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1

Ecological problems and how they are approached

Introduction

Much of ecology consists in making observations and then devising plausible explanations for the observations. Because alternative explanations of the observed phenomena frequently are available, the process by which the conclusions have been reached is known as "weak inference." It is not that the conclusions are necessarily wrong; the problem is that there is little assurance that they are right, and the widespread use of the approach has led to severe criticism, from both outside and inside the field.

In principle, manipulative experiments provide a preferable alternative, because their planning requires at least an implied prediction of the outcome, and making predictions is an integral part of science. The after-the-fact explanations mentioned earlier are sometimes called "predictions" by their promulgators, but there is no assurance that the information was not available before the prediction was made. There is no implication of dishonesty. The danger is as follows: All workers in ecology have a lot of factual information about the real world, and assuming that they are interested in understanding nature, they think about how things work. It is virtually impossible to separate known facts from the thought process. The knowledge is, perhaps unconsciously, taken into account in formulating hypotheses about how nature works. Thus, when a "test" is proposed, the prior knowledge is used, and the outcome is known in advance. Such a confirmation is, of course, spurious. I have selected an example from one of my own publications (Hairston 1964). In a consideration of the relationship between species abundance distributions and trophic level, I predicted that there should be a greater variance among the abundances of terrestrial carnivores than among the abundances of the coexisting herbivores. The reasoning was that the carnivores should be affected more by competitive interactions, which would be expected to be stable and hence would lead to large differences in abundance. Herbivores, on the basis of the arguments in Hairston, Smith, and Slobodkin (1960),

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should be affected by their respective intrinsic rates of increase, which should vary irregularly with weather conditions, involving frequent reversals. Thus, the herbivores would have less chance for long-continued trends in their respective abundances, and they were predicted to show less variance in abundance. After a tenuous series of assumptions and calculations, I presented evidence that confirmed the predictions for soil arthropods. It must be pointed out that my graduate students and I had carried out research on those organisms irregularly for thirteen years (Hairston & Byers 1954; Hairston 1959; Engelmann 1961), and much of the relevant information must have been in my mind, at least subconsciously, at the time that I made the predictions. Such lapses of rigor were common at the time, and remained largely unchallenged until the current controversy over hypothesis testing in ecology. [See the papers in Strong et al. (1984b), for example.]

Appeals are sometimes made to the complexity of nature, apparently in the hope of avoiding the rigorous thought that is required to formulate clear hypotheses, and to avoid devising proper tests to permit choices among competing hypotheses. The process of formulating clear hypotheses and devising acceptable tests, called "strong inference," was clearly described and vigorously promoted two decades ago in a famous paper by Platt (1964). An integral part of the process is planning experiments that will yield answers to the questions that are asked about nature. Some ecological questions are posed on such a broad scale and are of such complexity that satisfactory experiments have not yet been devised to answer them. Nevertheless, successful completion of many field experiments over the past twenty-five years has shown that some problems that once were considered unapproachable by experimentation have been attacked and solved.

Before considering the ecological problems that remain to be solved, we may as well admit that one person's solution is another's challenge. That is because ecologists are not in full agreement as to what is acceptable as "proof." There are some who regard at least one of the following questions as having been answered, and probably there are some who do not agree that these questions are important.

Ecological questions amenable to experimentation

All of the questions that follow have been attacked through field experiments, but few ecologists would argue that they have been

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answered fully. In later chapters there are descriptions and critiques of a number of these experiments. The experiments are arranged according to the various habitats in which ecologists have worked, rather than the kind of questions that follow. The reason for categorizing experiments by habitat is the hope that the arrangement will encourage an understanding of the ecological processes in each kind of setting, rather than trying to generalize over all settings. The field has not advanced to the stage where we even know if such generalizing is possible in principle.

What determines the abundance of species in nature?

This question continues to vex ecologists, despite much work on the subject since 1957, the date of the Cold Spring Harbor Symposium at which the proponents of various views vigorously aired their opinions. The stimulus for the symposium was the debate over density dependence versus density independence. One of its unfortunate aspects was that the protagonists never agreed on the terms of the debate. Both groups conceded the accuracy of the observations of the other. It was the relevance of the observations that was at stake. On the one hand, there were the plain correlations of abundance and population changes with aspects of weather (Davidson & Andrewartha 1948a,b), or the determination of the intrinsic rate of natural increase by laboratory-controlled temperature and moisture (Birch 1953). On the other hand, there were many laboratory populations showing a reasonably good fit to the logistic (the most density-dependent) model, long-term field studies showing fluctuations around a fairly constant mean, and the logical and mathematical argument that without density dependence, populations would fluctuate with increasing amplitude, eventually either going extinct or reaching completely unrealistic numbers. After the symposium, the debate was not so much settled as exhausted, and except for the exchange between Smith (1961,1963a) and Andrewartha (1963), most ecologists simply turned to other interests.

The dichotomy has been shown to be false, in that unexpected effects have been found. For example, it had been more or less assumed that the limitation of a population by its food supply automatically meant that the population was under density-dependent control. Yet Wise (1975) showed that spiders were food-limited, without their abundance

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being able to affect the supply of food, and Juliano (1986) reported a similar finding for scavenging carabid beetles. Filter-feeding sessile organisms in large bodies of water must frequently be in the same kind of situation.

As a result of work in the last three decades, the question is now posed in a more sophisticated manner, and we are concerned with whether density-dependent factors operate continuously or are interrupted by stochastic disturbances. Some ecologists are arguing that the disturbance itself is necessary for the stability of some ecosystems (Lewin 1986). If that is the case, we need to know the frequency of the disturbance, and especially the environmental factor that constitutes the disturbance. The dispersal phase in the life cycle seems to be especially sensitive to density-independent influences, especially when the dispersers are numerous and small and are carried passively by wind or water. Their success or failure in reaching a particular habitat has been known to determine the outcome of carefully executed experiments. For example, Paine's famous demonstration that a predatory starfish determined the composition of the community of sessile invertebrates (Paine 1966, 1974) could not be confirmed by his student Dayton (1971) because the mussels, which were the competitive dominant, failed to settle in large numbers during his study (Underwood & Denley 1984).

How important are interactions between species?

Ecological field experiments have established beyond question the fact that interspecific competition, predation, and mutualism are not rare in nature. What has not been settled is whether or not any of them, especially competition, is sufficiently pervasive to have an important effect on the dynamics and structure of assemblages of coexisting species. In two surveys of the literature that appeared almost simultaneously, Schoener (1983) and Connell (1983) reached different conclusions about the prevalence of interspecific competition, as shown by field experiments. The difference was only partly due to Connell's more restricted set of journals and years. Interpretation was more important. Connell was more rigorous in what he accepted as a satisfactory experiment, but he omitted from his analysis experiments involving an effect on one species at one time and place. As might be expected, he found interspecific competition less common than Schoener did. Schoener (1985) has reviewed the differences between the

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analyses, and it seems clear to me that the difference is largely related to the prior mind-sets of the two authors, Connell (1975, 1980) having moved away from an initial partiality toward the frequent occurrences of competition, and Schoener (1974, 1982) arguing strongly for their importance in ecological systems.

Mathematically derived community theory relies heavily on the assumption that interspecific competition is the primary negative interaction among species. Therefore, the question debated by Connell and Schoener is vitally important to our understanding of the sets of coexisting species that we call guilds. The term "community" is here used in its original sense to mean all organisms in an area – the living part of an ecosystem. Thus, the application of theory really applies almost exclusively to guilds, as restricted from the original proposal of Root (1967), to include by usage, if not by formal agreement, a group of taxonomically related species that presumably are competing for a common resource. The critical word here is "presumably," because even in cases where competition has been conclusively demonstrated by satisfactory experimentation, the finding is nearly always confined to fewer species than a prior choice of guild membership would dictate (Hairston 1984). Schoener (1986) has discussed the usages and defended the restrictions. I refrain from quoting his preferred term, and continue to use "guild" in the restricted sense. In no example is guild membership based on demonstrated interspecific competition among all necessary combinations of the proposed members. The existence of ecological or morphological differences has been used to justify the assumption that guilds are structured by competition among the members. But that leads to the circularity that the differences arose because competition was the force selecting for the development of the differences. Noncircular identification of guilds based on interspecific competition would be difficult; there has been no successful attempt in that direction.

Given this unsatisfactory state of affairs, our recourse must be to conduct the complete set of experiments necessary to test the postulated composition of a guild. Some authors accept the assumption that competition in the past was responsible for the differences and that therefore competition is no longer detectable. They ignore the fact that prevailing theory does not require the elimination of competition, only that it be reduced in intensity to the point where coexistence is possible. The experiments in which competition has been demonstrated have shown that it could still be detected. There have been rela-

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tively few examples in which even an approximately complete set of experiments has been carried out on all members of a proposed guild.

When predation is a relevant interaction, either with or without competition, the term "food web" is satisfactory; unlike "community," it is a term that has carried the same meaning for many years. A theory of food webs is being developed (Cohen 1978; Pimm 1982), but there is serious question that it will provide predictions of the outcomes of experiments, for a number of reasons explained by Paine (1988). It is true that both predation and competition have been demonstrated experimentally in some associations of species, but those phenomena were looked for independent of each other and independent of any unifying theory. One problem with current food-web theory is that it does not provide for competition at the lowest trophic level – an obvious shortcoming in most terrestrial ecosystems. Quantification of food-web relationships is a need that has caused difficulties in the construction of theory and has forced theoreticians to use qualitative relationships. The difficulty should be overcome by properly designed experiments.

Parasites constitute a different category, but one that is overlapping with predators. Mathematical models of their populations and those of their hosts have produced a variety of results. In some models, very regular cycles are predicted, a prediction that has been verified for some human viral diseases (Anderson & May 1979). Other kinds of parasites, with life cycles differing from those of viruses, carry quite different predictions (May 1985; Toft 1986). The rarity with which populations fluctuate cyclically in nature suggests either that they are unaffected by their parasites or that the important parasites of natural populations have some of the complex properties discussed by Toft (1986) or by Holmes and Price (1980). One example of an experimental test of the influence of a metazoan parasite on the population of its host is provided by the red grouse, *Lagopus lagopus scoticus*, and its nematode parasite *Trichostrongylus tenuis*. The parasite has been implicated in the long-term cycle of its host (A. Dobson, pers. commun.).

The natural history of mutualistic relationships has always fascinated ecologists. Only recently has mutualism been investigated quantitatively [see Addicott (1986) for a review]; its consequences for the structure and dynamics of guilds and communities are largely unknown (Schoener 1986). I predict that experimentation with mutualists will prove to be more difficult than has experimentation with

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competitors, whereas predator–prey systems will be intermediate in difficulty.

How important are competition, predation, and mutualism?

This question cannot be answered at present because of the uneven attention that has been paid historically to the three kinds of interaction. Competition has received the most attention, probably because of its central position in community theory. Sih et al. (1985) attempted to address this question, but their analysis misinterpreted the experiments, as far as the hypotheses of Hairston et al. (1960) are concerned, and the result is unsatisfactory. As already stated, mutualism lags far behind as a subject of experimentation.

Progress will be made in studying the relative importance of the different kinds of interaction only when experiments are planned to answer the specific question. My experiments on the salamander genus *Desmognathus* show that it is possible to obtain results in systems in which both predation and competition are operating (Hairston 1986), and the earlier work of Paine (1966, 1974) and Menge (1972) had done the same for the rocky intertidal habitat.

Do interspecific interactions affect larger ecological units than guilds?

Guilds are defined in such a way that competition is all-important within them, and although it is possible to imagine competition affecting communities of a variety of taxonomic groups, predation will be the interaction of interest where more than one trophic level is involved. Experiments have been conducted in the rocky intertidal, where it is difficult to confine the definition of a guild, a difficulty that appears to be due to the nature of the limiting resource: space on a solid substrate. The papers by Yodzis (1986) and Roughgarden (1986) analyze this situation. In terrestrial assemblages larger than guilds, there have been no attempts to separate the interspecific interactions discussed earlier from what are called "ecosystem processes" – production, consumption, and decomposition. Freshwater habitats, in contrast, have yielded important results on the interactions within entire communities. The experiments of Neill (1981, 1984), Neill and Peacock (1980), Schindler (1974), Hall, Cooper, and Werner (1970), and others are described in Chapter 7.

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Do interspecific interactions determine the composition of multispecies associations, or do these mostly reflect adaptations of individual species?

This question asks whether guilds and communities are "real" or are the products of our imagination. A negative answer to the former question, or a positive answer to the latter does not necessarily imply that species interactions are of trivial importance in ecology. That would mean that we would have no a priori means of estimating what array of species would have detectable interactions. Thus, a guild would be defined as a group of species among which competition has been demonstrated. There would be no means by which we could choose a set of species before the necessary experiments were conducted. Thus, sophisticated theories could be constructed to explain the mechanisms by which such guilds function and the abundances of the species involved, but it would not be possible to predict anything about guilds not yet identified. Community ecology would be in the position it has long occupied, that of writing theory to explain what is already known. The composition of many groups "of taxonomically related species that presumably are competing for a common resource" would be at least partly determined not by the strength of interactions among them but by the adaptations of the individual species to the physical environment.

What is the expected effect of any of these ecological forces in determining the direction of natural selection?

It is frequently stated that evolutionary questions are not approachable by field experiments, despite the fact that such experiments have been carried out. It is true that it is necessary to grant a basic assumption before accepting the result of such an experiment. That assumption is that the current ecological conditions will continue to provide the selective pressures that presumably led to adaptive differences between related populations. If the differences relate to the physical environment, physiological experiments will suffice to confirm adaptive differences. Where interspecific interactions are involved, it is much more difficult to meet the necessary conditions than it is where the physical environment provides the selective pressure, because proper experiments are a prerequisite for demonstrating the existence of the interactions. The whole question of demonstrating

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natural selection under field conditions has recently been treated at length by Endler (1986), and it should be noted that one experiment, described in less than a page of text, constitutes his treatment of field experiments.

How would the effects of these forces differ?

The answer to this question is likely to be highly specific to the individual situation. Theoretical work in both population biology and evolutionary ecology on the effects of competition and predation (Roughgarden 1979) has given fairly straightforward distinctions of the expected differences, but Dayton (1973) showed how interpretation could change when observations were followed by experimental analysis, and my experiments with *Desmognathus* showed that what had been interpreted as the result of competition was largely the result of predation (Hairston 1986). The topic is in need of much more critical work before any generalizations can be made.

A discussion of the ways proposed to solve the problems

The questions posed earlier are much the same as those posed throughout the history of ecology. It is true that the relative emphasis placed on the different questions has shifted over the years, with recent work concentrating on interspecific interactions. There have been dramatic changes in the methods used to attack the problems. During the past decade, the use of field experiments has increased exponentially (Schoener 1983), and a longer period beginning in the mid–1960s saw the dominance of mathematical models, including the introduction of at least two new journals to handle the flood of papers (Simberloff 1983). A review of the recent literature shows that all of the methods to be discussed next are actively used at present. There is, of course, variation in emphasis among ecological journals, depending on editorial policies and the tastes of contributors.

Field observations

Ecological problems are recognized through observations made in the field, and therefore such observations are vital to the science. To become preoccupied with theory or with methodology to the exclusion of looking at nature is surely to lose contact with the world

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that we are trying to understand. Such preoccupation always leads to oversimplification and thus to a limited vision of how nature works. It is true, of course, that some simplification is involved in any explanation of a natural phenomenon, and if we do not seek explanations, we can scarcely be said to have a science. Therefore, most publications of ecological observations are accompanied by interpretations. The emphasis in this book is to question the extent to which natural situations can be used to interpret the processes that brought them about. Interpretations of natural situations may be correct, but frequently they have been shown to be incorrect on subsequent experimentation. Despite the popularity of direct interpretation of ecological observations throughout the history of ecology and its advocacy by prominent ecologists, there are strong theoretical objections to this use of weak inference (Peters 1976); consequently, ecological experiments have become popular, even though they are "labor intensive, time-consuming and expensive" (Rosenzweig et al. 1985, p.194).

The members of one subset of direct observations have been called "natural experiments," and their importance in interpreting ecological processes has been defended vigorously by Diamond (1986). I argue that to label natural events experiments evades the issue of why manipulative experiments are conducted, which is first to test the validity of a specific idea, and second to avoid the charge of a posteriori reasoning.

There is no question that some situations and events in nature are especially favorable for constructing hypotheses about how the compositions of certain communities were determined and about how they function. This is especially true when a significant spontaneous event occurs after the start of a study, providing the very important initial conditions: those existing before the "experiment" began. Such a phenomenon provided the basis for the size-selective predation hypothesis of Brooks and Dodson (1965). After observations had been made on the plankton community in a small lake in Connecticut, it was colonized by a planktivorous fish, *Alosa pseudoharengus*. The subsequent difference in species composition among the planktonic crustaceans stimulated Brooks and Dodson to propose their hypothesis. Even though such events increase the likelihood that their interpretations are correct, that does stretch the concept of an experiment, and it exaggerates their significance to give them that name. Nature has no stake in being understood by us, and the so-called natural experiments universally lack important elements of experimental design, topics deferred to Chapter 2.

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