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THE PROBLEM OF PATTERN AND SCALE IN ECOLOGY

THE ROBERT H. MACARTHUR AWARD LECTURE
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by

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Abstract. It is argued that the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology. Applied challenges, such as the prediction of the ecological causes and consequences of global climate change, require the interfacing of phenomena that occur on very different scales of space, time, and ecological organization. Furthermore, there is no single natural scale at which ecological phenomena should be studied; systems generally show characteristic variability on a range of spatial, temporal, and organizational scales. The observer imposes a perceptual bias, a filter through which the system is viewed. This has fundamental evolutionary significance, since every organism is an "observer" of the environment, and life history adaptations such as dispersal and dormancy alter the perceptual scales of the species, and the observed variability. It likewise has fundamental significance for our own study of ecological systems, since the patterns that are unique to any range of scales will have unique causes and biological consequences.

The key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns. Typically, these mechanisms operate at different scales than those on which the patterns are observed; in some cases, the patterns must be understood as emerging from the collective behaviors of large ensembles of smaller scale units. In other cases, the pattern is imposed by larger scale constraints. Examination of such phenomena requires the study of how pattern and variability change with the scale of description, and the development of laws for simplification, aggregation, and scaling. Examples are given from the marine and terrestrial literatures.

Key words: heterogeneity; patchiness; pattern; scale; variability.

INTRODUCTION

Choosing the topic of this lecture was a difficult experience. The occasion was a unique opportunity to advance a personal view of the most fascinating questions in ecology, and several themes seemed appealing. First and foremost, since the lecture honors the contributions of Robert MacArthur, it seemed fitting to discuss the role of theoretical ecology: its historical roots, the influence of MacArthur in transforming it, and how it has changed in the years since his death. For one committed to demonstrating the importance of theory as an essential partner to empiricism, this challenge seemed almost a mandate.

However, another topic that has occupied much of my attention for the past decade seemed equally compelling: the interface between population biology and ecosystems science. The traditions in these two subdisciplines are so distinct that few studies seem able to blend them. Conservation biology and ecotoxicology manage to span the middle ground; but the chasm between evolutionary biology and ecosystems science is a wide one, and there is little overlap between the two in journals or scientific meetings. Yet neither discipline can afford to ignore the other: evolutionary changes take place within the context of ecosystems, and an evolutionary perspective is critical for understanding organisms' behavioral and physiological responses to environmental change. Furthermore, cross-system patterns that make the study of ecosystems more than simply the accumulation of unrelated anecdotes can only be explained within a framework that examines the evolutionary forces that act upon individual populations (e.g., MacArthur 1968, Orians and Paine 1983, Roughgarden 1989). The importance of bringing these two schools of thought together should be universally attractive.

Other topics also presented themselves as candidate themes: the interface between basic and applied science, the dynamics of structured populations, life history responses to variable environments, diffuse coevolution, the development of ecological pattern, metapopulations, and the problem of scale. Indeed, as I looked back over my career, which had included flirtations with each of these problems, I was struck by what a patchwork it seemed. What was the thread, if any, that had guided my wanderings? In retrospect, it became clear that a fascination with scale had underlain of all these efforts; it is, I will argue, the fundamental conceptual problem in ecology, if not in all of science.

Theoretical ecology, and theoretical science more generally, relates processes that occur on different scales of space, time, and organizational complexity. Understanding patterns in terms of the processes that produce them is the essence of science, and is the key to the development of principles for management. Without an understanding of mechanisms, one must evaluate each new stress on each new system de novo, without any scientific basis for extrapolation; with such understanding, one has the foundation for understanding and management. A popular fascination of theorists in all disciplines, because of the potential for mechanistic understanding, has been with systems in which the dynamics at one level of organization can be understood as the collective behavior of aggregates of similar units. Statistical mechanics, interacting particle systems, synergetics, neural networks, hierarchy theory, and other subjects all have concerned themselves with this problem, and I shall direct considerable attention to it in this paper.

Addressing the problem of scale also has fundamental applied importance. Global and regional changes in biological diversity, in the distribution of greenhouse gases and pollutants, and in climate all have origins in and consequences for fine-scale phenomena. The general circulation models that provide the basis for climate prediction operate on spatial and temporal scales (Fig. 1) many orders of magnitude greater than the scales at which most ecological studies are carried out (Hansen et al. 1987, Schneider 1989); satellite imagery and other means of remote sensing provide spatial information somewhere in between the two, overlapping both. General circulation models and remote sensing techniques also must lump functional ecological classes, sometimes into very crude assemblages (e.g., the "big leaf" to represent regional vegetation), suppressing considerable ecological detail. To develop the predictive models that are needed for management, or simply to allow us to respond to change, we must learn how to interface the disparate scales of interest of scientists studying these problems at different levels.

To scale from the leaf to the ecosystem to the landscape and beyond (Jarvis and McNaughton 1986, Ehleringer and Field, *in press*), we must understand how information is transferred from fine scales to broad scales, and vice versa. We must learn how to aggregate and simplify, retaining essential information without getting bogged down in unnecessary detail. The essence of modeling is, in fact, to facilitate the acquisition of this understanding, by abstracting and incorporating just enough detail to produce observed patterns. A good model does not attempt to reproduce every detail of the biological system; the system itself suffices for that purpose as the most detailed model of itself. Rather, the objective of a model should be to ask how much detail can be ignored without producing results that contradict specific sets of observations, on particular scales of interest. In such an analysis, natural scales and frequencies may emerge, and in these rests the essential nature of the system dynamics (Holling 1992).

The reference to "particular scales of interest" emphasizes a fundamental point: there is no single "correct" scale on which to describe populations or ecosystems (Greig-Smith 1964, Steele 1978, 1989, Allen and Starr 1982, Meentenmeyer and Box 1987, Wiens

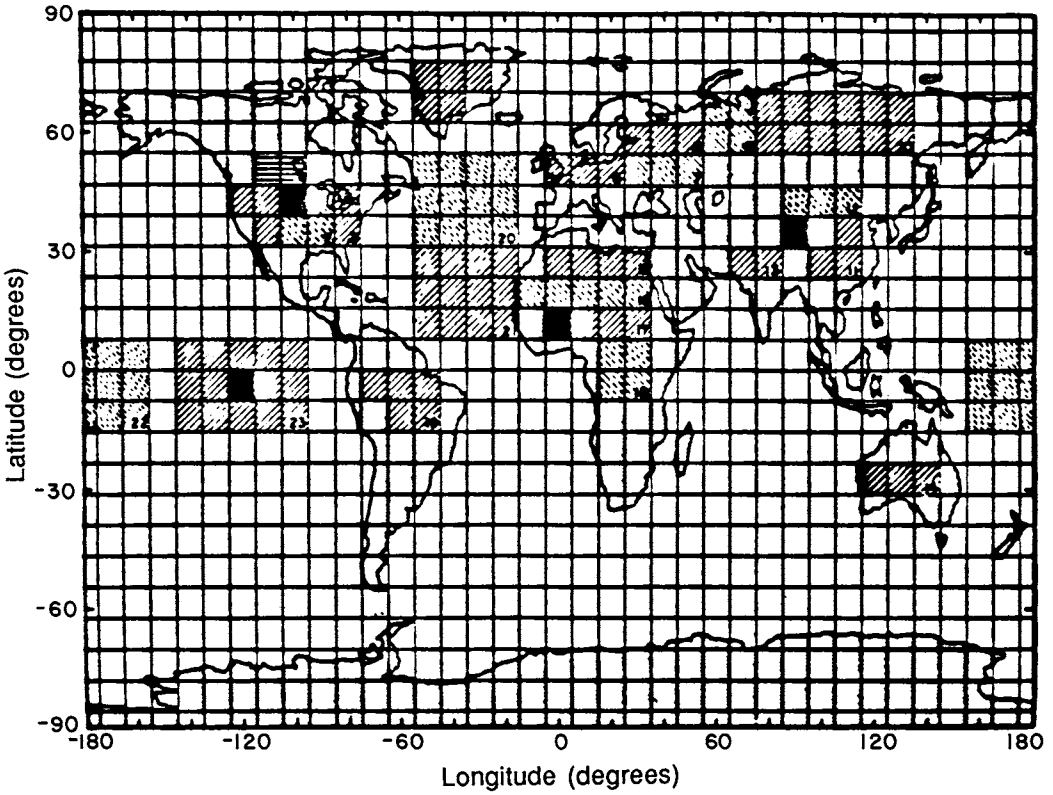

FIG. 1. Typical 10° grid for general circulation models (from Hansen et al. 1987). Current models allow much higher resolution, but still much coarser than typical scales of ecological investigation.

1989). Indeed, as I shall discuss in the next section, the forces governing life history evolution, shaped by competitive pressures and coevolutionary interactions, are such that each species observes the environment on its own unique suite of scales of space and time (see, for example, Wiens 1976). Moreover, the attention in the evolutionary literature to the distinction between diffuse and tight coevolution (e.g., Ehrlich and Raven 1964, Feeny 1976, 1983) makes clear that this point extends to biotic complexity as well. Where the linkage between species is tight, coevolutionary responses typically are species specific. On the other hand, where species interact weakly with large collections of other species, the biotic scale of evolutionary change is much broader and more diffuse.

Even for a given species, some evolutionary responses will be to a narrow range of environmental influences, and others will be diffusely linked to a broad range of influences. Indeed, as I shall discuss later in this paper, the distribution of any species is patchy on a range of scales, and different evolutionary forces will act on those different scales. Specific coevolutionary interactions can be intense on certain scales and not on others, because of the match or mismatch of species distributions; even intraspecific density dependence will vary with scale, and this effect will be exaggerated for interspecific interactions (Wiens 1986, Wiens et al. 1986, Sherry and Holmes 1988).

THE EVOLUTION OF LIFE HISTORY PHENOMENA

When we observe the environment, we necessarily do so on only a limited range of scales; therefore, our perception of events provides us with only a low-dimensional slice through a high-dimensional cake. In some cases, the scales of observation may be chosen deliberately to elucidate key features of the natural system; more often (Fig. 2), the scales are imposed on us by our perceptual capabilities, or by technological or logistical constraints (Steele 1978). In particular, the observed variability of the system will be conditional on the scale of description (Stommel 1963, Haury et al. 1978; Fig. 3).

All organisms face the same dilemma: for particular life history stages, the realized environmental variability will be a consequence of the scales of experience. Various life history adaptations, such as dispersal, dormancy, and iteroparous reproduction, have the effect of modifying the scales of observation, and hence the realized variability. For example (Schaffer 1974), the evolution of reproductive schedules and energy allocation will depend on the relative degrees of uncertainty experienced by juveniles vs. adults, which experience the environment on different scales.

In the case of dispersal or dormancy, the dispersion of a genotype in space or time has the advantage of

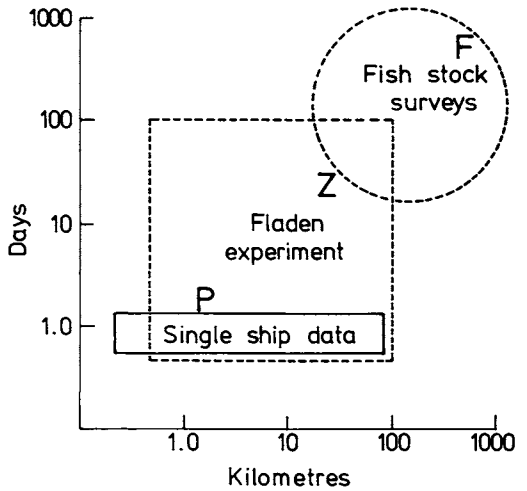

FIG. 2. The limitation of sampling programs to provide information on particular scales of space and time (from Steele 1978). F = fish; Z = zooplankton; P = phytoplankton.

"spreading the risk" (den Boer 1971, Reddingius 1972), converting a geometric mean of variation into an arithmetic mean (e.g., Strathmann 1974) and thereby reducing the variability faced by the subpopulation of individuals that share that genotype. (Of course, the potential is substantial here for parent–offspring conflict.) Environmental variability drives the evolution of such life history traits; these, in turn, modify the scale of experience, and hence the observed environmental variability. Since variability is not an absolute, but only has meaning relative to a particular scale of observation, the interaction of dispersal, dormancy, and similar traits can best be thought of in terms of coevolutionary processes between an organism and its environment. The consequence of differential responses of species to variability is a partitioning of resources, and enhanced coexistence.

The linkage between dispersal and dormancy, as ways to deal with environmental variability, can be explored theoretically. In Levin et al. (1984) and Cohen and Levin (1987), a theoretical model is developed for determining evolutionarily stable dispersal and dormancy strategies for annual plants, in relation to environmental variability; similar models for dispersal were discussed earlier by Hamilton and May (1977). Not surprisingly (Fig. 4), increasing environmental variability selects for higher rates of dispersal; analogous results were obtained for dormancy (e.g., Ellner 1985*a*, *b*, Cohen and Levin 1987). Furthermore, in the presence of dormancy, selection for dispersal is reduced (Fig. 5), and vice versa. When one considers both strategies simultaneously (Fig. 6), tradeoffs become evident; dispersal and dormancy are alternative ways to reduce the experienced variability, and selection for one reduces the selective pressure on the other because it changes the scale at which the environment is observed. Such theoretical predictions are borne out by data for a range of plant species (Werner 1979, Venable and Lawlor 1980).

In describing natural phenomena, we typically invoke a similar approach. At very fine spatial and temporal scales, stochastic phenomena (or deterministically driven chaos) may make the systems of interest

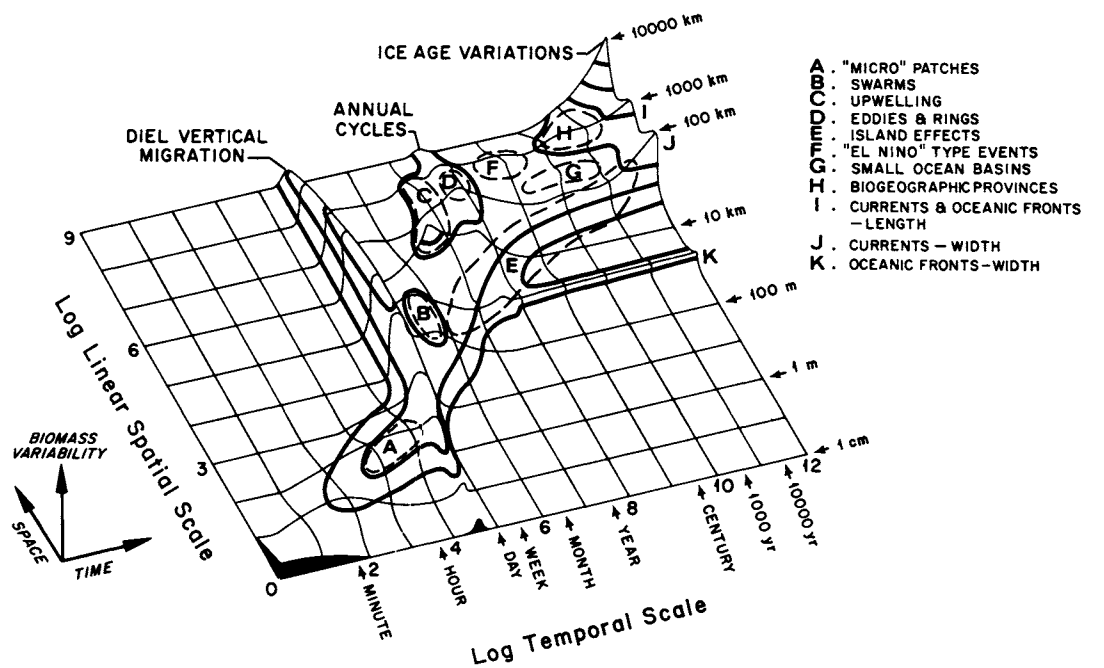

FIG. 3. Stommel diagram of spatial and temporal scales of zooplankton biomass variability (from Haury et al. 1978).

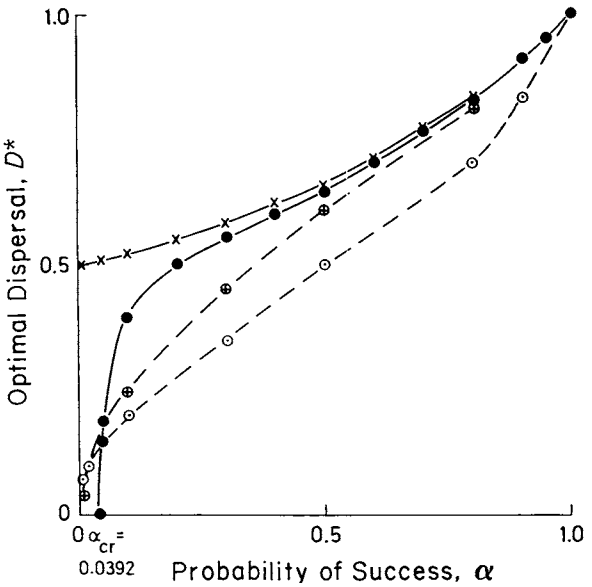

FIG. 4. Evolutionarily stable dispersal fractions for annual plants, for differing patterns of temporal environmental variation (from Levin et al. 1984). α = probability of success in finding new site; α_{cr} = critical value of α.

unpredictable. Thus we focus attention on larger spatial regions, longer time scales, or statistical ensembles, for which macroscopic statistical behaviors are more regular. This is the principal technique of scientific inquiry: by changing the scale of description, we move from unpredictable, unrepeatable individual cases to collections of cases whose behavior is regular enough to allow generalizations to be made. In so doing, we trade off the loss of detail or heterogeneity within a group for the gain of predictability; we thereby extract and abstract those fine-scale features that have relevance for the phenomena observed on other scales. In physics, this tradeoff is well studied, and goes to the heart of the problem of measurement (see, for example, Heisenberg 1932, Planck 1936). At fine scales, quantum mechanical laws must replace classical mechanical laws; laws become statistical in character, dealing only with probabilities of occupancy.

In population genetics, the same problem arises, and the same tradeoffs occur. Focusing on alternative definitions of fitness, Dawkins (1982) points out the tradeoffs, for example, among classical fitness, focusing on the unique properties of an individual; phenotypic measures that lump individuals together based on common phenetic traits; and genotypic measures that form even larger ensembles, for example by grouping all individuals together who carry a particular gene. As one moves up the hierarchy to larger and larger aggregates, one obtains more statistical predictability, while sweeping under the rug details of variation within an aggregate. Quantitative genetic approaches to evolution are based on a similar rationale.

The existence of these tradeoffs makes clear that there is no natural level of description: however one defines classes, there will be differential evolution among classes, and differential evolution within. Similar comments apply to the subdivision of a population, for theoretical analysis, say into trait groups (Wilson 1983) or epidemiological risk groups (Castillo-Chavez et al. 1989), or to any conceptualization of the population as metapopulation (Wright 1977, 1978, Gilpin and Hanski 1991). The interplay among different levels of selection presents one of the key conceptual problems in evolutionary biology (Eldredge 1985). Here, as in more strictly ecological settings (O'Neill et al. 1986), the problem is not to choose the correct scale of description, but rather to recognize that change is taking place on many scales at the same time, and that it is the interaction among phenomena on different scales that must occupy our attention.

PATTERN FORMATION

The concepts of scale and pattern are ineluctably intertwined (Hutchinson 1953). The description of pattern is the description of variation, and the quantification of variation requires the determination of scales. Thus, the identification of pattern is an entrée into the identification of scales (Denman and Powell 1984, Powell 1989).

Our efforts to develop theories of the way ecosystems or communities are organized must revolve around attempts to discover patterns that can be quantified within systems, and compared across systems. Thus, there has been considerable attention directed to techniques for the description of ecological or population pattern (Burrough 1981, Gardner et al. 1987, Milne

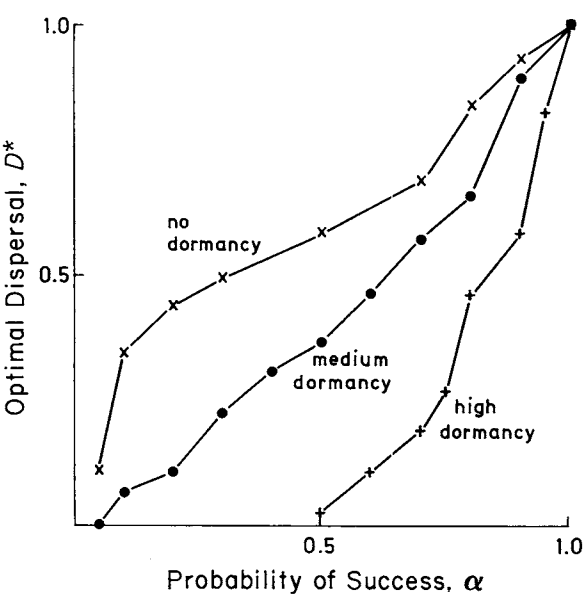

FIG. 5. Effects of dormancy on evolutionarily stable dispersal fractions (from Levin et al. 1984). α = probability of success in finding a new site.

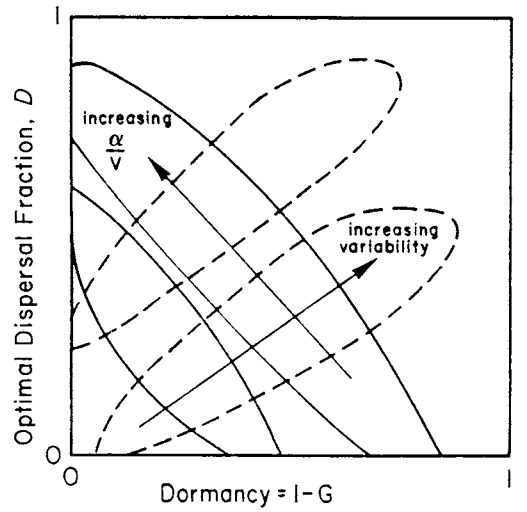

FIG. 6. Tradeoffs between evolutionarily stable dispersal fraction D and evolutionarily stable dormancy fraction (1 − G). α = probability of surviving dispersal episode, V = probability of surviving (1 yr) dormancy. Increasing variability selects for both; at given levels of variability, tradeoffs exist between dispersal and dormancy, with balance determined by α/V (from Cohen and Levin 1987).

1988, Sokal and Oden 1978, Sugihara et al. 1990). Once patterns are detected and described, we can seek to discover the determinants of pattern, and the mechanisms that generate and maintain those patterns. With understanding of mechanisms, one has predictive capacity that is impossible with correlations alone.

In developmental biology, considerable theoretical interest has been directed to the problem of how the predictable morphologies that are the defining characteristics of organisms develop from initially undifferentiated eggs. Early models, involving gradients of chemicals (morphogens) that carry the information guiding development, were shown by Turing (1952) to lead to symmetry-breaking, provided there were present both activator and inhibitor species, and provided the diffusion of the inhibitor was much more rapid than that of the activator. Under suitable conditions (Segel and Levin 1976), the destabilized uniform distributions give way to stable nonuniform patterns, which can provide the local information that specifies patterns of differentiation. The strengths of this model are that it requires no genetically determined blueprint, and through purely local interactions can give rise to almost every conceivable observed pattern (Meinhardt 1982); of particular interest (Murray 1988*a*, 1989) has been the application of these ideas to coat or wing patterns in animals.

However, the demonstration that a specific mechanism can in theory give rise to a range of observed patterns is not proof that that mechanism is indeed responsible for those patterns. In the absence of strong evidence for the existence of morphogens, or for their universal explanatory power, attention has turned to the search for alternative explanations. In recent years, for example, another class of models, involving mechanochemical interactions, has been shown to be equally feasible from a theoretical perspective, and equally flexible in its ability to give rise to patterns (Murray and Oster 1984). There are many roads to Rome; and in general, there will be many conceivable mechanisms that could give rise to any set of patterns. All that theory alone can do is to create a catalogue of possible mechanisms; experiments are then needed to distinguish among the candidate mechanisms. This is a lesson that must be borne in mind also as we consider the problem of pattern formation in ecology.

The problem of ecological pattern is inseparable from the problem of the generation and maintenance of diversity (Levin 1981). Not only is the heterogeneity of the environment often essential to the coexistence of species, but the very description of the spatial and temporal distributions of species is a description of patterns of diversity. Thus, an understanding of pattern, its causes and its consequences, is central to understanding evolutionary processes such as speciation, as well as ecological processes such as succession, community development, and the spread and persistence of species.

In the case of ecological systems, a range of mechanisms exists for generating pattern. Pattern is in part extrinsically determined, and a first step is to identify and factor out such external influences (Denman and

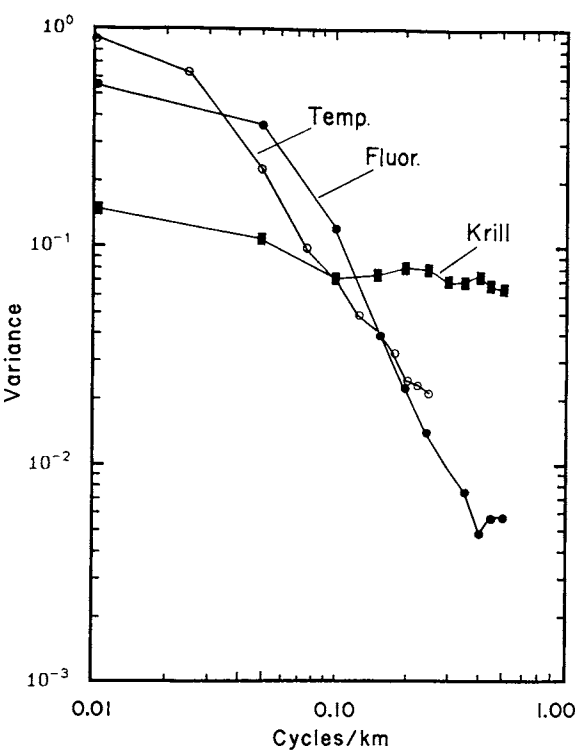

FIG. 7. Variance spectra for temperature, fluorescence, and krill in the Scotia Sea (from Weber et al. 1986).

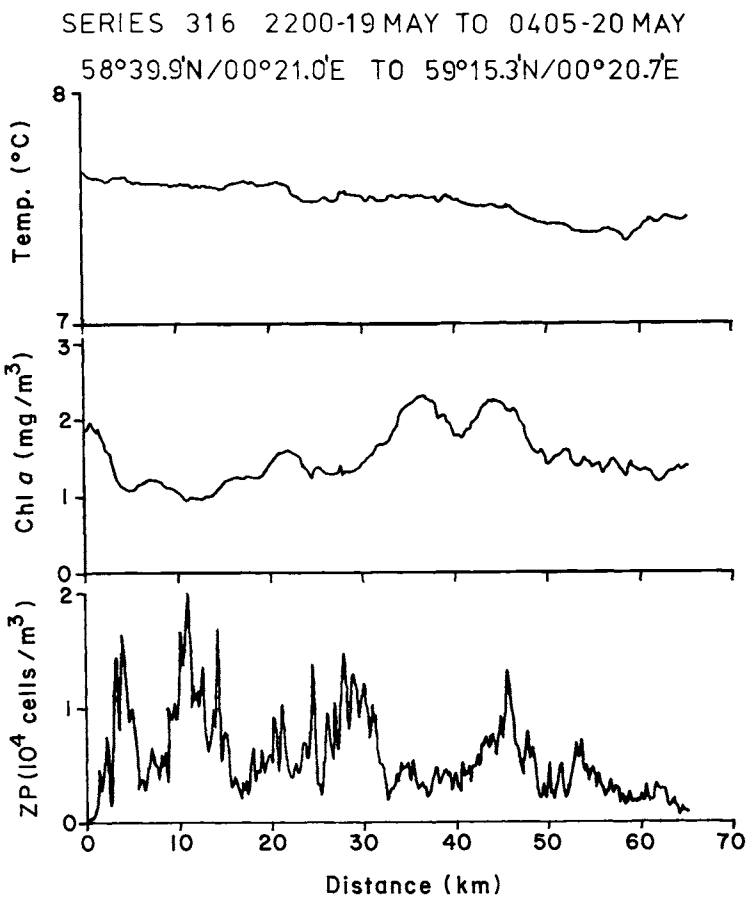

FIG. 8. Temperature, chlorophyll *a* concentration, and zooplankton (ZP) abundance in relation to latitude, for spring transect in North Sea (from Mackas 1977).

Powell 1984). Statistical similarities in the distributions of variables provide a natural place to start, and correlations provide stronger evidence. They do, however, provide only a starting point, and other approaches must be involved for the examination of causation.

For the krill populations of the Southern Ocean, spatial distributions have been shown to be patchy on almost every scale of description. This has fundamental importance both for the dynamics of krill, and for their predator species. Various studies have characterized the Fourier spectrum of variability for krill, and shown that variance decreases with scale (Fig. 7). However, substantial differences exist between the spectra for krill and those for temperature and fluorescence, and these differences are borne out by analysis of the cross correlations (Weber et al. 1986, Levin et al. 1989*b*). On broad scales, temperature (a passive marker of water movements), fluorescence (a measure of phytoplankton activity), and krill all have spectra that are consistent with the theoretical predictions of the Kolmogorov turbulence calculations (Tennekes and Lumley 1972). On fine scales, however, the krill spectrum is noticeably flatter, suggesting that krill are much more patchily distributed than their resource, or than can be explained by water movements alone. This observation is consistent with data of Mackas (1977), who showed more generally that zooplankton populations can exhibit much more fine-scale variation than phytoplankton (Fig. 8). For the krill, this patchiness appears to break down on the finest scales (Levin et al. 1989*b*).

The interpretation of these data is that large patches of krill and phytoplankton are being moved about by water movements, but that on fine scales some other mechanism must be invoked to explain pattern. Thus a two-scale model is needed, and a general lesson learned: no single mechanism explains pattern on all scales. In this case, pattern seems extrinsically driven on broad scales, and autonomously generated on fine scales. The explanation lies in the swimming behavior of krill, to which I shall return.

Similarly, Dayton and Tegner (1984) and Menge and Olson (1990) have discussed the range of scales at which the dynamics of communities are mediated, from biotic processes at the scale of metres to eddies and warm-water intrusions at the scale of tens of kilometres. Dayton and Tegner (1984) argue that "many ecologists . . .

focus on their small scale questions amenable to experimental tests and remain oblivious to the larger scale processes which may largely account for the patterns they study." One can equally point to other examples, however, such as models of general circulation, in which large-scale processes are overemphasized, at the expense of the fine scale. Rothschild and Osborn (1988) show how small-scale turbulence can have effects on predator–prey contact rates, and thus on broader scale dynamics. Butman (1987) discusses elegantly the interplay between small-scale processes such as active habitat selection and large-scale processes such as passive deposition in determining the settling of invertebrate larvae. In general, one must recognize that different processes are likely to be important on different scales, and find ways to achieve their integration (Denman and Powell 1984, Mackas et al. 1985, Levin et al. 1989*b*, Menge and Olson 1990). To date, this program of research has been more successfully carried out in marine than in terrestrial systems, but the situation is changing (Schimel et al. 1990).

For the krill populations of the Antarctic, once extrinsic influences have been subtracted, one still must find ways to explain what maintains fine-scale pattern. A natural first step is to consult the catalogue of ways that pattern can be created and maintained in aquatic systems. A prime candidate is the diffusive instability referred to earlier, in which phytoplankton serve as the activator species, and krill as the inhibitor (see, for example, Levin and Segel 1976). In contrast to other ways in which pattern can be generated, the notion of diffusive instability is well suited to continua such as the open ocean. However, the mechanism relies on the inhibitor (herbivore) species being more diffusive than the activator (resource) species, which will inevitably produce distributions in which the resource, rather than the herbivore, is more patchily distributed; this is inconsistent with observations. Similar objections apply to various alternative explanations, such as those that rely on favorable patches of nutrients (Kierstead and Slobodkin 1953, Okubo 1978, 1980) or physical features such as convective cells or warm core rings.

Fortunately, considerable life history information is available for krill, which are known to aggregate actively into swarms, and indeed into schools (Hamner et al. 1983, Hamner 1984). Using this information, Grünbaum (1992) has developed individual-based models of krill populations, whose collective behavior can give rise to the formation and maintenance of aggregations consistent with those observed. His model, building on earlier work of Okubo (1972) and Sakai (1973), considers both the random and directed forces imposed by the physical and chemical environment, and the behavioral responses of individuals to other individuals. Thus, on the fine scale, the explanation of krill distributions is in the ensemble behavior of individuals acting on even finer scales; on the broad scale, the explanation is in terms of oceanographic processes acting over even broader scales (Hofmann 1988). By interfacing individual-based models with fluid dynamic models, therefore, one seeks to interrelate phenomena acting on different scales; this approach must guide us in dealing with ever more complicated problems, involving wider ranges of scales. The challenges may be more difficult, but the principles are the same.

Patterns of Spread

The effort to explain the distribution of populations in terms of the movements of individuals is an extension of one of the most successful applications of mathematics to ecological phenomena, the use of random walk and diffusion models to describe dispersal. Diffusion approximations to the description of individual movements (the continuum limits of random walk models, with only first- and second-order terms retained) have been employed by biologists for nearly a century, and received considerable attention from population geneticists (Fisher 1937, Dobzhansky and Wright 1943, 1947, Haldane 1948). The basic idea is that, although organisms do not move randomly, the collective behavior of large numbers of such individuals may be indistinguishable (at the scale of the population) from what would result if they did. For example, even when individuals respond deterministically to chemicals or other cues, the presentation of those cues may be effectively random, at least on the perceptual scales of the external observer. Indeed, the philosophy behind the application of models is not that the finer detail does not exist, but that it is irrelevant for producing the observed patterns.

The same rationale is used, for example, to justify the application of the diffusion approach to the flow of heat, or of chemicals, and with the same limitations: the predictions of the models are excellent close to a source, but their validity diminishes as distance from source increases. Furthermore, diffusion models are based on an assumption of random collisions of molecules, which clearly is not technically valid. However, this suppression of detail is the strength rather than the weakness of the approach, because it allows the demonstration that the observed ensemble behavior can be explained entirely without reference to the extra detail. This is the kind of simplification that we must achieve more generally in learning how to connect phenomena on different scales.

The key to understanding how information is transferred across scales is to determine what information is preserved and what information is lost as one moves from one scale to the other. In the case of the diffusion approximation, the notion is that only certain macroscopic statistics of the distribution of individual movements is relevant; more generally, the goal of research into scaling is to discover what the most relevant macroscopic statistics are that inform the higher levels about lower level behaviors.

In the case of the application of random walk models

in ecology, the last 40 yr have seen tremendous activity. The most important paper undoubtedly was that of Skellam (1951), who synthesized the general theory, and anticipated a range of applications that have occupied the attention of researchers since: the spread of pest species, and of colonizing species following climate change; the patchiness of species distributions; and geographical clines. Okubo (1980), in a fascinating book, provides the most complete treatment of the application of diffusion models in ecology, introducing a range of novel applications.

It is perhaps not surprising that generalized diffusion models, incorporating advective movements due to winds, currents, and gravitational forces, work well to describe the passive spread of seeds and pollen (Liddle et al. 1987, Okubo and Levin 1989), or of invertebrate larvae (Hofmann 1988). It may be more surprising, however, that they also work well for organisms that can use detailed environmental cues to direct their movements. In the first rigorous test of the use of such models, Kareiva (1983) released flea beetles on collard plants in one-dimensional habitats, and tested their movements against the predictions of a diffusion model. He later expanded this approach to other phytophagous insects, relying on studies reported in the literature. His conclusions were that the diffusion models provided remarkably good agreement with the observed data in 7 cases out of 11, and were a reasonable first approximation in the other cases. For the latter, a habitat-dependent movement model provided the necessary extra detail. Grünbaum's individual-based models of krill population dynamics are a further application of this approach. Again, the general philosophy is to incorporate a minimum of necessary detail, complicating the model only when necessary. In general, adding more parameters to a model may be expected to give a better fit to observed data, but may result in a less reliable model for prediction (see, for example, Ludwig and Walters 1985).

One of the most powerful applications of the diffusion model has been in dealing with the spread of introduced species. Indeed, this was the application that first captured the attention of population geneticists such as Fisher (1937), interested in the spread of advantageous alleles. By adding a growth process to the diffusion model, Fisher used intuitive arguments to conclude that there would be an asymptotic speed of propagation, equal to twice the square root of the product of the intrinsic rate of increase at low density and the diffusion coefficient; this brilliant insight was confirmed formally by Kolmogorov et al. (1937), and extensions have occupied some of the best efforts of mathematicians since (e.g., Bramson 1983). Skellam (1951) applied the approach to the spread of various species, including oaks and muskrats, and the last decade has seen an increasing attention to the problem (e.g., Lubina and Levin 1988, Murray 1988*b*, Andow et al. 1990) for applications ranging from spores and viruses to invertebrate agricultural pests to vertebrate species such as muskrats and otters. In some cases (Fig. 9), this simple model provides excellent agreement with observed data; in other situations, it can underestimate rates of spread by an order of magnitude. The problem is again one of scale: the spread of organisms is a multistage process involving the establishment of new centers, and the spread from those centers (Fig. 10). Our scale of observation is such that the diffusion model may work very well on the fine scales, but be unable to deal with the broader scales (or at least require a separate parameterization there). The establishment of secondary foci, involving "great leaps forward," requires an extension of the diffusion approximation to include other factors, e.g., higher order moments (Mollison 1977) or Rvachev's intercity models of influenza transmission (Rvachev and Longini 1985).

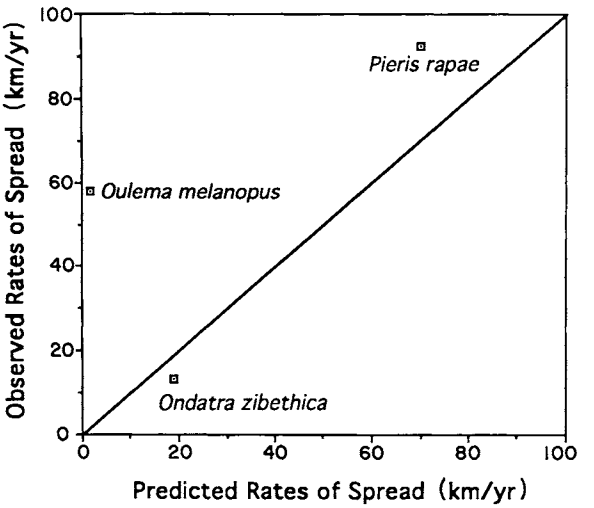

FIG. 9. Predicted and observed rates of spread for three introduced species (data from Andow et al. 1990).

I have described diffusion models in such detail not because they are to be taken as gospel, but because they provide a clear example of a general approach. Various alternatives to diffusion models have been utilized, for example, percolation models to describe the spread (and persistence) of species in fragmented habitats (Durrett 1988, Gardner et al. 1992), or correlated random walks to describe the movement of insects (Kareiva and Shigesada 1983), or the clonal growth of branching organisms (Cain 1990, 1991). All these alternatives attempt to understand behavior at one level in terms of ensembles of units at lower levels. I will take the same approach in this paper as I discuss the dynamics of communities and ecosystems, and potential interactions with global climate systems.

PATTERN AND SCALE IN TERRESTRIAL SYSTEMS

The approach described earlier for aquatic systems can be applied equally to terrestrial systems. Tech-

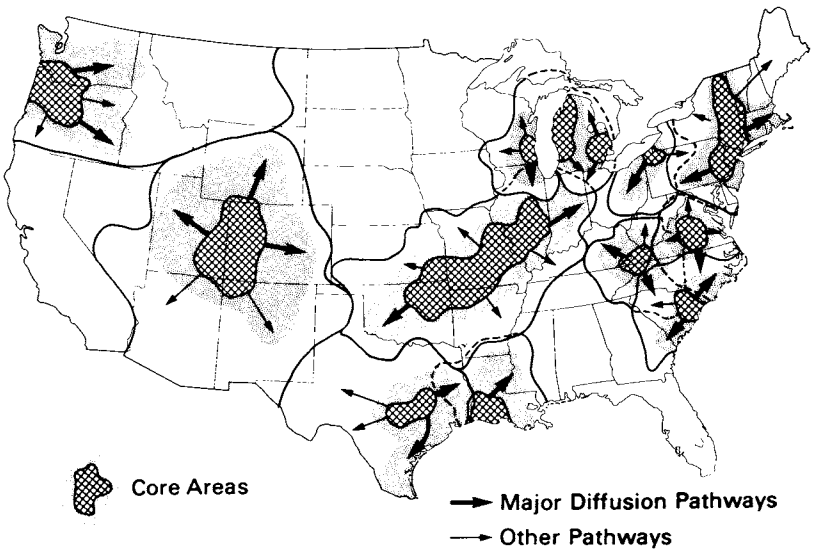

FIG. 10. Patterns of two-level spread of influenza during start of 1967–1968 season (from G. F. Pyle 1982).

niques such as remote sensing, in concert with spatial statistics, can be used to describe the broad-scale distributions of plant species and the factors that might influence them. Theoretical studies, including computer simulations, can be used to bridge to smaller scale experimental studies, to generate and test hypotheses concerning how fine-scale processes interact with those on other scales to produce observed pattern. In this program, it is helpful to have available a suite of models of increasing complexity and detail; in this way, one can strip away detail and explore how much finer scale information is relevant to describing observed pattern at broader scales. At one extreme are models that attempt to capture as much detail as possible, within the constraints imposed by parameter estimation problems; at the other extreme are grossly oversimplified models that retain as few features of the real system as possible, in order to explore systematically and in isolation the influence of particular factors. Combining those simple models to reassemble the ecosystem is the next step, and is analogous to the problem of trying to understand the evolution of populations in terms of the dynamics of individual loci.

A case in point is the quantification of plant competition in terrestrial communities. In a very important series of papers, Pacala and Silander (1985) (see also Pacala 1989) have developed neighborhood models that quantify the competitive influence of plants on each other as a function of the distances between them. That detail certainly determines the microdistribution of plants (see, for example, Lechowicz and Bell 1991); but how much of the detail is relevant to the distribution of species even at the field level, much less at the landscape level? Theoretical explorations of models that incorporate the detail can be helpful; in such work, increasing levels of aggregation are applied while model outputs are compared with field data, to determine what information (if any) at the broad scale is lost as a result of aggregation.

A similar approach is called for when one is dealing with systems in which asynchronized random disturbances play an important role. These clearly include gap phase systems, discussed in detail by A. S. Watt in his presidential address to the British Ecological Society (Watt 1947), and later by Levin and Paine (Levin and Paine 1974, Paine and Levin 1981) for a range of systems, including especially the rocky intertidal. The notions of patch dynamic phenomena introduced in those works have been expanded, developed, and improved in a virtual explosion of studies (see especially Forman and Godron 1981, 1986, Pickett and White 1985), and are closely related to metapopulation ideas that have become so important in evolutionary theory and population biology (e.g., Fahrig and Paloheimo 1988*a*, *b*, Harrison and Quinn 1989, Hastings and Wolin 1989, Gilpin and Hanski 1991). In a novel application of these ideas, McEvoy et al. (1993) have shown how the balance between disturbance, colonization, and successional development is critical to the biological control of ragwort.

In systems in which localized disturbances play an important role, the local dynamics are unpredictable, except in terms of statistical averages over longer time scales. The local unpredictability and variability present opportunities for species that would be eliminated competitively in constant environments, and greatly increase diversity at intermediate levels of disturbance. Indeed, for many species, local unpredictability is globally the most predictable feature of the system (Levin and Paine 1974). As the scale of description is increased beyond the scale of individual disturbances, variability declines, and predictability correspondingly increases.

Levin and Paine (1974), taking the view that the rocky intertidal community can best be understood as a metapopulation of patches, focused on two scales of dynamics. On the large scale, attention was directed to the demography of patches; within patches, a more rapid and smaller scale successional dynamic dominated. Through a modeling approach that explicitly recognized these scales, Paine and Levin (1981) were able to examine the role of disturbance as a structuring agent. Other investigators (e.g., Coffin and Lauenroth 1988, Green 1989, Clark 1991*a*) have subsequently quantified the dynamics of patches in a range of systems, and demonstrated the validity of this approach and the importance of disturbance in maintaining the character of those systems. A similar approach can be taken for the colonization of host patches by parasites, for example plant pathogens or animal parasites (e.g., Holmes 1983).

As I have already discussed, not all systems allow subdivision neatly into hierarchical scales of organization. In the case of a host–parasite system, the units are fairly discrete and distinct; in the case of terrestrial vegetation, the gradations are more like those already discussed for Antarctic krill: patches do not have a narrow range of sizes, but are found across a broad spectrum. That is, patchiness is found on almost every scale of observation. In this case, there is no unique natural scale, even though some scales may provide more natural biological vantage points (e.g., O'Neill et al. 1991*a, b*). One must recognize that the description of the system will vary with the choice of scales; that each species, including the human species, will sample and experience the environment on a unique range of scales; and that, rather than trying to determine the correct scale, we must understand simply how the system description changes across scales. This explains why there has been so much fascination in ecology, as in other fields, with the theory of fractals (Mandelbrot 1977, Sugihara and May 1990), which emphasizes both the scale-dependence of data and descriptions of phenomena, and the more hopeful note that there may be scaling laws.

To begin to address the question of how system description changes with scale for disturbance-mediated systems, Levin and Buttel (1987) used landscape models for a grid in which local growth simulators were linked together through common disturbance, interpatch dispersal, and competition. Earlier models (Levin 1974) assumed local dynamics that were deterministic, in the tradition of Lotka and Volterra, and linked cells together through an interaction matrix describing movement of propagules or individuals. For disturbance-mediated applications, however, local dynamics must incorporate stochastic elements (representing disturbance and colonization events), which may be spatially correlated. The simplest description was through an interacting particle model in which each cell was in one of a small number of successional states. Local state could be altered due to invasion (and capture) by species with later successional characteristics, or by disturbance, which reset cells to the initial state. Dispersal ability was taken to be inversely correlated with competitive ability, and disturbance intensity and frequency tied to the present state of a cell (Levin and Buttel 1987). In particular, later successional stages were susceptible to higher disturbance rates, and those disturbances were allowed to radiate outwards to neighboring cells. Spatial correlations arise in such models due to this latter phenomenon, which resets groups of contiguous cells to the initial successional stage; spatial correlations can also arise due to dispersal among neighboring cells, and due to other influences such as competition.

In homogeneous environments, spatial and temporal variability will be a function of the size of the window used to view the world; as window size is increased, variability will decay. The exact relationship between variability and window size is difficult to predict (see empirical methods, for example, in Kershaw 1957, Cain and Castro 1959, Greig-Smith 1964, Mead 1974), but will be determined by the way spatial correlations fall off with distance (see, for example, Hubbell and Foster 1983, Robertson et al. 1988, Carlile et al. 1989). In general, the relationship will follow a power law within the correlation length of the system (which is determined by such influences as the disturbance size distribution, and the dispersal curve), and then will fall off asymptotically as the inverse of the number of cells in the window. On a log-log plot, this yields a straight line of characteristic slope (usually between 0 and -1) within the correlation length, asymptoting to a slope of minus one (Fig. 11) for very large window sizes; such relationships have been described both for model output (Levin and Buttel 1987) and for data from terrestrial systems (Moloney et al. 1992).

The evidence presented in Fig. 11 supports the view that there is no correct scale for describing the system, that the description of variability is contingent upon the window through which the system is viewed, but that there may be scaling laws that allow one to make comparisons among studies carried out on different scales. These results are reminiscent of similar observations that form the basis of the theory of fractals, and the power law relationships are identical to what is seen in statistical physics, in the study of critical phenomena (Wilson 1983).

The slope of the line in Fig. 11, within the correlation length, is determined by the spatial correlations. With no correlations, one expects the variance to fall off as the inverse of the number of cells, as it does well beyond the correlation length; this would give a slope of minus one in Fig. 11. With perfect spatial correlation, the slope would be zero. Observed slopes typically lie somewhere in between (Levin and Buttel 1987), reflecting the degree of correlation.

Simulation models allow easy exploration of the in-

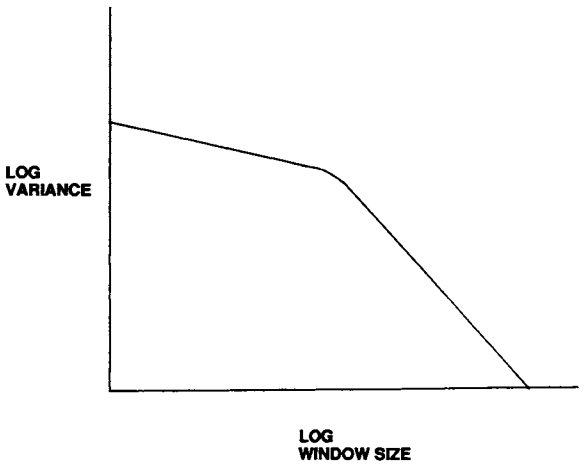

FIG. 11. Theoretical relationship between variance and window size. Within correlation length, characteristic slope reflects rate of decay of correlation with distance; beyond correlation length, −1 slope reflects absence of correlation.

fluence of factors such as dispersal and disturbance in determining the slope, and of biological consequences of disturbance, such as persistence or extinction. The technique is not perfect. As with any such method, it is limited at the fine scale by the minimum size of a cell, and at the broad scale by the extent of the grid.

Theoretical explorations can carry one just so far, and are meant primarily to guide empirical studies. The next stage is to search for such patterns in natural systems, and to use models to explore causes. In the serpentine grassland of Jasper Ridge, California, we (S. A. Levin, with Kirk Moloney and Linda Buttel) in collaboration with Hal Mooney, Nona Chiariello, and others, have sought to understand the dynamics of the vegetation as mediated by soil factors and by the activities of gophers and ants, which disturb the soil and the vegetation (Hobbs and Hobbs 1987, Levin et al. 1989*a*, Hobbs and Mooney 1991, Moloney et al. 1992). Related models have been developed by Coffin and Lauenroth (1989) for the dynamics of the shortgrass prairie. The random disturbance model described above must be modified here, because both the soil factors and the disturbing forces show similar evidence of strong spatial correlations, and the same characteristic curves for the relationship between variance and window: on a log-lot plot, variance falls off linearly, with a characteristic slope, within the correlation length, and with asymptotic slope equal to minus one. These correlating influences add another set to the list of those that can be structuring the vegetation, and the goal of research is to sort out the various influences. In a modeling approach that is an extension of that introduced by Levin and Buttel (1987), we (Levin et al. 1989*a*, Moloney et al. 1992) have focused on four annual grasses in the serpentine, and on the influence of gopher disturbances on their dynamics (Fig. 12). Timing and magnitude of disturbance are both of importance. It is easy to see from such models how some disturbance regions lead to the extinction of particular species, while others maintain coexistence through ergodic spatiotemporal mosaics (Fig. 13). Thus, the simulation model becomes a powerful complement to other experimental techniques.

Similar models are being developed for a forested watershed in northwestern Connecticut, where disturbances create forest gaps. In collaboration with Steve Pacala, John Silander, and Charles Canham, we are utilizing both raster (grid) -based models and vector (individual tree) -based models to explore the consequences of local detail concerning competition regimes. Local growth simulators, extensions of those in wide use in ecology (Botkin et al. 1972, Shugart and West 1981, Shugart 1984, Horn et al. 1989) provide the starting points, and are complemented with models of dispersal and disturbance. In both cases, model output is being interfaced with broader scale information derived from remote sensing and other studies, in work with William Philpot, Kyu-Sung Lee, and David Weinstein. Existing patterns of topography, rainfall, temperature, and soil factors will be analyzed, and compared with distributions in vegetation patterns. Modeling and empirical studies will then be used to explain the variation in vegetation patterns not accounted for by physical factors.

The localized effects of tree gaps, small fires, wave disturbance, or gopher and ant mounds are special cases of situations where systems may be viewed as spatiotemporal mosaics, variable and unpredictable on the

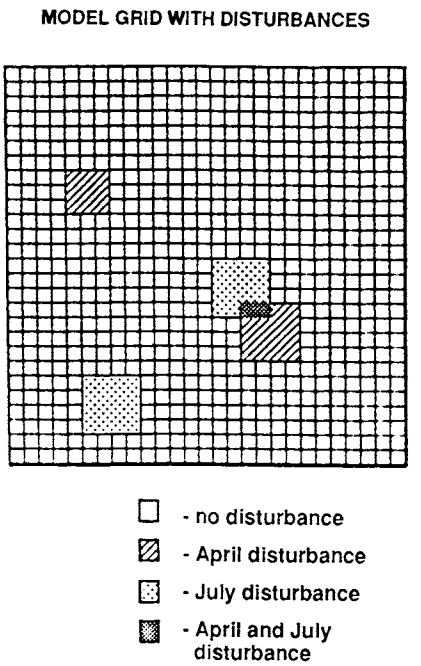

FIG. 12. Basic grid for grassland simulation model (from Levin et al. 1989*a*).

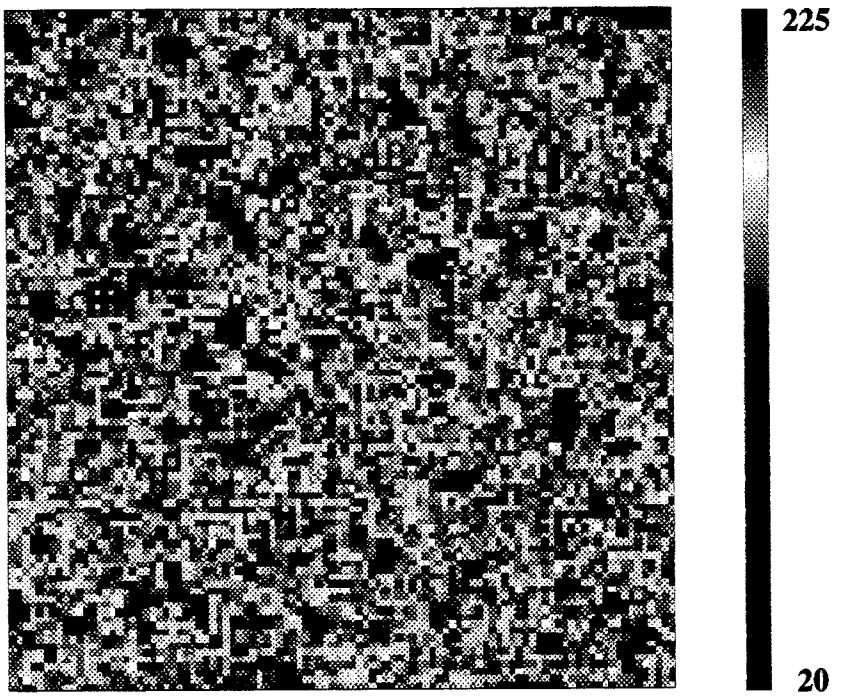

FIG. 13. Sample output from grassland simulation; snapshot of distribution of *Plantago erecta*. Colors denote population levels (see key).

fine scale, but increasingly predictable on large scales (Watt 1947, Levin and Paine 1974, Wright 1974, Minnich 1983, Urban et al. 1987, Clark 1989, 1991*a, b*). For such systems, transient dynamics are often ignored, and steady-state properties treated as the objects of interest. Yet some events have effects on too broad a spatial scale to permit such a perspective; the affected systems do not achieve statistical equilibrium over realistic temporal and spatial scales. In such situations modeling approaches still can be useful in explaining how patterns of spread are mediated at the local level. Models of this sort have been discussed earlier for spread of introduced species, and also have been utilized to study the dynamics of epidemics and forest fires (Cox and Durrett 1988, von Niessen and Blumen 1988).

METAPOPULATION MODELS

One of the most important theoretical contributions of Robert MacArthur was his work with E. O. Wilson in developing the theory of island biogeography (MacArthur and Wilson 1967). Although that work, which focused on the turnover rates in island faunas, was directed to islands that were sustained by a mainland source, the ideas could be extended to archipelagoes in which the dynamics of the system became closed. In population genetics, similar considerations led to pool or stepping-stone models (Levene 1953, Kimura and Weiss 1964) of genetic correlation.

The view of systems as mosaics of islands has taken a number of interesting directions. The concept of patch dynamics (Watt 1947, Levin and Paine 1974, Paine and Levin 1981, Pickett and White 1985) has become a popular theme in both the terrestrial and marine literatures, and has led to new views of community structure. Metapopulation models, in which systems are viewed as composed of interacting populations of local demes, have been shown to be of importance in conservation biology (Armstrong 1988, Fahrig and Paloheimo 1988*a, b,* Burkey 1989, Gilpin and Hanski 1991, Nuernberger 1991), evolutionary theory (Levene 1953), and epidemiology (Levin and Pimentel 1981), and have become the focus of considerable theoretical effort (e.g., Nee and May, *in press*), especially in terms of the role of the metapopulation structure in facilitating coexistence of species.

The metapopulation perspective involves an explicit recognition of scales, and an explicit separation of within-patch and among-patch dynamics. In the intertidal, wave damage creates gaps whose demographic changes occur on a time scale of years and a spatial scale orders of magnitude larger than the typical size of a patch; within a patch, successional dynamics occur on a somewhat more rapid scale. Similar separation of scales has proved useful in viewing forest gap systems (Grubb 1977, Runkle 1982, Pickett and White 1985, Canham 1988, Clark 1990, 1991*b*) and gopher-mediated grassland systems (Hobbs and Hobbs 1987, Hobbs and Mooney 1991). Host–parasite systems provide yet another important application, in which the individual host is the patch (Gilbert 1977, Anderson and May

1981, Denno and McClure 1983); the interplay between within-patch and among-patch evolutionary changes explains the evolution of intermediate levels of virulence, for example in the myxoma–*Oryctolagus* system (Fenner and Ratcliffe 1965, Lewontin 1970, Levin and Pimentel 1981) discussed earlier. Similar multiscale phenomena are important within our own genomes, in which the evolution of selfish DNA results from a conflict between the individual benefits to the segment of DNA and the costs to its host organism; or in bacteria, in which evolutionary forces on plasmid-borne DNA must be distinguished from those on the bacteria. Finally, host plants form islands that can be colonized by insect pests (Gilbert 1977, Denno and McClure 1983, Harrison and Thomas 1991, McEvoy et al. 1993), and that recognition has led to important insights into the dynamics of these systems.

Food Webs

One of the most natural ways to describe a community or an ecosystem is in terms of the trophic relationships among species, and the tangled web that results (Elton 1958, Paine 1966, 1980, Levin et al. 1977, Odum 1983). Considerable theoretical interest has been directed to regularities that can be detected in the topological structure of such webs (Cohen 1977, 1989, Pimm 1982, Sugihara 1982, Yodzis 1989). This seems all the more remarkable given the fact that such patterns seem to hold true regardless of the criteria used to define the elements of a web, or the criteria for deciding that a link exists between two species (but see Cohen 1989, Schoener 1989). Indeed, there clearly is no unequivocal way to characterize a web. Is a taxonomic subdivision most appropriate, or would a functional one serve better? Should subdivision stop at the species level, consider different demographic classes, be partitioned according to genotype, etc.? However a class were defined, one could partition it further according to a variety of kinds of criteria, reducing variability within a class while sacrificing the predictability that can be achieved for larger assemblages. This is the same kind of problem confronted when one deals with spatial and temporal scale, but with added layers of complexity.

In an important study, Sugihara et al. (1989) examine the robustness of observed food web properties to aggregation of trophic groupings. Specifically, they look at such properties as chain length, existence of rigid circuits, and particular trophic ratios, and show that these are roughly invariant under lumping. The degree to which such regularities represent deep biological truths vs. statistical anomalies is still to be resolved. What is important about their paper is the explicit recognition that one must take into consideration the biases attributable to the investigator's choice of scale, and examine specifically how system description changes with scale.

A critical question regarding food web structure is whether there is a natural hierarchical decomposition of webs, or whether the particular filter imposed by a given aggregation scheme is just an arbitrary point on a continuum. Paine (1980), in his insightful Tansley lecture, introduced the notions of interaction strength, and strong and weak linkages, to suggest a fruitful way to dissect food web structure; similar ideas have proved very powerful in the sector decomposition literature in economics (Simon and Ando 1961, Iwasa et al. 1987, 1989). The general question remains unresolved, however, and a rich area for research.

Global Climate Change and Ecological Models

Global climate change, and changes in the concentrations of greenhouse gases, will have major effects on the vegetational patterns at local and regional scales (MacArthur 1972, Clark 1985); in turn, changes that occur at very fine scales, such as alterations in rates of stomatal opening and closing, ultimately will have impacts at much broader scales (Jarvis and McNaughton 1986). General circulation models (GCMs), which form the basis of climate prediction, operate on scales of hundreds of kilometres on a side, treating as homogeneous all of the ecological detail within (Hansen et al. 1987, Schneider 1989). On the other hand (Fig. 14), most ecological studies are carried out on scales of metres or tens of metres (Kareiva and Anderson 1988); and even ecosystem studies are at scales several orders of magnitude less than those relevant to GCMs. Thus, a fundamental problem in relating the large-scale predictions of the climate models to processes at the scale of ecological information is to understand how information is transferred across scales (Jarvis and McNaughton 1986, Levin, *in press*).

As in the research described previously, there is a need both for statistical and correlational studies, and for modeling designed to elucidate mechanisms. A useful place to begin is in the quantification of spatial and temporal variability as a function of scale (e.g., Kratz et al. 1987, McGowan 1990). Long temporal and spatial series can be used to examine similar patterns in the variation of climate and ecosystem components; where scales of variation match, there is at least the basis for investigation of mechanistic relationships. An example is provided by the continuous plankton recorder surveys of the North Atlantic, providing data on spatial variations in the distributions of phytoplankton and zooplankton over half a century (see, for example, Colebrook 1982, McGowan 1990). The evidence from these studies has been that the larger spatial and temporal scales show the greatest variations, and that these correlate well with large-scale climatic variations (Dickson et al. 1988, McGowan 1990). The approach taken (Radach 1984), similar to that described earlier, is first to ask how much of the variation can be explained by variation in the physical environment, and then to look to autonomous biological factors to

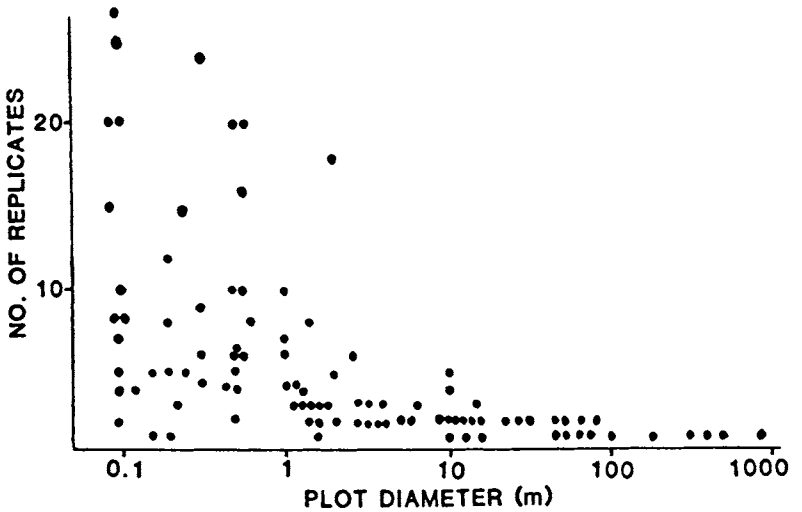

FIG. 14. Size and number of replicates in experimental community ecology. Each point is taken from a different paper published in *Ecology*. Every paper from January 1980 to August 1986 was included if it involved experimental manipulation of resources or populations "in order to learn about community dynamics or community properties" (from Kareiva and Anderson 1988).

account for the balance. This mode of attack, which is the conventional one and the one that I have relied on in this paper, perhaps requires scrutiny, given the possibility that intrinsic biotic factors might account for some climatic variation. Only mechanistic approaches that examine how effects scale can address this puzzle.

Ågren et al. (1991) review models of the linkage of production and decomposition, and discuss as well the linkages of process at different scales. The problem of scaling from the leaf to the ecosystem and beyond poses fundamental challenges in predicting the effects of global change (Norman 1980, Ehleringer and Field, *in press*). Ågren et al. point out that ecosystem models that operate at only one level of integration are not likely to incorporate mechanisms properly, and that it is essential to develop methods for integrating from finer scales; this reiterates the central theme of this paper. A related problem is the need to interface processes that are operating at different levels of integration, as for example, in the linkages between grassland biogeochemistry and atmospheric processes (Parton et al. 1989, Schimel et al. 1990).

It is worth noting (C. J. Holling, *personal communication*) that separating climatic and biotic influences upon changing ecosystem patterns can be extremely problematic. Extrinsic influences can serve to trigger qualitative changes in systems dynamics (Levin 1978); cases in point may involve fires or outbreaks that are triggered by climate change, but show very little correlation with it (e.g., Holling, *in press*).

Patterns of Evolution at the Community Level

One of the greatest barriers to the development of interfaces between population biology and ecosystems science is the perceived scale mismatch, especially as regards evolutionary processes. To some extent, this is a misconception; for example, the evolution of responses to strong selective pressures, such as heavy metals in the environment, or antibiotics, can occur in ecological time, whereas ecosystem scientists concerned with global change must place great importance upon an understanding of the evolutionary record. Similarly, much of the study of macroevolutionary processes, such as speciation, must involve spatial scales comparable to those of relevance in ecosystem or landscape studies. Thus, there is considerable overlap between the spatial and temporal scales of interest to the population biologist and the ecosystem scientist.

Organizational complexity is another matter, by definition. Population biologists are concerned with changes taking place among and within populations; where coevolution has been documented, it is usually tight coevolution, such as in parasite–host systems, in which the fate of a small number of species (usually two), are intimately linked. Furthermore, the occasional tendency in ecosystems science to explain the evolution of ecosystem-level phenomena in terms of what is good for the ecosystem suggests to the population biologist a lack of sensitivity to the mechanisms of evolution, which they see as operating primarily at the individual level. On the other hand, to some ecosystem scientists, such attention to detail seems to miss the forest for the trees. It is hardly surprising that in some bastions of population biology, ecosystems science is scarcely tolerated, whereas in some schools of ecosystems science, population biology is seen as an academic enterprise of limited relevance to ecosystem-level problems.

A growing number of ecologists and evolutionary biologists, however, recognize the folly of failing to address the issues of mutual importance to the two

communities (Roughgarden 1976*b*, Orians and Paine 1983, Schneider and Louder 1984, Rummel and Roughgarden 1985, Ehrlich 1991, papers in Levin 1976). As mentioned earlier, ecotoxicology and conservation biology represent two applications where systematics, population dynamics, evolutionary biology, and ecosystems science have built partnerships. Similar progress has been made in understanding the dynamics of aquatic systems, and the linkages between community structure and ecosystem processes (Bormann and Likens 1979, Carpenter and Kitchell 1988, Howarth 1991). For example, Carpenter and Kitchell (1988), in discussing the results of large-scale experimental manipulations of lakes, demonstrate the temporal and spatial dependence of the results, and attribute the differences to the evolutionary history of the trophic interactions experienced; whole-lake experiments elicit processes over long time scales that involve diffuse interactions with large numbers of species. Yet central issues, such as the explanation of the evolution of community and ecosystem-level patterns in terms of forces acting on individual species, remain virtually untouched. Though various models attempt to explain how species subdivide the resources in a community, given their particular demographic characteristics (MacArthur 1970, May and MacArthur 1972), few address the question of how those demographic characteristics evolve in relation to each other (but see Lawlor and Maynard Smith 1976). And, whereas cross-system comparisons of different ecosystems may show regularities and allow functional classifications in terms of successional patterns (Connell and Slatyer 1977), trophic organization (Pimm 1982, Cohen 1989), diversity (May 1978, 1981, Levin 1981), or ecosystem processes (Ulanowicz 1986), few if any studies attempt to account for the evolution of those patterns in terms of the forces acting on individuals. The challenge is the familiar one of trying to understand patterns observed at one level of detail in terms of mechanisms that are operating on other scales. The study of such processes provides a challenging collection of problems of surpassing importance for understanding, for example, how ecosystems might be expected to change over long time scales in response to anthropogenic stresses.

As an example, consider the description of the patterns of chemical defenses and detoxification mechanisms found in communities of plants and their herbivores. Such patterns are important in defining the chemical context for introduced species, and for a variety of other problems; indeed, the study of patterns of chemical interactions in plant–herbivore communities is surely one of the most intellectually exciting in ecology (Feeny 1976, Futuyma 1983). In some cases, this evolution has been in response to tight and therefore strong interactions between pairs of species; but more often than not, the evolutionary pressures have come from diffuse influences, such as those acting to shape the vertebrate immune system. How then, do we develop a theoretical framework to address such problems?

The problem, actually, is not much different than what we face when attention is on individual populations, and on the evolution of ecological parameters. Classical theories have developed a rich literature for dealing with single loci, and for tight interactions among pairs of loci. Yet many and probably most traits of ecological importance are quantitative, controlled at many loci, each of which contributes in a small way. To address such problems, the theory of quantitative genetics was developed (Falconer 1960, Lande 1976). In quantitative genetics, one deals with broad phenotypic classes, suppressing variation within those classes, and focusing on macroscopic parameters such as population means and variances. One of the fundamental debates in that subject involves the appropriateness of ignoring certain levels of detail and heterogeneity, and the correct way to derive ensemble properties from information on individual dynamics.

The same problem must be confronted in developing quantitative descriptions of diffuse coevolution. Phenotypic classes must be broader, lumping individuals together not only within a species, but also across species, and phenomenological descriptions of the dynamics of macroscopic statistics must be achieved by aggregating lower level phenomena. When this is done (Levin and Segel 1982, Levin et al. 1990), one can derive quantitative descriptions of changes at the community level, analogous to the equations of quantitative genetics. In this way, for example, one can derive equations for the rate of change of the mean level of resistance to herbivory within a community in terms of the variance and the statistics of the distribution of detoxification chemicals in the herbivore community (Levin et al. 1990).

Undoubtedly, the same objections will be raised against quantitative approaches at the community level as are lodged against the use of quantitative genetics, albeit more forcefully. After all, the approach is simply quantitative genetics carried a step further; by lumping together individuals across species, quantitative approaches would ignore the barriers to interbreeding that define species boundaries. Such objections should insert a note of caution, and a reminder to be sensitive to how aggregation and simplification are done; they must not, however, prevent the development of such theories, which seem one of the most hopeful ways to bridge a yawning chasm. It cannot be the case that every detail of interspecific evolutionary interactions is essential for understanding patterns at the community level, any more than it is necessary (or useful) to account for every species in models of ecosystems dynamics. To be effective at developing appropriate descriptions at any level in terms of lower level phenomena, it is as important to know what detail to ignore

as it is to know what detail to include (Ludwig and Walters 1985).

Evolutionary theory has made great advances, and efforts over the next decade in molecular evolution will expand our understanding greatly of the mechanisms underlying evolutionary change. Yet unless we can find ways to relate detailed information at the molecular level to patterns of change at the level of the individual, the population, and the community, we will not have advanced our understanding of the evolution of the biosphere. Indeed, the disruptive selection regime, by which population genetics becomes more molecular while ecosystems science becomes more global, may enhance the speciation of the two communities of scientists unless novel efforts are made to relate the phenomena that transpire on the disparate scales of interest. Now, more than ever, we need to develop mechanistic evolutionary theories of how ecosystem patterns arise and are maintained.

CONCLUSION

Two fundamental and interconnected themes in ecology are the development and maintenance of spatial and temporal pattern, and the consequences of that pattern for the dynamics of populations and ecosystems. Central to these questions is the issue of how the scale of observation influences the description of pattern; each individual and each species experiences the environment on a unique range of scales, and thus responds to variability individualistically. Thus, no description of the variability and predictability of the environment makes sense without reference to the particular range of scales that are relevant to the organisms or processes being examined.

Such issues are most clear for spatial and temporal scales, but apply as well to organizational complexity. The recognition in marine fisheries that total yield in multispecies fisheries remains fairly constant over long periods of time, though the species composition may change dramatically (May 1984), is a consequence of broadening the scale of description. Similarly, a claim that microbial communities are stable to perturbations, such as introductions of genetically engineered organisms, results from the application of a taxonomically broad filter, perhaps because only a fraction of the microbial community can be identified. In ecosystems research, one is likely to be concerned with a functional guild of microorganisms that perform a particular service to the ecosystem, and to refer to functional redundancy to explain why it is acceptable to ignore changes within a guild. This is the key to scaling and interrelating phenomena at different scales: knowing what fine detail is relevant at the higher levels, and what is noise.

There are several stages in the examination of the problem of pattern and scale. First, one must have measures to describe pattern (Gardner et al. 1987, Milne 1988), so that criteria can be established for relating that pattern to its causes and consequences. Cross-correlational analyses can provide initial suggestions as to mechanisms, but may miss emergent phenomena that arise from the collective behavior of smaller scale processes. Theoretical investigations of the various mechanisms through which pattern can arise provide a catalogue of possibilities, and may suggest relevant experiments to distinguish among hypothesized mechanisms.

All ecological systems exhibit heterogeneity and patchiness on a broad range of scales, and this patchiness is fundamental to population dynamics (Levin 1974, Roughgarden 1976*a*), community organization and stability (Holling 1986, Kareiva 1987), and element cycling (Bormann and Likens 1979). Patchiness is a concept that cuts across terrestrial and marine systems, and provides a common ground for population biologists and ecosystem scientists. Patchiness, and the role of humans in fragmenting habitats, are key to the persistence of rare species, and the spread of pest species. The level of species diversity represents a balance between regional processes, e.g., dispersal and species formation, and local processes, such as biotic interactions and stochasticity (Ricklefs 1987).

The consequences of spatial pattern and patchiness for the biota are many. Patchiness in the distribution of resources is fundamental to the way organisms exploit their environment (Schoener 1971, Wiens 1976, Mangel and Clark 1986, Pulliam 1989). Environmental heterogeneity provides a diversity of resources that can lead to coexistence among competitors that could not coexist in homogeneous environments (Levin 1970, 1974, Horn and MacArthur 1972); but the problem of how to count the number of resources is a vexing one. Trivially, no environment will be completely homogeneous, but how different must resources be to support different species? This question, a central one in community ecology (MacArthur 1970, May and MacArthur 1972, Whittaker and Levin 1977), goes to the heart of the problem of scale. Species can subdivide the environment spatially, concentrating on different parts of the same plant (Broadhead and Wapshere 1966), different layers of vegetation (MacArthur et al. 1966), or different microenvironments; or temporally, partitioning a successional gradient (Levin and Paine 1974) or a seasonal one. Thus, resource partitioning can result in temporally constant spatially nonuniform patterns, or spatially constant temporally nonuniform ones, or spatiotemporal mosaics (Levin and Paine 1974, Whittaker and Levin 1977, Paine and Levin 1981, Tilman 1988).

Because the variability and patchiness of the environment affects persistence and coexistence, it also affects species' evolutionary responses. Differential persistence occurs both among species and within species, and the latter will result in evolutionary changes that alter the species' response to environment, and hence the species' perception of the environment. Since the

environment of a species is made up to a large extent of other species, the evolutionary response of one must affect the environmental variability experienced by others; thus ensues a coevolutionary dynamic that shapes the observed patterns of biotic and environmental variability.

All of this reinforces the recognition that there is no single correct scale at which to view ecosystems; the individualistic nature of responses to environment means that what we call a community or ecosystem is really just an arbitrary subdivision of a continuous gradation of local species assemblages (Whittaker 1975). It also carries important implications for predicting the responses of the biota to global change. Communities are not well integrated units that move en masse. They are collections of organisms and species that will respond individualistically to temporal variation, as they do to spatial variation. This is also true, of course, with regard to the evolutionary responses of populations. Thus, if there are predictable patterns that may be observed in what we define as communities and ecosystems, they have arisen through the individualistic ecological and evolutionary responses of their components, rather than some higher level evolution at the ecosystem level, Gaia notwithstanding (Lovelock 1972; see also Schneider and Boston 1991, for a wide range of views).

That there is no single correct scale or level at which to describe a system does not mean that all scales serve equally well or that there are not scaling laws. This is the major lesson of the theory of fractals (Mandelbrot 1977, Milne 1988, Sugihara and May 1990). The power of methods of spatial statistics, such as fractals, nested quadrat analysis (Oosting 1956, Greig-Smith 1964), semivariograms or correlograms (Sokal and Oden 1978, Burrough 1981, 1983*a*, *b*, Sokal et al. 1989), or spectral analysis (Chatfield 1984); or of allometry (Calder 1984, Platt 1985, Brown and Nicoletto 1991, Harvey and Pagel 1991) is in their capability to describe how patterns change across scales. Thus, such methods have been used in ecology to quantify change in soils and in ecosystem properties at sub-field levels (Robertson et al. 1988) or landscape levels (Krummel et al. 1987), and in marine systems to quantify the distribution of physical factors, primary producers, and consumers (Haury et al. 1978, Steele 1978, 1991, Weber et al. 1986, Levin et al. 1989*b*).

The simple statistical description of patterns is a starting point; but correlations are no substitute for mechanistic understanding (Lehman 1986). Modeling can play a powerful role in suggesting possible mechanisms and experiments, in exploring the possible consequences of individual factors that cannot be separated easily experimentally, and in relating fine-scale data to broad-scale patterns.

Because there is no single scale at which ecosystems should be described, there is no single scale at which models should be constructed. Methods from statistics and dynamical systems theory can play an important part in helping to determine the dimensionality of underlying mechanisms, and of appropriate models (Schaffer 1981, Takens 1981, Schaffer and Kot 1985, Sugihara et al. 1990). We need to have available a suite of models of different levels of complexity, and to understand the consequences of suppressing or incorporating detail. Models that are insufficiently detailed may ignore critical internal heterogeneity, such as that which is responsible for maintaining species diversity (Holling 1986); it is clear, for example, that the broad brush of the general circulation models ignores detail that is relevant for understanding biotic influences on climate systems, and vice versa. On the other hand, overly detailed models provide little understanding of what the essential forces are, will have more parameters and functional forms to estimate than the available data justify, will admit multiple basins of attraction, and are more prone to erratic dynamics that hamper prediction and parameter estimation. Just as we would not seek to build a model of human behavior by describing what every cell is doing, we cannot expect to model the dynamics of ecosystems by accounting for every individual, or for every species (Ludwig et al. 1978). We must determine what the appropriate levels of aggregation and simplification are for the problem at hand.

In an extremely instructive study, Ludwig and Walters (1985) have shown clearly that in some cases aggregated models can serve as better management tools than highly detailed models, even when the data used to fit the parameters of the model have been generated by the detailed model; in retrospect, this should accord well with intuition. The problem of aggregation and simplification is the problem of determining minimal sufficient detail (Levin 1991, Rastetter et al. 1992).

Classical ecological models (Scudo and Ziegler 1978) treated communities as closed, integrated, deterministic, and homogeneous. Such models are simplifications in real systems, and provide a place to begin analysis. However, each of these assumptions must be relaxed if we are to understand the factors governing the diversity and dynamics of ecosystems. Virtually every population will exhibit patchiness and variability on a range of spatial and temporal scales, so that the definition of commonness or rarity is scale dependent (Schoener 1987). Virtually every ecosystem will exhibit patchiness and variability on a range of spatial, temporal, and organizational scales, with substantial interaction with other systems and influence of local stochastic events. These phenomena are critical for the maintenance of most species, which are locally ephemeral and competitively inferior, and which depend upon the continual local renewal of resources and mechanisms such as dispersal to find those opportunities. Fragmentation, local disturbance, and variability also can have major consequences for patterns of nutrient cycling (Bormann and Likens 1979), persistence (Pimm

and Gilpin 1989), and patterns of spread of introduced species (Mooney and Drake 1986, Durrett 1988). The key is to separate the components of variability into those that inhibit persistence and coexistence, those that promote these, and those that are noise (Chesson 1986).

To address such phenomena, we must find ways to quantify patterns of variability in space and time, to understand how patterns change with scale (e.g., Steele 1978, 1989, Dagan 1986), and to understand the causes and consequences of pattern (Levin 1989, Wiens 1989). This is a daunting task that must involve remote sensing, spatial statistics, and other methods to quantify pattern at broad scales; theoretical work to suggest mechanisms and explore relationships; and experimental work, carried out both at fine scales and through whole-system manipulations, to test hypotheses. Together, these can provide insights as to how information is transferred across scales, and hence how to simplify and aggregate models.

The problem of relating phenomena across scales is the central problem in biology and in all of science. Cross-scale studies are critical to complement more traditional studies carried out on narrow single scales of space, time, and organizational complexity (Steele 1978, 1989, Meetenmeyer and Box 1987, Levin 1988, 1989, Holling 1992), just as measures of β-diversity are needed to complement within-community measures of α-diversity (Whittaker 1975). By addressing this challenge, using the insights gained from similar studies in other sciences and the unique approaches that must be developed for ecological systems, we can enhance greatly our understanding of the dynamics of ecosystems and develop the theoretical basis necessary to manage them.

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