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ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF PATCHINESS: A MARINE-TERRESTRIAL PERSPECTIVE

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INTRODUCTION

A quantitative description of patchiness and the assessment of its effects on ecological and evolutionary processes represents a major research focus as well as a challenge for ecologists and evolutionary biologists (e.g., Pickett and White 1985, Shorrocks and Swingland 1990, Kolasa and Pickett 1991). Patchiness is neither unique in origin nor characteristic of particular temporal or spatial scales; rather, patchiness emerges from the interactions between physical and biotic processes (Levin 1976, 1978) and is apparent at any scale of resolution. The scale dependency of patchiness and the complexity it generates calls attention to the need for new modeling approaches where spatial and temporal heterogeneity is explicitly incorporated (e.g., Hassell et al. 1991, Deutschman et al., this volume) and for new methodological tools to deal with problems of scale (e.g., Milne 1992, Garcia-Moliner et al., this volume).

In this chapter we address some of the ecological and evolutionary consequences of patchiness in both terrestrial and marine ecosystems. To do this we focus on the interactions across space and time scales. We illustrate particular phenomena by means of simulation models and by pointing out new approaches and conceptual frameworks for the analysis of patchiness and its consequences. We emphasize that the ecological and evolutionary consequences of patchiness vary according to the scales at which different organisms operate within a particular environment (intrinsic component), as well as on the scales of abiotic variability that characterize each environment (extrinsic component). First we compare terrestrial and marine ecosystems with respect to their characteristic spatial and temporal scales of variability. Next we address some of the ecological consequences of patchiness at two levels: population and landscape. Finally, we discuss the consequences of patchiness for microevolutionary change and macroevolutionary patterns and demonstrate the connections with the ecological scales. Throughout the chapter, the word *patchiness* is used to refer to both spatial and temporal heterogeneity or environmental variability.

THE TEMPORAL AND SPATIAL SCALES OF SOME ECOLOGICAL PHENOMENA: A MARINE-TERRESTRIAL COMPARISON

There are many ways to contrast marine and terrestrial systems (e.g., Fuentes and Jaksic 1988). Here we will compare temporal scales of some ecological variables in both systems.

This approach has been used by Steele (1989, 1991a) and by Dayton and Tegner (1984). We start by exploring some consequences of marine and terrestrial physical variability for life-history attributes. Later, we focus on a particular methodology that can help in contrasting marine and terrestrial systems and explore some of the resulting insights.

Types and Scales of Variability

Variability in the physical environment has several aspects that are important for understanding biological heterogeneity and how it differs between terrestrial and marine ecosystems. Environments of low abiotic variability may still be highly variable as a consequence of the behavior of the organisms themselves (e.g., treefall gaps in forests, foraging activities of predators). However, under highly variable abiotic conditions, the processes that produce biotic variability will tend to be disrupted. The limit cycles associated with simple predator-prey interactions might not be expected in nature if they are readily disrupted by other sources of variability.

The scales of variability also govern whether a species with a given life history perceives a particular source of variance as a general feature of its environment or as a rare event. In the former case, an organism might adapt to the heterogeneity it is sure to face on a regular basis. In the latter case, the cost of adaptation to a perceived rare event might outweigh the benefit that is realized only occasionally.

Predictable events are perceived much differently than are unpredictable ones. Highly predictable variability in time includes periodic "events" (e.g., diel, fortnightly, seasonal) and temporally autocorrelated processes, such as dissipative structures in ocean currents. Organisms can adapt to variability that is highly predictable in time. Zooplankton migrate vertically with diel variation in light. Many temperate angiosperm plants construct relatively inexpensive leaves each year, shedding them in step with the highly predictable climate variation represented by seasonal changes. The predictability of events in this sense appears to be reflected in the life-history strategies of the dominant organisms present in an environment. Predictable variability can be the focus of much behavioral and physiological adaptation. For population persistence, the critical aspects are environmental changes where variance is large, unpredictable, and of a time scale that demands adaptation. There is a great diversity of responses or bet-hedging strategies (Stearns and Crandall 1981). These include iteroparity of a relatively resistant mature stage, dispersal to spatially restricted sites of recruitment, and dormancy (Cohen 1966, Gadgil 1971, Roff 1975, Levin et al. 1984, Levin 1985, Cohen and Levin 1985, 1991). In this case the organism must integrate over areas and/or times of unfavorable conditions in order to realize comparatively large reproductive gains at suitable times and places. In general, the gains realized during rare favorable periods must be sufficiently large to offset the losses that accumulate during unfavorable times. Marine/terrestrial comparisons are interesting here, because of some general patterns in costs associated with bet-hedging strategies in the two environments. Consider the role of dispersal. Seeds possessing built-in carbohydrate reserves have a greater chance of survival. However, such reserves are not conducive to dispersal by wind. Due to the physical characteristics of the atmosphere, adaptations that result in high atmospheric residence times (e.g., structures that decrease drag) are almost universally achieved at the cost of low seed reserves. Because of the high juvenile mortality associated with low seed reserves, terrestrial plants are not expected to engage in a bet-hedging strategy of high dispersal rates. It is likely that the costs of high dispersal are a strong force regulating many aspects of terrestrial plant assemblages.

On the other hand, the physical characteristics of marine environments (gravity is not a problem) renders increased stored reserves less costly in terms of dispersal and subsequent juvenile survival, setting a different scenario for the evolution of bet-hedging strategies. As pointed out by Strathmann (1990), differences in the physical characteristics of terrestrial and marine habitats have resulted in the prevalence of different life histories in these environments. These relationships between life history and the physical environment may provide some insights for understanding the regularities observed in Stommel diagrams.

The Stommel Diagram

Stommel diagrams summarize variability in natural systems. They are plots that identify which scales contribute most to the total variance of the system (Figure 1). The characteristic scale of a phenomenon can be defined as the length or time interval necessary for the variable of interest to show a significant degree of variation (Powell 1989). Stommel diagrams (or their heuristic equivalents) have been used as descriptors of the most relevant spatial and temporal scales of physical phenomena (Stommel 1963), zooplankton biomass (Haury et al. 1978), or as an aid in defining the relevant scales in paleobiological phenomena (Schopf 1972). Other diagrams (e.g., Steele 1978, 1989, 1991a; Delcourt et al. 1983; Harris 1986; Wiens 1989) are also used to portray the spatial and temporal scales of the most relevant phenomena. Haury et al.'s (1978) Stommel diagram is, to our knowledge, the only one that has been published for an ecological variable. An important feature of Haury et al.'s diagram is that it shows that biomass variability peaks at the largest spatial and temporal scales, implying that only phenomena characterized by large temporal scales produce changes at the large spatial scale.

Technically, the Stommel diagram is a three-dimensional representation of the power spectrum, Sq, of a relevant record q (i.e., q represents some variable, phenomenon, process, etc.) as a function of frequency (W) and wave number (K) (see Figure 1). Since period (T) $\alpha\ W^1$ and wave length (λ) $\alpha\ K^1$, the analyst commonly plots S_q vs T (a measure of temporal scale) and λ (a measure of spatial scale). The volume under the S_q surface represents the total variance associated with the record (Figure 1).

Some ecological variables may be poorly suited for spectral analysis, violating some necessary assumptions (for examples see Haury et al. 1978). One case is represented by variables that show secular trends in space or time (i.e., are non-stationary), such as species richness. Further, large variability may be related to single (i.e., non-stationary) catastrophic events. Moreover, one can also envision situations in which there are no apparently characteristic time or spatial scale associations. Another difficulty is that in marine and terrestrial systems (e.g., Harris 1986, Pagel et al. 1991) longitudinal, latitudinal, and vertical (altitudinal) transects are likely to produce different dominant scales. In this case, one might plot different contours for the different axes. Finally, the existence of a maximum spatial scale value, given by the size of the earth, implies that at some point the matching between temporal and spatial scales is no longer possible.

Because of the difficulty in collecting the appropriate data for the largest time and space scales, Stommel diagrams are likely to be the result of educated guesses in these spatial and temporal domains. In our case (Figure 2), we followed Haury et al. (1978) in completing the diagrams with our best knowledge and best guesses (in some other cases inferring the patterns from the processes). Therefore, the diagrams are schematic representations; plots with real data might be restricted to smaller scales. Nonetheless, we believe the general
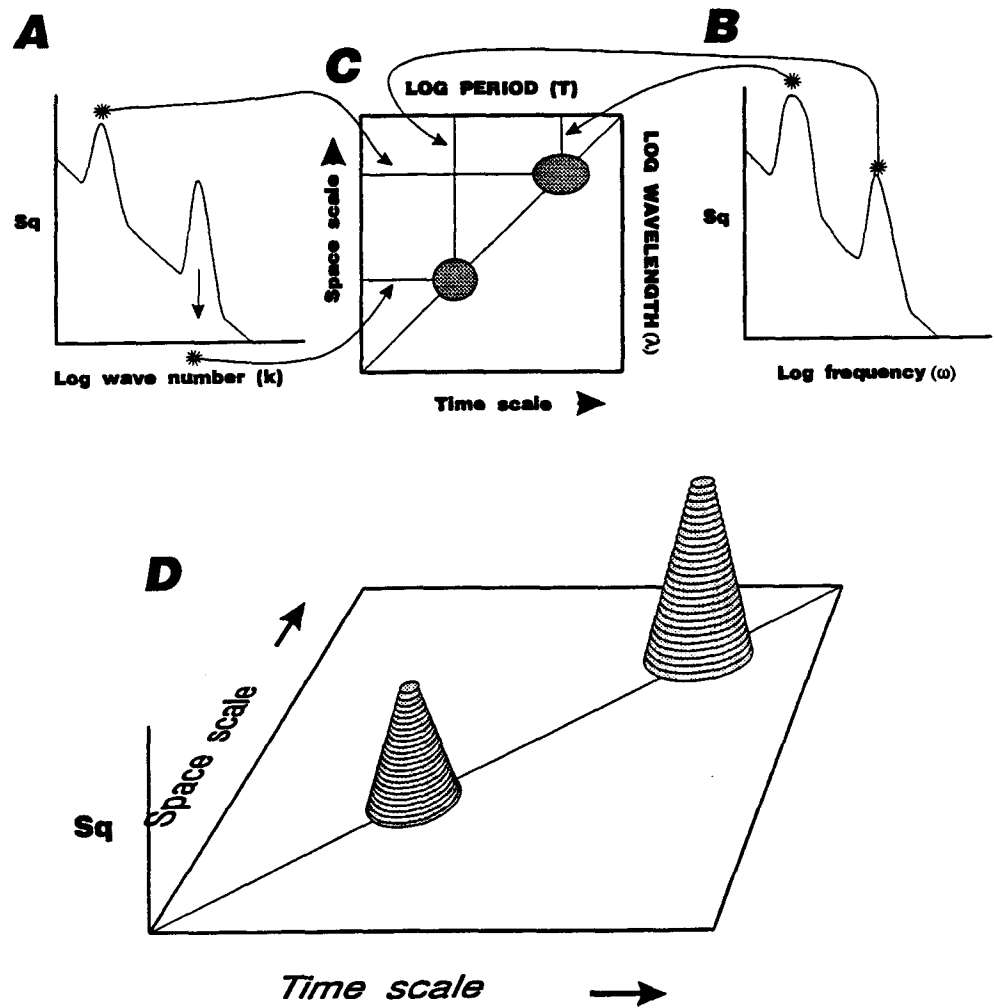
Figure 1. Schematic representation of the procedure to construct a Stommel diagram. Panel A represents the power spectrum, S_q, of a spatially distributed variable, while panel B represents the spectrum of a time series. Panel C represents the resulting Stommel diagram. Notice that the peaks in the spectral diagrams represent the most energetic frequencies or wave numbers (i.e., the important scales). The peaks in time and space are matched in the Stommel diagram. Panel D is a three-dimensional depiction of panel C.
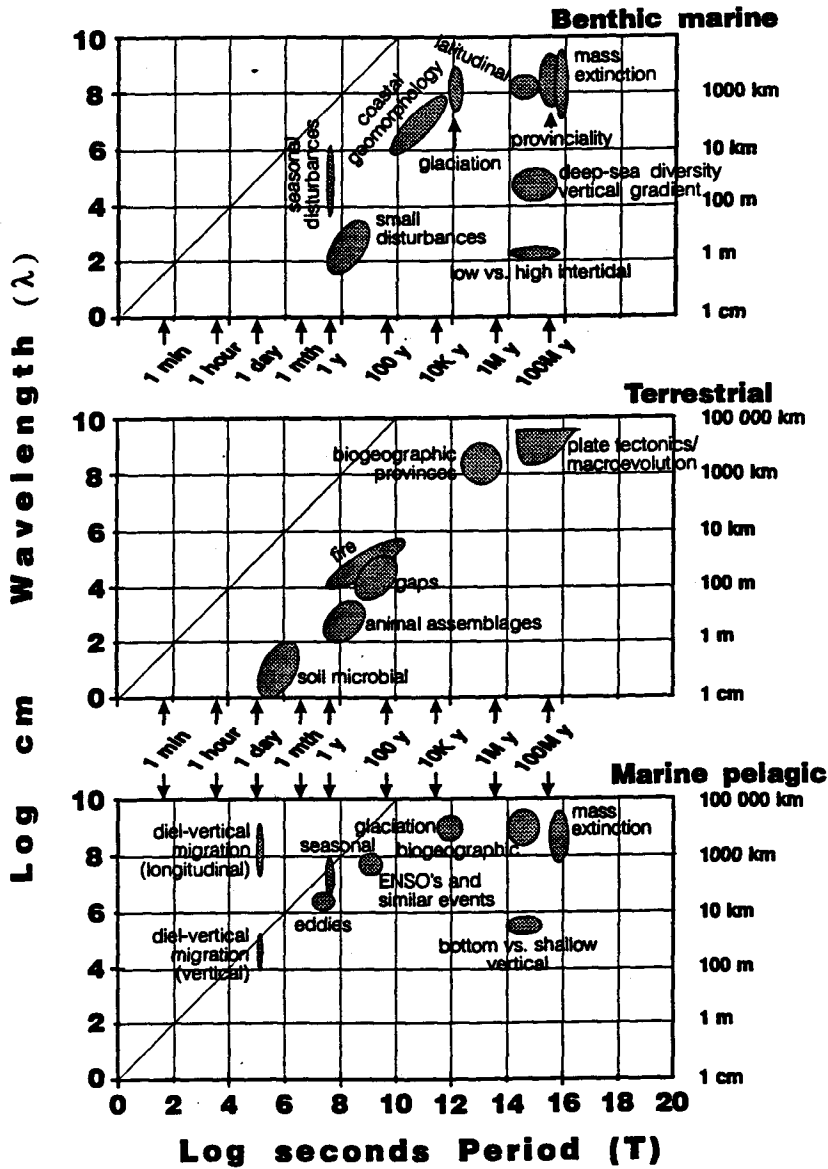
Figure 2. Stommel diagrams for species richness. Marine benthos, marine pelagic, and terrestrial systems. Marine benthos does not include coral communities. (ENSO = El Niño-Southern Oscillation). Stippled figures represent contours of maximum variance (see text for an explanation).

features of our diagrams will persist, despite some fine-tuning that may occur as more data accumulates.

Marine-Terrestrial Comparisons: Species Richness

Stommel diagrams for terrestrial, pelagic marine, and benthic systems (Figure 2) show the general features of a positive relationship between spatial and temporal scales. The terrestrial pattern is displaced to the right (to larger temporal scales) of that for pelagic marine; in this aspect, these diagrams parallel the one obtained independently by Steele (1991a). Further, the pelagic diagram is also displaced to large spatial scales. For benthic and pelagic systems, the phenomena with large temporal scale and small spatial scale are all associated with vertical gradients, such as the deep vs. shallow sea species diversity gradient, the low vs. high intertidal in the benthic marine, and the bottom vs. shallow vertical in the pelagic marine (Figure 2). It is also to be expected that most phenomena with small temporal scales and large spatial scales are those associated with astronomical cycles (diel, lunar, yearly). This is most obvious in the marine pelagic diagram for diel-vertical migration (longitudinal). This particular pattern emerges when comparing species richness at, say, noon and midnight at two sites separated 180° in longitude. The positive association of these dominant scales has been noted by several authors (Haury et al. 1978, Steele 1978, Delcourt et al. 1983). It has been explained on the basis of the underlying scaling relationships that govern the physical heterogeneity in the sea (Stommel 1963). Steele (1991b) also notes the regular pattern that emerges with trophic status in pelagic systems, where organisms high on the food chain are larger, thereby foraging over larger spatial scales and living longer. Steele's comparison of such patterns for marine and terrestrial environments featured the offset between the two curves. He suggests that the scales of physical variability differ between the two environments. Because of its more predictable nature, physical variability in the marine environment provides an opportunity for specialization. He cites the example of a near-universal pelagic habit for larval stages. In contrast, much of the physical variability in terrestrial environments provides no opportunity for adaptation because of its high frequency and unpredictability. Thus, terrestrial biotic environment is less tightly coupled with the physical environment.

In the next sections we discuss and illustrate the effects of temporal and spatial variability on some ecological and evolutionary processes responsible for some of the patterns observed in Stommel diagrams.

ECOLOGICAL CONSEQUENCES OF PATCHINESS

At small spatial and temporal scales, biotic and physical variability in the environment is of paramount importance in affecting ecological patterns and processes. In this section, we discuss some specific implications of patchiness on ecological processes, starting with the characterization of patch properties with an emphasis on boundary effects. We then consider some of the population and landscape-level ecological consequences.

Patch Boundary Properties and Ecological Processes

The bulk of the literature on patchiness emphasizes patch size and shape as salient features of patches, while comparatively little attention has been directed to the functional

characteristics of boundaries and their potential influence on ecological processes. In part this is because, in order to characterize and understand ecosystem processes, terrestrial researchers have focused primarily on homogeneous regions, avoiding the heterogeneous areas linking them. As a result, properties of boundaries have been overlooked, and their spatial representation often reduced to a line on a map. In marine systems, however, boundaries associated with water masses such as fronts, thermoclines, or pycnoclines are well-studied features (e.g., Le Fèvre 1986; Steele 1989, 1991b; Barry and Dayton 1991) and are generally regarded as having, sometimes, characteristic communities (Steele 1991b, Ray 1991).

The boundary of a patch can be viewed as the location in space at which the rate of change of a given variable or assemblage of variables is the highest (Burrough 1986). This definition encompasses both structural and functional boundaries (Allen and Starr 1982). While some boundaries may completely surround a patch, others simply denote a discontinuity in rate of change, structure, or composition between adjacent systems (O'Neill et al. 1986). From a dynamic point of view, boundaries and ecotones are transition zones, at which flux of material or energy and other ecological processes take place (Margalef 1963, Naiman and D'Camps 1990).

The terms *boundary* and *ecotone* were primarily used to define the limits between terrestrial biomes based on vegetation types. Recently they have been extended to account for discontinuities that occur at all spatial scales. At a given scale, boundary edges might be perceived in a series of forms, ranging from a sharp to a fuzzy transition zone (Ferson 1988). The detection of boundaries depends on the scale of observation; boundaries that at some scale are recognized as a whole ecosystem, such as intertidal systems, can be viewed as an ecotone or even a very sharp edge at larger scales. Boundary properties have recently started to be the focus of an increasing number of studies in terrestrial environments (e.g., Forman and Godron 1986). This reflects the relative ease in visualizing them (e.g., forest-prairie, hemlock-maple groves) compared to pelagic realms, where patches and their boundaries are much more dynamic. Indeed, at small scale in aquatic ecosystems, patches due to biological behavior grow and decay at a speed that does not allow the observer to make accurate assessments of the patch size and its boundary. For these ecosystems, a statistical definition of patchiness using variance/mean indices may be more appropriate (Downing 1991). On the other hand, boundaries in large-scale pelagic communities are generally determined by mesoscale physical dynamics such as fronts and pycnoclines (Brinton 1962, McGowan 1972, Brandt and Wadley 1981) and are typically more persistent in time than small scale boundaries. This is also apparent in terrestrial ecosystems, where physical variables such as temperature may impose limits on the geographical distribution and survival of organisms such as birds (Root 1988) or trees (Davis et al. 1986, Davis 1987). Although the importance of large-scale boundaries as a general feature of pelagic ecosystems is well established, our perceptions may be biased to some degree by the limited capabilities of sampling pelagic habitats on smaller scales. The further development and use of new methodologies such as remote sensing and continuous recording systems—including fluorometry, flow cytometry, hydroacoustics, and optical plankton counters—may change our view of the dominant sizes, shapes, and boundary characteristics of patches in the pelagic realm.

Patch dynamics refers to the temporal response of patches to either autonomous (intrinsic) or induced (extrinsic) processes or forces. A patch may react to these forces by changing its internal state, thus reinforcing or reducing the difference between the patch and its surroundings, which in turn leads to changes in boundary properties. In terrestrial landscapes, the shape of boundaries has implications for ecological processes such as

colonization: forest recovery is faster when forest patches present concave boundaries rather than convex ones (Hardt and Forman 1989), due to the combined effect of microclimate and larger seed pool. In the same way that boundary shape may affect the dynamics of some ecological processes, other processes such as spatial competition, disturbance, or organismal response to environmental changes may influence the shape of boundaries (Forman and Godron 1986, Paine and Levin 1981, Navarrete and Castilla 1990). Thus, there is a two-way interactive process where the ecological phenomena influence the properties of the boundary and where the boundary characteristics may determine specific biological and ecological responses.

Boundaries affect processes occurring at disparate spatial scales, from local movements of an individual up to processes such as long-term species migration or dispersal. However, whatever the scale, a boundary acts either as a barrier or as a permeable membrane (Wiens et al. 1985). The degree of permeability might be different for fluxes leaving or entering the patch and could depend on the process or species involved. The interaction among boundary shape, permeability, and patch size is particularly important in the outcome of migration processes. Stamps et al. (1987) explored the impact of geometry and permeability of boundary on emigration in a patch using computer simulations. Patch shape and size were not found to be relevant as long as the degree of permeability was low. These results were supported by field studies of some terrestrial insects (Turchin 1986) and vertebrates (Stamps et al. 1987).

Permeability influences population interactions such as competition and predator-prey dynamics by varying the rate of dispersal of different species across heterogeneous systems. For example, a refuge is a patch where the boundary is less permeable to the predator than to its prey. Taylor and Pekins (1991) found such a functional boundary in the case of wolf-deer interactions. A refuge for the deer was a patch that the wolf cannot occupy due to behavioral constraints. Similarly, Menge et al. (1985) found that the survival of many intertidal organisms, and thus diversity and community structure, depend on the availability of refuges from both vertebrate and invertebrate predators.

Boundaries are a salient feature of patches. Their functional characteristic can strongly affect the outcome of species interactions and species persistence on heterogeneous landscapes. Their characterization is important for a more complete understanding of the ecological consequences of patchiness, and for a more precise assessment of the effect that alteration of landscape heterogeneity (mainly by humans) can have on species survival. One of the effects of human use of the landscape is to modify the shape of patches by straightening the boundaries. In this way, the edge-to-area ratio is altered, and this in turn may affect the level of permeability. Besides acting at the boundary level, humankind also fragments the landscape in such a way that suitable patches for a given species become discontinuous and usually smaller. This discontinuity and size alteration can be critical depending on the dispersal capabilities of each species, and on its minimum territorial requirements. Thus, some aspects of landscape management, such as reserve planning, should take into account not only boundary characteristics but also the spatial requirements of the species involved. This is a difficult task to accomplish in terrestrial landscapes, and this kind of space management may not be applicable at all in seascapes.

Some Population-Level Consequences of Patchiness

Much of the appreciation for the importance of patchiness on population dynamics was stimulated by the classic work of Huffaker (1958). Unfortunately, logistical constraints have

severely limited the amount of experimental work conducted in natural systems (Kareiva 1990, Kareiva and Anderson 1988). Thus much of the work in this field has been conducted using mathematical models (see reviews by Taylor 1990, Hastings 1990, Reeve 1990, Harrison, in press). These models explore the relationship between patchiness and population persistence and demonstrate the importance of species attributes (e.g., life history and dispersal behavior).

The importance of both patchiness and species dispersal capabilities is illustrated by a predator-prey model recently developed by Schumaker and Wallin (in prep). This model (Table 1) tracks predator and prey population dynamics on a 50 x 50 gridded landscape. Populations dynamics for each grid cell are calculated independently using standard Lotka-Volterra difference equations (Table 1). For all simulations, a limited proportion of the landscape is defined as suitable habitat. The remainder of the grid cells are defined as unsuitable for both predator and prey. The grain specifies the size distribution of suitable patches. For a grain size of one, suitable patches are randomly placed onto the landscape one grid cell at a time. For a grain size of two, suitable patches of two-grid cells by two-grid cells are randomly placed on the landscape. As grain size increases, the suitable habitat occurs in a smaller number of larger blocks and the inter-patch distances increase (Figure 3). At the maximum grain size all of the suitable habitat is present in a single large block.

When predator or prey populations in a grid cell exceed a predefined carrying capacity (see Table 1), the excess individuals disperse. Individuals can move through unsuitable grid cells, but they must continue to walk until they die from natural causes (Table 1) or find a suitable grid cell with a population size below the carrying capacity.

The edges of the landscape are wrapped into a torus so that animals experience a continuous landscape. The dispersal track for an individual animal consists of one or more segments or "steps," and the characteristics of the track are defined by three movement parameters (Table 1). For both predator and prey, the direction of the first step is selected at random and the direction of all subsequent steps is constrained by the species directional autocorrelation. The prey uses an uncorrelated walk; that is, the direction of each step is independent of the previous step direction. The predator uses a self-avoiding walk; after random selection of the initial direction, the animal continues in the same direction. The length of each step is variable; an integer value is selected at random between the range of zero and the species' maximum step size. During dispersal, animals are assumed to experience higher mortality rates. The more steps involved in a dispersal track, the lower the survival rate. The predator and prey each have a specified survival probability per step.

Two sets of simulations were conducted (Table 1). In the first set, the predator's maximum step size (a measure of dispersal distance) was set to 1.0; in the second to 2.0. Each set of simulations included thirty model runs, five for each grain size. For each run, summary statistics for the predator population were computed without considering the first 100 time steps, in order to eliminate transient responses due to initial conditions. For both sets of simulations, there is a highly significant, positive relationship between mean predator population size and habitat grain (Figures 4a, 4b; $r^2 = 0.89$ and 0.50, respectively, $P < 0.05$). For the less mobile predator (i.e., small step size), population size is considerably reduced in the fragmented landscapes (i.e., small grain size, Figure 3a). For the more mobile predator, population size is not as strongly affected by grain size. Figures 4c and 4d present the coefficient of variation in population size for these two predators ($r^2 = 0.46$ and 0.77, respectively, $P < 0.05$). For the less mobile predator, there is a significant, inverse relationship between the coefficient of variation and habitat grain (Figure 4c). For the more

Table 1. Model parameters and initial conditions.

Simulation Length: 250 time steps
Landscape in suitable habitat: 22%
Habitat grain sizes:1, 2, 4, 8, 16, 23
Five replicate simulations run for each grain size
Lotka-Volterra Equations:

$$H_{t+1} = c_1 H_t - c_2 P_t H_t$$

$$P_{t+1} = -d_1 P_t + d_2 P_t H_t$$

$$c_1 = 2.0 \qquad d_1 = 0.1$$

$$c_2 = 5.0 \qquad d_2 = 0.2$$

	Prey (H)	Predator (P)
Initial Population Size	5000	500
Maximum Density/Cell	12	5
Maximum Step Size	2	1 or 2
Directional Auto-Correlation	0	1.00
Survival Probability/Step	0.8	0.70

mobile predator, the relationship between the coefficient of variation and habitat grain is positive (Figure 4d).

Given that a high coefficient of variation in population size implies a high probability of extinction (Pimm et al. 1988), our results suggest that the less mobile predator is at a higher risk in fragmented landscapes. Extinctions occurred in three of five simulations with the less mobile predator in the most highly fragmented landscape. In these cases, it appears that following local extinctions of prey, the fragmented landscape and the predator's limited dispersal capabilities make it difficult to reach new concentrations of prey. Conversely, the more mobile predator is at a higher risk of extinction in large intact blocks of habitat. With the more mobile predator, extinctions occurred in eight of fifteen simulations in landscapes with the three largest grain sizes. In these large blocks of habitat, it appears that the prey are unable to find refuge from these highly mobile predators. The predators quickly build up to very large population sizes and drive the prey and themselves to extinction. Although additional simulations need to be conducted over a wider range of conditions, these results demonstrate that conclusions about the effect of habitat heterogeneity on population persistence cannot be made without knowledge of species dispersal capabilities and life history attributes
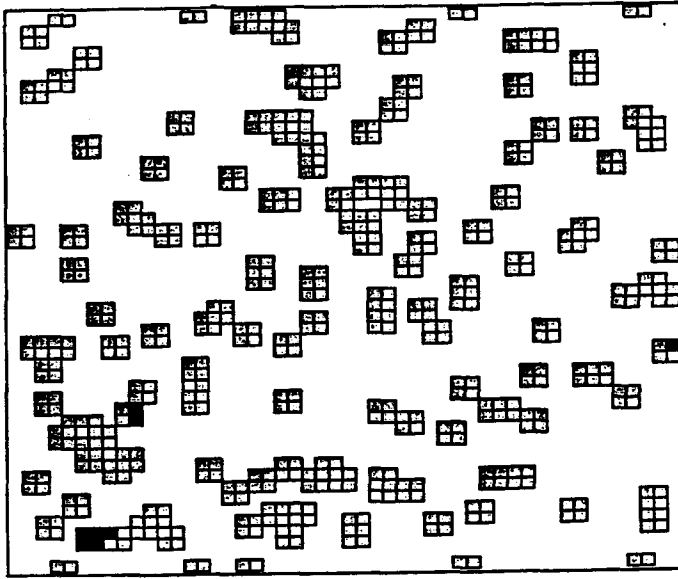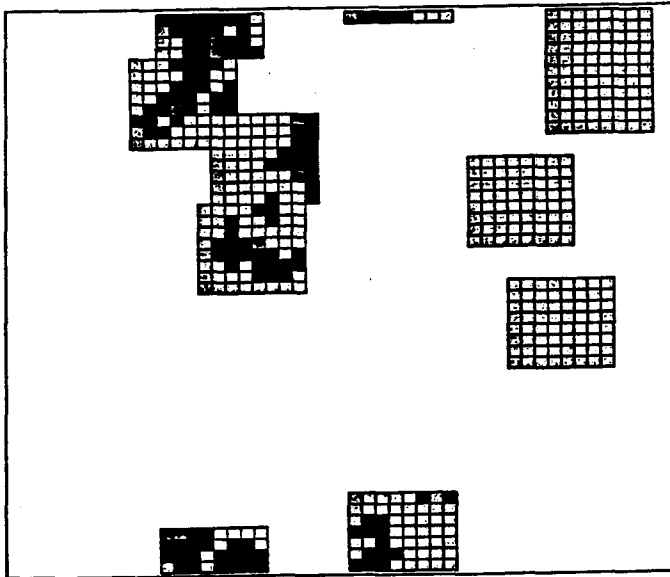
Figure 3. Sample landscapes used in the simulations. Total landscape size is 50 x 50 cells. Cells outlined in black represent suitable habitat; remaining white background is unsuitable habitat. The solid black cells contain predators and prey; dark grey cells—predators only; light grey—prey only; open cells are unoccupied. (a) habitat grain = 2; (b) habitat grain = 8.
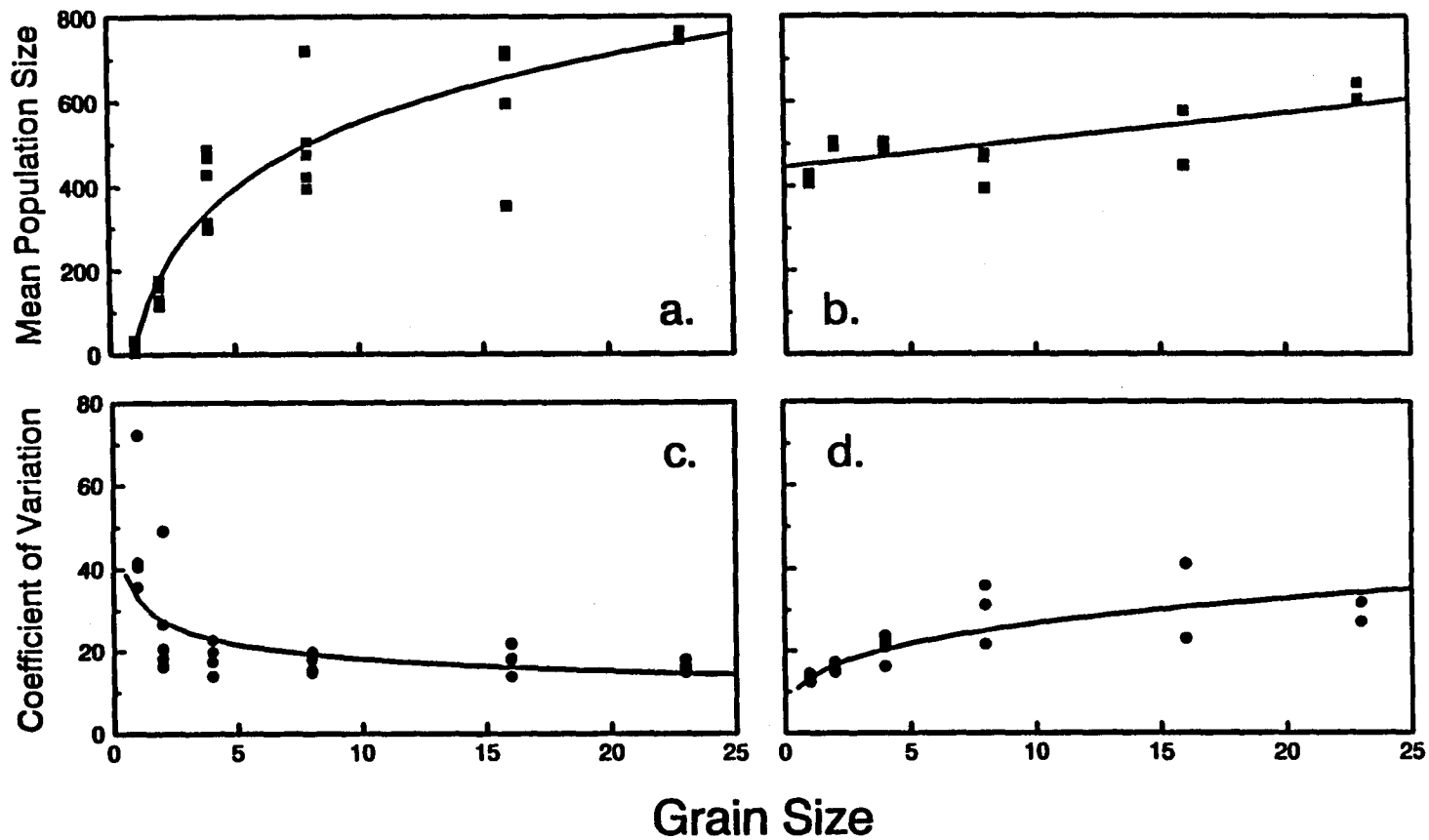
Figure 4. Predator population size and corresponding coefficient of variation as function of habitat grain. Approximately 22% of the landscape in suitable habitat. Each point based on the last 150 time steps of a 250-step simulation. See text for additional details. (a,c) Maximum predator step size = 1; (b,d) Predator step size = 2.

related to habitat requirement. As pointed out by Kareiva (1987, p. 389), "...instead of making robust generalization about habitat fragmentation (such as "patchiness is stabilizing") we should seek predictions that are based on the details of an organism's dispersal behavior and demography." For some species, population persistence may be highest in fragmented landscapes; other species may do best in large blocks of habitat. Unfortunately, the life history and dispersal characteristics for many species are not well known. Nevertheless, an important conclusion is that major changes in habitat grain—e.g., due to anthropogenic factors—are likely to have a major impact on population dynamics. For species that have evolved in environments with a large habitat grain, a substantial reduction in grain is likely to increase the probability of extinction. Such changes are also likely to increase the likelihood of invasions by species that have evolved in fine-grained habitats. This could ultimately result in substantial shifts in species composition and biodiversity.

Ecological Consequences of Landscape-Level Patchiness

The importance of landscape patchiness has been widely recognized in the study of both terrestrial (Wiens et al. 1985) and marine ecosystems (Paine and Levin 1981, Steele 1991b). Here, we focus on two aspects: the effect of landscape patchiness on the spread of disturbances, and landscape patchiness as it affects the redistribution of available resources and species survival.

Patchiness and the spread of disturbance. One of the challenges for landscape ecologists is to understand how disturbance, as an ecological process, spreads across heterogeneous landscapes (Turner et al. 1989, Green 1989, Costanza et al. 1990). A process-based landscape model, developed by Wu (1991), simulates fire spread across a Rocky Mountain foothill landscape and suggests that different interactive overlays of landscape patchiness such as vegetation, fuel complex, stand age, topography, and weather conditions affect fire spread differentially. Wu found that some vegetation patches in the study area, such as juniper woodlands, may play an important role in fire spread under conditions of high wind speed but not at low wind speed because of the distance between individuals trees. Usually, fuel complex correlates to stand age, as older stands accumulate higher fuel loadings and have a higher fire spread rate. However, steep slopes reduce fuel accumulation rate and therefore alter the effect of stand age on fire spread. Also, stand age composition may be a consequence of the effect of topography on fire. Thus, the interaction of abiotic and biotic patchiness plays an important role in fire spread. In other words, all the modeled components of landscape patchiness interact to determine the spread rate of fire. It is also suggested that under different conditions there may be different components of patchiness controlling the process.

Disturbance regimes may significantly affect landscape stability. For fire spread in woodland ecosystems, a set of disturbance regimes creates a set of landscape patterns; and, by the same logic, a set of landscape patterns makes a set of disturbance regimes more prevalent than others. This dynamic property suggests the existence of metastability in landscape patchiness. This means that landscape patchiness will remain relatively unchanged under a disturbance regime of a certain frequency and intensity, but could undergo a radical change at others (O'Neill et al. 1989). By way of example, disturbances of low frequency and high intensity may create a landscape with low patchiness. In contrast, disturbances of high frequency and low intensity may prevail in highly patchy landscapes. Different recurrence times for fire in different landscapes have been reported (Clark 1989, Wu 1991), suggesting

that variable fire regimes may control different landscape patchiness (even-aged stand mosaics). For example, as Turner and Romme (1991) found out, a fire cycle of 26 - 113 years in interior Alaska creates landscape patches of less that 200-year-old stand age (Yarie 1981). But with a 434-year cycle, the patch mosaic of the landscape may include many stands with age greater that 1000 years old.

Patchiness and the effect of resource distribution on species survival. Landscape patchiness affects the spatial and temporal availability and distribution of resources and the way species use those resources. At the landscape level, several questions on patchiness and resource utilization may be asked:

(1) How do the abundance and spatial distribution of resources affect species survival?
(2) How is landscape patchiness important for species?
(3) Are there any threshold effects of patchiness on species survival?

Individual-based landscape modeling has provided a new context for the study of interactions among landscape patchiness, resource redistribution, and animal foraging (Houston et al. 1988; Hyman 1990; Turner et al. 1991; Johnson et al., in press; Milne et al., in press). A landscape simulation model of winter foraging by large ungulates has been developed by Turner et al. (1991) to study elk and bison responses to spatial distribution of resources and landscape patchiness in the northern range of Yellowstone National Park. In agreement with the model predictions, the degree of landscape patchiness affects both foraging efficiency and movement energy costs. When resources are patchily distributed, ungulates forage more efficiently and have higher fragmentation tolerance as the search area and movement scale get larger. The model also suggests that there might be a threshold effect of patchiness on ungulate survival. A distinct decline in ungulate survival, after 90 days of simulation, was caused by a sharp reduction in the daily consumed biomass during the simulation, and by the highly negative energetic balance resulting from drastic increases in movement energy costs. When changes in landscape patchiness are considered, it is apparent that the proportion of resource pixels (P) declines through winter as ungulates are foraging, which means a decrease of available forage biomass (Figure 5a). However, there is no evidence that the decline of P value directly affects ungulate survival after 90 days of simulation. An interesting result relates to a rapid increase in the number of patches in the landscape that shows up around 80 days of simulation (Figure 5b), which means that before the decline in ungulate survival the landscape speeds up its fragmentation rate. Also, resource patches decrease dramatically in size (from 600 to less than 200 pixels) after 90 days of ungulate foraging, suggesting that survival is strongly affected by the decay rate of large resource patches.

Several conclusions can be drawn from the simulations:

(1)   As resources become limited, their spatial distribution becomes more important for species survival.
(2)   Ungulate survival declines when the landscape increases its degree of patchiness;
(3)   The decay of large resource patches in a landscape may strongly influence winter foraging and ungulate survival;
(4)   As resource patches are rapidly fragmented, they may have a critical influence on ungulate survival.
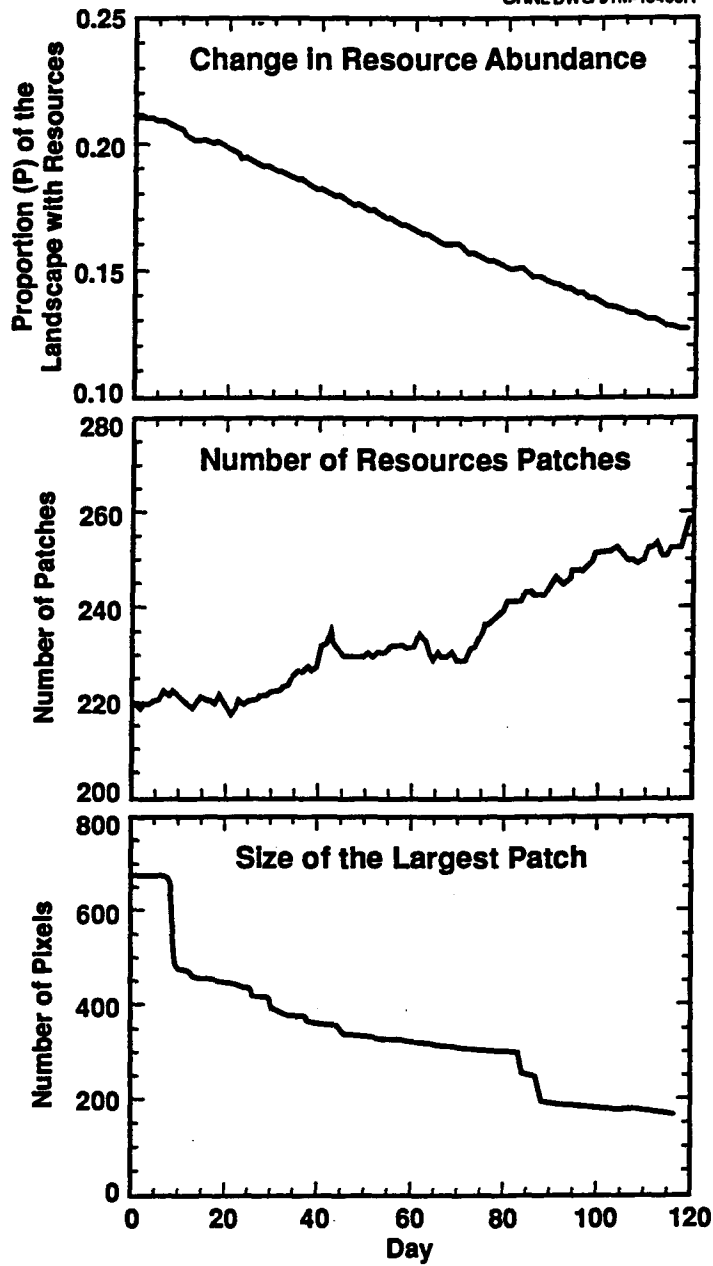
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Figure 5. The changes of landscape patchiness by ungulate foraging. (a) Proportions of resource pixels, (b) number of resource patches, and (c) number of pixels for the largest resource patch (from Turner et al. ms.).

EVOLUTIONARY CONSEQUENCES OF PATCHINESS

Evolutionary processes are typically characterized by spatial and temporal scales much larger than those commonly used to describe ecological dynamics. However, since patchiness is apparent at all spatial and temporal scales of resolution, it is worth assessing its consequences at the evolutionary level. In this section, we outline the conceptual basis that makes patchiness a relevant phenomenon for understanding both microevolutionary and macroevolutionary processes. We also show how ecological and evolutionary processes can be integrated within the framework of populations' responses to patchy environments.

Microevolutionary Consequences

Microevolution is defined to be genetic change that occurs within populations and species. In principle, patchiness may influence all the driving forces of microevolution (the mutational input of new variation, and its fate due to genetic drift, gene flow, and natural selection) that collectively determine the mean phenotype of a given species, the amount of variation maintained in that species, and how that variation is partitioned within and among local populations. The word "patchiness" is one way to refer to the general topic of environmental heterogeneity. There is an enormous literature in evolutionary biology dealing with the consequences of heterogeneity, for instance, in the evolution of strategies to cope with heterogeneity (e.g., "bet-hedging," Seger and Brockmann 1987; the evolution of dispersal and diapause strategies, Levin et al. 1984), and the maintenance of genetic variation (e.g., Hedrick 1986). Rather than attempt to review this unwieldy literature, this section outlines the relationship between some of the topics discussed elsewhere in this chapter and microevolution.

Whenever one studies a local population, it is important to remember that that population is the latest successful pass through an immensely complex sieve of past temporal and spatial environments. But the sieve that is relevant to understanding the composition of a given population is a biased sample of the array of available past environments. This biasing results from a number of distinct processes, including habitat selection (Holt 1987), spatial variation in population abundance, asymmetrical dispersal rates, and the basic distributional limits imposed upon a species by its fundamental niche (Holt and Gaines, ms). Although these biases will themselves evolve in response to environmental heterogeneity, they will never be absent, and their combined effects clearly must be incorporated in any analysis of microevolutionary dynamics within a species (Kitchell 1990). Above we used Stommel diagrams to contrast temporal and spatial scales of variability between marine and terrestrial systems. Though we did not explicitly say so, a Stommel diagram is constructed relative to a defined sampling regime (e.g., in Figure 2b the variance components are computed from data from sample points on continents, not in the intervening seas). The suggestion we now explore is that to characterize the role of patchiness in microevolution, one must similarly relativize environmental variation to the array of "sampling units"—individuals—that comprise a given phylogenetic lineage, and that a useful heuristic device for doing so is provided by constructing a "phylogenetic envelope" on a space-time or space-time-environment diagram (see also Holt and Gaines, ms).

Ever since Darwin, it has been conventional to portray biotic diversification in a phylogenetic lineage as a branching tree. The tree is a retrospective view of the historical relationships among organisms in different species. Within a biological species, it is more

sensible to display phylogeny (at the level of individuals) as a reticulated web (Maynard Smith 1989). To envisage the relationship between spatial and temporal variability and microevolutionary processes, let us overlay this phylogenetic web onto a space-time diagram. The basic idea is that the phylogenetic web, when placed on a space-time-environment plot, provides the relevant, appropriately biased sample of past environments for analyzing microevolution.

Start with a particular local population (loosely defined as that set of individuals that interbreed to produce the subsequent generation). For simplicity, assume that the organism in question is bisexual with an annual life cycle, and that we census at the beginning of generation t (at the zygote stage). There are several ways one can overlay the phylogenetic web on a space-time plot. The simplest, and the one developed here, is to let the x-axis represent the actual spatial position of individuals in a population and their ancestors; and the y-axis, time. The origin is the spatial position of the population at a given point in time. Each zygote in our sample, of course, had a father and a mother, who themselves were zygotes one year earlier. Their spatiotemporal birth position can also be represented by dots, and their successful production of offspring (one or more) in the current generation is delineated by lines connecting the dots of successive generations (Figure 6).

This graphical representation can be iterated as many generations into the past as is useful; obvious break-off points might be the time of speciation in a peripheral isolate, or invasion from a distant locality. Individuals that leave no descendants can be represented as the terminal ends of such lines. The actual phylogenetic web of successful individual genealogies leading to a particular population is penetrated and surrounded by a penumbra of such termini. Moreover, some ancestors may be members of populations that leave descendants in other contemporaneous populations, and of course some ancestors are more successful at leaving descendants than are others (either due to chance or to selective advantages).

If there is a large number of individuals in the local population, and we are considering evolutionary processes over many generations, this graph will be a very dense, complex skein of entangled threads (which might be more efficiently described by a density function). This skein is surrounded by an envelope, the shape of which describes the slice of the earth relevant to interpreting the genetic composition of one's study population. At a grander level, one could repeat the same process sketched here at various spatial scales, from the home range of single individuals up to the entire ensemble of populations comprising a species range. Figure 7 shows some examples.

The shape of the phylogenetic envelope reflects the interplay of intrinsic biotic factors and external constraints. If the upper boundary of the phylogenetic envelope has a very shallow slope (e.g., Figure 7a), the contemporaneous population is descended from sets of ancestral individuals that are similarly spatially circumscribed. Moreover, if the mean location of these ancestors is the same as their descendants, the population is tied to a particular piece of turf. This may be a reasonable approximation of some oceanic island populations, which are panmictic within-island but receive very few immigrants from outside (Grant and Grant 1989). In this case, microevolution to a first approximation involves within-population microevolutionary processes. Patchiness at small spatial scales within the island can, of course, be very important—for instance, in determining population size (thereby affecting genetic drift) or in setting the relative fitnesses of alternative genotypes or phenotypes—but it seems fair to say that spatial heterogeneity expressed over large spatial scales will not be
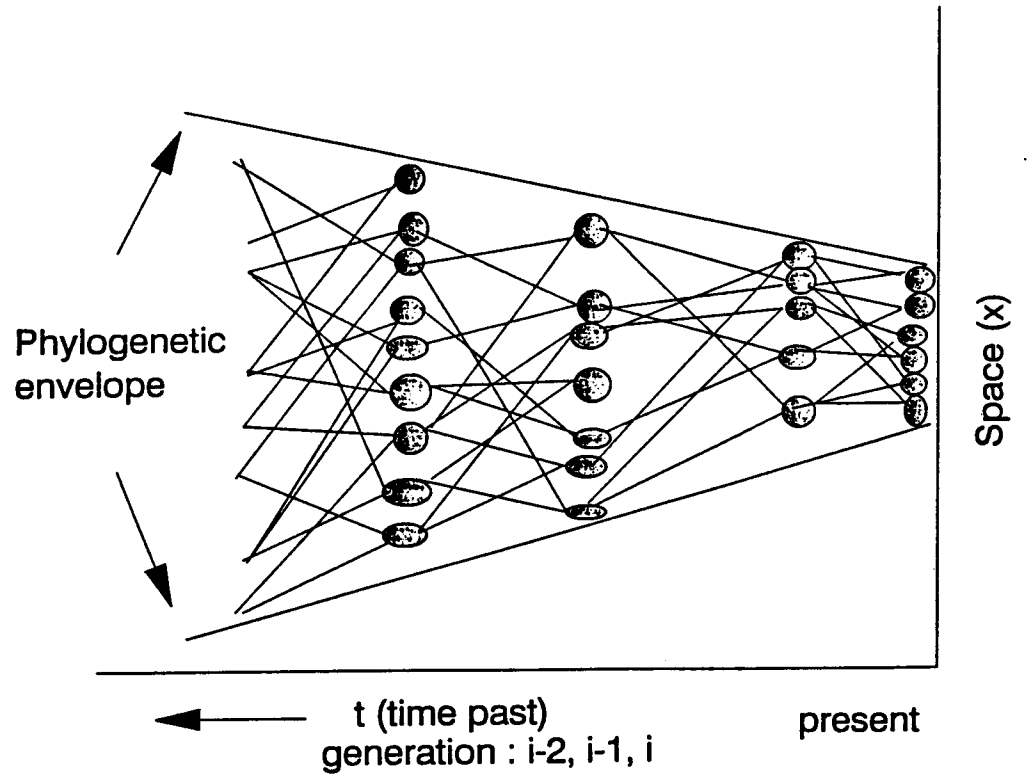
Figure 6. The phylogenetic web in a space-time diagram. In a diploid population with discrete generations, every freshly created zygote has a spatial position, indicated by open circles against the right-hand axis. Each individual descends from two parents, whose own spatial positions at the time of their birth are indicated by open circles one generation past. This graphical depiction of the phylogenetic web that actually progenerated the current population can be iterated as many generations into the past as seems useful. The outer boundary of this web in the space-time plot is called the "phylogenetic envelope."
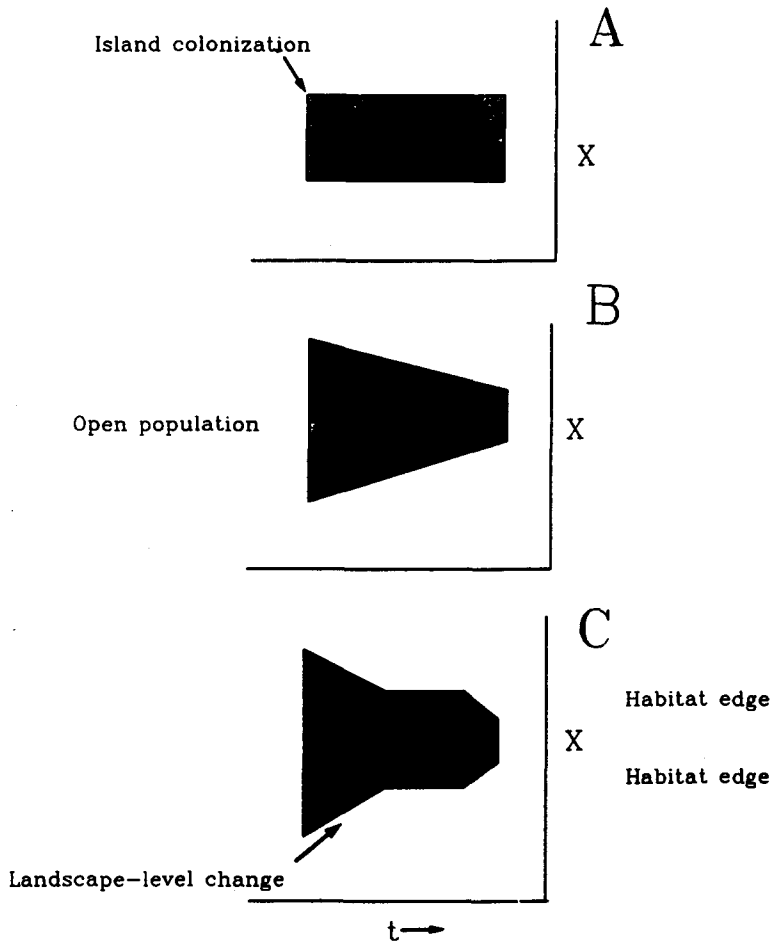
Figure 7. Examples of phylogenetic envelopes. (A) Panmictic population on a homogeneous, oceanic island. Following the initial colonization episode, there is no further dispersal from outside, and the spatial domain of the current population describes that of all ancestral populations, post-colonization. (B) Open population of low vagility on homogeneous portion of a large continent. The ancestors of the current population came from a much larger spatial expanse than contained in that population, and the spatial expanse of that ancestry increases with increasingly distant (in time) ancestors. (C) Open population of low vagility in heterogeneous landscape, which itself changes over a long time scale. As in (B), over a short time scale the spatial extent of the local population's ancestry increases. But this reaches an asymptote at a level set by discrete boundaries between different habitat types (e.g., an island of forest in a sea of prairie). Over still longer time scales, the forest itself moves on the landscape, and was part of a larger contiguous block at some time in the past. Hence, ancestors of the current population may be drawn from a large spatial domain at some sufficiently long temporal scale.

germane to interpreting that population's evolution (except insofar as it influences temporal trends in the local environment).

If the upper boundary of the phylogenetic envelope is steep (Figure 7b), the ancestors of the current population will have been drawn from widely scattered localities. This in effect implies that there is substantial gene flow among populations. This has a number of potentially important implications. First, the population size that is relevant in models of neutral evolution will be somewhat larger than the local population size (Kimura 1983), allowing more variation to be maintained locally than in a similar, isolated population. Second, if the local selective environment differs from the average environment inhabited by the ancestors of the local population, the average phenotypes in the population are likely to be displaced from the local selective optima (or ESSs). In other words, the spatial scale defining the local "population" is too small to gauge accurately the action of natural selection on phenotypic evolution.

Patchiness typically leads to spatial variation in both density and dispersal rates. An alpine plant, for instance, may have reasonable rates of dispersal and high abundances within large patches of alpine tundra, but low abundance and dispersal rates between such patches. This leads to an envelope with a steep slope at low temporal scales that levels off at longer scales (Figure 7c). But at yet longer scales, climatic variation may have led to shifts in entire vegetation zones, so that today's isolated tundra patches are remnants of a much larger past area of tundra; hence the ultimate ancestors of a local population may have been drawn from a much larger area.

The effect of patchiness on gene flow and selection is governed crucially by the temporal stability of patches. Broadly speaking, if a landscape of habitable patches surrounded by an inhospitable matrix is temporally stable (so that within-patch carrying capacities are constant), dispersal tends to be disadvantageous. This leads to a low rate of gene flow and should allow the population to adapt more precisely to local environmental idiosyncrasies. However, if a genetic variant appears in one local population that potentially is advantageous in all, the patchy distribution of the species and the low rate of dispersal between patches slows down the rate at which this allele reaches fixation in the species as a whole. Patchiness thus has opposing effects on local versus species-wide adaptation.

By contrast, if the habitable patches are transient pieces in a shifting mosaic, dispersal is strongly favored. A species occupying transient patches is likely to show frequent local extinctions and recolonizations, which implies that many local populations may ultimately descend from a relatively few ancestral populations. This tends to homogenize the genetic composition of populations (Slatkin 1987). Alleles adapted to particular local environments should have low life expectancies, whereas alleles with species-wide advantages should be able to become fixed relatively quickly.

The effect of spatial variation in the selective environment on adaptive evolution is difficult to gauge in more detail without developing explicit models that specify the nature of the variation and the constraints acting on the character(s) in question. Spatial variation in selection within a population can promote the maintenance of genetic variation if different genotypes are favored in different environments. However, this is easiest to achieve if selection is soft rather than hard (i.e., selections occurs at a life stage different from that at which density-dependence occurs, Jaenike and Holt 1991), and if organisms cannot vary their phenotype plastically to match different environments. Spatial variation in selection between populations can lead to different alleles' being favored in different populations, and a polymorphism will be maintained if dispersal rates are not too great and if spatial variation

in local population density is not large (as with competing species, Levin 1974). Such polymorphisms are vulnerable to invasion by phenotypically plastic strategies that exhibit the "best" phenotype in each environment.

In an ecological community, different local populations are likely to exhibit different phylogenetic envelopes. Those populations descending from a long line of resident, ancestral populations are more likely to exhibit finely honed local adaptation than populations recently derived from a melange of spatially separated ancestral populations.

Ideally, one should add other dimensions to these figures in order to characterize the abiotic and biotic factors that influence population growth rates and fitness in this lineage. For the reasons sketched above, organisms within a species x spatial units apart are more likely to inhabit more similar environments than two randomly placed sample points, and this will be expressed to different degrees in different species.

The phylogenetic envelope describes the appropriately biased sample of the environment needed for an analysis of microevolution relevant to a defined local population or species. One could in principle carry out the spectral analysis sketched in Figure 1, for a weighted space-time sample, where the weights are simply the actual occurrence of a species in given environments leading to species-specific Stommel diagrams. Because of range shifts, habitat selection, etc., variance peaks in the general physical spectrum might not correspond to peaks in the spectrum as experienced by a particular phylogenetic lineage. Species assemblages are highly variable in space and time, and biotic components of the selective regime are likely to be similarly variable for any particular species. But different species are likely to experience quite different spatiotemporal patterns of variability in biotic components of selection.

Just as species richness is likely to show peaks on a Stommel diagram, so should intraspecific variability (e.g., as measured by mean heterozygosity, or the additive genetic variance for a quantitative character). If an entire species goes through a bottleneck on a long-time scale (e.g., due to glaciation), variance should be depleted shortly after the bottleneck and cumulate up to the next bottleneck, so there will be a variance peak at this time-scale. It would be particularly interesting to compare Stommel diagrams for species richness and for intraspecific genetic variation.

Macroevolutionary Consequences

So far, patchiness has been shown to affect ecological processes as well as microevolutionary change in both marine and terrestrial systems. In this section we are concerned with patchiness as it affects the origin and subsequent evolutionary changes in the biological properties of an existing higher taxon. In particular, we will propose that differences in physical and biotic scales of variability among systems (terrestrial and marine in particular) not only promote ecological differences or the prevalence of different adaptive strategies among them, but are capable of giving rise to different macroevolutionary dynamics. This is an inquiry into the mechanisms responsible for the transmission of change from ecological to microevolutionary up to macroevolutionary scales.

For ecological phenomena, patchiness expresses itself as affecting persistence and distribution of local species populations (e.g., Kareiva 1990, Hassell 1991), whereas for macroevolutionary phenomena, heterogeneity, represented by major environmental changes and disturbance events, affects extinction and diversification rates of taxa, giving rise to patterns of taxonomic diversity over the Phanerozoic (Benton 1988, Knoll 1991, Raup and

Sepkoski 1984, Valentine and Jablonski 1983b). It is apparent that the effect of patchiness at ecological, spatial, and temporal scales differs from that at macroevolutionary scales, but they are intimately related. In the following paragraphs we elaborate on such a relationship in the context of organism responses to patchy environments.

The link between ecological and evolutionary dynamics can be exemplified by taking, as a starting point, a simple single-species metapopulation model proposed by Levins (1969) to study the extinction of species by way of the dynamics of the extinction and founding of its local populations:

$$dp/dt = mp (1 - p) - ep \qquad (1)$$

where (p) represents the proportion of patches occupied, (m) is the colonization rate of empty patches and (e) is the extinction rate of occupied patches (for further elaboration of this model see Hanski 1982, 1991; Gotelli 1991). From this model it is readily apparent that taxa with different colonization or extinction rates will be characterized by different metapopulation dynamics, giving rise to contrasting patterns of local, regional, and global extinction and diversification. Under this scenario, a large-scale irreversible shift in landscape heterogeneity could increase the extinction or colonization rate of a particular group of species, thus affecting both their local population persistence and the extinction probability of their lineage over evolutionary time. The above example stresses that adaptations to cope with heterogeneity in ecological timeframes are also relevant for understanding patterns arising at the macroevolutionary level. For example, ecological requirements related to habitat or resource use are known to be correlated with speciation and extinction rates within a lineage (Rensch 1959, Eldredge 1979). In particular, generalist species capable of using different resources in alternative environments (such as a lineage might encounter through time) or specialist species whose resource patches are abundant, widespread, and persist through time, are subjected to less directional selection, and their lineages to low speciation and extinction rates, as exemplified for African large mammals (Vrba 1980, 1987). Within a species' geographic range, spatial heterogeneity in the environment provides the template for the kind of population structure envisioned by Levins (1969); a necessary condition for the effective action of processes responsible for the origination of higher taxonomic units as envisioned by the shifting-balance theory of evolution (e.g., Wright 1982).

Dispersal and life history traits are known to be important in affecting ecological and macroevolutionary dynamics in both terrestrial and marine environments. Dispersal capabilities, hence propensity to isolation of local populations, affect speciation rate. Dispersal is an axis along which it is possible to gain insights into the differences between terrestrial and marine ecosystems. In particular, the capability of long distance dispersal in most marine organisms, usually related to hydrodynamic phenomena, contrasts with the limited dispersal of most terrestrial species. Long-distance dispersal in marine systems prevents genetic tracking of local biological changes that might otherwise result in high isolation and subsequent speciation. In fact, terrestrial mammal speciation rates are seven or more times higher than those of Late Tertiary bivalves (Stanley 1973). Additionally, within marine systems, variation among species with regard to modes of dispersal and larval characteristics greatly influence speciation/extinction dynamics (for a review, see Jablonski and Lutz 1983). For example, it is known that weak dispersal in marine gastropods that lack planktotrophic larvae results in narrow geographic ranges, and consequently in higher rates of extinction as well as of speciation. In contrast, species with planktotrophic larvae generally have low extinction rates

and low speciation rates (Valentine and Jablonski 1983a,b). Thus dispersability and related life history traits are strongly correlated with patterns arising at macroevolutionary level and also affect ecological time processes related to local and regional persistence of populations in patchy environments.

At large spatial and temporal scales, distinct patterns of environmental heterogeneity will promote selective extinction and diversification of particular taxa with different ecological and life history traits. A good example comes from pelagic ecosystems, where macroevolutionary trends have been driven by changes in the circulation patterns throughout the world's oceans, affecting the vertical and horizontal heterogeneity of the environment due to changes in temperature gradients over large spatial scales. Those changes have regulated species dynamics by fostering episodes of proliferation and extinction of species with different life history strategies and trophic relations within pelagic ecosystems (see Lipps 1986 for a review). It would be of great interest to compare macroevolutionary patterns of extinction and diversification of taxa for ecosystems that differ in terms of spatial and temporal variability in the environment (e.g., deep-sea benthic vs. terrestrial vs. pelagic marine) as shown for Stommel diagrams (Figure 2). Unfortunately, the vagaries of the fossil record for some systems, and the difficulties in correlating marine and non-marine stratigraphic sequences, make these comparisons difficult. However, their relevance to understanding current patterns of taxonomic diversity among ecosystems (e.g., Ray and Grassle 1991) makes these comparisons worth pursuing.

Finally, it is worth mentioning that patches are not necessarily restricted to landscape-level heterogeneity but can also be discerned at larger spatial scales. Depending on the scale of resolution, terrestrial and marine systems could be thought of as two large patches with different patterns of variability giving rise to different macroevolutionary dynamics (Boucot 1983, Benton 1988). The same is true for continental biomes, and major oceanographic systems (e.g., Westrop 1991). At larger spatial scales, the dynamics of fragmentation and connection that patches such as seas and continents underwent during the Phanerozoic have been an important determinant of clade diversity through time (e.g., Flessa and Sepkoski 1978). Further, dispersal and isolation within landmasses and seas, through the creation of corridors and barriers, respectively, have dramatically affected the composition of actual biotas and the subsequent history of ecological interactions (e.g., The great American biotic interchange, see Stheli and Webb 1985, Vermeij 1991).

The Stommel diagram teaches us that patchiness affects biological phenomena across a continuum of spatial and temporal scales. Environmental variability affects ecological dynamics at the population, community, and landscape levels, as well as micro and macroevolutionary change. We believe that more effort must be directed to questions emphasizing the connection between processes operating at different time and spatial scales, with special concern directed to the relationship between ecology and macroevolution.

PERSPECTIVES AND CONCLUSIONS

Spatial heterogeneity and temporal variability have far-reaching ecological and evolutionary consequences. In particular, different patterns of spatiotemporal variability in terrestrial as compared to marine ecosystems may not only affect the prevalence of distinct life history strategies among the organisms that inhabit them, but may also afford different macroevolutionary patterns. The same is true when we consider systems within marine or terrestrial environments, such as terrestrial biomes or pelagic vs. benthic marine systems. One

way to assess the spatial and temporal variability that characterize a system is through Stommel diagrams, which depict the relevant spatial and temporal scales across which the variance in a particular physical or ecological variable is distributed. Although they are constrained in terms of precision at large temporal and spatial scales, their utility in describing the spatiotemporal variability of systems, at those scales that are logistically feasible, has not been fully appreciated.

Comparative studies regarding regional and local persistence of populations in patchy environments that focus on organisms with different life histories, ecological requirements, and body size are badly needed for a better understanding of the extinction processes in both ecological and evolutionary time. A comparative metapopulation biology is required, which would provide a tool to reveal new patterns and deeper insights into the processes of extinction and microevolutionary change, and how they relate to patterns of environmental heterogeneity.

A closer interaction between theoretical and empirical approaches is crucial in addressing patchiness phenomena (e.g., Moloney et al., in press). As recently pointed out by Kareiva (1990), to say that spatial heterogeneity has important consequences for population dynamics and species interactions may appear so obvious to the field ecologist as to be trite. Indeed, a vast number of theoretical studies (reviewed above and elsewhere in this volume) underscoring this point have accumulated over recent years. Yet this large body of theoretical work has not been met with a commensurate amount of experimental work; predictions of the consequences of spatially heterogeneous environments to the population dynamics of plants and animals have largely remained untested. Kareiva (1990) bemoaned this point, citing only one marine and three terrestrial field studies employing experimental manipulations of habitat subdivision. (Indeed, it may be of interest that the single marine study was the only one to fail to detect an effect of habitat subdivision.) This is clearly an area that would benefit from further work, be it in terrestrial or marine ecosystems, although overcoming the formidable logistical constraints of performing experimental manipulations in the pelagic realm remains particularly challenging.

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