Revista Chilena de Historia Natural
63: 309-315, 1990

DOCUMENT

Ecology 2000: an essay on future directions in ecology*

Ecología 2000: un ensayo sobre las futuras direcciones en Ecología

JOHN A. WIENS

Department of Biology, Colorado State University,
Fort Collins, Colorado 80523 USA

ABSTRACT

I comment on several areas of important activity in ecology as we approach the 21st century. Investigations founded on mechanisms operating at the level of individual organisms may lead to better understanding of higher-level patterns. Ecologists should consider the effects of spatial and temporal scales and of the degreee of openness of ecological systems on the patterns they document and the explanations they offer. Spatial heterogeneity, especially as it is expressed in the spatially explicit patterns of environmental mosaics, should also become a focus of study. The distinction between basic and applied ecology is detrimental to progress and should be abandoned.

Key words: mechanistic ecology, scale, landscape ecology, spatial patterns, applied ecology.

RESUMEN

Se comenta sobre diversas áreas de actividad importante en ecología, a medida que nos acercamos al siglo 21. Las investigaciones basadas en los mecanismos que operan al nivel de organismos individuales pueden llevar a una mejor comprensión de los patrones de alto nivel. Los ecólogos deberían considerar los efectos de las escalas temporales y espaciales y del grado de apertura de los sistemas ecológicos, sobre los patrones que ellos documentan, y las explicaciones que ofrecen. La heterogeneidad espacial –particularmente en la forma en que ella se expresa en los patrones espacialmente explícitos de mosaicos ambientales– debería llegar a ser también un foco de estudio. La distinción entre ecología básica y aplicada es dañina para el progreso, y debería ser abandonada.

Palabras claves: Ecología "mecanística", escala, ecología del paisaje, patrones espaciales, ecología aplicada.

INTRODUCTION

The science of ecology has undergone an explosive growth over the past three decades. Journals have proliferated, professional societies have been formed, and new subdisciplines have sprung to life. The parallel development of public concern about environmental problems has revitalized interest in conservation and produced significant political movements in many countries. Ecology has become important to people other than ecologists.

As it has grown, ecology has changed from a descriptive and often qualitative discipline to one that is increasingly quantitative, hypothetico-deductive, and experimental (Haila 1982, McIntosh 1985, 1989, Loehle 1987, Wiens 1989a). The conceptual and theoretical foundation of ecology has become richer, but at the same time more contentious (Pielou 1981, Roughgarden 1983, Cherrett 1989, Wiens 1989b). Controversies have developed over such questions as the importance of competition in structuring communities; the role of density-dependent factors in population dynamics; the degree to which communities or ecosystems are deterministic, cybernetic systems or are governed by stochastic processes; the use of null models; the importance of local details versus general patterns; the level at which selection operates in ecological systems; whether or not the concept of succession (or, indeed, any concept) is useful or realistic; or whether behavior or physiological responses to environmental stress are opti-

* Adapted from an address delivered at the ceremony marking the twentieth anniversary of the Facultad de Ciencias Biológicas. Pontificia Universidad Católica de Chile, Santiago, on 8 August 1990.

mized. To some degree, these controversies stem from misunderstandings among ecologists about the appropriate scale for investigations (Wiens 1989c) or their use of different forms of causal explanation, but they also reflect fundamental differences of opinion about how nature is structured and how science should be done. Schoener (1986a) observed that the debate over the relative importance of intraspecific versus interspecific processes has at times "been so acrimonious that it has frightened some away from the field and evoked a wonderment in others as to what could possibly be so controversial." Perhaps to assuage such disharmony, calls for a pluralism of approaches in ecology have become more frequent (Schoener 1986b, McIntosh 1987). Ecology, like many of the systems it studies, has become increasingly fragmented.

Is it possible, amid this splinterning, to develop some outlook on where ecology might (or should) be headed as we approach the twenty-first century? The inventory of both basic and applied ecological problems awaiting solution is quite large, and one might enumerate a correspondingly large list of directions and approaches that ecologists should follow (Lubchenco *et al.* 1991; see also Kawanabe *et al.*, 1990, May & Southwood 1990). Here I offer a personal perspective on the future of ecology, focusing on several features that must become central to investigations in any area of ecology.

MECHANISTIC ECOLOGY

Traditionally, ecological explanations have been largely phenomenological. A pattern is observed and matched with the predictions of a theory that postulates a certain linkage between pattern and process. The observations are then explained as the result of the presumed operation of the postulated process in nature. The documentation of the pattern is empirical, but the underlying explanation is inferential. There are formidable difficulties with this approach, not the least of which is the problem of multiple causation –the same pattern may be produced by several processes (Wiens 1989b). Because of their heavy reliance on inference (or analogy), phenomenological exlanations are often based more on faith than on empirical evidence. If we instead frame explanations of population, community, and ecosystem phenomena in terms of their underlying mechanisms, the role of inference can be reduced and our understanding of pattern-process linkages sharpened. Mechanistic ecology, which is already receiving some attention (Price 1986, Schoener 1986a, Huston *et al.*, 1988), will become a major focus of ecology in the future.

The mechanisms underlying ecological phenomena are rooted in what individual organisms do. The feeding habits of animals determine the trophic dynamics of ecosystems; their movements and habitat selection establish the spatial structure of populations, gene flow, and the assembly patterns of communities; and their behavior affects reproduction, demography, and microevolutionary change. In a like manner, the capacities of plant organisms to accumulate biomass, utilize nutrients, fix nitrogen, and the like not only affects the distribution and demography of plant populations and communities, but also provides both the food and elements of habitat structure upon which consumer communities are built.

Three aspects of individual activities are particularly important contributors to patterns at higher levels. First, individual movements and dispersal affect virtually all aspects of an organism's ecology –its probability of encounter with food, shelter, or mates; its predation risk; its exposure to physiological stress; its habitat occupancy and interactions with competitors; and so on. For example, organisms that move in approximately linear pathways (*e.g.* ants moving to and from a rich food source, dispersing juveniles of many species) are likely to encounter a greater variety of patches in a given landscape mosaic than are individuals following a more convoluted track with more frequent and extreme turns (*e.g.* desert isopods searching for shelter, predators engaged in area-restricted search). As a consequence, they may have greater opportunities for actively selecting the habitat patches to occupy. Because they encounter a more diverse landscape, however, they may also experience a more uncertain environment. It is easiest to visualize these consequences for highly mobile animals, but even sessile organisms such as barnacles or trees have a mobile, dispersal phase. Although this phase may comprise only a small fraction of the life cycle, it may have disproportionate effects on many population, community, and ecosystem patterns.

Habitat selection is a second major component of mechanistic ecology. Many organisms respond actively to the mosaic of habitats they encounter, avoiding some and preferring others. The outcome is that the occupancy and use of habitats differs markedly from the proportion of habitat types found in an area. Habitat selection is often a hierarchical process —individuals respond to certain features at broad scales and then further refine their use of habitats at finer scales (Kotliar & Wiens 1990). Individuals may thus aggregate by habitat at several scales of resolution, and this aggregation may influence population structure and demography, the directions and frequencies of species interactions, community composition, and energy and nutrient flow pathways. Neither the process of habitat selection nor its consequences has received much empirical or theoretical study (but see Cody 1985).

The third critical element of mechanistic ecology, resource acquisition, has been a traditional focus of ecological investigations, albeit in the guise of competitively driven resource partitioning among species. Resources are the foundation of ecological processes ("You are what you eat"), yet they are often vaguely defined and poorly quantified (Tilman 1982, Wiens 1984, Abrams 1988). The effects of resource abundance and availability in habitats on individual performance or fitness and population dynamics need to be documented in much greater detail if we are to understand such central concepts as "resorce limitation," "competition," "resource use efficiency," or "trophic efficiency."

To some ecologists, a focus on mechanisms raises the spectre of a descent into the black hole of reductionism. They fear that we will be drawn into increasingly detailed examinations of increasingly particular situations, and little if any light on the central questions of ecology will emerge. Instead of becoming more mechanistic, it is proposed that we should focus on large-scale "macroparameters" such as multispecies distribution patterns or global patterns in biodiversity (May 1988, Brown & Maurer 1989).

This proposal has merit. Some phenomena are driven by events occurring at broad scales (*e.g.* El Niño), and some patterns are apparent only when a large-scale perspective is used (*e.g.* core-satellite species-abundance distributions; Hanski 1982). Broad-scale features of ecological systems may act as constraints on the patterns and dynamics that are expressed at finer scales (Ricklefs 1987, Brown & Maurer 1989). Of course, some macroecological patterns *are* determined by processes operating at broad scales (*e.g.* atmospheric circulation dynamics), and reduction to finer levels would be likely to obscure rather than reveal these mechanisms. More often than not, however, macroecological patterns may derive from mechanisms operating at the level of individuals that are overlooked if one resorts to broad-scale, inferential explanations. A macroecological approach can serve as a guide for judicious reductionism, but it should not preclude the search for mechanisms at the level where ecological dynamics are frequently played out $\frac{1}{m}$ the individual organism.

SCALE

It is apparent from these comments that ecological investigations can be conducted at various scales. Over the past decade, it has also become apparent to many ecologists that the patterns we see in nature depend very much on the scale on which they are viewed. Ecological phenomena are scale-dependent in time and space (Wiens 1989c). Until quite recently, however, ecologists have largely ignored scale-dependency, designing their investigations with little regard for the "natural" or intrinsic scaling of the systems they study. When Natasha Kotliar and I conducted a survey of papers published in *Ecology* over a 5-yr interval in the 1980s, we discovered that most investigators used a grain size (*i.e.* minimum sample-unit area or quadrat) of 1 m^2, whether they were studying small or large organisms, plants or animals, or individuals or ecosystems. It seems unlikely that such a wide range of ecological phenomena and systems would operate on such a convenient scale. The danger, of course, is that measurements recorded from systems at inappropriate scales may reveal patterns that are only artifacts. Because we are good at telling stories about whatever patterns we see in nature, we can often explain such patterns to the satisfaction of our peers (who also love a good story!). The patterns and their process explanations are then perpetuated in the literature.

The openness of systems further exacerbates such scaling problems. Ecological dynamics are rarely contained within the boundaries of the area or time selected for study. Interactions and influences from outside the system (as we arbitrarily define it) may have substantial effects on the patterns and dynamics we observe. As a result, explanations that treat the system as closed will be incomplete. Terms such as "metapopulation" or "supply-side ecology" (Hanski 1989, Roughgarden *et al.*, 1987) focus attention on the openness of ecological systems; the key to understanding the effects of differing degrees of openness, however, may lie in mechanistic ecology, particularly investigations of movement patterns.

Future progress in ecology depends on our recognizing and dealing with scale-dependency and openness. We must regard scaling not just as a bothersome feature of study design but as a subject meriting study in its own right –a science of ecological scaling (Meentemeyer & Box 1987). This science might have as its foundation the definition of *domains* of scale: regions of a scale spectrum within which patterns and their relationships with underlying processes either do not change or change monotonically with changes in scale (Wiens 1989c). The transition from one domain, where patterns are determined by one set of factors, to an adjacent domain, where other factors predominate, may be relatively abrupt and may be characterized by complex nonlinearities and apparent chaos, much like phase transitions in physical systems. Relationships (and explanations) may be relatively stable and predictable within a domain, but not between domains. The challenges of specifying these domains, determining their generality over ecological systems and phenomena, and defining the "translation rules" between domains will be formidable, but they cannot be ignored. The first task is to establish that domains of scale actually exist; at present, we do not know if this concept has any value at all, or whether ecological patterns and processes may instead change quantitatively and qualitatively with every change in scale.

SPATIALLY EXPLICIT ECOLOGY

Environments vary in time and space. Temporal dynamics have received considerable attention, especially in population studies, and as long-term investigations become more fashionable (Likens 1989, Armesto 1990, Oliver & Larson 1990) our understanding of the temporal dimension of variation is bound to grow. Ecologists have also recognized the effects of spatial heterogeneity on systems (Pickett & White 1985). To a large degree, however, this recognition has been limited to distinguishing between homogeneous and heterogeneous environments or evaluating heterogeneity as expressed in various statistical indices.

The recent development of landscape ecology (Turner 1989) has brought an awareness that the explicit locational relationships of habitats and organisms may have profund effects on a wide variety of ecological phenomena. The susceptibility of a local population to predation or parasitism, for example, depends not only on the characteristics of the habitat patch occupied, but also on features of the adjacent patches in a spatial mosaic. Unfortunately, landscape ecology has not yet developed either the theoretical framework or the rigorous empirical base to permit a predictive understanding of spatially explicit patterns, effects, and linkages.

There are several ways to develop a spatially explicit ecology. Statistical analyses of spatial patterns (Ripley 1981, Haining 1990) are necessary to document spatial relationships, but they do little to reveal dynamics. It is becoming increasingly feasible to model large spatial matrices (*e.g.* Costanza *et al.* 1990), and such models may provide a powerful way to explore possible spatial effects on system dynamics at multiple scales and to design the empirical studies necessary to substantiate the results. Mechanistic approaches that link movement patterns and habitat or patch selection with patch-boundary conditions and spatially explicit mosaics (*e.g.* Stamps *et al.* 1987, Wiens *et al.* 1985, Wiens, Stenseth, Van Horne, & Ims, in preparation) may permit us to link fine-scale mechanisms with broader scale demographic or nutrient-flow dynamics in a spatially sensitive (and sensible) manner. This approach could forge a connection between mechanistic ecology and macroecology. Work in this area is just beginning, but the pervasiveness of spatial heterogeneity and the consequences of variations in explicit mosaic structure indicate that it must be a major focus of future activity.

BASIC AND APPLIED ECOLOGY

As ecology has grown, the distinction between basic and applied work has become increasingly formalized. Just this year the Ecological Society of America has launched *Ecological Applications*, which joins *Journal of Applied Ecology* and *Forest Ecology and Management* as a journal focused on ecology dealing with applied problems. Applied ecologists often work for business or government agencies, basic ecologists for universities. The polarization of these approaches is further nurtured by attitudes, some applied ecologists regarding basic ecologists as unrealistic dreamers or charlatans while some basic ecologists consider those working in applied areas to be inferior scientists or mercenaries.

To distinguish between basic and applied ecology is senseless. What is important is whether or not the science is good, not whether it addresses problems that only ecologists or the public at large finds important. The catalog of "applied" environmental problems is huge: pollution and degradation of environments by human activities, an accelerating loss of biological diversity, global climatic change and its effects, devising sustainable development plans that balance human needs with biospheric integrity, and (by no means least important) communicating ecological knowledge and findings to the public and to those making policy and management decisions. Each of these problems provides ample opportunities to conduct basic reserach, and each rests on findings from such research for its resolution. These are not applied problems; they are *ecological* problems. Who ever said that ecological research has to be irrelevant to be good? Ecology of the future must include collaborative efforts and unrestricted communication between those who might now consider themselves "applied" or "basic" scientists, regardless of where they are employed.

CONCLUDING COMMENTS

The themes I have developed here are general and conceptual, not specific or detailed. Certainly future directions in ecology will be strongly influenced by methodological advances, especially technologies imported from other disciplines (*e.g.* fractal geometry, remote sensing systems, chaos theory, computer scanning, molecular probes, genetic engineering). These advances by themselves will make ecology a more demanding subject, fostering specialization and diversification. The spectrum of problems and approaches will demand greater operational and philosophical variety —ecology cannot become just experimental, or solely hypothetico-deductive. In the face of these forces, it will be difficult for ecology to avoid further fragmentation. Yet the challenges we face demand cohesion, not fragmentatation. Perhaps the threads I have outlined here— mechanisms, scaling, spatial explicitness, and a merging of basic and applied approaches —will provide the fabric to bind ecology and ecologists together.

ACKNOWLEDGMENTS

I am grateful for the invitation to come to Chile to join in the dedication ceremonies for the Facultad de Ciencias Biológicas, and therefore the impetus to think about the future of ecology. Jane Lubchenco graciously provided a draft copy of the report. "The Sustainable Biosphere Initivative: an Ecological Research Agenda for the Nineties." prepared for the Ecological Society of America. Dan Binkley, Tom Crist, and Bea Van Horne commented on a draft of this paper. My research has been supported by the United States National Science Foundation (BSR-8805829) and Department of Energy (DE-FGO2-88 ER60715).

LITERATURE CITED

ABRAMS P (1988) How should resources be counted? Theoretical Population Biology 33: 226-242.

ARMESTO JJ (1990). Estudios a largo plazo: una prioridad para la investigación ecológica de hoy. Revista Chilena de Historia Natural 63: 7-9.

BROWN JH & BA MAURER (1989) Macroecology: the division of food and space among species on continents. Science 243: 1145-1150.

CHERRETT JM, (ed) (1989) Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World, Oxford: Blackwell Scientific Publications.

CODY ML, (ed) (1985) Habitat Selection in Birds. New York: Academic Press.

COSTANZA R, FH SKLAR & ML WHITE (1990) Modeling coastal landscape dynamics. BioScience 40: 91-107.

HAILA Y (1982) Hypothetico-deductivism and the competition controversy in ecology. Annales Zoologici Fennici 19: 255-263.

HAINING R (1990) Spatial data analysis in the social and environmental sciences. Cambridge: Cambridge University Press.

HANSKI I (1982) Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210-221.

HANSKI I (1989) Metapopulation dynamics: does it help to have more of the same? Trends in Ecology and Evolution 4: 113-114.

HUSTON M, D DeANGELIS & W POST (1988) New computer models unify ecological theory. BioScience 38: 682-691.

KAWANABE HT, T OHGUSHI & M HIGASHI (1990) Ecology for Tomorrow. Kyoto: Physiology and Ecology Japan, Vol. 27.

KOTLIAR NB & JA WIENS (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

LIKENS GE, (ed) (1989) Long-term Studies in Ecology. Approaches and Alternatives. New York: Springer-Verlag.

LOEHLE C (1987) Hypothesis testing in ecology: psychological aspects and the importance of theory maturation. Quarterly Review of Biology 62: 397-409.

LUBCHENCO J, AM OLSON, LB BRUBAKER, SR CARPENTER, MM HOLLAND, SP HUBBELL, SA LEVIN, JA MACMAHON, PA MATSON, JM MELILLO, HA MOONEY, CH PETERSON, HR PULLIAM, LA REAL, PJ REGAL, PG RISSER (1991) The sustainable biosphere initiative: an ecological research agenda. Ecology, 72, 371-412.

MAY RM (1988) How many species are there on earth? Science 241: 1441-1449.

MAY RM & TRE SOUTHWOOD (1990) Introduction. In Living in a Patchy Environment, (ed) Shorrocks, B. & I.R. Swingland, pp. 1-22. Oxford: Oxford University Press.

McINTOSH, RP (1985) The Background of Ecology: Concept and Theory. Cambridge: Cambridge University Press.

McINTOSH RP (1987) Pluralism in ecology. Annual Review of Ecology and Systematics 18: 321-341.

McINTOSH RP (1989) Citation classics of ecology. Quarterly Review of Biology 64: 31-49.

MEENTEMEYER V & EO BOX (1987) Scale effects in landscape studies. In Landscape Heterogeneity and Disturbance, (ed) Turner, MG, pp. 15-34. New York: Springer-Verlag.

OLIVER CD & BC LARSON (1990) Forest Stand Dynamics. McGraw-Hill, New York.

PICKETT STA & PS WHITE (eds) (1985) The Ecology of Natural Disturbance and Patch Dynamics. New York: Academic Press.

PIELOU EC (1981) The usefulness of ecological models: a stocktaking. Quarterly Review of Biology, 56, 17-31.

PRICE MV (1986) Introduction to the symposium: mechanistic approaches to the study of natural communities. The American Zoologist 26: 3-4.

RICKLEFS RE (1987) Community diversity: relative roles of local and regional processes. Science 235: 167-171.

RIPLEY BD (1981) Spatial Statistics. New York: John Wiley & Sons.

ROUGHGARDEN J (1983) Competition and theory in community ecology. The American Naturalist 122: 583-601.

ROUGHGARDEN J, SD GAINES & SW PACALA (1987) Supply side ecology: the role of physical transport processes. In Organization of Communities: Past and Present, (ed). Gee JHR & PS Giller, pp. 491-518. Oxford: Blackwell Scientific Publications.

SCHOENER TW (1986a) Mechanistic approaches to community ecology: A new reductionism? The American Zoologist 26: 81-106.

SCHOENER TW (1986b) Overview: kinds of ecological communities —ecology become pluralistic. In Community Ecology, (ed) Diamond, J & Case TJ, pp. 467-479. New York: Harper & Row.

STAMPS JA, M BUECHNER & VV KRISHNAN (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. The American Naturalist 129: 533-552.

TILMAN D (1982) Resource Competition and Community Structure. Princeton, NJ: Princeton University Press.

TURNER MG (1989) Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Stematics 20: 171-197.

WIENS JA (1984) Resource systems, populations, and communities. In A New Ecology: Novel Approaches to Interactive Systems, (ed) Price, PW, CN Slobodchikoff, & WS Gaud, pp. 397-436. New York: John Wiley & Sons.

WIENS JA (1989a) The Ecology of Bird Communities, Vol. 1. Cambridge: Cambridge Univ. Press.

WIENS JA (1989b) The Ecology of Bird Communities, Vol. 2. Cambridge: Cambridge University Press.

WIENS JA (1989c) Spatial scaling in ecology. Functional Ecology 3: 385-397.

WIENS JA, CS CRAWFORD & JR GOSZ (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421-427.