0.0$ ) landscapes and at  $p_{\text{crit}} = 0.45$  for the clumped ( $H = 1.0$ ) fractal landscapes (Figure 4). At a coarser scale of analysis (Rule 3), however, landscape connectivity in fractal

landscapes declines more as a linear function of habitat loss than as a threshold (Figure 5). Correlation length exhibits a threshold for random landscapes at about the point predicted by the percolation threshold ( $p = 0.6$  for Rule 1 and  $p = 0.3$  for Rule 3), but exhibits a linear decrease as a function of habitat loss for fractal landscapes (Figures 4–5). None of the other patch-based metrics used in this study exhibit threshold behavior. The size of the largest patch increases nearly linearly with habitat abundance (Figures 4–5). The amount of edge habitat peaks at  $p = 0.5$  for all landscapes (Figures 4–5). The number of patches on the landscape peaks around  $p = 0.3$  in random landscapes (Rule 1, Figure 4), but does exhibit a sharp reduction at  $p < 0.1$  if patch connectivity is defined by Rule 3 (Figure 5). Dispersal thresholds were not strongly defined in random landscapes, however. Thus, conventional measures of patch structure do not appear to capture the changes in landscape structure at  $p < 0.1$  responsible for the thresholds in dispersal success.

The lacunarity index, a measure of the gap structure of the landscape, does exhibit a pronounced

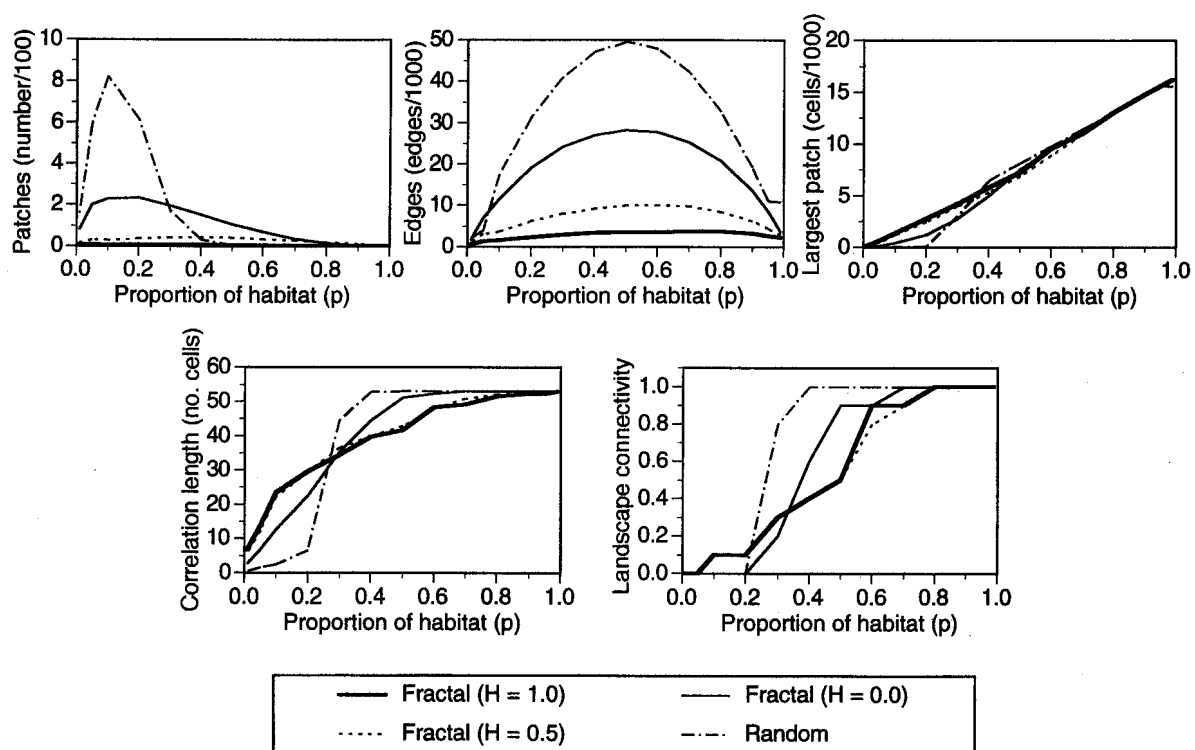


Figure 5. Patch-based metrics for random and fractal neutral landscapes as a function of habitat abundance ( $p$ ). 'Patch' is defined by a 12-cell neighborhood rule (Rule 3). Curves represent the average statistic based on an analysis of 10 maps for each type of neutral landscape at each level of  $p$ .

threshold at low levels of habitat abundance ( $p < 0.1$ ) in fractal landscapes, however, which correlates with the abrupt declines observed in dispersal success (Figure 6). The highest lacunarity values are obtained when the scale of the analysis is the same as the grain size of the landscape pattern (i.e., box size = 1). The lacunarity curves for random and fractal landscapes are equivalent at the finest scale of analysis (box size = 1, Figure 6). When box size is equal to the grain size of the map, the lacunarity index is solely a function of the proportion of habitat on the landscape and is independent of the spatial distribution of habitat (Plotnick et al. 1993). At the next scale of analysis, however, random maps have fairly uniform gap sizes as evidenced by the low lacunarity index (box size = 2, Figure 6), and no threshold is evident in random maps at larger scales of analysis. A threshold in lacunarity does persist at larger scales for fractal maps, and is most evident in maps of greater spatial contagion. At larger scales (increasing box size), there is a decrease in lacunarity for all landscapes, but the difference in gap structure between highly fragmented (e.g.,  $H = 0.0$ ) and clumped ( $H = 1.0$ ) landscapes

becomes more pronounced, particularly when habitat is rare (Figure 6). The highly fragmented fractal landscapes have more uniform gap sizes than the clumped fractal landscapes at these larger scales (box size = 2, 5, and 10; Figure 6).

Thresholds in lacunarity are coincident with thresholds in dispersal success. Thus, the gap structure of the landscape may be an important determinant of dispersal success in fractal landscapes.

## Discussion

The focus of much theoretical and empirical research in ecology has been on how patchiness affects ecological processes such as movement, dispersal and patch colonization (e.g., Fahrig and Merriam 1985; Kareiva 1990; Doak et al. 1992, and references therein; Wiens et al. 1993; Gustafson and Gardner 1996). There has been a preoccupation in landscape ecology with the patch structure and spatial scaling of landscapes. The connectivity of habitat patches is a 'vital element of landscape structure' (Taylor et al. 1993), which not

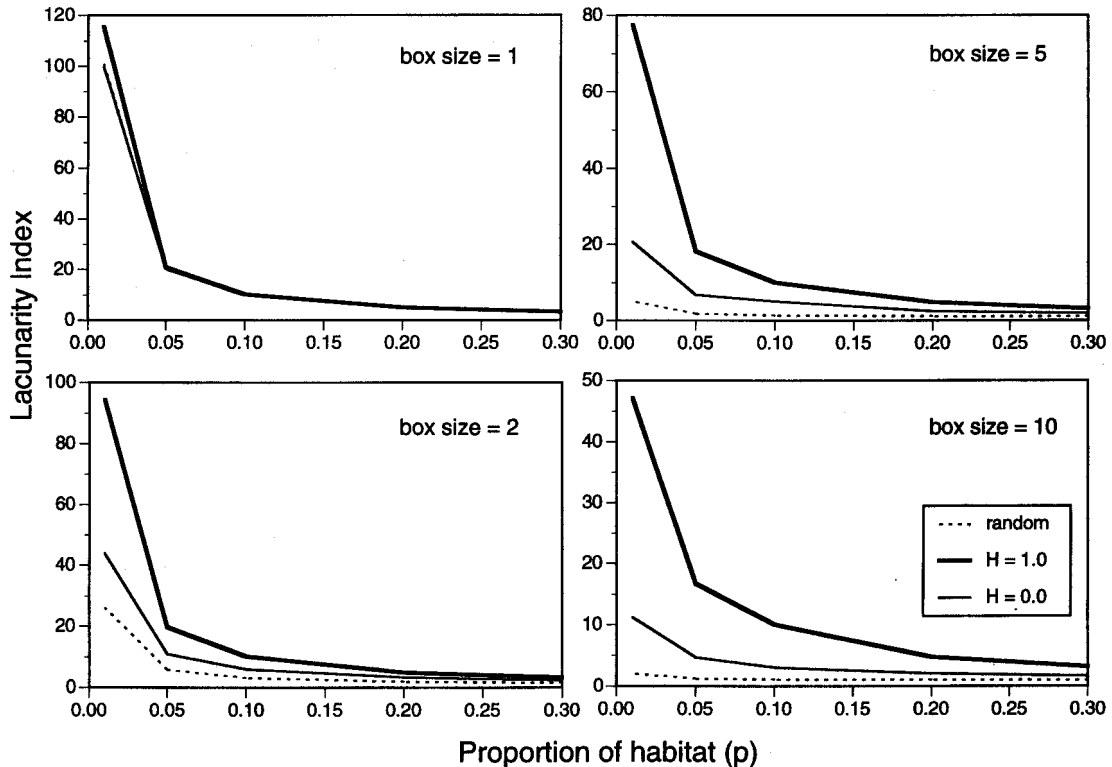


Figure 6. A comparison of lacunarity thresholds for random and fractal landscapes ( $H$ ) at different spatial scales (box sizes). A threshold in gap structure occurs at  $p < 0.1$ ; gap sizes become extremely variable in this range as evidenced by the high lacunarity indices. Curves are equivalent for all maps at the finest scale (box size = 1) because the scale of measurement is the same as the grain of the landscape pattern; only the abundance of habitat affects the lacunarity index at this scale. At larger scales, however, fractal landscapes exhibit thresholds in gap structure, whereas gap sizes are essentially uniform in random landscapes (low lacunarity indices).

only affects dispersal success and colonization rates, but ultimately population persistence and community dynamics (e.g., Opdam 1990; Hansson 1991). To be meaningful, measures of landscape connectivity should thus be based on dispersal or movement behavior. Studies have begun to emerge, however, that suggest that measures of patch connectivity may fail as predictors of dispersal success on fragmented landscapes. For example, Schumaker (1996) found weak correlation between nine commonly employed indices of landscape pattern (e.g., contagion, perimeter-area ratios) and dispersal success.

The gap structure of the landscape has not been explicitly addressed in most analyses of landscape pattern. Although lacunarity analysis was first presented as a measure of 'landscape texture' or gappiness, it was ultimately used as a multiscale analysis of landscape pattern that could be used to identify the patch structure of ecological data (Plotnick et al. 1993, 1996). The discovery of critical thresholds in lacunarity suggests that dramatic changes in the gap structure

of fractal landscapes occurs at low levels of habitat abundance. The variability in gap sizes between habitat patches increases precipitously as habitat falls below 10% (Figure 6). This should make it more difficult for dispersers to find suitable habitat, which is evidenced by the abrupt declines in dispersal success in fractal landscapes (Figure 3). Dispersal success in our model is generally high in fractal landscapes because of the greater spatial contagion of habitat, which produces a more clumped distribution than random, and because individuals begin their search for suitable habitat within a patch. As habitat becomes scarce, patches become smaller and more isolated and individuals are forced to traverse larger gaps in search of suitable habitat. Past a certain threshold in gap sizes, the disperser perishes before finding a suitable habitat cell, particularly in landscapes with extensive gaps, such as clumped ( $H = 1.0$ ) fractal landscapes. Thus, dispersal success is alternatively enhanced (when searching for suitable habitat within the natal patch) and diminished (when disperser leaves patch) in landscapes with



clumped habitat distributions; a similar finding was reported by Doak et al. (1992) in their simulation model of dispersal on artificial patchy landscapes. Other theoretical models have also demonstrated that interpatch distance has a strong effect on search behavior and on the ability of dispersers to locate suitable habitat or discriminate between 'good and bad' patches (e.g., Walsh 1996).

Other studies have recently emerged in which thresholds in movement behavior or population responses are evident when habitat is limiting on the landscape. Tenebrionid beetles traversing experimental microlandscapes, constructed as random mosaics of sand and grass, exhibited a strong threshold in several movement parameters (e.g., net displacement) at  $p_{\text{grass}} < 0.2$  (Wiens et al. 1997). Movement rates were significantly reduced in plots with grass cover ( $p_{\text{grass}} \geq 0.2$ ), which suggests that grass patches are less permeable to beetles and/or that beetles have a preference for grass and tend to remain in this cover type, especially when there is little grass cover available. In either case, beetles may be modifying their behavior when they encounter patch boundaries. Patch boundary effects are expected to be greatest in landscapes with a high patch edge-to-area ratio, which occurs when habitat is rare (e.g.,  $p_{\text{grass}} < 0.2$ ) and patches tend to be small and isolated. In a recent series of simulations, Fahrig (1997) demonstrated that habitat fragmentation – the disruption of habitat into numerous small patches – had the greatest effect on population persistence at  $p < 0.2$ . Extinction risk increased precipitously when <20% habitat remained on the landscape; above this, the amount of habitat had a much greater effect on extinction probability than fragmentation (Fahrig 1997). These results are similar to the literature survey Andrén (1994) performed to assess the effects of habitat fragmentation on birds and mammals, in which the total amount of suitable habitat was a better predictor of species abundance than fragmentation *per se*. The threshold at which fragmentation effects became important was  $p = 0.1\text{--}0.3$ . It was in this range that interpatch distances increased exponentially and that the spatial arrangement of patches became critical. Because habitat fragmentation involves, by definition, a change in the gap-size distribution (i.e., interpatch distances) of landscapes, we propose that the disruption in dispersal or movement behavior that has been observed to occur at low levels of habitat abundance ( $p < 0.2$ ; Wiens et al. 1997, this study) may directly impact population-level phenomena such as popula-

tion sizes and contribute to thresholds in population persistence (Andrén 1994, Fahrig 1997).

In summary, gap structure is an important feature of landscapes that may profoundly affect ecological processes such as movement and dispersal, and perhaps more so than patch structure. Gap structure is not the inverse or 'mirror image' of patch structure. Landscapes with similar levels of patchiness can have different gap structures as was shown for patterns of Cantor dusts (Plotnick et al. 1993) and Sierpinski carpets (Mandelbrot 1983). The discovery of lacunarity thresholds may resolve the apparent dilemma posed by discordant thresholds in ecological responses to landscape structure and percolation thresholds of patch connectivity. It is intriguing that thresholds in movement behavior, dispersal success, and population distributions have been found in the vicinity of  $p = 0.1$ , the same domain at which lacunarity thresholds occur (e.g., Andrén 1994; Fahrig 1997; Wiens et al. 1997; this paper). We suggest that more explicit attention should be given to the gap structure of both natural and model landscapes. Both the lacunarity index and fractal dimension of landscape patterns will be necessary to predict dispersal success and other ecological responses to habitat fragmentation.

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### References

- Allain, C., and Cloitre, M. 1991. Characterizing the lacunarity of random and deterministic fractal sets. *Physical Review A* 44: 3552–3558.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.

- Doak, D.F., Marino, P.C., and P.M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology* 41: 315–336.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603–610.
- Fahrig, L., and Merriam, G. 1985. Habitat patch connectivity and population survival. *Ecology* 66: 1762–1768.
- Fahrig, L., and Paloheimo, J. 1988. Determinants of local population size in patchy habitats. *Theoretical Population Biology* 34: 194–213.
- Gardner, R.H. 1998. RULE: a program for the generation and analysis of landscape pattern. In press in *Landscape ecological analysis: issues and applications* (J.M. Klopatek, and R.H. Gardner, editors). Springer-Verlag, New York.
- Gardner, R.H., and O'Neill, R.V. 1991. Pattern, process and predictability: the use of neutral models for landscape analysis. In *Quantitative methods in landscape ecology*. pp. 289–307. Edited by M. G. Turner and R.H. Gardner. Springer-Verlag, New York.
- Gardner, R.H., Milne, B.T., Turner, M.G., and 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., and Turner, M.G. 1993. Ecological implications of landscape fragmentation. In *Humans as components of ecosystems: subtle human effects and ecology of populated areas*. pp. 208–226. Edited by S.T.A. Pickett and M.G. McDonnell. Springer-Verlag, New York.
- Gardner, R.H., O'Neill, R.V., Turner, M.G., and Dale, V.H. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecology* 3: 217–227.
- Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140–1162.
- Greenwood, P.J., and Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13: 1–21.
- Gustafson, E.J., and Gardner, R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77: 94–107.
- Hansson, L. 1991. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society* 42: 89–103.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London B* 330: 175–190.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* 130: 624–635.
- Mandelbrot, B.B. 1983. *The fractal geometry of nature*. W.H. Freeman and Company, New York.
- O'Neill, R.V., Milne, B.T., Turner, M.G., and Gardner, R.H. 1988. Resource utilization scales and landscape pattern. *Landscape Ecology* 2: 63–69.
- 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.W., Dale, V.H., and Graham, R.L. 1988. Indices of landscape pattern. *Landscape Ecology* 1: 153–162.
- Opdam, P. 1990. Dispersal in fragmented populations: the key to survival. In *Species dispersal in agricultural habitats*. pp. 3–17. Edited by R.G.H. Bunce and D.C. Howard. Belhaven Press, New York.
- Pearson, S.M., Turner, M.G., Gardner, R.H., and O'Neill, R.V. 1996. An organism-based perspective of habitat fragmentation. In *Biodiversity in managed landscapes: theory and practice*. pp. 77–95. Edited by R.C. Szaro and D.W. Johnston. Oxford University Press, Oxford.
- Pickett, S.T.A., and Cadenasso, M.L. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269: 331–334.
- Plotnick, R.E., and Gardner, R.H. 1993. Lattices and landscapes. In *Lectures on mathematics in the life sciences: predicting spatial effects in ecological systems*, vol. 23. pp. 207–224. Edited by R.H. Gardner. American Mathematical Society, Providence, Rhode Island.
- Plotnick, R.E., Gardner, R.H., and O'Neill, R.V. 1993. Lacunarity indices as measures of landscape texture. *Landscape Ecology* 8: 201–211.
- Plotnick, R.E., Gardner, R.H., Hargrove, W.W., Prestegard, K., and Perlmutter, M. 1996. Lacunarity analysis: a general technique for the analysis of spatial patterns. *Physical Review E* 53: 5461–5468.
- Saupe, D. 1988. Algorithms for random fractals. In *The science of fractal images*. pp. 71–113. Edited by H.-O. Petigien and D. Saupe. Springer, New York.
- Schumaker, N. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77: 1210–1225.
- Taylor, P.D., Fahrig, L., Henein, K., and Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571–573.
- Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171–197.
- Turner, M.G., and Gardner, R.H., editors. 1991. *Quantitative methods in landscape ecology*. Springer-Verlag, New York.
- Walsh, P.D. 1996. Area-restricted search and scale dependence of patch quality discrimination. *Journal of Theoretical Biology* 183: 351–361.
- Wiens, J.A., Stenseth, N.C., Van Horne, B., and Ims, R.A. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66: 369–380.
- Wiens, J.A., Schooley, R.L., and Weeks, Jr., R.D. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78: 257–264.
- With, K.A. 1997. The application of neutral landscape models to conservation biology. *Conservation Biology* 11: 1069–1080.
- With, K.A., and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76: 2446–2459.
- With, K.A., and King, A.W. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* 79: 219–229.
- With, K.A., and King, A.W. *in press*. Extinction thresholds for species in fractal landscapes. *Conservation Biology*.
- With, K.A., Gardner, R.H., and Turner, M.G. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78: 151–169.