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Ecological mechanisms and landscape ecology

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Landscape ecology deals with the effects of the spatial configuration of mosaics on a wide variety of ecological phenomena. Because problems in many areas of conservation biology and resource management are related to landscape use, development of a rigorous theoretical and empirical foundation for landscape ecology is essential. We present an approach to research that focuses on how individual-level mechanisms operating in a heterogeneous mosaic produce ecological patterns that are spatially dependent. The theoretical framework that we develop considers the density and distribution of a population among patches as a function of (a) within-patch movement patterns of individuals; (b) emigration from patches as a function of population density, patch configuration, patch context, and within-patch movement; and (c) loss of individuals as they disperse through landscape elements. This theoretical framework is coupled with an empirical approach that emphasizes the use of experimental model systems (EMS), small-scale systems occupying "microlandscapes." Such systems are amenable to experimental manipulation with adequate replication and control and may serve as analogs of systems occurring at broader landscape scales, where rigorous empirical work is more difficult. We illustrate the use of EMS with examples from our studies of beetles and ants in North America and of voles in Norway. Finally, we consider some factors that may constrain extrapolations from EMS to other systems, scales, or levels. We believe that implementation of a mechanistic approach to landscape ecology is essential to deriving generalizations about how spatial heterogeneity influences ecological systems.

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The world is composed of landscapes, be they natural or altered by human activities. Such spatial mosaics are the focus of the emerging discipline of landscape ecology (Forman and Godron 1986, Turner 1989, Zonneveld and Forman 1990). Landscape ecology began in central Europe in the 1960's as a merging of human geography and holistic ecology, with infusions from landscape architecture, land management and planning, and sociology (Naveh and Lieberman 1984, Schreiber 1990, Zonneveld 1990). Over the past decade, it has become broadly international, with all the attributes of an established scientific discipline – journals, books, societies, international congresses, and jargon. Although there are regional variations, the main focus of landscape ecology has been on spatially explicit patterns of landscape mosaics and interactions among their elements, primarily at the scale of kilometers (Risser et al. 1984, Forman and Godron 1986).

From an ecological perspective, landscape ecology offers a way to consider environmental heterogeneity or patchiness in spatially explicit terms. The effect of patchiness has become a major focus of research in many areas of ecology (Shorrocks and Swingland 1990, Kolasa and Pickett 1991), including optimal foraging theory and behavioral ecology (Kacelnik and Cuthill 1987, Houston et al. 1988, Krebs and Houston 1989),

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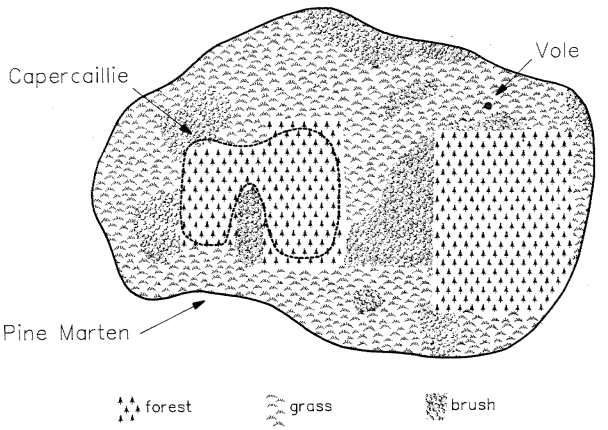

Fig. 1. A typical boreal forest-clearcut mosaic in Scandinavia, showing the relative home-range scales of a vole (ca 0.05 ha; Ims 1988), a capercaillie cock (ca 50 ha; Rolstad and Wegge 1987), and a pine marten (ca 500 ha; Storch 1988).

population and metapopulation structure (Rogers 1987, Bernstein et al. 1991, Gilpin and Hanski 1991), and community and ecosystem dynamics (Pickett and White 1985, Caswell and Cohen 1991). Most of these "patch dynamics" studies have considered spatial heterogeneity in terms of simple, internally homogeneous, shapeless patches embedded in a featureless and ecologically neutral matrix. There has been little appreciation of the rich texture of explicit spatial patterns and their potential effects, which is the focus of landscape ecology. On the other hand, the emphasis in landscape ecology on holism has made it difficult to unravel the mechanisms underlying landscape dynamics, and the focus on landscapes at the scale of human perception has constrained statistical hypothesis testing and precluded the use of replicated experiments, limiting the scope of research questions. A coherent paradigm for landscape ecology has yet to emerge.

An integration of these approaches may unify the study of spatially explicit ecological processes and enhance the rigor of landscape ecology. We develop one approach to such an integration here, emphasizing the dynamics of mobile organisms in terrestrial ecosystems. Although this approach may not apply to systems such as long-lived clonal plants, similar thinking may be applied to sessile or modular organisms that have a well-defined and frequent dispersal phase in their life history (Reiners and Lang 1979, Pacala and Silander 1985, Pacala 1986, Matsuda 1987, Sato and Iwasa in press). We do not consider such systems here.

An example may serve to illustrate the kinds of problems to be addressed (Fig. 1). A vole (e.g. *Microtus*) moving through a patch of grass in a clearcut in Scandinavian boreal forest encounters a boundary with a brushy area. Should it leave the grass and enter the brush patch or remain in the grass? Its decision will be influenced by features of the patch it occupies (e.g. food supply, predation risk, competitive pressure, physiological stress, behavioral constraints) as well as those of the patch it encounters (e.g. an open area or a habitat corridor leading to other grassy areas) (Hansson 1977, Stenseth 1983, Lidicker 1988, Stenseth and Lidicker 1991). Its movements through the "landscape" within the clearcut are predicated not only on the quality of local habitat patches, but on their explicit locational relationships within a mosaic – their sizes, shapes, arrangement, and connectedness (Franklin and Forman 1987, Stamps et al. 1987, Wiens 1992).

At a broader scale, the movement patterns of individual voles within and between home ranges translate into variations among landscape elements in population density, survival, and reproduction (Van Horne 1982). For forest grouse occurring in the same area, such as capercaillie (*Tetrao urogallus*), the distinction between patches of grass and brush within the clearcut may be irrelevant, but the structure of the forest-clearcut mosaic determines individual movements and, over a broader scale, the location of display leks and population dynamics (Rolstad and Wegge 1987, Rolstad et al. 1988, Wegge et al. 1990).

Even though they respond to the structure of "landscapes" at different scales, the dynamics of vole and capercaillie populations are linked. The landscape structure resulting from modern forestry leads to high densities of voles in clearcuts (Hansson 1977, Henttonen 1989). Here, predators that prey on voles and capercaillie, such as pine martens (*Martes martes*), may respond functionally and/or numerically (Andersson and Erlinge 1977). Because pine martens use forest and clearcut patches within a daily home range (Fig. 1), predation in the clearcuts may extend into adjacent forest patches to affect capercaillie population dynamics (Andrén et al. 1985, Angelstam 1986, Rolstad and Wegge 1989), especially if the forest fragments are relatively small (Andrén and Angelstam 1988). The effects of land-use practices are thus expressed, mechanistically, as consequences of individual activities within home ranges and their translation into population distributions and variations in net recruitment in "landscapes" over a range of scales (Van Horne 1991).

The above example is but one of a broad range of more general phenomena, including mating probabilities (Ims 1990), population densities and dynamics (Gilpin and Hanski 1991), predator-prey interactions (Taylor 1990, Bernstein et al. 1991), community structure (Bengtsson 1989), biomass and nutrient distribution (Pastor and Post 1986, Risser 1990), or the spread of disturbances such as fire or insect epidemics (Turner 1987), that are influenced by the spatial structure of mosaics. A broadened approach to landscape ecology thus integrates questions at many biological levels and spatial scales.

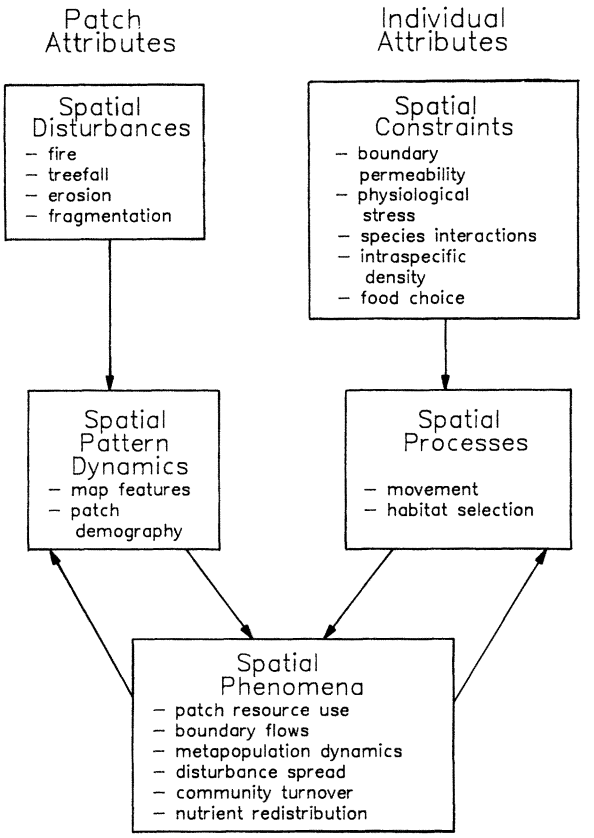

Fig. 2. A mechanistic framework for investigating the effects of explicit spatial patterns on spatial phenomena. Temporal changes in spatial patterns may be produced by external disturbances or by feedback effects of the spatial phenomena, as mediated by the regeneration dynamics of the patch type. Spatial processes may be constrained by the spatial consequences of the pattern-process interaction and by system constraints unrelated to spatial patterning.

A conceptual framework

How can we integrate the approaches of landscape ecology and patch dynamics to increase our understanding of both basic and applied problems in ecology? Advocates of hierarchy theory (e.g. O'Neill 1989, Allen and Hoekstra 1991) propose that the mechanisms underlying ecological phenomena expressed at a particular hierarchical level should be sought at the next lower level in the hierarchy (however defined). Because of its central role in biological interactions, however, the organism can generally be regarded the basic unit in ecology (Stenseth 1985a, Łomnicki 1988), regardless of its position in a given hierarchy (hierarchies, after all, are abstract constructs). Accordingly, we focus on mechanisms operating at the level of individual animals, such as the behavior of voles and their predators described above. These individual mechanisms, expressed in a spatially patterned environment, produce ecological

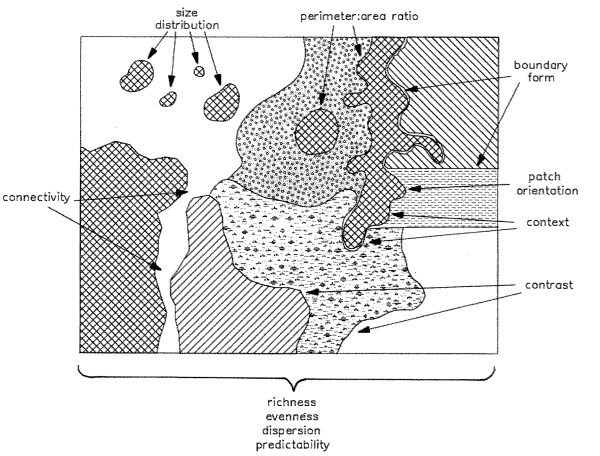

Fig. 3. An example of a landscape-mosaic map, showing the parameters that may be measured (Table 1).

phenomena that are sensitive to the effects of spatial variation (Fig. 2).

Spatial pattern is expressed in several measures of mosaic structure (Fig. 3), which may be mapped and quantified at a particular point in time. To do this requires that one specify the scale and criteria that will be

Table 1. Measurable features of landscape mosaics (Fig. 3).

Feature	Description
Size distribution	Frequency distribution of sizes of patches of a given type
Boundary form	Boundary thickness, continuity, linearity (e.g. fractal dimension), length
Perimeter: area ratio	Relates patch area to boundary length; reflects patch shape
Patch orientation	Position relative to a directional process of interest (e.g. water flow, passage of migrants)
Context	Immediate mosaic-matrix in which a patch of a given type occurs
Contrast	Magnitude of difference in measures across a given boundary between patches
Connectivity	Degree to which patches of a given type are joined by corridors into a lattice of nodes and links
Richness	Number of different patch types in a given area
Eveness	Equivalence in numbers (or areas) of different patch types in a mosaic (the inverse of the degree of dominance by one or a few patch types)
Dispersion	Distribution pattern of patch types over an area
Predictability	Spatial autocorrelation; the degree to which knowledge about features at a given location reduces uncertainty about variable values at other locations

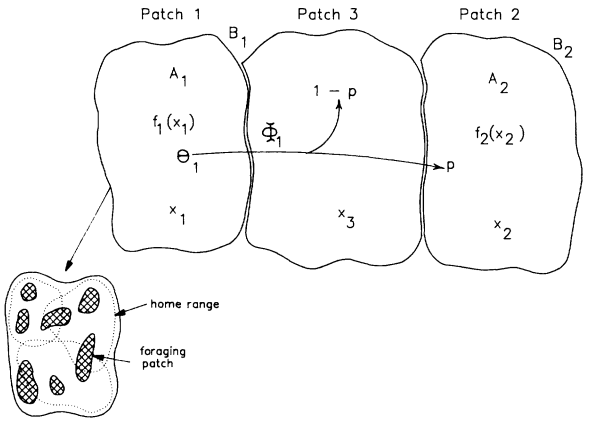

Fig. 4. Terms in eqs (1) and (2) linking population dynamics and density distributions between two "reproduction" patches in a mosaic (patches 1 and 2) and an intervening "transition" patch (patch 3). Terms are described in the text. The inset illustrates the heterogeneity within individual home ranges that are nested within these patches. Patchiness within home ranges may affect daily foraging behavior, but only indirectly influences population dynamics.

used. The appropriate scale will depend on the questions asked, the organisms studied, and the time periods considered (Wiens 1989). Criteria based on vegetation composition or structure are usually used to map habitats in terrestrial environments, but thermal discontinuities may be more important for defining daily use patches for ectothermic organisms such as lizards or ants (Huey 1991), whereas soil characteristics may be appropriate criteria in mapping landscapes relevant to plants. The criteria used to map mosaics should be relevant to the organisms of interest.

To analyze the explicit spatial pattern of a landscape mosaic, patch boundaries must first be defined. In environments heavily modified by humans, such boundaries are often sharp, but in natural settings they may be less distinct. Here, methods of image analysis (Overington and Greenway 1987, Brunt and Conley 1990) may be useful in detecting patch edges. Once a mosaic map has been derived, one can measure a variety of attributes of the mosaic (Table 1). Various methods are available for measuring these variables (Haggett et al. 1977, O'Neill et al. 1988, Haining 1990, Turner and Gardner 1991). Landscape mosaics are not static, of course, but have temporal dynamics produced by disturbances and by the regeneration time lags characteristic of particular patch types (Shugart 1984, Franklin and Forman 1987, Turner et al. 1989). Phenomena that result from the interplay of spatial patterns and individual processes, such as bark beetle (*Ips typographus*) or spruce budworm (*Choristomeura occidentalis*) outbreaks (Rykiel et al. 1988, Berryman and Stenseth 1989), may also generate spatial patterns that change over time.

In systems including mobile organisms, many ecological phenomena have their mechanistic roots in two features of individual behavior: movement and patch (habitat) choice. The movement rate and pathway of an organism determine the probability that it will move from one location in a mosaic to another during a specified time period. Movement pathways have been analyzed using models of simple diffusion (Okubo 1980, Turchin 1989), percolation networks (Gardner and O'Neill 1991), and correlated random walks (Kareiva and Shigesada 1983, McCulloch and Cain 1989, Hastings 1990, Turchin 1991). The other process, patch choice, expresses how an individual responds when it encounters a patch boundary and therefore determines its probability of movement to adjacent patches.

Both processes are constrained by factors that vary spatially in their effects (Fig 2). For instance, movement may be more difficult through some patch types than others, and patch boundaries may differ in their "permeability" to movement by organisms (Wiens et al. 1985, Stamps et al. 1987). Correspondingly, highly vagile organisms may perceive mosaic heterogeneity on different scales than more sedentary animals (Kolasa and Rollo 1991). As a result, movement pathway characteristics vary among patch types and organisms. Similarly, patch choice may be based on a variety of patch features, such as resource levels, population densities, habitat structure, predation risk, and social interactions (Nishimura 1988, McNamara and Houston 1990, Smith and Peacock 1990, Rosenzweig 1991). Many of these constraints are often considered collectively as "patch quality," but this term is not useful unless it is partitioned into mechanistically defined components (Van Horne 1983). The interplay of these spatial processes and constraints with the pattern of a spatial mosaic produces spatial dependencies in a wide array of ecological phenomena (Fig. 2).

Linking spatial patterns and processes

Concepts are all well and good, but unless they can be expressed in operational terms they are of little value in empirical work. Implementing this mechanistic framework requires not only quantification of critical features of mosaics and movements, but an interplay of theoretical and empirical approaches as well.

Theoretical approaches

We believe that landscape ecology theory must integrate individual and population approaches if it is to be mechanistically based. Accordingly, we emphasize linkages of individual space use (e.g. foraging behavior, dispersal) to population and metapopulation phenomena. A logical starting point is to build on the tradition of simple patch models of population dynamics (Stenseth 1986, Pulliam 1988, Pulliam and Danielson 1991),

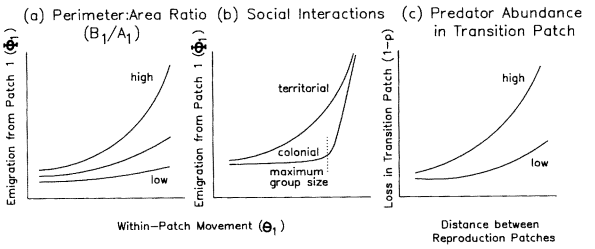

Fig. 5. Hypothesized relationships between (a) movement within a patch, $\theta_i(x_i)$, and emigration from the patch, $\varphi_i(x_i, x_j)$ for $i \neq j$, as a function of different patch perimeter:area ratios (B_i/A_i); (b) within-patch movement and emigration for organisms with territorial (repulsive) vs colonial (attractive) social organization (above a critical group size, colonies repel individuals, increasing emigration); and (c) distance separating reproductive patches and the loss of individuals during immigration between patches, under different intensities of predation in the transition patch (patch 3 of Fig. 4).

in which spatial variation is included but individual variation is not. Although parameter values may be obtained from observations of many individuals, they are expressed in terms of the "average" individual (see also Łomnicki 1988).

Consider a population occupying a mosaic consisting of three patches (Fig. 4). Patches 1 and 2 are suitable for reproduction ("reproduction" patches), whereas individuals can move through or inhabit patch 3 but do not reproduce there ("transition" patch). Reproduction patch i has an area, A_i, and a boundary length, B_i. Individual probabilities of survival and reproduction are relatively homogeneous among individuals within these reproduction patches but differ between patches, so we may specify patch-specific net population growth rates, $f_i(x_i)$, where x_i is the density of individuals of a given species in patch i. Population density dynamics in the two patches can then be expressed as:

$$\begin{aligned} dx_1/dt &= f_1(x_1)x_1 - \varphi_1(x_1,x_2)x_1 + p\varphi_2(x_2,x_1)x_2(A_2/A_1) \\ dx_2/dt &= f_2(x_2)x_2 - \varphi_2(x_2,x_1)x_2 + p\varphi_1(x_1,x_2)x_1(A_1/A_2) \end{aligned} \quad (1)$$

where $\varphi_i(x_i,x_j)$ for $i \neq j$ is the patch-specific emigration rate and p is the proportion of individuals leaving patch i (1) that immigrate to patch j (2) (or vice versa). Patch-specific immigration is a function of both the relative areas of source and recipient patches (e.g. A_2/A_1) and of densities in the patches (x_i, x_j). Through mortality, dispersal out of the system, or by taking up residency as nonbreeders, 1-p individuals are "lost" in patch 3.

Individuals respond to patchiness at within-home-range and between-home-range scales (Van Horne 1991), although there may be several levels of response at each scale (Kotliar and Wiens 1990, Orians and Wittenberger 1991). Movements within home ranges are generally considered by patch foraging theory (Stephens and Krebs 1986), whereas those beyond home-range boundaries constitute dispersal (Fig. 4). One possible algorithm for modeling such movements is developed by Stamps et al. (1987). We consider individual movement within a patch or landscape-mosaic element as a function of density by specifying the function, θ_i, which expresses the patch-specific, per individual movement per unit time. Movement pathways are characterized by a distribution of turning angles and increment lengths, which produce aggregate pathway properties such as net squared displacement (the total distance traveled during a specified time interval), mean direction, and tortuosity or fractal dimension (Crist et al. in press). Because within-patch movements determine the probability that an average individual will encounter a patch boundary and emigrate, between-patch movement, φ_i, is given by:

$$\varphi_i[\theta_i(x_i), x_j(B_i/A_i)] \text{ for } i \neq j \quad (2)$$

where B_i/A_iexpresses the perimeter:area ratio of patch i and x_j is the density in patches adjoining patch i. In contrast to most patch models (Stenseth 1986), emigration or dispersal is dependent on density and spatial pattern in a patch-specific manner.

Patch choice enters in two ways: the average individual may decide whether or not to remain within its current patch upon encountering a boundary, or it may make such a decision on encountering another boundary (e.g. patch 2) after entering the transition patch (patch 3). The former decision may be included in the specification of $\varphi_i(x_i, x_j)$, while the latter is a component of p.

This approach links spatial patterns and processes through the dynamics of $\theta_i(x_i)$, $\varphi_i(x_i, x_j)$, and 1-p, which may differ among patches in a mosaic. Patches with greater values of $\theta_i(x_i)$, for example, will experience greater emigration loss $[\varphi_i(x_i, x_j)]$, although this relationship will be influenced by patch area (A_i) and boundary (B_i/A_i) (Fig. 5a; Stamps et al. 1987). The form of density-dependence specified by $\varphi_i(x_i, x_j)$ may also vary with differences in the social organization of the organisms considered (Fig. 5b). The value of 1-p will increase if predator abundance in patch 3 is high and/or patch 3 is large (Fig. 5c; Gilpin 1987). Emigrant losses $(1 - p)$ are therefore dependent on the distance separating patches 1 and 2; such effects might be modeled as a distance-decay function (Okubo 1980). If predation is frequency-dependent, the abundance of the organism in patch 3 (x_3) becomes important, and $p(x_3)$ should be substituted for p in eq. (1). This describes the vole-pine marten example we gave earlier; to extend it to the broader vole-capercaillie-pine marten interactions requires a multispecies model with feedback effects of x_3 and 1-p on $f_i(x_i)$.

Additional complexity can be built into this model in several ways. For example, if corridors link patches in a mosaic, emigrating individuals may move either across a transition patch or through the corridor. This effect may be incorporated by substituting the term

$p\varphi_i(x_j,x_i)x_j$

by

$qp_1\varphi_i(x_j,x_i)x_j + (1-q)p_2\varphi_i(x_j,x_i)x_j$

where q is the proportion of dispersers moving through the transition patch at a cost $1\text{-}p_1$, and $(1\text{-}q)$ is the proportion moving through the corridor with a cost $1\text{-}p_2$. The one-species, three-patch system of Fig. 4 may also be extended to consider mosaics with a more complex array of patches and several species by making each x_i a vector with elements x_{ij} representing the density in patch i of species j. Predator-prey interactions may be modeled following Holt (1983) and Bernstein et al. (1991), while Caswell and Cohen (1991) and Danielson (1991) describe protocols for incorporating competition between species. As more species are included, more assumptions must be made about the form of species interactions, and multiple equilibria become more likely.

Such extensions involve changes in the model structure. Other ecological phenomena may be included in existing model parameters. For example, source patches, in which net reproductive output is positive, may be distinguished from sink patches, in which reproduction does not occur or net per-capita reproduction is negative (Pulliam 1988). We may define a source patch as one for which $f_i(x_i) > 0$ for some values of x_i and sink patches as those in which $f_i(x_i) < 0$ for all values of x_i. Of course, not all patches for which $f_i(x_i) > 0$ are of the same "quality." The Fretwell-Lucas (1969) model considers how individuals may be distributed among patches as a function of patch quality. In spatial terms, both φ_i and θ_i may change with changes in $f_i(x_i)$, and the patterns of patch occupancy become dependent on values of $1\text{-}p$ in the transition patches as well as patch "quality" (see also Pulliam and Danielson 1991). Because φ_i is density-dependent, population dynamics in the sink patches may exhibit an indirect or induced density-dependence as well (R. Holt, pers. comm.). Not all source or sink patches in a mosaic may be occupied at any one time (Levins 1970); the likelihood that such patches will be colonized (and, consequently, the dynamics of the metapopulation) depends on the values of φ_i and p (or $1\text{-}p$). Site fidelity or philopatry reduces the magnitude of θ_i and thereby reduces the probability of between-patch colonization. Of course, all of these functions may vary with the structure of the spatial mosaic.

Although the model as formulated can be used directly in order to understand some of the emerging properties of the system, it is necessary to aggregate the microvariables (x_i) and microparameters of the system into a few macrovariables. This is one of the major challenges in theoretical ecology (Stenseth 1985a, b). Theorists have deduced the conditions under which an aggregated system corresponds exactly to the original system formulated by using microvariables (Iwasa et al. 1987, 1989). This corresponds to deducing relations such as the gas laws in chemistry on the basis of the microscopic properties of the motion of the molecules, and is closely related to similar efforts in economic modeling (Simon and Ando 1961). Ludwig (1983, Ludwig and Walters 1985) has in fact done this rather successfully for one system by grouping – and aggregating – microvariables changing on fairly similar rates (i.e. fast and slow; Iwasa et al. 1987).

At present, the value of the theory we have developed is primarily heuristic: it helps us understand the effects of explicit spatial patterns by expressing population dynamics as functions of features of individual behavior, by posing questions in terms of explicitly defined variables such as φ_i, θ_i, or $1\text{-}p$. The framework may be expressed in a discrete-time rather than a continuous form to simplify numerical solutions, which may often be more useful than obtaining stability (equilibrium) solutions. By varying net population growth in a patch-specific manner, relating dispersal to B_i/A_i, and varying immigration (p) in accordance with features of the transition patch ($1\text{-}p$), we can determine the influence of spatially explicit patch relationships on population density and distribution, both within patches and over an entire mosaic.

Although this analytical approach may enable one to explore interactions among patch-mosaic configuration, individual-level behavior, and population distribution, it does not permit us to consider individual differences in behavior. Likewise, the "cellular automata" approaches of Caswell and Cohen (1991) or of Langton (1990), in which the dynamics of populations occupying a matrix of cells (patches) are described by nonlinear Markov chain or other transition rules governing cell state, also ignore individual variation. In stochastic modeling, however, individual attributes can be drawn at random from probability distributions of patch-specific behavioral traits for the sampled population (Andersen 1991, Chesson 1991, Clark 1991). These values may then be used as input parameter values to project population-level dynamics, as in the above model.

Simulation models constitute another approach. For example, individual movement properties have been simulated within a percolation network of accessible and inaccessible sites (Gardner et al. 1987, 1989). Such models may be especially useful in establishing null expectations for specified movement patterns in theoretical or actual landscapes (Gardner and O'Neill 1991, Johnson et al. in press). Spatial simulation models that evaluate interactions among cells in grid-mosaics (e.g. Huston et al. 1988, Smith and Huston 1989, Bartell and Brenkert 1991, Fahrig 1991, Hyman et al. 1991, Sklar and Costanza 1991) provide a powerful approach to modeling the spatial dynamics of complex systems based on individual-level properties. Simulation models based on diffusion processes (e.g. Okubo 1980, Turchin 1989, 1991, Andow et al. 1990) or correlated random

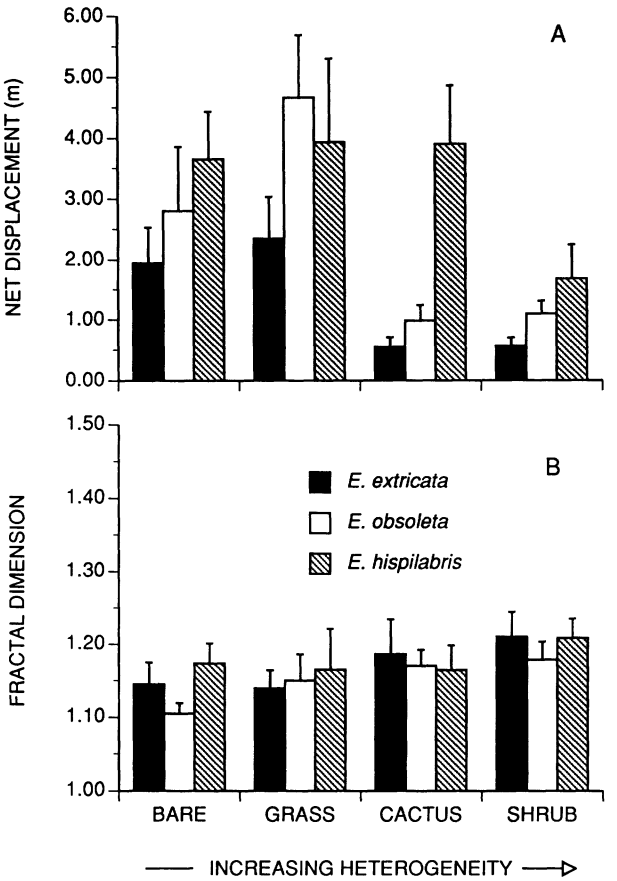

Fig. 6. Net squared displacement (A) and fractal dimension (B) of movement pathways of three beetle species (*Eleodes*, Tenebrionidae) in natural microlandscape mosaics of increasing spatial heterogeneity (from Crist et al. in press).

walks (e.g. Kareiva and Shigesada 1983, Cain 1989, McCulloch and Cain 1989) can be used as null models to test the actual patterns of animal movement. Models that are based on diffusion, random walks, or probability distributions of turn angles and distances (e.g. Siniff and Jessen 1969), however, generally ignore the effects of individual patch-choice decisions that are contingent on explicit mosaic structure. Folse et al. (1990) have dealt with this problem using artificial intelligence approaches, which also provide a way to link analytic and simulation models (c.f. Turchin 1991).

Empirical approaches: experimental model systems

Empirical tests are necessary to determine whether the premises and predictions of such theoretical models are valid or general. Although mechanisms can be inferred from well-designed comparative studies (Parker and Maynard Smith 1990, Harvey and Pagel 1991), experimental manipulations have much greater power to reveal pattern-process linkages (Hairston 1989, Underwood 1990). For obvious reasons, experimental tests are difficult to conduct at the broad scales of human-defined landscapes (but see Lovejoy et al. 1986). In contrast, experiments at small, "microlandscape" scales may be adequately replicated, and large sample sizes may increase the precision of response estimation (Wiens and Milne 1989). By choosing organisms that operate at manageable spatial scales, the ways in which spatial patterns influence movement and patch choice and how these translate into features of foraging behavior, population dynamics, or ecosystem flows can be determined. Such experiments may function as "experimental model systems" (EMS; Ims and Stenseth 1989, Matter and Mannan 1989), in which studies conducted at relatively fine scales may be used to obtain insights about pattern-process relationships in similar systems operating at broader scales. Because spatial patterns can be manipulated at a microlandscape scale, EMS may be especially valuable in landscape ecology. We illustrate this with two examples from our own studies.

Wiens and Milne (1989, Johnson et al. 1992) are using a model system of tenebrionid beetles (*Eleodes* spp.) and harvester ants (*Pogonomyrmex* spp.) in semiarid grasslands, in concert with theories of diffusion and percolation (Okubo 1980, Gardner and O'Neill 1991) and the model described in eqs (1) and (2), to determine how the explicit pattern of habitat mosaics influences within-patch movement, among-patch distribution, and population dynamics. In the beetle studies, the focus has been primarily on quantifying components of θ in relation to the fine structure of heterogeneity within patches. Individual movement pathways in 25-m^2 microlandscapes are mapped and related to the mosaic structure and fractal dimension of the microlandscape. These studies have shown that beetle "diffusion" through a mosaic is more complex than a correlated random walk, and that individuals appear to avoid cells in a matrix having particular fractal dimensions of coverage of bare soil. Such features of movement pathways as net squared displacement are clearly affected by the structure of the microlandscape, and these effects are more pronounced for some species than for others (Fig. 6A). The fractal dimension of the movement pathway, on the other hand, does not vary among species or with habitat heterogeneity (Fig. 6B; Crist et al. in press). Thus, although differences in measured features of movement pathways are apparent when considered at a particular scale, the pathways exhibit similar levels of tortuosity when scaled relative to the movement rates of the different species. Experimental modifications of the mosaic structure of microlandscapes are being used to probe these relationships further, and to develop the local, within-patch "rules" that may permit extrapolation of individual movements to population distributions over larger landscape mosaics.

In another study, Ims et al. (unpubl.) have introduced populations of the root vole (*Microtus oecono-*

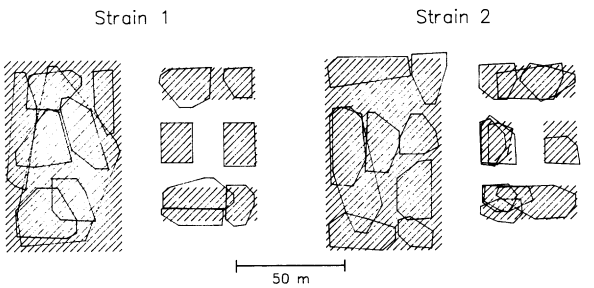

Fig. 7. Home ranges of females from two behaviorally distinct strains of *Microtus oeconomus* on fragmented and continuous experimental plots. Strain 1 = aggressive (territorial) strain from northern Norway; Strain 2 = more docile strain from southern Norway. Home ranges are plotted as outer convex polygons including 95% of the radiotelemetry records (from Ims et al. unpubl.).

mus) into 0.5-ha enclosures of homogeneous meadow vegetation in southeastern Norway to explore the effects of habitat fragmentation on individual space-use and reproduction and demography. In the fragmentation treatments, replicate plots were mowed to create a mosaic of large (675 m^2) and small (300 m^2) patches of dense meadow vegetation embedded in a mowed matrix. Females from an aggressive strain of *M. oeconomus* from northern Norway (Strain 1) established non-overlapping territories within individual habitat fragments, whereas females of a less aggressive strain from southeastern Norway (Strain 2) occupied extensively overlapping home ranges in the fragmented treatments (Fig. 7). Such dependences between individual behavioral differences and space-use responses to habitat fragmentation may explain differences in the responses of species to fragmentation at broader spatial scales. Thus, the capercaillie forms leks of single territorial cocks on small isolated forest islands (Rolstad and Wegge 1989), whereas some understory rainforest birds aggregate into small forest fragments following logging (Lovejoy et al. 1986).

Experimental model systems have long been used in ecology in the study of population and community dynamics (e.g. Gause 1934, Nicholson 1950, Holling 1959, Park 1962, Kareiva 1986, Spiller and Schoener 1988, Foster and Gaines 1991), ecosystem functioning (e.g. Taub 1974, Giesy 1980), and toxicity testing (e.g. Metcalf et al. 1971, Pritchard 1981, Giddings 1983). In most cases, such as the classic *Tribolium* systems of population dynamics, the model system is an artificially constructed abstraction of selected elements of the natural world. Such experiments may reveal whether and how certain mechanisms operate, but because much of the detail of the real world is excluded, the results bear more on the plausibility of general theoretical postulates than on their operation in specific situations. In contrast, EMS drawn from natural systems sacrifice some control of extraneous variables but contain more of the detail that is relevant to real-world pattern-process linkages. Moreover, because EMS are physical rather than mental or theoretical abstractions of broader-scale systems, they have an internal structure that, on closer probing, may reveal additional details that mathematical models or synthesized experimental systems cannot.

Extrapolation and judicious reductionism

The value of EMS (and, ultimately, of mechanistic theory) will be limited if one cannot extrapolate findings and predictions to other scales, organizational levels, or systems. To extrapolate across scales, one asks whether the system would behave in the same way at other spatial or temporal scales or whether abrupt, nonlinear changes occur between "domains" of scale (Krummel et al. 1987, O'Neill et al. 1989, Wiens 1989, King 1991). Extrapolation between scale domains involves the problem of transmutation (O'Neill 1979, Chesson 1981), in which the causes of patterns change qualitatively with scale. These nonlinearities produce "amplifying effects" (Huston et al. 1988) that preclude deriving patterns at a given scale (or hierarchical level) by some simple (e.g. additive) function that amalgamates average values from observations at a finer scale (or lower hierarchical level) (Gardner et al. 1982, Cale et al. 1983, Welsh et al. 1988, King et al. 1991). If transmutation effects are large, it may not be possible to extrapolate beyond a certain, restricted range of scale. One way to assay the magnitude of these effects is by combining mathematical functions for a given scale with spatially explicit simulation models to define scaling functions that predict the patterns expected where transmutation is absent.

Another form of extrapolation involves building from one level of ecological organization to another. Defining the "rules" for translating individual space use to population dynamics, for example, requires an interplay between theoretical studies and empirical investigations. Our theoretical model [eqs (1) and (2)] shows one way in which the properties of "average" individuals may be integrated to define patterns at the population level (see also Maynard Smith 1974, Huston et al. 1988, Łomnicki 1988, Persson and Diehl 1990, Hyman et al. 1991). Similar approaches could be used to build from models of individual movement and patch choice to explain variations in, for example, the β-diversity of communities across heterogeneous landscapes.

The third form of extrapolation is relevant to the use of EMS. Can one extrapolate from an EMS study of a vole to predict the responses of a capercaillie, or from a beetle to a bison? Clearly, the differences between these organisms are such that one would not attempt an extrapolation in detail, even after adjusting for the differences in scale (e.g. home-range sizes). Nonetheless, general extrapolations may be justified if the compari-

sons are restricted on the basis of shared attributes of interest. Thus, one might balk at extrapolating from a dung beetle to a moose if one's question deals with resource-defined space use, but a comparison among organisms of similar physiology and trophic status (e.g. a mouse and a moose) might be appropriate. What sorts of extrapolations are sensible depends on the questions asked. Here also simulation models may be helpful. One might, for example, develop a spatially explicit simulation model that reliably predicts mouse patch occupancy using "local rules" that encode mouse movements and patch choice. The same model, with appropriately modified rules, might then be applied to simulate the distribution of moose over a macrolandscape (Johnson et al. 1992).

Our approach emphasizes the individual level, even though many of the phenomena of interest characterize populations, communities, or ecosystems. To many ecologists, such an approach risks the peril of being drawn into the black hole of reductionism, in which one becomes so preoccupied with the details of every situation that generalizations never emerge. The distinction between reductionism and generalism or holism in ecology, however, is specious. One does not need to study every species in every situation to obtain an understanding of the important (and perhaps general) mechanistic linkages between explicit spatial patterns and processes. One may practice reductionism judiciously, selecting for investigation focal species or situations that occupy key positions on gradients in life-history strategies, body size, spatial heterogeneity, and the like (e.g. Keddy 1991). For example, one might define a matrix based on life-history attributes and structural attributes of reproduction patches and then select a few cells located on orthogonal dimensions of this matrix for study. Comparisons among such carefully defined sample systems may provide a powerful reductionist route to generalizations at higher levels of organization.

Conclusions

The mechanistic framework we advocate here suggests new lines of ecological research. Existing theory needs to be reformulated in explicitly spatial terms and new theory must be developed to integrate spatial patterns and processes and to consider scaling functions. Empirical research needs to be focused on carefully selected model systems that occupy key positions in ecological or environmental matrices. Comparisons among such systems may produce the generalizations or "rules" that will enhance our understanding of how spatial heterogeneity influences ecological systems. Because human activities disrupt the spatial patterns of nature, these generalizations may be the key to ecologically-based resource management as well. Ultimately, problems in reserve design (Simberloff 1988), habitat fragmentation (Saunders et al. 1991), the maintenance of biodiversity (Wilson and Peter 1988), or sustainable development (World Commission on Environment and Development 1987) all require a mechanistic understanding of landscape ecology.

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