Landscape Ecology vol. 3 no. 2 pp 87-96 (1989)
SPB Academic Publishing bv, The Hague

Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective

John A. Wiens[1] and Bruce T. Milne[2]
[1]Department of Biology and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523 USA, and [2]Department of Biology, University of New Mexico, Albuquerque, NM 87131 USA

Keywords: landscape ecology, fractals, tenebrionidae, beetles, grassland

Abstract

Research performed on microlandscapes embodies the essence of landscape ecology by focusing on the ecological consequences of the mosaic structure of different landscape elements. As an illustration, observations and simulations were used to test whether the fractal structure of grassland microlandscapes affected the movement patterns of tenebrionid beeetles in natural environments. The significant tendency of beetles to avoid 1 m^2 cells with fractal dimensions of 1.85 to 1.89 (indicating the area-filling tendency of bare ground) demonstrated the role of landscape structure as a modifier of beetle movements or diffusion in heterogeneous landscapes. Experiments in microlandscapes may accelerate the development of quantitative conceptual frameworks applicable to landscapes at all scales.

Introduction

The distinctiveness of landscape ecology as a discipline lies in its focus on entire landscapes as the objects of study and the way in which it draws together different disciplines about this focus. But what is a 'landscape'? Perhaps because landscape ecologists represent a variety of disciplinary backgrounds, the term 'landscape' conjures up different images to different people. The prevalent view, however, is that landscapes are the arenas in which humans interact with their environments on a kilometres-wide scale (Troll 1968; Zonneveld 1979; Naveh and Lieberman 1984; Forman and Godron 1986). Because landscape ecology began as a discipline in the extensively modified landscapes of West Germany and The Netherlands (Naveh 1982), this focus on the dynamic role of humans in the landscape is not surprising.

We approach landscape ecology from the perspectives of the discipline of ecology. In this context, we believe that the primary contribution of landscape ecology, its raison d'être, is its capacity to focus our attention on the structure of patch *mosaics* and, thereby, to develop our understanding of environmental heterogeneity and its effects beyond simple considerations of patchiness and patch dynamics. By this view, landscape ecology addresses how landscape elements or patches are configured in relation to one another in an overall mosaic and how such landscape structure influences a wide variety of ecological patterns and processes.

There is nothing in this perspective that restricts it to human-modified landscapes or to areas scaled to the human level of perception. Considerations of mosaic patterns and their effects should be scaled to the organisms and phenomena being investigated and the questions being asked (Wiens *et al.* 1986, Addicott *et al.* 1987; Wiens in press). A landscape that is heterogeneous from the perspective of a ground-dwelling harvester ant, for example, may be contained within one or two seemingly homogeneous patches from the perspective of a foraging bird or a grazing ungulate.

Our thesis is that the ideas and approaches of landscape ecology should apply at any scale of investigation and that landscape ecology is likely to develop a strong conceptual and theoretical foundation only if we shed the preoccupation with human-scaled landscapes and adopt a multi-scale perspective on landscape patterns and dynamics. In particular, we advocate investigations of landscape patterns and their effects at small, 'microlandscape' scales. Studies at such scales may have the potential to serve as a model of larger-scale landscape systems, in a manner analogous to microcosm studies of trophic dynamics or nutrient cycling in laboratory ecosystems (Taub 1974). There are several advantages of this microlandscape approach: (1) measurements may be taken with a level of detail that is difficult to attain at a broader scale; (2) sample sizes may be greater or sampling at a given intensity may provide a more accurate representation of the phenomenon being investigated; (3) experimental manipulations may be conducted with relative ease, and (4) experiments or observations may be replicated over many plots or treatments with relative ease. Collectively, these features enhance our ability to study landscapes in a rigorous fashion and to move from Troll's assessment of landscape ecology as 'an attitude' (Zonneveld 1979) to a firmer scientific base for the discipline.

Our objectives in this paper are twofold. First, we will illustrate the way in which a microlandscape approach can be applied, using results from our ongoing studies of beetle movements in relationship to habitat mosaic structure in semiarid grasslands. We will then discuss the relevance of such studies, not only to our knowledge of beetle ecology, but also with regard to how this approach can be applied at other, more conventional, landscape scales. We will conclude with some general comments about scaling of investigations in landscape ecology.

Microlandscape patterns and beetle movements

Tenebrionid beetles (Coleoptera: Tenebrionidae) are conspicuous elements of the arthropod fauna of most deserts and grasslands of the world (Crawford 1981). They are primarily detritivores, although some species are partially herbivorous. Individuals may be associated with burrows to which they return, but they often range widely when foraging. Calkins and Kirk (1973), for example, found average straight-line movement distances for five species of *Eleodes* to be > 300 m over a 10-day period, with maximum distances for the most vagile species, *E. obsoleta*, of 3,600 m. Other investigators have reported movement rates on the order of 6–20 $\mathrm{m\,h^{-1}}$ (Kramm and Kramm 1972) or 15–35 $\mathrm{m\,d^{-1}}$ (Doyen and Tschinkel 1974).

Beetles rarely move in straight lines, however. Instead, they follow a tortuous pathway, turning frequently to head in new directions. Our initial observations indicated that beetles move rapidly across bare, unvegetated ground but move more slowly when traversing dense clumps of grass. Grass clumps interspersed among areas of bare ground constitute the landscape of a beetle, and may therefore have important effects on their movement patterns. To evaluate this premise, we tested the null hypothesis that the movement patterns of beetles are unrelated to variations in the mosaic pattern of the microlandscape they occupy.

Methods

To test this hypothesis, Milne measured the patterns of beetle landscapes and beetle movements in a semiarid grassland dominated by *Bouteloua gracilis* in the Sevilleta National Wildlife Refuge (a Long Term Ecological Research site), 115 km S of Albuquerque, New Mexico. This system was chosen because it shares characteristics with percolating networks (Stauffer 1985; Orbach 1986), which have been used to develop diffusion equations for fractally heterogeneous patch networks. Without flowering culms the grasses average ca. 10 cm in height and form open sods with anastomosing patches of bare ground.

Ten 5 × 5 m plots were established within a ca. 0.04-ha area. Each plot was subdivided into a nested series of grid cells measuring 1 m, 1/2 m, 1/4 m, 1/8 m and 1/16 m on a side. The grids defined measurement scales of increasingly higher resolution that included 1, 0.25, 0.0625, 0.0156, and 0.0039 m^2, respectively, with 5–80 grid cells along each edge of the study plots. The observations and analyses reported here were obtained in one of these plots.

Landscape patterns

We used a measure of fractal geometry to determine the landscape patterns encountered by beetles moving in this plot. Each grid cell at each scale of measurement was categorized according to whether or not it contained > 25% coverage of bare ground. Bare ground was assumed to be the 'environment' within which beetles moved most readily, much like the cells studied in percolation theory (Stauffer 1985; Orbach 1986; Gardner *et al.* 1987). We used an arbitrary standard of 25% bare-ground coverage rather than some other equally arbitrary standard because this value maintained a constant criterion of 'cover' among the scales of measurement, which differed sequentially as powers of 2. In this way, we could compare directly the cell counts at the finest resolution of 0.0039 m^2 with those obtained at broader scales of measurement. At each scale, the number of nested cells at the next finer scale that contained > 25% bare-ground cover was counted.

We quantified landscape heterogeneity within each 1 m^2 cell of the 5 × 5 m plot by regressing the log of the cell counts at each of the finer scales of measurement against the log of resolution (*i.e.*, the number of cells along one side of the 1 m^2 cells at a given measurement scale). The slope of the regression is the fractal dimension, D, of bare ground (Mandelbrot 1983; Milne 1988). In this case, D was most sensitive to the manner in which bare ground 'filled' the plane of the study plot (Milne 1989). A fractal dimension of $D = 2$ implied continuous cover of bare ground at all scales, whereas values of $D < 2$ indicated that grasses broke up the 2-dimensional plane occupied by bare ground, thereby creating a more sinuous or 'linear' network of bare ground. Maps of (1) bare-ground coverage at various resolutions and (2) fractal dimensions in each 1 m^2 cell were created by kriging (Davis 1986) the coverage data and fractal dimensions, respectively, using the Surfer software from Golden Software, Inc.

Beetle movements

To determine how beetles responded to the mosaic pattern of this microlandscape, we used a total of six individuals of *Eleodes sponsa* Lec., *E. longicollis* Lec., and *E. caudifera* Lec. The beetles were similar in length (mean = 24.0 mm, s.d. = 2.37) and had the same movement speeds over open expanses of bare ground (mean = 0.11 m/s, s.d. = 0.05). Field trials were conducted between 17 June and 8 July 1987 from 0730 to 1130 MST (to avoid heat effects on activity; air temperature range = 23–30°C). During a 'trial', an individual beetle was released at the center of a randomly selected cell among the central nine 1 m^2 cells of the plot. In order to minimize effects of handling on movement patterns, beetles were covered by an opaque container for 2 min prior to release. A remote control was used to remove the cover to release the beetle. The position of the beetle was then marked every 5 s by placing a numbered toothpick at its posterior end. Movements were monitored in this way for 500 s or until the beetle exited the plot. The movement trajectory was then mapped to the nearest cm.

Our null hypothesis was that beetle movements were independent of landscape complexity. In order to test this hypothesis, we must determine whether beetle movement through cells of different types departs significantly from that expected on the basis of random occupancy of the cells. We used model simulations of beetle movements to generate expected patterns. There are many alternative models for simulating beetle movement under this null hypothesis. Kareiva and Shigesada (1983) described correlated random walks based on empirical distributions of displacement and turning angles. The simulations we used relied on empirical

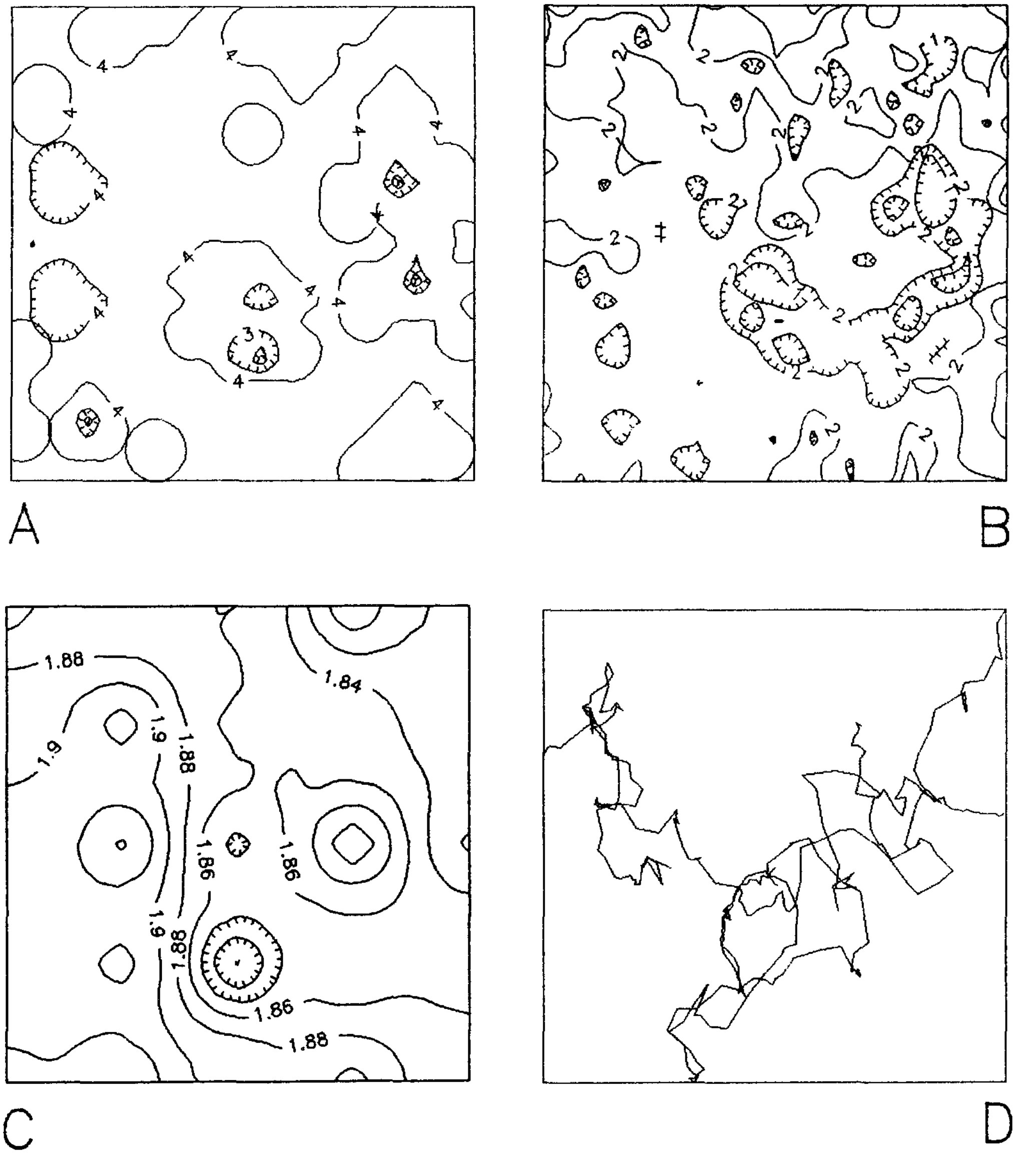

Fig. 1. Characterization of plot number 1 and beetle movements. Each panel represents the same 5 × 5 m study plot. (A) Kriged surface representing the number of 0.0156 m^2 cells that were occupied by > 25% bare ground within each 0.0625 m^2 cell. (B) Kriged surface describing the number of 0.0039 m^2 cells containing > 25% bare ground within each 0.0156 m^2 cell. (C) Kriged surface of fractal dimensions calculated for each 1 m^2 cell. (D) Beetle pathways observed in the field.

probability distributions of displacement but assumed that turning angles were distributed uniformly between 0 and 360 degrees. Our assumptions represent one of two parsimonious alternative models of correlated random walks. By emphasizing biases in displacement rather than turning angle, the simulations focused on the tendency of beetles to move from one 1 m^2 cell to another. Landscape heterogeneity could also impart biases to the turning angle if beetles were deflected by obstacles that are difficult to traverse (*e.g.*, clumps of grass). Deflection and altered turning angles could explain a significant deviation between the observed behavior and simulations, if one were found.

The empirical displacements were used to generate a probability distribution describing the distances beetles traveled during each 5-s interval. This probability distribution was then resampled to regulate the distances traveled each 5 s during 1,000 independent simulations of beetle movement trials. As in the field trials, simulated beetles were allowed to 'walk' through the plot for 500 s or until exiting the plot, whichever occurred first. These rules resulted in simulations of 98,122 time intervals during which beetles walked about the plot.

The locations of simulated beetles within the 1 m^2 cells were tallied at each time step. The tallies were used to measure the likelihood of visiting cells of a given fractal dimension, given that the simulated beetles lacked knowledge of environmental complexity. The simulations therefore provided expected frequencies of beetle visits to each 1 m^2 cell, regardless of its fractal dimension.

We measured the effects of landscape structure on beetle movement by comparing the frequencies at which particular cells were visited by real beetles to the visitation frequencies for simulated beetles. Because cells located near the center of the plot where the simulated beetles were 'released' had intermediate fractal dimensions (see Fig. 1C), we expected that the simulated beetles would exhibit a higher frequency of visitation to such cells. The Kolmogorov-Smirnov test (Sokal and Rohlf 1969) was used to test whether the empirical (field) probability distribution could have been obtained from the simulated distribution. Rejection of the null hypothesis in the Kolmogorov-Smirnov test would suggest that the movements of real beetles were affected by landscape heterogeneity, as expressed by fractal dimension.

Results

Microlandscape patterns

The sample plot exhibited a complex pattern of vegetated and unvegetated areas. Not surprisingly, this pattern varied at the different scales of resolution (Fig. 1A vs. B). Because the patterns are so scale-dependent, it is difficult to judge which pattern a beetle might actually experience in its movements about a plot, and therefore which pattern should be compared with the beetle-movement data.

We circumvented this difficulty by deriving the fractal dimension of the patterns. Because the fractal dimension is calculated across the several scales, it integrates the complexity of patterns over these scales and permits a simultaneous consideration of the patterns shown in Fig. 1A and B. The success of the fractal approach in integrating scale-dependent patterns across these scales is indicated by the close fit of the regressions (of log cell count versus log resolution) used to estimate the fractal dimensions ($R^2 = 0.98$ to 0.99).

The landscape patterns revealed by the fractal dimension of the cells (Fig. 1C) differed qualitatively from the patterns suggested by the raw coverage data (Fig. 1A and B). Cells with low fractal dimensions (D) had exponentially less bare ground at all scales than did high-dimensional cells. For example, relative to cells in which $D = 1.95$ at 0.0039 m^2 resolution, cells in which $D = 1.90$ or 1.85 had 13% and 24% less bare ground, respectively. The presence of grass in a plane of bare ground represented an exponential increase in the fragmentation of the bare-ground pattern.

Beetle movements

The movement trajectories of the six beetles released appeared to be non-random, or perhaps non-Brownian (Fig. 1D, see Mandelbrot 1983; Peitgen and Saupe 1988). Non-Brownian movement is characterized in part by mean square displacements greater than zero. Half the beetles left the plot before 500 s elapsed. Beetle displacement during 5-s intervals was highly skewed (Fig. 2); 50% of the displacements were < 10 cm long. Even so, beetles moved > 35 cm roughly 5% of the time (Fig. 2).

Simulated beetles ($N = 98{,}122$ steps) and real beetles ($N = 486$ steps) visited plots of different fractal dimensions at significantly different frequencies (Kolmogorov-Smirnov $D_{0.01,486} = 0.074$, $D_{obs} = 0.202$, $p << 0.01$; Fig. 3). Simulated beetles exhibited a propensity to visit cells of intermediate fractal dimensions ($D = 1.85$ to 1.89; Fig. 3), perhaps because such cells were clustered

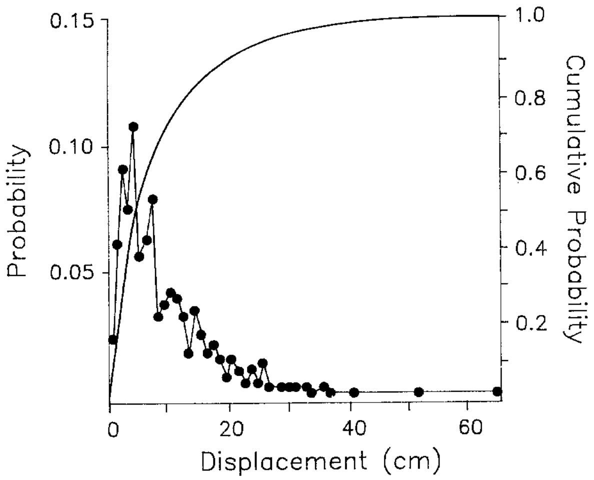

Fig. 2. Beetle displacement probabilities obtained from field observations. Solid dots represent probabilities of obtaining a given displacement in 5 s. The smooth curve traces the cumulative probability of displacement (n = 486).

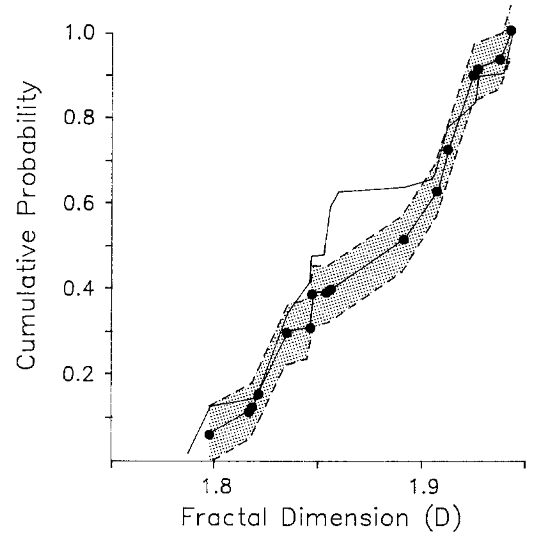

Fig. 3. Cumulative probabilities of beetles visiting 1 m^2 cells with various fractal dimensions for 486 empirical observations (curve with solid dots) and 98,122 simulated observations (solid line). Dashed lines and the shaded zone represent the 95% confidence interval for the empirical observations. For the simulated distribution, confidence limits are indistinguishable from the curve.

near the center of the plot (Fig. 1C). Despite the fact that they were released in the same portion of the plot, real beetles visited cells of intermediate fractal dimensions significantly less often than the simulated beetles. The frequency of occurrence of real beetles in cells of low (D = 1.80–1.84) or high (D = 1.91–1.95) fractal dimension did not differ from that expected from the simulations. Although the overall range of fractal dimensions among the cells appears to be relatively small, the differences in landscape patterns are considerable (because D is calculated from logarithmic measures). The departure of observed distributions of beetles from model expectations in cells of intermediate fractal dimension therefore represents a very real pattern.

Relevance of the microlandscape approach

Our study of beetle movements emphasizes an approach to, and a perspective on, landscapes. We believe that our studies are relevant not only to studies of beetles, but relate as well to broader considerations involving other animals and how landscape ecology as a discipline might develop. The relevance is perhaps most apparent in the sorts of questions we are led to ask.

Relevance to studies of beetles

Eleodes beetles in this semiarid grassland clearly respond to the patch structure of their habitat in a non-random fashion. Here, grass cover rarely formed a continuous sward; cells with a fractal dimension of bare soil < 1.82 were scarce (Fig. 1C). The frequency of beetle use of such portions of the mosaic was therefore low, but it did not differ from that expected on the basis of the simulations (Fig. 3). By the same token, cells with high fractal dimensions (essentially $> 25\%$ bare-ground cover at all scales) occurred infrequently in the plot, and their use by beetles did not differ from expectations (Fig. 1C, Fig. 3). The significant deviation of the observed from the expected frequencies in grid cells of intermediate fractal dimension, however, suggests that the beetles were deflected from grassy areas, despite the proximity of such areas to the release points.

Why did the movements of real beetles differ from expectations at intermediate values of D? Perhaps the structure of the simulation model itself is an explanation. We used a correlated random walk algorithm that emphasized displacement but randomized turning angle. If both turning angle and displacement are influenced by microlandscape structure, beetle movement might deviate from movement patterns expected on the basis of displacement alone, owing to the convoluted protrusion of grass cover into bare ground ($D < ca. 1.90$). Other features of beetle biology or life-history (*e.g.*, whether they are moving in search of food, a burrow, or a mate) may also relate to the mosaic structure of their landscape in ways that are associated with a particular range of fractal dimensionality. Our studies indicate what that range of landscape heterogeneity might be and thereby serve to focus subsequent investigations of causal mechanisms underlying beetle movement patterns on specific aspects of landscape structure.

Landscape heterogeneity reflects differences in landscape structure that are apparent when the same landscape is analyzed at different levels of resolution or grain (Milne 1989). Differences in microlandscape structure were evident in the simplest representations of bare-ground coverage at two scales (Fig. 1A vs B). The 'scale-dependence' of landscape structure relative to beetle movements may render analyses conducted at just one scale of resolution equivocal, because of uncertainty about the resolution at which beetles perceive landscape heterogeneity (Milne *et al.* 1989; Wiens in press). The fractal dimension represents landscape structure at a variety of scales and thus unifies landscape patterns that otherwise appear to be different at each scale of resolution (compare Fig. 1A and B with Fig. 1C). A general concordance between the beetle movement pathways (Fig. 1D) and the fractal surface in Fig. 1C shows the tendency of beetles to walk 'upslope' in Fig. 1C toward areas of more bare ground and reinforces the results shown in Fig. 3.

The approach we have used to document the responses of beetles to their landscape may be extended to other questions. For example: How are the movement trajectories of individuals altered as the level of heterogeneity is changed (*e.g.*, as a result of heavy grazing by ungulates)? Do beetles concentrate their activities within particular portions of a mosaic as patches become smaller and/or less interconnected? How do beetles move in a landscape containing little bare ground, as in a shortgrass prairie sward? Is there a critical level of interconnectedness of patch types within a landscape that permits beetles to move readily across the landscape, as predicted by studies of percolating networks (Orbach 1986; Gardner *et al.* 1987)? How are population densities of beetles and the stability of their populations related to landscape structure and patch interconnectedness (Fahrig *et al.* 1983)? How do the non-random movements of beetles in a heterogeneous landscape influence the movement and redistribution of materials in the system (Risser *et al.* 1984; Wiens *et al.* 1985)?

Relevance to other animals

Such questions relate to animal movement in complex landscapes in general, and they are therefore relevant to other kinds of organisms that may live in seemingly different landscapes and that move with different rates at different scales (*e.g.*, Senft *et al.* 1987). By considering the mosaic structure on scales that are relevant to the organisms being studied, the biases and errors that accompany the imposition of an arbitrary scale (*e.g.*, kilometers-wide landscapes) on the system are reduced. By analyzing landscape structure in terms of its fractal geometry, mosaic patterns at a variety of scales may be compared in a scale-independent fashion (Mandelbrot 1983). The behavioral responses to landscape structure of, say, an antelope or a jackrabbit occupying the desert grassland certainly appear to us to be vastly different from those of a beetle. The differences may be somewhat illusory, however; once the systems are appropriately scaled to adjust for the size and home-range differences between the organisms, their landscape mosaics may turn out to be geometrically and contexturally similar. Are the movements of an antelope or a jackrabbit or a beetle within appropriately scaled landscapes fundamentally similar, just as the music of Beethoven, Ba-Benzele pygmies, and American blues share a common mixture of randomness and predictability when properly scaled (Voss and Clarke 1975)? Are differences interpretable in terms of differences in diet, life-history features, physiology, or social organization among the organisms? Can we use the responses of organisms to the fractal geometry of their landscapes to develop scale-independent theories of how, say, landscape fragmentation might influence organisms of quite different sizes that perceive their environments in quite different ways (Wiens in press; Milne *et al.* 1989)?

Relevance to landscape ecology

These questions strike us as new and different sorts of questions, both about organisms and about landscapes and their effects. They emerge because we have applied the basic notions of landscape ecology at different, multiple scales of study, and because we have also attempted to define landscape structure in a way that is relevant to the organism but is independent of the specific scale of measurement. Many of these questions may be addressed by investigations of landscapes at microlandscape scales. In addition to monitoring the movements of beetles released in carefully measured plots, for example, we might experimentally alter the scale and/or configuration of patches in a plot, or create landscape patterns of different fractal dimensions, and test the responses of beetles in these arenas.

Even though scale-independent measures such as fractal dimensions are constant over a finite range of scales, however, landscape patterns or the responses of organisms to those patterns may still vary as functions of scale. Scale *does* make a difference in the patterns we record and the ways we interpret them (Wiens *et al.* 1986, 1987), and our ability to extrapolate findings from microlandscape studies to landscapes at broader scales is undoubtedly limited. As long as landscape studies are conducted in a way that is insensitive to scale or that is confined to a narrow range of human-perceived scales, we are not likely to develop an understanding of the limits to extrapolation of the results of any study, regardless of the scale on which it is conducted. We propose that, by adopting a multi-scale conceptualization of landscapes and by conducting studies over a range of scales, we may be able to define the *domains* of scale that apply to particular patterns, processes, or phenomena. Within a given domain, the pattern of landscape mosaics or the responses of organisms to that pattern may not change or may change monotonically with changes in scale (Wiens in press). The findings of studies conducted at one scale may be extrapolated to other scales within the domain of that scale, but not into other domains of scales, where patterns, processes, and relationships are fundamentally different. There are limits to extrapolation, but domains are not likely to be so small that no extrapolation is possible. One way to recognize the domains of scale is to analyze the fractal geometry of the patterns over a range of scales and determine at which points the fractal dimension changes (*e.g.*, Krummel *et al.* 1987; Palmer 1988). A constant fractal dimension over a range of scales defines a domain within which the patterns, and perhaps the processes causing them, are repetitive and therefore predictable.

Conclusions

Studies of diffusion in heterogeneous landscapes offer rich and seemingly endless opportunities for exploring how landscape structure affects the performance of organisms (*e.g.* Kareiva 1985). By developing models that predict random movements through landscapes under various constraints, we may move from a focus on descriptions to an approach that emphasizes testing of formal hypotheses. Many alternative random-walk models remain to be explored, including high-order Markov chains, models that represent biases in turning angle, and models that incorporate the fractal geometry of landscapes (*e.g.*, Milne 1988). Such fractal models represent landscape heterogeneity explicitly. Their application in broad landscapes, however, requires measurements of spatial complexity similar to those reported here. Fortunately, remotely sensed measurements of landscape patterns can be used to estimate fractal dimensions for kilometers-wide regions (Milne 1989; De Cola 1989), and random or neutral models may provide ways of evaluating whether or how such patterns are remarkable (Gardner *et al.* 1987). Thus, the approaches applied in a microlandscape context are also amenable to studies of broad-scale landscapes.

Microlandscape studies embody the essence of landscape ecology (*e.g.*, Naveh and Lieberman 1984; Forman and Godron 1986) by focusing on consequences of heterogeneity for the movement of resources, organisms, and energy (see Risser *et al.* 1984). Consequences of heterogeneity probably occur to similar degrees both for beetles traversing grassland networks and for ungulates moving across savannas or mountainous terrain, although adjustments must be made for body size (Swihart *et al.* 1988). Heterogeneity in landscapes that occur on vastly different scales may be quantified by a rich array of fractal models (Mandelbrot 1983; Milne 1988, 1989, in press), thereby allowing disparate systems to enjoy similar conceptual treatments. The understanding derived from observations and experiments in microlandscapes may accelerate the development of rigorous approaches that apply to landscapes at all scales.

Acknowledgments

We thank S. Loftin, T. Morse, and S. Andrews for field assistance and C. Crawford for beetle identifications. I. Burke, S. Grogan, and N. Kotliar helped to clarify an early draft of the manuscript. Support was provided the National Science Foundation (grants BSR-8806435 and BSR-8614981 to BTM and BSR-8805829 to JAW) and by the Department of Energy (grant DE-FG04-88ER60714 to BTM and DE-FG02-88ER60715 to JAW). This paper is Sevilleta LTER contribution no. 3.

References

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. and Soluk, D.A. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340–346.

Calkins, C.O. and Kirk, V.M. 1973. Distribution and movement of adult false wireworms in a wheat field. Ann. Entomol. Soc. Am. 66: 527–532.

Crawford, C.S. 1981. Biology of Desert Invertebrates. Springer-Verlag, New York.

Davis, J.C. 1986. Statistics and Data Analysis in Geology, 2nd ed. John Wiley & Sons, New York.

De Cola, L. 1989. Fractal analysis of a classified Landsat scene. Photogrammetric Engineering and Remote Sensing 55: 601–610.

Doyen, J.T. and Tschinkel, J.T. 1974. Population size, microgrographic distribution and habitat separation in some tenebrionidae beetles (Coleoptera). Ann. Entomol. Soc. Am. 67: 617–626.

Fahrig, L., Lefkovitch, L. and Merriam, G. 1983. Population stability in a patchy environment. *In* Analysis of Ecological Systems: State-of-the-art in Ecological Modeling. pp. 61–67. Edited by W.K. Lauenroth, G.V. Skogerboe and M. Flug. Elsevier, New York.

Forman, R.T.T. and Godron, M. 1986. Landscape Ecology. John Wiley & Sons, 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. Landsc. Ecol. 1: 19–28.

Kareiva, P.M. 1985. Finding and losing host plants by Phyllotreta: patch size and surrounding habitat. Ecology 66: 1809–1816.

Kareiva, P.M. and Shigesada, N. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56: 234–238.

Kramm, R.A. and Kramm, K.P. 1972. Activities of certain species of Eleodes in relation to season, temperature, and time of day at Joshua Tree National Monument (Coleoptera: Tenebrionidae). Southw. Natur. 16: 341–355.

Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V. and Coleman, P.R. 1987. Landscape patterns in a disturbed environment. Oikos 48: 321–324.

Mandelbrot, B. 1983. The Fractal Geometry of Nature. W.H. Freeman and Co., New York.

Milne, B.T. (in press). Lessons from the application of fractals in landscape ecology. *In* Quantitative Methods in Landscape Ecology. Edited by M.G. Turner and R. Gardner. Springer-Verlag, New York.

Milne, B.T. 1988. Measuring the fractal geometry of landscapes. Appl. Mathem. Comput. 27: 67–79.

Milne, B.T. 1989. Heterogeneity as a multi-scale characteristic of landscapes. *In* Ecological Heterogeneity. Edited by J. Kolasa and S.T.A. Pickett. Springer-Verlag, New York.

Milne, B.T., Johnston, K.M. and Forman, R.T.T. 1989. Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model. Landsc. Ecol. 2: 101–110.

Naveh, Z. 1982. Landscape ecology as an emerging branch of human ecosystem science. Adv. Ecol. Res. 12: 189–237.

Naveh, Z. and Lieberman, A.S. 1984. Landscape Ecology. Theory and Application. Springer-Verlag, New York.

Orbach, R. 1986. Dynamics of fractal networks. Science 231: 814–819.

Palmer, M.W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. Vegetatio 75: 91–102.

Peitgen, H.-O. and Saupe, D. (eds.) 1988. The Science of Fractal Images. Springer-Verlag, New York.

Risser, P.G., Karr, J.R. and Forman, R.T.T. 1984. Landscape ecology: directions and approaches. Illinois Nat. Hist. Surv. Spec. Publ., 2: 1–18.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37: 789–799.

Sokal, R.R. and Rohlf, F.J. 1969. Biometry. W.H. Freeman and Co., San Francisco.

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

Swihart, R.K., Slade, N.A. and Bergstrom, B.J. 1988. Relating body size to the rate of home range use in mammals. Ecology 69: 393–399.

Taub, F.B. 1974. Closed ecological systems. Ann. Rev. Ecol. Syst. 5: 139–160.

Troll, C. 1968. Landschaftsökologie. *In* Pflanzensoziologie und Landschaftsökologie. pp. 1–21. Edited by R. Tüxen. Dr W. Junk Publishers, The Hague.

Voss, R.F. and Clarke, J. 1975. '1/f noise' in music and speech. Nature 258: 317–318.

Wiens, J.A. (in press). Spatial scaling in ecology. Functional Ecology.

Wiens, J.A., Addicott, J.F., Case, T.J. and Diamond, J. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. *In* Community Ecology. pp. 145–153. Edited by J. Diamond and T.J. Case. Harper & Row, New York.

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

Wiens, J.A., Rotenberry, J.T. and Van Horne, B. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48: 132–147.

Zonneveld, I.S. 1979. Land Evaluation and Land(scape) Science. International Training Center, Enschede, The Netherlands.