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Chapter 6

Discussion:
Population Dynamics and Species
Interactions

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Ecology is the scientific discipline that attempts to determine the causes of patterns in the distribution, abundance, and dynamics of the earth's biota. The earth's ecosystems are complex. In any given habitat, there are tens to hundreds or even thousands of different species. These influence each other both through direct pairwise interactions and through indirect interactions mediated by intermediate species, processes, or substances (Levine 1976; Holt 1977; Vandemeer 1980; Schaffer 1981). Because it is impractical, if not impossible, to observe all the potential interactions among all species and processes, ecological research involves the simplifying assumption that much of the complexity of nature is either unimportant or can be subsumed within a few summary variables. Schaffer (1981, p. 383) defined such simplification as the process of ecological abstraction: "Accordingly, when the empiricist fits data to equations describing the growth rates of particular species, he has, in a sense, 'abstracted' these species from a more complex matrix of interactions in which they are embedded. Nevertheless, because the species studied, as opposed to the variables in the abstracted equations, continue to interact with the remaining, unspecified components of the ecosystem, the parameter values obtained perforce reflect, in part, the species and interactions omitted from the model."

The study of population dynamics and population interactions is, of necessity, a process of ecological abstraction. Ecologists attempt to find, through empirical observation, experimentation, and theory, the critical subset of parameters and interspecific interactions that are needed to describe and predict ecological patterns. How might the process of ecological abstraction best proceed? This paper presents five somewhat related points that may increase the efficiency of ecological research. These musings are based, in part, on discussions at the Asilomar

Conference, but have been colored by my predispositions. Although some points may seem obvious, the approach they encompass has not been used as frequently as such a categorization would imply.

STUDY MAJOR, BROAD, REPEATABLE PATTERNS

Because the purpose of ecology is to understand the causes of patterns in nature, we should start by studying the largest, most general, and most repeatable patterns. The wealth of natural-history information that has already been collected is an invaluable but all too often overlooked guide in choosing the organisms, habitats, and questions for study. All ecological research, of necessity, is performed in a particular locality on a particular group of organisms and environmental processes, at a particular time. This tends to make any particular study narrow, but can be overcome if the study is used as a test of the potential causes of broader patterns. Although ecologically unique and unusual events have a certain appeal, studies of the unique and unusual are done to the unavoidable exclusion of studies of broad, major, general patterns. With well over two million species of plants and animals on the earth, there are an almost unlimited number of unique events caused by the peculiarities of the life history, morphology, physiology, or behavior of a particular species, and by chance environmental events. Although all studies of natural history have some value, we must choose research questions based on their generality if we are to avoid having too great a proportion of the resources available for ecological research spent studying rare events and unusual patterns. For instance, oscillations in the density of a small mammal species in a particular locality would be of interest if the pattern were repeatable through time. The oscillations would be of greater interest if this same species exhibited similar oscillations in many other localities. If other species of small mammals also exhibited similar oscillations across many habitats, the phenomenon would be highly general and repeatable, and thus of great interest. Patterns that are global in extent should be studied before those that are purely local. However, both local and global studies are needed to determine which patterns are general and which are unique. This seeming contradiction is resolved later in this chapter.

Some of the classic papers of our discipline have been those that pointed out major patterns (e.g., Cowles 1899; Tansley 1949; Elton and Nicholson 1942; Hutchinson 1959, 1961; MacArthur and Wilson 1967). May (1986) took this approach in his MacArthur Award lecture, highlighting some intriguing, general patterns in food-web structure, in relative abundance patterns among species, in the relationship between the physical size of species and their species richness, and the relationship between the size of individuals and their abundance in a region. Some of these patterns are relatively well studied. Others are unstudied. For instance, we do not yet have a single terrestrial food web that has been studied

in sufficient depth that all species on all trophic levels, including the decomposer level, have been quantified. Until such work is accomplished, patterns in food webs will be inadequately described, and it will be impossible to determine their causes.

There are many ways to judge ecological generality. A few years ago, a paper was presented at the annual meeting of the Ecological Society of America in which it was suggested, as a tongue-in-cheek response to Hurlbert (1984), that all ecological experiments had an element of pseudoreplication unless they were replicated on different planets on which life had independently evolved. After all, all organisms on earth are derived from a single ancestor, and thus their responses are potentially constrained by this common heritage! This raises an important point. Should we not, as ecologists, first seek those general features of life that are likely to be repeatedly observed given the general constraints of a planet such as earth? Although we cannot explore other solar systems, we can make comparisons among continents whose biota have been geographically isolated for eons. There are many patterns in the morphology, physiology, life history, behavior, and dynamics of species, and in the structure of communities and ecosystems, that reoccur from continent to continent even though the taxa are often unrelated (e.g., Beard 1944, 1955, 1983; Cody 1969, 1973; Whittaker 1975; Mooney 1977; Cody and Mooney 1978; Orians and Paine 1983; Walter 1985). In allocating the limited time each of us has in our careers, and the funds that are available to support research in our discipline, should we not seek the causes of such similarities before we study less general processes? General patterns provide a framework within which less general patterns can be more effectively studied.

Because all habitats and all species have unique features, patterns that are repeatable across many habitats or from one species to another are unlikely to be explained by the unique features of each habitat or species. Rather, the existence of broad, general patterns suggests the existence of broad, general causative forces. If this is so, theory based on these forces should be able to predict the major patterns we see in nature. Ecology is conceptually young. Our highest priority should be to understand these forces and their ramifications for patterns in nature. Every such advance will allow us to explain some of the variance we see in nature and to determine the patterns that are not explained by these forces. It is the unexplained patterns—the unexplained variance—that then guide our future research.

LOOK FOR ENVIRONMENTAL CONSTRAINTS AND ORGANISMAL TRADE OFFS

The forces that cause pattern in ecology result from the constraints of the abiotic and biotic environment and from the unavoidable trade-offs that organisms encounter in dealing with these environmental constraints. An environmental constraint is any factor that acts to reduce the reproductive rate or increase the

mortality rate of a population. There are many such constraints. As has long been recognized, the most general constraint comes from the universal requirement of all living organisms for energy and matter. Hutchinson (1959) expressed this well when he said, "In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum 'eat or be eaten,' but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view."

Each individual organism exists within a web of consumer-resource relations. Its reproductive rate is constrained by the availabilities of the items it consumes—its resources. Its survivorship is constrained by the organisms that attempt to consume it. The universality of consumer-resource interactions has motivated both theory and experiments (e.g., MacArthur 1972; Schoener 1971, 1976, 1986; and Tilman 1977, 1980, 1982, 1988), but has not yet become as central a concept in ecology as its universality demands. In addition to consumer-resource interactions, populations are also constrained by physical factors such as temperature, humidity, and pH, and by mortality from nonbiological agents of disturbance, such as fire, windstorms, waves, or climatic variability. These physical factors can be included in a consumer-resource approach by explicitly stating how they influence resource availability, resource-dependent growth, and mortality (Tilman 1982, 1988).

In dealing with environmental constraints, individual organisms face trade-offs. If there were no trade-offs, there would be no forces favoring biotic diversity, genetic polymorphisms, or individual plasticity (e.g., Tilman 1982:234–65). The reproductive rate and survivorship that an organism attains when it experiences a particular suite of environmental constraints is determined by its morphology, physiology, life history, and behavior. Any beneficial traits that can be attained without giving up other beneficial traits should rapidly become fixed in a population. The differences among individuals, then, should be based on unavoidable trade-offs. (An unavoidable trade-off is a type of "constraint," but I prefer to call it a trade-off because it exists only if the cost of gaining one beneficial trait is the loss of some other beneficial trait or traits.)

What types of trade-offs are likely to be unavoidable? All traits that are based on allocation of some limiting item are subject to an unavoidable trade-off. Thus, a plant that allocates a carbon or nitrogen atom toward the production of a leaf cannot allocate that same atom toward the production of a root or stem or seed (Tilman 1988). For a plant to gain the ability to grow on nutrient-poor soils, it must necessarily give up some of the leaf area or stem biomass that would allow it to grow better on a rich soil. Similarly, an animal that allocates some protein to locomotor musculature cannot also allocate that protein to digestive functions. Protein allocated to one physiological process cannot also be allocated to a different physiological process. Time allocated to one method of foraging cannot be allocated to a different method. Time allocated to courtship and mating cannot be

used for foraging or the raising of young. The process of allocation of any limiting item—energy, protein, a trace metal, time, and so on—necessarily effects not just the process to which it is allocated, but also the processes to which it is not allocated. Different patterns of allocation lead to different morphologies, physiologies, life histories, and/or behaviors. A potentially beneficial trait is gained, but at the unavoidable expense of a different potentially beneficial trait. Thus, the suite of traits that leads to maximal fitness for an individual in response to one set of environmental constraints is unlikely to do so in response to a different set of constraints.

Ecological patterns result from the interplay between environmental constraints and the trade-offs that organisms face in dealing with them. General and repeatable constraints will lead to general and repeatable patterns if there are unavoidable trade-offs that organisms face in dealing with these constraints. Many components of an organism's morphology, physiology, life history, and behavior are determined by the pattern of allocation to these components, and thus represent unavoidable trade-offs. Individual organisms overcome some of these trade-offs, to some extent, through plasticity. However, there are limits to plasticity because plasticity has costs. An individual, though plastic, rarely can assume the full range of variation observed within an entire species. Species, though variable both from individual plasticity and from genetic differences among individuals, do not have the full range of variation that is observed among species. This, in its own right, is a general pattern that merits further consideration.

If the existence of general patterns implies that organisms face similar constraints, then an important step in studying such patterns is to determine what the environmental constraints are and what the patterning of each constraint is with respect to the others. This is most easily done experimentally. Based on Hutchinson's assertion, it might be best to consider initially the position of a species in its food web, and thus to determine experimentally which resources limit it. It is also necessary to manipulate the densities of the organisms that consume it, to determine their effect on the species. Observational studies of the relationships between the density of a species, the availability of its limiting resource(s), and the densities of species that consume it would help determine the generality of the patterns suggested by the manipulative experiments. Other experimental studies might reveal other environmental constraints.

THEORY SHOULD EXPLICITLY INCLUDE CONSTRAINTS AND TRADE-OFFS

Whatever the environmental constraints might be, theory should be developed to deal explicitly with those constraints. The constraints may be separate and distinct, or they may be interdependent. Such interdependence, if it exists, is impor

tant to include, because it can greatly influence the ecological pattern that a theory predicts. If a large, general, repeatable pattern is being studied, theory should start by considering only the most universal constraints. It is also necessary to determine which traits are important in species' responses to these constraints, and the unavoidable trade-offs that individual organisms face with respect to these traits. A theory that explicitly dealt with the major constraints and trade-offs could then explore their logical implications. It could determine the extent to which broad, general patterns and deviations away from these patterns could be explained by these constraints and trade-offs.

Environmental constraints and organismal trade-offs represent the underlying mechanisms whereby organisms interact with each other and with their environment. Most ecological theory has been more phenomenological than that called for above. Rather than explicitly dealing with environmental constraints and organismal trade-offs, it has sought greater generality by using summary variables that are not explicitly tied to the mechanisms of interaction between environmental constraints and organismal trade-offs (Schoener 1986). This has been valuable in establishing a conceptual framework for ecology. Although further theory of this sort will be useful, there is an even greater need for theory that more explicitly deals with mechanism (Tilman 1987).

Clearly, phenomenology and mechanism are not absolute entities but idealized ends of a spectrum. Any theory that explicitly includes environmental constraints and organismal trade-offs will be more mechanistic than most current theory. It is likely that, along the spectrum from phenomenological to mechanistic theory, there will be a point that is optimal for explaining any given ecological pattern. It is very possible to produce theory that is too mechanistic, that loses generality without gaining significant predictive power. The optimal point will be found only through the usual trial-and-error process of science. It is always possible to produce a theory that is either more or less mechanistic than a given theory. I do not present mechanistic theory as an absolute good, but rather suggest that many present theories may lack predictive power because they are not sufficiently mechanistic, that is, they do not explicitly deal with environmental constraints and organismal trade-offs.

THEORY, OBSERVATION, AND EXPERIMENT MUST INTERACT

Let me start this section by offering a simplified view of the scientific process, which is often described as having three parts: observation, hypothesis formation, and experimentation. Scientific advances come from the repetitive application of these three activities. Observations lead to hypotheses that are often formalized in mathematical theory. Theory is used to make predictions that are tested with

experiments or additional observations. This leads to the rejection, modification, or extension of the theory, and thus to new predictions that are again testable through observation or experimentation. Thus observation, experimentation, and theory are interdependent. Each gains its value from the others. Theory is valuable if it explains patterns that have been observed and makes testable predictions. Observations are valuable as tests of theoretical predictions and as they suggest new hypotheses. Experiments are valuable as tests of theoretical predictions.

Theory, observation, and experimentation advance together and cannot stand alone. The more each relates to the other, the more powerful each becomes. Even the most ardent empiricist is, of necessity, a theoretician, for it is impossible to measure everything in an ecosystem. The act of choosing some items for measurement and ignoring others represents the formation of a hypothesis as to the possible causes of pattern. Theory that is based on easily observed or easily measured items is more easily tested than theory based on abstract summary variables. Environmental constraints, by their nature, are often easily observed and measured, for they are the entities to which organisms are actually responding. Theory based on them is more easily related to observation and experimentation than theory based on more abstract summarizations.

Although many models of predator-prey or host-parasite interactions have been based on directly measurable items and processes, many models of the growth of a single population and of interspecific competition have not. Rather, models of intraspecific and interspecific competition have too often been based on the inclusion of density dependence, even though there is little evidence of direct density dependence in such interactions. Direct density dependence implies that an increase in the density of a species is directly responsible for a decrease in per capita growth rate. With the exception of territorial animals whose density is regulated in response to aggressive interactions, most population regulation is mediated through some intermediate entity, usually one or more limiting resources. Woodpecker reproduction can be limited by the number of suitable nesting holes; *Daphnia* reproduction by the density of algae. A change in *Daphnia* density influences algal density, and algal density, in turn, influences growth rate. As such, intraspecific and interspecific competition is often a consumer-resource interaction. Even for territorial animals, it is difficult to imagine how territoriality would evolve except in response to consumer-resource interactions.

Theory that describes the phenomenon of competition by using density-dependent summary variables may be broadly applicable to all types of competition, but the density-dependent summary variables cannot be directly observed. Lotka-Volterra models of competition use an abstract concept, the competition coefficient α , that cannot be directly observed but must be measured via field experiments. This has meant that many studies of competition have served merely to measure α (e.g., see reviews in Schoener 1983; Connell 1983).

Alpha, though, is just a measure of the effect of the density of one species on the growth rate of another. As soon as it is admitted that species are imbedded in a matrix of many other species, an alpha measured in the field is an ecological abstraction that depends on the densities of all other species at the time it is measured (Schaffer 1981; Tilman 1987), and is thus highly specific to those conditions. Work motivated by a "general" theory becomes highly specific and is of limited utility in seeking the causes of broad ecological patterns.

Alternatively, studies of competition based on a more mechanistic approach might gather information on the foraging behavior of species and on the availabilities of the limiting resources for which they were competing. Like alphas, information on foraging is obtained through experiments. However, unlike alphas, foraging information is potentially applicable to habitats other than that in which it is obtained and can be used to predict the dynamics and outcome of competition in other habitats. As such, a seemingly less general study of consumer-resource interactions may be generalizable to many more habitats than a study based on the "more general" Lotka-Volterra model. Indeed, this has been the case for studies of nutrient competition among freshwater algae (e.g., Tilman 1977, 1982; Tilman, Kilham, and Kilham 1982; Sommer 1983; Tilman et al. 1986). The inclusion of a few simple mechanisms of interaction related to environmental constraints (limitation by phosphorus and silicon) and species trade-offs (superior competitive ability for silicon being gained at the expense of competitive ability for phosphate) has allowed prediction of phytoplankton patterns in a wide range of lakes around the world.

If ecology is to develop a general theory, it will probably be based on consumer-resource interactions because of the universality of consumer-resource interactions. What other approach is so easily extended to whole food webs and ecosystems, as well as to the evolution of morphology, foraging behavior, physiology, and life histories? Although future research may be able to identify universal aspects to consumer-resource interactions, there are many aspects that are likely to be specific to the constraints of the physical environment and the patterning among these constraints. Such a consumer-resource-based theory may well prove to be the foundation for MacArthur's (1972) vision of ecology, as quoted by May (1986): "I predict that there will be erected a two- or three-way classification of organisms and their geometrical and temporal environments, this classification consuming most of the creative energy of ecologists. The future principles of the ecology of coexistence will then be of the form 'for organisms of type A, in environments of structure B, such and such relations will hold.'"

TREAT ECOLOGY AS A SINGLE DISCIPLINE

Our graduate students are trained, our papers are reviewed, and our grants are funded as if ecology consists of subdisciplines: evolutionary ecology, population

ecology, community ecology, and ecosystem ecology. Although there are pragmatic reasons for the National Science Foundation to use such categories, the lack of communication and synthesis among subdisciplines limits our training and vision. The natural world is not divided into evolutionary, population, community, and ecosystem spheres. Organisms have evolved in and live in a single world. Explanations for patterns in this world must be consistent not only within a particular subdiscipline, but across all of these. An explanation of an ecosystem-level phenomenon that is inconsistent with evolutionary theory is either incorrect, or evolutionary theory is incorrect, and vice versa. If evolutionary theory had been rigorously applied to many of the ideas suggested by Clements (1916), we could have avoided decades of misdirected research that treated communities and ecosystems as superorganisms. Conversely, if population ecologists had started, in 1916, to seek the causes of the broad, general patterns Clements described, that subdiscipline could have advanced much more quickly. There is much about the evolution of organismal traits that can be best understood in terms of ecosystem-level constraints, just as there are many ecosystem-level patterns that are best explained in terms of constraints on the evolution of individual organisms. The vastness of the ecological literature makes it difficult for anyone's knowledge to bridge these subdisciplines. However, major advances are likely to come from those who attempt syntheses across these subdisciplinary boundaries, for this will allow them to test their hypotheses against the accumulated knowledge of all of ecology, not just that of a single subdiscipline.

The study of consumer-resource interactions is a natural starting place for such a synthesis. The life histories of organisms, their morphology, physiology, and behavior are already studied in an evolutionary context. It is these traits that are directly relevant to the interactions between a species and its resources and between a species and other species for which it is a resource. Constraints of optimal foraging, for instance, have ramifications for community and ecosystem structure and dynamics that can be determined as soon as they are applied to a complete food web. Although I am arguing, contrary to the Clementsian view, that ecosystem structure should be predictable, in principle, from knowledge of lower-level processes, I am also arguing that evolutionary, population, and community ecology must be done in the context of the whole ecosystem.

Recent discussions of indirect effects (e.g., Levine 1976; Holt 1977; Lawlor 1979; Vandermeer 1980) have emphasized the problems inherent in interpreting interactions in multispecies communities as if only the species of interest existed. Of all the food-web linkages that exist, probably the most overlooked link is that controlled by decomposers. An indirect result of the life of a decomposer is the resupply of the mineral nutrients that are required by and often constrain plants. Because the amounts and proportions of these nutrients can have a large impact on competitive interactions among plants (Tilman 1982, 1988), all processes that influence the decomposer species are potentially important. For instance, if the litter of different plant species differed in its suitability as food for decomposers,

this could lead to changes in nutrient mineralization rates (Pastor, Naiman, and Dewey 1987). In theory, this could form a positive feedback loop that would magnify initial differences in local species composition, leading to multiple stable equilibria. Differential grazing by herbivores on plants that differed in litter quality could have similar feedback effects (Pastor, Naimon, and Dewey 1988). Only further observation, experimentation, and theory will determine if such feedback effects are important, and which aspects of food-web structure need to be considered to predict particular types of patterns.

SUMMARY

Ecological research is the process of seeking simplifying assumptions that allow us to abstract much of the complexity of nature into a few variables. There are many reasons to be optimistic that this is a viable process. The very existence of broad, general, repeatable patterns suggests that many of the unique aspects of organisms and habitat are of minor importance. Schaffer (1981) showed that there is a conceptual foundation for ecological abstraction. Much of the dynamics of complex models can often be predicted by a few equations (Tilman 1988). However, we do not yet know the level of mechanism and detail at which this abstraction might be most effectively pursued. A comparison of the mechanistic studies reviewed in Schoener (1986) with studies that are more traditional suggests that our field is still in a phase for which inclusion of additional mechanistic detail can lead to major gains in predictive ability.

In this paper, I have suggested that we should study broad, general patterns. In studying such patterns, we should pursue ecological abstraction by using the simplest possible approach that explicitly includes the most universal constraints of the environment and the unavoidable trade-offs that organisms face in dealing with these constraints. The most universal constraints may come from consumer-resource interactions because all species are, of necessity, parts of food webs. A major advantage of studies at this level of mechanism is that the critical variables (availabilities of various resources, foraging behavior, morphological or physiological processes relevant to resource acquisition and use) can be directly observed. Theories based on these observations are less likely to be habitat-specific than those based on more phenomenological summary variables. Moreover, such an approach is easily expanded to additional trophic levels, as needed. The process of seeking ecological abstraction may be accelerated if there is closer interaction among empiricists, experimentalists, and theoreticians. Such an interaction would be aided if theory were based on variables that could be directly observed. Finally, such a process should cut across the current interdisciplinary lines in ecology: an observation of a general pattern on any conceptual level is of potential importance in testing concepts that had initially been developed on other levels.

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