

Animal movements and population dynamics in heterogeneous landscapes

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Abstract

Organisms respond to environmental heterogeneity at different scales and in different ways. These differences are consequences of how the movement characteristics of animals – their movement rates, directionality, turning frequencies, and turning angles – interact with patch and boundary features in landscape mosaics. The interactions of movement patterns with landscape features in turn produce spatial patterns in individual space-use, population dynamics and dispersion, gene flow, and the redistribution of nutrients and other materials. We describe several theoretical approaches for modeling the diffusion, foraging behavior, and population dynamics of animals in heterogeneous landscapes, including: (1) scaling relationships derived from percolation theory and fractal geometry, (2) extensions of traditional patch-based metapopulation models, and (3) individual-based, spatially explicit models governed by local rules. We conclude by emphasizing the need to couple theoretical models with empirical studies and the usefulness of ‘microlandscape’ investigations.

Introduction

Landscapes are spatially heterogeneous, and this heterogeneity has important ecological implications for the animals inhabiting the landscape (Risser *et al.* 1984; Forman and Godron 1986; Turner 1989). Spatial heterogeneity can influence the movement patterns of organisms, and thus affect dispersal rates and foraging behaviors. Additionally, in a patchy environment, different regions of the landscape may vary in their suitability for use by an organism according to differing levels of resource availability (Milne *et al.* 1989), differing degrees of exposure to predation, or differing opportunities for mating and probabilities of reproductive success (Wiens, in press). Environmental patchiness can therefore be expected to play an important role

in population dynamics (Shorrocks and Swingland 1990).

Landscape ecology is directly concerned with the ecological implications of spatial heterogeneity. Elucidating the interactions between animals and the heterogeneous landscapes in which they dwell – requires both a solid theoretical foundation and careful empirical investigations. In our view, the successful wedding of theory and experiment is essential if landscape ecology is to realize its potential as a science.

We propose a set of theoretical and empirical tools for the study of the behavior and dynamics of animals in complex, heterogeneous landscapes. The theoretical components are: (1) scaling relations derived on the basis of percolation theory and fractal geometry, (2) the incorporation of landscape

descriptors into patch-based population dynamics models, and (3) individual-based, spatially-explicit models with dynamics governed by local rules. On the empirical front, we emphasize the potential value of experimental model systems (**micro-landscapes**) as tools for testing theoretical predictions and for generating new hypotheses.

The approaches outlined in this paper should not be viewed as an exhaustive list of possibilities for the study of animals in heterogeneous landscapes. Other theoretical and empirical approaches are undoubtedly applicable and necessary. However, the approaches discussed here, taken together, constitute a program that, if pursued, may significantly advance our understanding of the influence of landscape heterogeneity on animal movements and population dynamics.

Animal movements and diffusion

Theory of diffusion in heterogeneous landscapes

The movement of a group of organisms is frequently treated as a diffusion process, with movements of the individuals treated as a random walk (Okubo 1980; Berg 1983). In a homogeneous environment, assuming that steps are chosen at random and independently, the behavior of a large collection of random walkers follows the diffusion equation:

$$\frac{\partial \rho}{\partial t} = u + D \nabla^2 \rho \quad (1)$$

where ρ is the local density of random walkers, treated as a function of both time and spatial location, D is the diffusion coefficient, and ∇^2 is the Laplacian operator, equal to the sum of the second partial derivatives of ρ with respect to each of the spatial coordinates. The drift term, u , reflects the net effect of directional biases in the random walk. If the probabilities associated with movement are independent of direction, then $u = 0$. A salient feature of solutions to this equation is that, when averaged over a large number of random walkers, squared distances of the walkers from their center of mass (**i.e.**, the mean squared displacement) increase linearly with time. Diffusion that can be

described by this equation is termed Fickian (Okubo 1980).

Random walkers that have no fixed directional bias but do have a biased distribution of turning angles can lead to non-Fickian diffusion. In this case, successive steps are no longer statistically independent, so the process is often referred to as a correlated random walk. Several researchers have used correlated walks to model animal movements (Karieva and Shigesada 1983; Bovet and Benhamou 1988; Marsh and Jones 1988; **McCullough** and Cain 1989). The mean squared displacement for correlated walks departs from a linear increase with time, at least over some range of time and space scales.

Spatial heterogeneity in the environment can also induce departures from Fickian diffusion. A substantial body of theory has recently developed in the physical sciences regarding non-Fickian diffusion caused by spatial heterogeneity. Since this theory was developed in the context of physical applications, an associated jargon has arisen which will be unfamiliar to most ecologists. We have found it useful to adopt some of the vocabulary from the physical sciences in order to maintain consistency with the existing scientific literature. Our focus; however, is on the ecological applications of the theory, so we will stress the ecological significance, rather than the original physical referents, of the terms we employ.

Particularly relevant are studies of simple (**uncorrelated**) random walks on fractal lattice structures, where a lattice can be viewed as a map represented in raster format. (Gefen **et al.** 1983; Havlin and Ben-Avraham 1983, 1987; McCarthy 1988; Mitescu and Rossenq 1983; Rammal and Toulouse 1983; Pandey **et al.** 1984; Rammal 1984). Most of this work has focused on random walks on percolation clusters, which are formed by taking a regular (e.g., square) lattice and randomly classifying every lattice site as being accessible to random walkers, with probability p , or inaccessible, with probability $1 - p$. In an ecological context, this can be viewed as partitioning the environment into habitat and non-habitat. The random walker starts on an accessible site and is restricted to moving only to accessible neighboring sites. This protocol produces **non-Fickian** diffusion, in which the mean squared dis-

placement scales with time as:

$$\langle R^2(t) \rangle \sim t^{d_s/d_f} \quad (2)$$

where $\langle R^2(t) \rangle$ represents the mean squared displacement at time t (averaged over a large number of random walkers), d_f is the fractal dimension of the accessible sites of the lattice, and d_s is the fracton, or spectral, dimension (Alexander and Orbach 1982; Rammal and Toulouse 1983; Orbach 1986). In the context of random walks, the significance of the spectral dimension is that it governs how the number of distinct sites visited during a random walk increases with time. Specifically:

$$\langle S(t) \rangle \sim t^{d_s/2} \quad (3)$$

where $\langle S(t) \rangle$ is the number of distinct sites a random walker has visited by time t (sites visited more than once are counted only once) averaged over a large number of random walkers (Rammal and Toulouse 1983; Havlin and Ben-Avraham 1987).

As noted above, percolation clusters are formed by randomly occupying a lattice with accessible sites at a specified probability p . A distinct transition occurs at a specific value of p (approximately 0.5928 on a square lattice). Clusters formed below this threshold value are all finite in size. Above this threshold, an infinite cluster appears. This means that, if one looks at lattices that are large but of finite extent, above the percolation threshold there will be a cluster that spans the lattice from one side to the other. For diffusion on percolation clusters formed above the percolation threshold, non-Fickian behavior is observed up to a characteristic length and time scale, after which a return to Fickian diffusion is observed (Redner 1983).

As an alternative to the mean squared displacement, the collective behavior of random walkers can be characterized by the time required for each walker to first cross a given circle centered on the origin of the walk. The diffusion behavior can then be investigated in terms of the scaling of the mean first-passage time as a function of the radius of the circle.

For a simple random walk in a homogeneous environment, such mean first-passage times scale proportionately to the square of the radius of the circle. Based on work by Seshardi and West (1982),

Angles d'Auriac *et al.* (1983) derived the following scaling relation governing first-passage times for simple random walks on a fractal:

$$\langle T_1(r) \rangle \sim r^{2d_f/d_s} \quad (4)$$

where $\langle T_1(r) \rangle$ is the average time required to first cross a circle of radius r , and d_f and d_s are, respectively, the fractal and the spectral dimensions of the accessible sites.

The origin of anomalous diffusion on percolation clusters can be seen by considering the path of a single random walker (Fig. 1). The walker often has an unobstructed path for movements over short distances. As we consider displacements greater than a few grid cells, however, the shortest path between two points becomes increasingly convoluted, thus increasing the length of time required to traverse a specified straight-line distance. The walker's progress is further impeded by the presence of cul-de-sacs in the spatial arrangement of accessible sites. The cumulative effect of the convolutions and cul-de-sacs inherent to the structure of a percolation cluster is to slow the rate of diffusion, such that (for simple random walks) the exponent in equation (3) assumes a value of 0.71, as opposed to 1.0 for Fickian diffusion in a homogeneous environment.

The precise scaling relations derived for uncorrelated random walks on percolation clusters cannot be expected to hold in nature: real landscapes are not percolation maps (Gardner *et al.* 1987) and the movements of real organisms are seldom uncorrelated, at least over short time scales (Karieva and Shigesada 1983). Yet studies of random walks on percolation lattices and other fractal structures nonetheless enable us to make certain qualitative predictions about the diffusion behavior of real organisms in real landscapes. We expect that (1) mathematical descriptions of animal diffusion will need to be scale-dependent (non-Fickian at some scales, and Fickian at others), (2) power-law scaling relations for mean squared displacement and mean first-passage time will be observed, and (3) the exponents in these power laws will depend on the fractal geometry of the environment.

In general, there are two characteristic length scales that affect diffusion dynamics: (1) the typical size of barriers to the organism's movement (ξ_1),

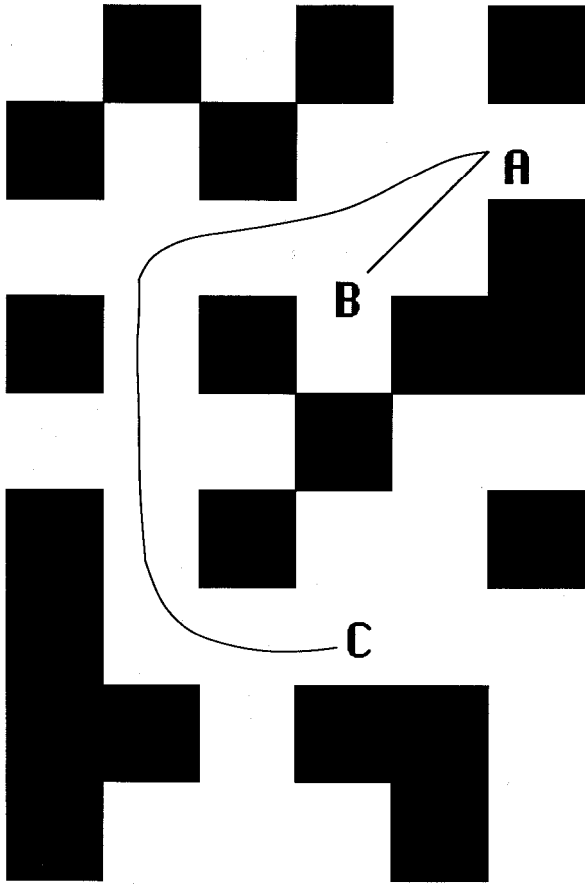


Fig. 1. In a heterogeneous landscape, short distances (such as from point A to point B) can often be traversed by a direct path, whereas longer distances (such as from point A to point C) necessitate a more circuitous path.

and (2) the distance over which correlations would persist in the organism's movements in the absence of barriers (ξ_2). Analogous characteristic scales can also be defined in the temporal domain: (1) the time required to move around a typical barrier (τ_1), and (2) the time required for correlations in the unimpeded movement pattern to decay (τ_2) (similar to the 'time to independence' of Swihart *et al.* 1988). Assume that observations are made at a spatial resolution L and a temporal resolution T , such that movement dynamics over distances less than L or over time intervals less than T are not recorded (i.e., these represent the 'grain' of the investigation; Wiens 1989, 1990). As illustrated in Fig. 2, at coarse spatial or long temporal resolution ($L \gg \xi_1, \xi_2$ or $T \gg \tau_1, \tau_2$) we would expect the diffusion to ap-

pear Fickian. At the opposite extreme ($L \ll \xi_1, \xi_2$ or $T \ll \tau_1, \tau_2$) non-Fickian diffusion is expected, with power-law scaling relations whose exponents depend upon both the details of the landscape pattern and the movement behavior of the organism. Depending upon the relative magnitudes of ξ_1 versus ξ_2 and τ_1 versus τ_2 , there may also exist an intermediate scale that yields scaling exponents that are a function of only the landscape or the organism's movement, but not both. For instance, if $\tau_2 \ll T \ll \tau_1$, the organism's movements should appear as a simple random walk (since any correlations would have decayed at the resolution of the observations) constrained by the fractal heterogeneity of the landscape. The mean first-passage time exponent would thus be a function of the landscape, but not of the details of the animal's movement behavior.

That such theory may have relevance to natural situations is indicated by preliminary simulation studies we have conducted of correlated random walks on percolation maps and on digitized maps of natural semi-arid grasslands. The temporal and spatial scales used in the simulation were chosen to correspond to the scales used in parallel field studies of the movements of tenebrionid beetles. Over the range of scales investigated, power-law scaling dynamics were observed, with scaling exponents that depended upon both the landscape pattern and the parameters of the correlated random walk.

Experimental studies of diffusion

Numerous researchers have applied diffusion models to account for observed movements of organisms in the field. Insects are particularly convenient study organisms for use in experimental situations, so much research has focused on them. Much of the resulting literature is summarized in Okubo (1980) and Kareiva (1983). Additionally, diffusion models have been applied to analyze historical records of the invasion dynamics of introduced species, as in Lubina and Levin (1988) and Andow *et al.* (1990).

Many of the experimental studies reported that a

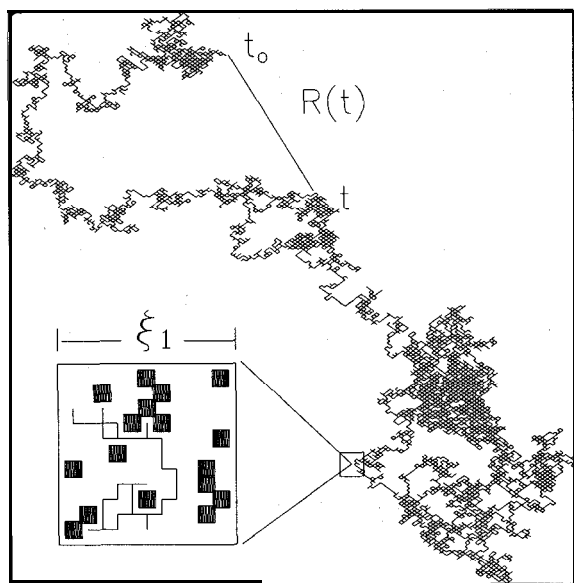


Fig. 2. Schematic representation of a random walk showing displacement, $R(t)$, from the origin at t_0 to the location at time t . At scales $< \xi_1$, as shown in the inset, barriers slow the movement and induce non-Fickian diffusion.

Fickian diffusion model provided an adequate fit to the data. In cases where non-Fickian dynamics were observed, it was typically attributed to movements of individuals which departed from a simple random walk (e.g., Kareiva and Shigesada 1983). However, it should be noted that most experimental studies have been conducted in field situations specifically chosen for their spatial homogeneity. Spatially non-uniform rates of range expansion have been noted in data on invading species, and this has led researchers to compute separate diffusion coefficients for different ad hoc regions of the landscape (e.g., Lubina and Levin 1988, Andow *et al.* 1990). However, these studies have not explored the possible role of spatial heterogeneity in producing non-Fickian diffusion dynamics.

We have used the microlandscape approach to study the dynamics of diffusion of animals in a heterogeneous landscape. As an experimental system, we chose to study the movements of beetles (*Eleodes* spp.: Tenebrionidae) in their semi-arid grassland habitat (i.e., a mosaic of bare soil and vegetated patches) and in artificially constructed mosaics of bare soil and grass. The experimental plots are either 5 x 5 m or 20 x 20 m. An individ-

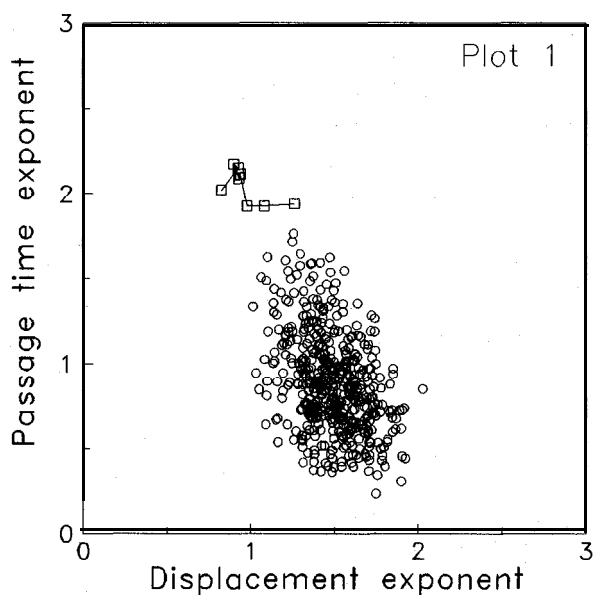


Fig. 3. Scaling exponent for mean squared displacement and mean first-passage time for Plot 1. Circles: exponents calculated for 500 bootstrap samples of field data. Squares: exponents calculated from simulations of correlated random walks on digitized map of the plot.

ual beetle is released near the center of the plot and its location is recorded at 5-s intervals (Wiens and Milne 1989). From this information, its trajectory can be reconstructed and summary statistics for ensembles of beetles (such as their mean squared displacements, or mean first-passage times) can be computed.

Preliminary analysis of the frequency with which areas of a plot are actually visited by beetles, as opposed to the frequency expected by chance, indicate that landscape structure does influence beetle movements (Wiens and Milne 1989). The real beetles showed a significant tendency to avoid regions of the microlandscape with local fractal dimensions of bare soil in the range of 1.85 to 1.89.

Accounting for the influence of landscape heterogeneity on beetle movements has proven more difficult. Motivated by the results of simulations of correlated random walks on fractal lattices discussed above, we have calculated scaling exponents for the mean squared displacements and mean first-passage times observed for the actual beetles. Results for a typical plot (Fig. 3) indicate that the real beetles diffuse more efficiently than

any of the simulations using correlated random walks (see also Milne 1991).

In our simulations, correlations were introduced into the walks by enhancing the probability of moving in the 'forward' direction, *i.e.*, in the same direction of movement as the previous step. Yet even when the probability of moving forward is set quite high (e.g., $P_f = 0.97$), these correlations may not persist over large distances, particularly in a heterogeneous landscape where obstacles frequently force a change in direction. Thus, to mimic the movement behavior of individual beetles properly, movement rules need to be based on more than just the direction of movement in the last time step. Longer-range correlations could be introduced if the beetles are actually navigating, perhaps by the use of landmarks or sun angle. Further studies are needed to elucidate the local rules needed to mimic beetle behavior.

Foraging behavior and population dynamics

Metapopulation models

An ecological framework for the study of spatial heterogeneity has developed under the rubrics of 'patch dynamics' and 'metapopulations'. Building on the work of Watt (1947), some plant ecologists have viewed ecological succession or disturbance in terms of the temporal dynamics of patches (Shugart and West 1981; Pickett and White 1985). Separately, some population biologists and behavioral ecologists (e.g., Levene 1953; Levins and MacArthur 1966; MacArthur and Pianka 1966; Emlen 1966; Fretwell and Lucas 1969; Fahrig and Paloheimo 1988) began to extend models based on homogeneous systems to consider how individuals and populations respond to heterogeneity in habitat or resource distribution (see also Stephens and Krebs 1986; Shorrocks and Swingland 1990). These models typically allow for movement of organisms between various patch types, with patch-specific net energy gains, reproductive rates or other population parameters. The dynamics of the 'metapopulation', consisting of the ensemble of local (within-patch) populations, is the focus of attention.

In a single species system, the fragmentation of the habitat into discrete patches would be expected to lead to a higher extinction rate within each patch. If movement between patches is sufficiently restricted, this could lead to a reduced probability of persistence for the metapopulation as a whole. However, for multispecies systems with predator-prey or competitive interactions, local extinctions and recolonizations at the patch level may lead to coexistence of species in the metapopulations which could not coexist in a homogeneous environment (Hassell and May 1973; Vandermeer 1973; Levin 1974; Hastings 1977; Ziegler 1977; Sabelis and Diekmann 1988; Taylor 1990; Pacala *et al.* 1990). This regional stabilization of locally unstable interactions is one mechanism by which spatial heterogeneity can contribute to population persistence and to ecological diversity.

Traditional patch-based models of metapopulation dynamics have considered relatively simple, internally homogeneous patches, embedded in an ecologically neutral matrix and linked by between-patch dispersal. Details of patch size, shape, juxtaposition, perimeter complexity, and the presence or absence of corridors have not been explicitly considered. In work in progress, Wiens, Stenseth, Van Horne and Ims have extended the traditional patch-based formulation of population dynamics models in an effort to incorporate such factors. Other researchers are also engaged in adapting metapopulation for use in addressing problems of landscape ecology (e.g., Opdam 1991).

The theoretical approach adopted by Wiens and his colleagues can be summarized as follows (Fig. 4). Assume that there are three patches, and that the animal of interest can live in and reproduce in patches 1 and 2, but moves through or resides in patch 3 without reproducing. Each patch covers an area, A_i , and is enclosed by a boundary of length B_i (where $i = 1$ or 2 ; area and boundary length of patch 3 do not enter into the model). The animal population in each patch is at a density x_i , and is subject to a patch-specific growth rate, $f_i(x_i)$. The emigration rate from patch 1 is $\Phi_1(x_1, x_2)$. A proportion, p , of these emigrants are assumed to successfully immigrate in patch 2, while the remainder, $1 - p$, are 'lost' in patch 3, either through

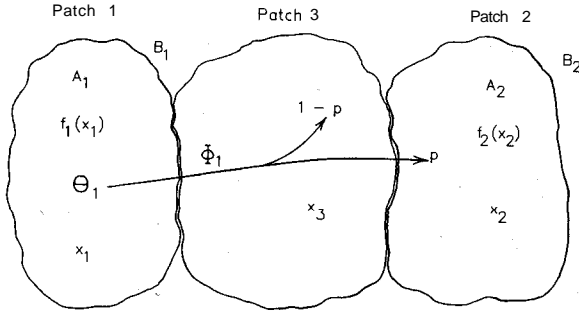


Fig. 4. Illustration of the basic three patch metapopulation model developed by Wiens, Stenseth, Van Horne and Ims (unpublished).

mortality, dispersal out of the system, or as **non**-reproducing residents. Analogous considerations govern migration from patch 2 to patch 1.

Given these assumptions, the following equations governing the metapopulation dynamics can be derived:

$$\begin{aligned} \frac{dx_1}{dt} &= [f_1(x_1)]x_1 - [\Phi_1(x_1, x_2)]x_1 + \\ &\quad [p\Phi_2(x_2, x_1)]x_2 \left(\frac{A_2}{A_1} \right) \\ \frac{dx_2}{dt} &= [f_2(x_2)]x_2 - [\Phi_2(x_2, x_1)]x_2 + \\ &\quad [p\Phi_1(x_1, x_2)]x_1 \left(\frac{A_1}{A_2} \right) \end{aligned} \quad (5)$$

Within-patch movements determine the probability that individuals will encounter a patch boundary and thus be able to emigrate (Buechner 1987; Stamps *et al.* 1987; Wiens in press). Individual within-patch movements may be summarized by a function $\theta_i(x_i)$. Emigration rates can then be expressed as $\phi_i(\theta_i(x_i), x_j, B_i/A_i)$, incorporating an explicit dependence on within-patch movement behavior and on the amount of edge (expressed as the ratio of boundary length to enclosed area).

The model may also be extended to incorporate the effect of corridors. If a corridor links patches 1 and 2, organisms may move between these patches either along the corridor, or by diffusing through the matrix, represented by patch 3. Let q represent the proportion of dispersers moving through the matrix (of which a proportion p_m successfully

reach the other patch), and $1 - q$ represent the proportion moving through the corridor (of which a proportion p_c successfully reach the other patch). Then, for the terms represented above as

$$[p\Phi_i(x_i, x_j)]x_i \quad (6)$$

substitute

$$q[p_m\Phi_i(x_i, x_j)]x_i + (1 - q)[p_c\Phi_i(x_i, x_j)]x_i \quad (7)$$

For the sake of simplicity, we have thus far considered only a 3-patch, 1-species version of the model. In principle, a more complex mosaic of patches and multiple dispersing species can be incorporated by converting each x_i into a vector with elements x_{ik} representing the density of species k in patch i . Representing the dispersal dynamics will become more complicated as more patches are included, and a multispecies version of the model would need to modify the existing terms or include additional terms to represent species interactions.

Modeling approaches such as this represent an advance over previous patch-based metapopulation models. However, even this formulation represents landscape patterns in terms of overall descriptors, such as patch areas and boundary lengths. Certain details of patch shape or orientation are lost or subsumed into the emigration function. We consider now modeling approaches in which such details are explicitly retained.

Individual-based models

Landscape heterogeneity may be explicitly represented in a computer as maps digitized in a raster format. Such maps can be thought of as **two**-dimensional arrays, where each array element has a value representing some spatially-distributed property of the landscape (e.g., cover type, nutrient concentration, temperature). These arrays can be envisioned as a two-dimensional lattice of sites, in which each site has four immediately adjacent nearest-neighbors. The spatial patterns in the landscape may be displayed using pixels that are **color**- or intensity-coded to represent the numerical value of the corresponding array.

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may be simulated on the lattice using **individual-based** models that employ local rules. The rules are local in the sense that the behavior or dynamics of each individual is specified as a function of only those lattice sites in some finite region surrounding the animal's current location.

This sort of modeling strategy has been employed in some simulations of animal foraging behavior. One notable example is the work of researchers at UCLA in simulating ant foraging and trail following behavior (Collins and Jefferson 1992; Jefferson *et al.* 1992). Artificial ant-like organisms are allowed to move and forage on a two-dimensional lattice. Each ant is a member of a particular colony, with a nest located at a lattice site. Food particles are scattered at various lattice sites in the environment. Each individual ant can move to an adjacent lattice site, sense the presence of food or pheromones in a lattice site, pick up a food particle, or deposit a pheromone signal. Each ant executes these behaviors according to its own set of 'rules', which are encoded in a recurrent artificial neural network (Wasserman 1989). Simulations last for many generations of artificial ants, with natural selection being imposed to select those colonies with the most successful foraging behaviors. These behaviors are encoded in a numerical 'chromosome' which is subject to mutation and genetic recombination in each generation. The evolutionary dynamics of foraging strategies can thus be studied.

Another individual-based, spatially explicit foraging model was studied by Milne *et al.* (in press). This model simulates the foraging behavior of mammalian herbivores in a dynamic, spatially heterogeneous landscape. Each animal establishes a home range. As long as sufficient food can be gathered within the home range, the location of the home range remains fixed. If, however, the available food within the home range falls below a critical threshold, the animal will move at random until a location with sufficient food is found. The model is designed such that once the body mass of the herbivore is specified, factors such as home range size, ingestion rate, metabolic rate, movement speed, and transportation costs are determined by **allometric** relationships (Peters 1983). In contrast to the

preceding model, the local rules determining animal behavior are the same for all individuals and do not evolve over time; however, the distribution of resources in the landscape does change with time.

A simple individual-based model of **predator-prey** dynamics has been discussed in *Scientific American* (Dewdney 1984). In this model, predators and prey move on a two-dimensional lattice with environmental heterogeneity in which sites are of two types: those accessible to the animals, and inaccessible sites. Both predator and prey move in this lattice environment, encounter one another, eat, and reproduce according to simple rules. Population dynamics arise spontaneously from the collective behaviors of the simulated individuals. Wiener and **Pinson** (1990) provide a listing of computer code, written in C++, for implementing this model using object-oriented programming techniques.

Another local rule model, called RAM, has been developed by researchers at UCLA (Taylor *et al.* 1988). In RAM, each animal is simulated as a separate computer program. Environmental processes, such as weather, are represented as separate programs also. The programs are executed concurrently, and are able to interact by exchanging information. Interactions occur within a two-dimensional grid of lattice sites. Each animal typically inspects nearby lattice sites and the animals occupying those sites. On the basis of the information gathered from nearby sites, internal state variables, and learned behaviors, each animal executes some action, such as moving, eating, or reproducing, from which the overall population dynamics emerge.

A number of other local-rule models have been developed. Ackley and Littman (1992) describe a model, called ERL, which uses a combination of neural network and genetic algorithm techniques to simulate natural selection in a two-dimensional grid landscape. The series of models developed by Conrad and his associates also simulate evolution in a one- or two-dimensional discretized space (Conrad and **Pattee** 1970; Conrad and Strizich 1985; Rizki and Conrad 1985, 1986). Finally, the modeling strategies of Hogeweg are also based on local rules (Hogeweg and Hesper 1981; Hogeweg 1988).

These various models differ in numerous details, but we wish to emphasize a feature the models share in common. In all cases, the dynamics of the model over large spatial scales and long temporal scales emerge naturally from the collective behavior of individuals, each of which acts in accord with local rules that are specified at a much finer spatiotemporal scale. Because landscape heterogeneity can be explicitly represented by environmental variables associated with each lattice site, the influence of spatial patterns on population dynamics and other ecological phenomena can readily be investigated.

Experimental studies of population dynamics

The use of experimental model systems has a long history in population biology. In single species systems, fragmentation of the habitat leads to higher extinction probabilities (Forney and Gilpin 1989). However, the story for multispecies communities may be different. Huffaker's (1958) classic study of the role of spatial heterogeneity on population dynamics in a predator-prey system, for example, indicated that increased spatial heterogeneity may dampen predator-prey oscillations and promote the persistent coexistence of the predator and prey populations. Similar experimental evidence for the role of spatial heterogeneity in 'stabilizing population dynamics is provided in the studies by Pimentel *et al.* (1963), van den Ende (1973) and Pacala *et al.* (1990).

We believe there is much more that could be learned from experimental systems such as these. The types of spatial heterogeneity incorporated in the models could be made more realistic by including complex gradients, patches of varying size and shape (with complex boundaries), or the presence of landscape features such as corridors. Systems with greater species richness and more diverse species interactions would also be of great interest. We feel the time is ripe for detailed experimental studies of population dynamics in heterogeneous micro-

Microlandscapes as experimental systems

It is difficult to conduct experimental manipulations at the large spatial scales that are the traditional focus of landscape ecology. Those large-scale experiments which are conducted, such as the study of Amazonian forest remnants conducted by Lovejoy and his associates (Lovejoy *et al.* 1986), are extremely valuable, but logistic and economic constraints limit the number of such studies that can be carried out and the replication that can be achieved. Additional useful data can be obtained through careful observational studies of anthropogenic activities (e.g., deforestation, agriculture, pollution) or natural phenomena (e.g., fires, hurricanes, volcanic eruptions) that alter the landscape at the scales of interest. It seems likely, however, that certain aspects of the ecological role of landscape heterogeneity will remain elusive unless the landscape pattern can be directly manipulated in a controlled, experimental setting, with the possibility of replication.

Experimental studies conducted using smaller spatial units, 'microlandscapes' can provide a valuable means of investigating the role of heterogeneity (Wiens and Milne 1989). By choosing organisms that operate at manageable spatial scales, the influence of spatial patterns on movement behavior, foraging success, and population dynamics can be studied. We believe that from such studies, general ecological principles will emerge that may be translated to other organisms and larger spatial scales.

The use of fine-scale ecological systems as experimental models for broad-scale systems is not new to ecology (see Ims and Stenseth 1989). It is, in fact, the prevailing philosophy behind the use of experimental 'microcosms', which have been widely used in the study of ecosystem dynamics and in toxicity testing (Giesy 1980; Pritchard 1981; Giddings 1983; Cairns 1985). Our interest is in the relationship between microcosms as experimental models and the real-world ecosystems they are supposed to represent. The nature of this correspondence is an issue that has been consciously addressed in the microcosm literature.

Microcosms can be broadly categorized as being either synthetic or naturally-derived. Synthetic

microcosms are artificially constructed and stocked with a species assemblage determined by the researcher (e.g., Metcalf *et al.* 1971; Taub 1969; Taub and Crow 1980). Naturally-derived microcosms consist either of excised portions of natural ecosystems (Giddings 1986; Van Voris *et al.* 1985) or a system inoculated by a natural assemblage of organisms (e.g., Leffler 1980). Synthetic microcosms usually contain species assemblages that have no direct counterpart in nature, and thus are generally used simply as toxicity screening tools or to investigate generic ecological processes common to all ecosystems (Giddings 1983). For naturally-derived microcosms, a closer correspondence to natural ecosystems is usually assumed, although many authors warn against the facile assumption that microcosms simply mimic natural ecosystems (Leffler 1980; King 1980; Heath 1980; Giddings 1983). Factors that might cause a microcosm to diverge from its parent ecosystems include the exclusion of larger organisms, the reduced degree of material and energy exchange with the surroundings, artificial conditions imposed by the laboratory environment, surface effects of the container walls, reduced species richness due to species-area effects, distortions in relative proportions of ecosystem components, and unsuccessful incorporation of the spatial heterogeneity of natural systems.

Despite these difficulties, it is widely believed that microcosm studies can be used to make inferences about the corresponding natural ecosystems. Researchers have noted the need to **rescale** results of microcosm studies in order to extrapolate them to large-scale ecosystems, but scaling techniques are generally lacking (but see Shirazi *et al.* 1984 for a scaling approach which may be useful for extrapolating results from soil microcosms).

Some workers (e.g., Heath 1980) view microcosms as heuristic rather than predictive tools. A more flexible analysis of the relationship of microcosms to natural ecosystems is offered by Hill and Wiegert (1980). These authors discuss the role of ecological models (of the mathematical or simulation variety) in providing a logical framework for comparing the properties of microcosms and natural ecosystems. We believe that mathematical or

simulation models can provide a crucial bridge between experimental model systems (microcosms or microlandscapes) and the natural systems they are intended to represent.

We can elucidate the relationship between microlandscapes, as experimental models, and the larger macrolandscapes they represent, as follows. On the microlandscape, one typically studies small organisms that operate over a relatively limited spatial scale (e.g., insects or small mammals). At the level of the macrolandscape, one may be concerned with organisms that operate over much larger spatial extents (e.g., birds or large ungulates). Landscape heterogeneity can be found at all scales; in the microlandscapes, the spatial pattern can be experimentally manipulated to match the patterns of observed variation at the macroscale (e.g., Burrough 1986). However, the consequences of this spatial heterogeneity for animal movement patterns and population dynamics will depend on the individual behaviors exhibited by the organisms in the landscape. It seems unlikely that, say, a beetle moving through an experimental microlandscape follows behavioral rules that are simply the appropriately **rescaled** version of what some other organism, such as an elk, is doing at the macrolandscape level. This does not mean that the resulting movement patterns of the beetle and the elk are totally dissimilar, but simply that the correspondence is probably one of analogy, in which no quantitative transformation of one onto the other exists.

On the basis of studies at the microlandscape level, however, one may be able to develop a spatially explicit simulation model that reliably predicts beetle movements (at least in a statistical sense) using local rules that encode individual beetle behavior. This same model, with appropriately modified local rules, might be applied to simulate the movement of elk on the macrolandscape. Thus, a quantitative correspondence could be established between the simulation model and the movement of beetles on a microlandscape, and, with a change in local rules, a quantitative correspondence could be established between the simulation model and elk moving on the macrolandscape. The simulation model thereby bridges the gap, establishing a relationship between the micro- and macrolandscapes

that could not be established directly. A major justification for the use of microlandscapes is the utility of these controllable, manipulable, experimental systems for the development of predictive models that can then be employed to predict dynamics at larger scales.

Concluding remarks

Animals move, eat, reproduce, live and die in spatially heterogeneous landscapes. The consequences of such spatial heterogeneity for population dynamics demands serious investigation. Addressing this issue will require an integrated approach, incorporating a variety of theoretical and empirical techniques.

We have suggested three theoretical approaches: (1) the derivation of scaling relationships to describe non-Fickian diffusion, (2) the modification of patch-based metapopulation models to explicitly incorporate aspects of landscape pattern, and (3) the development of individual-based, spatially explicit models governed by local rules.

These theoretical approaches will lead to predictions that will require empirical testing. The verification or falsification of hypotheses generated by the theory will probably be most readily accomplished by true experiments, in which features of the landscape pattern and other experimental variables can be controlled and manipulated, and in which replicate units are available, so that the resulting data can be analyzed statistically. For this purpose, we advocate the use of microlandscapes as small-scale experimental model systems. Mathematical or simulation models that are developed in parallel with the microlandscape studies can form a bridge for extrapolating the experimental results to make predictions at the larger, macrolandscape scale.

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