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FORUM

On the practice of ecology

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Progress in ecology

Despite inspiration from their subject and an unwavering belief in its importance, ecologists often seem to be in a state of self-doubt about progress in ecology. When we observe the advances occurring in other fields, such as cellular and molecular biology, we cannot help noting that our own science does not appear to be progressing in the same way. We are debating many of the same issues today that we were decades ago. While there appears to be progress on some specific questions, we have not observed major advances in our understanding of fundamental ecological processes. Recently, an author of one of the best and most widely used general ecology textbooks told me that when he and his coauthors sat down to do the second edition of their book, they found very little that was substantively new in ecology in the years since the publication of their first edition. In contrast, a colleague who is the author of one of the best textbooks in developmental biology tells me that he has to rewrite major sections of his text for every new edition because the field is moving so fast. Frustration with the apparent lack of progress has led numerous ecologists to question the way scientific research in ecology is done (e.g. Dayton 1979; Pielou 1981; Simberloff 1981, 1983; Hall 1988; Keddy 1989; Peters 1991). The criticisms of ecology have emerged primarily from within the field, often from established and successful researchers. This essay attempts to outline a useful critique of ecological research. The motivation is not philosophical issues of epistemology, but the more practical problem of progress within our science.

Many ecologists attribute the lack of progress in ecological science to the nature of the 'beasts,' not to methodological issues. It is unclear to what extent many ecological phenomena are controlled and therefore predictable. For example, current ideas that communities may not be near equilibrium, and the recent re-emphasis on the necessary role of historical explanations (e.g. Gould 1986; Ricklefs & Schluter 1993) mean that ecological systems will never be as predictable as physical or chemical processes, but many researchers think that the way ecology is done could be part of the problem.

I will argue for a general critique of ecological research based on principles that are widely held among ecologists. From this critique we can make some modest proposals for improving the way ecological research is pursued. These principles include

1 the need for predictive models and testable explanatory theories;

2 an appreciation of the role of natural history vis à vis ecology;

3 the need for pluralism and diversity, and especially for new approaches within our young science.

Testable theories

Most of the criticisms of ecology over the past 25 years have been based on the Popperian notion of refutability (Popper 1968; Popper 1972; Schilpp 1974). According to Popper, science advances by generating theories that make claims about the world – predictions that can be tested. The problem of induction cannot be solved, therefore nothing in empirical science can ever be 'proven' – theories can only be tested and, at best, not rejected. Scientific progress comes from generating better and better theories that survive ever more stringent tests, although in practice this process of rejecting and replacing theories may occur intermittently, when whole 'paradigms' are changed, rather than in a slow continuous fashion (Kuhn 1970).

While the central role of refutability of scientific theories is widely accepted among practising scientists, including ecologists, a few ecologists have argued that falsifiability has been over-emphasized. Fagerström (1987) states that the importance of testability has been exaggerated, and other qualities such as beauty are equally important attributes of a scientific theory. The anarchistic 'anything goes' philosophy of science advanced by Feyerabend (1975) has been invoked to argue against criticisms of ecological theory (May 1981). Such a view, however, destroys the materialistic core of science, replacing the admittedly difficult concepts of truth or reality with those of taste and aesthetics. This leads to a sort of nihilistic postmodern view of ecology, where there is no truth, only stories, and the choice among stories is a question of individual taste (and power). To the degree that we reject the notion of falsifiability as a criterion for ecological theory, we reject the claim of ecology to be an empirical science, and consign it to the humanities. One of the essential differences between science and other forms of knowledge is that science makes claims about the world in the form of predictions that serve as testable hypotheses.

Critics concerned about testability have serious problems with much of the theoretical and empirical work in ecology. They point out that most of what is called 'ecological theory' is not theory at all, but deductive games that seem to provide 'insight' but are not testable (Peters 1991). In those cases where theoretical models have made predictions, they have been rejected (Hall 1988). Rather than being testable, ecological models are often assumed to have deductive validity ('the model captures the essence of the system') because they follow mathematically from simple, reasonable assumptions. Popperians are also critical of much ecological data collection. They argue that the role of data should be to test hypotheses, but ecological data are often collected without any clear theoretical question in mind. Ecological field data often seem to be collected and treated like case studies, which are then put into apparently causal narratives that give us the feeling of understanding processes and phenomena. Such explanations have more in common with what is called explanation in fields like history than with explanation as we know it in other sciences.

In response to such criticisms one might argue that given the difficulty in generating testable ecological theories, we are doing as well as can be expected. But evolutionary biology, which appears to be more historical and less amenable to the scientific method than ecology, has had much more success in generating testable theories. The theory of inclusive fitness, for example, has resulted in a substantial advance in our understanding of the behaviour of many animal species, and it has generated numerous testable hypotheses about the behaviour of individuals as a function of their degree of relatedness. Even historical theories, such as those regarding meteor impacts, have generated testable predictions (e.g. world-wide presence of iridum layers in sediments of a certain age, and simultaneous extinctions across a wide geographic range). Although much of evolutionary theory cannot be tested experimentally, hypotheses have been tested using the comparative method. Ecology has been much less successful.

'Naive falsificationism'

While the core of the criticism of ecology based on testability is compelling, those critiques which have been based solely upon this idea have been much too narrow. For example, R. H. Peters takes an extreme 'naive falsificationist' position in his controversial book *A Critique for Ecology* (1991). Peters accurately describes many of the ills of ecology, and concludes that ecologists should focus on generating testable predictions. The best way to do this, he argues, is through statistical fitting and extrapolation of empirical relationships, not by seeking mechanistic explanations. This prescription for ecological research does not distinguish between explanatory theories and what Loehle (1983) calls calculation tools. Calculation tools are atheoretical prediction devices such as most statistical and phenomenological models (e.g. 'curve-fitting'). Criteria such as goodness of fit and accuracy of predictions are sufficient for evaluating a calculation tool. Theories, in contrast, are mechanistic explanations.

> A good theory should do more than predict, it should explain. Its structure should be interpretable in terms of the real world. ... We can accept a [calculation tool] as being sufficiently accurate, but we can only fail to reject a theory. (Loehle 1983)

Loehle gives regression as an example of a calculation tool, because the statistical model is usually not a functional (mechanistic) model. But since calculation tools do generate testable predictions, Peters is satisfied with them. As an alternative to mechanism, Peters advances a sort of positivist 'behaviourism' (in the sense of the behavioural psychologist B. F. Skinner), in which there are no explanatory theories, only black box predictions: inputs and outputs fitted by regression.

Although calculation tools are an extremely important part of science and engineering, scientific understanding ultimately comes from explanatory theories. Calculation tools are one of the best methods for generating predictions in ecology today, and therefore they must occupy a central place in modern ecology. But ecologists should also seek explanatory theories. Mechanistic explanation is not only consistent with the goal of producing testable predictions, but explanatory theories give rise to much broader and therefore stronger predictions. A more general mechanistic model will make predictions over a much wider range of conditions and is ultimately a more useful model, although in many instances a calculation tool will make more accurate predictions in a narrower domain (Levins 1966). According to Peters's prescription, we would be satisfied with developing prediction equations for the probability of getting a specific disease as a function of different environmental, genetic and behavioural variables. Time spent looking for the 'cause' of a disease would be discouraged as too abstract and deductive, and not likely to yield immediate predictions. But the analysis of quantitative trends in the study of diseases has been most valuable in providing clues for mechanistic understanding of diseases. Peters either does not believe there are mechanisms in ecology, or he believes that they may exist but could never be uncovered. In a sense, his prescription for ecology is engineering without science.

Where do theories come from?

The concept of testability establishes one relationship between theories and data. But where do the testable theories come from? This difficult question is often ignored, but the need for testable theories requires that we try to address it. In addition to imagination and speculation, we can point to two activities that can play an important role in the development of explanatory theories: (1) the search for and analysis of patterns in nature, and (2) the construction of deductive mathematical models.

PATTERNS IN NATURE

Data are not just useful in testing hypotheses; they are first of all a source of patterns. The search for patterns at all levels is one of the most critical parts of the science of ecology today. Examples include patterns in community structure (e.g. Brown & Maurer 1989; Cornell & Lawton

1992) and food webs (e.g. Pimm *et al.* 1991), correlations among traits in different species and environments (e.g. Bazzaz 1979; Keddy 1992), and allometric trends (e.g. Shipley & Dion 1992). The study of natural patterns could be called quantitative natural history. Patterns can be used to generate calculation tools, and may provide clues about underlying processes. In an important sense, such patterns, not individual facts or models, are the subject of ecology. One of the difficulties confronting ecological research is that we do not even know at which levels we can expect generality and predictability. Although there have been numerous calls for generality in ecology (e.g. Keddy 1989), generality has to be found, it cannot simply be declared. The study of patterns is the most important source of clues, and the existence of so many patterns is the basis for our conviction that ecology can become a predictive as well as a descriptive science.

Although most ecologists would probably agree with the statement that the search for patterns is an important aspect of ecological research, it is not widely accepted as a conscious goal in practice by journals and granting agencies. How many ecologists write their grant proposals and papers in terms of hypotheses and tests retroactively, even though the work was not conceived in this way?

Much ecological data collection does not seem to be directed by a search for patterns *or* the testing of hypotheses. A large fraction of the research published in our empirically oriented journals seems to describe individual case studies, e.g. 'the ecology of community (or species) X.' Phytosociologists continue to describe and classify vegetation types as a goal in itself, even though the biological meaning of the categories and their contribution to understanding of processes in vegetation are questionable. Of course, a certain amount of empirical knowledge is necessary before we can say anything about a system, and description of individual cases is necessary before we can find patterns, but the practical question is how many case studies can be reasonably justified in this way.

DEDUCTIVE MODELS

The construction of deductive mathematical models can make important contributions to the development of explanatory theories. Deductive models can show what is possible. Reality is one of many imaginable worlds, and to a large extent science asks why the observed world occurs and not the others. Deductive models are logical instruments that demonstrate the mathematical consequences of clearly stated assumptions, and thus require that the assumptions be clarified. Mathematical formality can help to make verbal models evolve into predictive theories, and offers the promise of generality (Caswell 1988; Murdoch *et al.* 1992).

Although deductive models can make a major contribution to the development of explanatory theories, they don't seem to have done so in ecology. For example, the Lotka–Volterra population models have been around for decades, and they are still the subject of intensive theoretical investigations, although they show little sign of producing testable predictions. One can ask what hope there is of obtaining testable theories from other classic models such as niche theory, or from currently fashionable models such as nonlinear dynamics, lottery models, nonequilibrium thermodynamics, fractals, and exergy. Rather, the mathematical developments in our theoretical journals seem to grow more and more remote from empirical predictions. Theoreticians could counter that some hypotheses have been generated by these models (e.g. Pimm 1991; Law & Morton 1993), and that advances in their analysis may suddenly lead to testable theories.

Not only have theoretical models in ecology rarely yielded testable predictions, but, when they have made predictions, they have been refuted (Hall 1988). For example, the Lotka–Volterra predator–prey model predicts oscillations (either neutral stability, limit cycles, or damped oscillations that converge on an equilibrium point) in which the predator and prey cycle out of phase. In the models, oscillations in the prey population drive oscillations in the predator populations, and vice-versa. In nature, oscillations in predators and prey are observed, but while predator oscillations often track prey oscillations, I know of no known case in the field in which evidence supports the hypothesis that predator oscillations are responsible for those of the prey. Rather, the prey population oscillates even when the predator is removed. Indeed, despite numerous attempts, starting with Gause & Huffaker, I know of only one case in which anything like the oscillations of the models have been obtained in the lab (Utida 1957). Yet, despite the lack of support for the core prediction of the Lotka–Volterra predator–prey models, they remain a staple of mathematical ecology and are still employed extensively in theoretical studies, because they are believed, on deductive grounds, to 'capture the essence of the system,' or they are considered of interest because the models have 'interesting dynamics'. Generation of testable predictions does not seem to be a primary goal of theoretical ecology.

I would suggest that one of the major reasons why most theoretical work in ecology does not yield testable hypotheses is that theories often do not address patterns of nature. Rather, most theoretical work addresses abstract questions. As one example of this, I relate a recent discussion with a colleague who (like many of us at one time or another) was working on a model in which species with similar niches are able to avoid competitive exclusion. I inquired as to which of the many patterns of species diversity observed in nature his model would address. He replied that his model was not directed towards any pattern in the field. Rather, he hoped to explain species diversity 'in one place,' not differences in species diversity in different places (or times). This is a fallacious notion of what an ecological theory can do. One cannot explain diversity in one place (except perhaps in a Zoo or Botanical Garden); one can only hope to explain differences in diversity over time and space.

Theorizing would be more likely to produce testable theories if the 'problem' to which a model is addressed is some pattern observed in nature, rather than abstract questions of a general nature (Grimm 1994).

I have noted that the colleagues with whom I discuss these issues are *either* very critical of undirected collection of data *or* of abstract model building. There seems to be a centrifugal force in ecology that keeps theory and data far apart from each other and from what we are trying to understand. While the situation is improving, both theoretical work and data collection in ecology often have a tendency to follow their own internal logic rather than attack ecological questions. We need to fight against these centrifugal forces by pulling theory and empirical work together and directing them both towards questions in ecology. These questions come from the study of natural history.

Natural history and ecology

The relationship between ecology and natural history is central to one's conception of ecology as a science, and therefore to its practice. For example, in his attempt to make ecology more predictive, Peters (1991) tried to drive a huge wedge between the study of natural history and the science of ecology. He pointed out that the former is more of an art; the latter a science. Thus, we are to conclude that they have little to do with each other. But this inference belies a major misunderstanding of how ecology has advanced at all, and how it can advance farther. While natural history and ecology may represent very different approaches, they share something extremely important: their subject. In fact, the art of natural history is more advanced than the science of ecology, and natural historians make more testable predictions than do theoreticians. For example, there are scores of field ecologists who can go to a site in the field that they have never visited before and make strong claims about the management history, testable predictions about the future course of succession or the effects of specific grazing regimes, fertilizer applications, etc., even if they are unable to provide a satisfactory theoretical account of the basis for these predictions. There is much knowledge in the art of natural history, and one of the goals of ecological science is to transform this intuitive knowledge into scientific knowledge, and thus enable us to extend it.

I view natural history as a craft rather than an art, because it can be used to do things and to make things, and therefore it must be able to make predictions. Using the craft of natural history, ecologists can create a wetland similar in most measurable ways to naturally occurring wetlands. We know enough to influence the vegetation in an area in a desired direction, and in many cases we know how to manage an area to protect specific species, etc. There is a wealth of ecological knowledge, but most of it today is in the form of the craft of natural history rather than the science of ecology. Natural history and the intuitive understanding of many natural phenomena by field ecologists are perhaps the best available 'technologies' for ecological decision-making today, better in many cases than currently available calculation tools. It is the successes of natural history that offer hope to the science of ecology, because they show us that there are patterns out there which should be amenable to scientific attack.

The fundamental flaw in the attack on natural history is that the question of how to advance ecological science is very different from the purely philosophical questions of epistemology. There may be an epistemological gulf between natural history and ecology, but that does not mean that this distinction is a good basis for decisions about practice. I would like to advance the historical hypothesis that most of the major advances in ecology have been made by scientists with either an extensive background in field natural history or at least a very large treasure of biological knowledge in their heads. I invite the reader to make her/his own list of the 10 greatest contributors to the science of ecology. I predict that a strong interest and background in natural history will be a more common trait among the individuals on the list than any other scientific interest or background.

On the other hand, natural history *can* be a distraction, just as mathematics can be. There certainly are many ecologists who are so immersed in the details of their 'systems' that they seem to think that ecology is the study of particulars, and characterize any attempt to build a model as 'oversimplified'. One can see a parallel, in terms of progress in ecology, between the undirected collection of ecological facts or data, and the building of totally abstract mathematical models.

Pluralism in ecology

According to the argument advanced here, ecology needs new ideas, approaches and theories. Thus, we need diversity and pluralism in ecological research. Since we are working in a young science and don't know which approaches are most likely to bring progress, we should try many different ones, and see what works. If our central dogmas are weak, we should not be very concerned about defending them. Abrahamson *et al.* (1989) have argued convincingly that ecologists should be more bold and open to new ideas, and less concerned about the dangers of fads.

If we are to try new approaches and bring theory and data together, we will probably have to take on somewhat smaller bits of nature: narrower domains in which to search for patterns and theories. General theories of population dynamics, species diversity, etc., have not been very successful in generating testable hypotheses (Murdoch *et al.* 1992). The old debate about what limits population size, density-independent or density-dependent factors, assumes that population size is controlled by the same factors in all species in all communities. Such an assumption is probably not justified, and this is part of the richness and fascination of the natural world. If we could understand the basis of some diversity gradients, or predict population sizes of some groups of species, we would be making very good progress. Just as it was not possible to find a cure for diseases in general, but possible to make progress in understanding and curing classes of diseases (environmental, genetic, infectious, etc.), it may be possible to understand some diversity gradients or predict the population dynamics of certain species. The testable theories we have seen in ecology (e.g. concerning plant defences, causes of succession in particular classes of habitats, and food webs) seem to address somewhat narrower questions than the general abstract models of the 1960s and 70s. Ecology may not be one relatively homogeneous subject. Pluralism means less grandiose, but more useful, ecology.

Recommendations

From the general arguments above, I advance the following modest recommendations for ecological research.

1 *Ecological theory.* Theoretical work should eventually contribute to the development of testable theories. How long is eventually? Totally abstract theoretical development without attention to immediate predictions is desirable because it may eventually contribute to the development of testable theories, but if a line of theoretical work does not yield predictions after several years (or decades or scores of publications), it might be worth questioning if this particular approach is likely to meet this criterion in the future. I suggest that each theoretical project be directed towards some observed pattern in nature, rather than addressing abstract questions such as 'What is the behaviour of a model with assumptions A, B & C?'

2 *Empirical work.* Data can be used to:

(a) Look for patterns that can be the bases for generating hypotheses and theories. Case studies are necessary steps to seek patterns, especially in the exploration of previously little-studied systems, but one can ask how long this phase should be pursued if it does not yield compelling patterns.

(b) Develop and calibrate empirical calculation tools which can be used for making atheoretical predictions.

(c) Test calibrated calculation tools and explanatory theories.

3 *The organization, politics and funding of ecological research.* The general argument outlined above also leads to some recommendations for how ecological research is organized. The need for pluralism argues strongly against concentration of power within the ecological research establishment. Ecological research will not be served well by the presence of dominant 'schools of thought,' whether they be systems analysts, phytosociologists, mathematical modellers, or any other single perspective. Since there is neither a clear best road ahead, nor any technology that will clearly lead us forward, research funds would perhaps be better distributed more widely in smaller amounts, rather than concentrated in a few influential institutions.

4 *The teaching of ecology.* Ecology should be taught with a relatively high degree of scepticism and criticism, rather than as a body of accepted theory. At the stage of our science today, we should be teaching approaches rather than facts, and emphasizing the patterns that are our subject. Many of the best teachers of ecology already do this.

Ecology on its own terms

Ecology is a unique subject which to some degree has to be defined in its own terms. We cannot apply what we see in other sciences to ecology directly, nor should we try to make ecology look as much like other sciences as possible. We cannot make ecology like physics by simply acting like physicists, any more than one can make an automobile fly by acting like an airline pilot instead of an automobile driver. Ecology may require special approaches, methodologies and skills. For example, MacFadyen (1975) argued that, unlike other scientists, ecologists should remain broad and resist the urge to specialize. I would like to extend MacFadyen's argument: The solution usually put forward to bridge the gap between theoreticians and empiricists in ecology is that they should talk to each other. This certainly seems like a good idea, and it is espoused more often than practised. I would like to suggest that discussions between theoreticians and empiricists may not be enough. Rather, individual ecologists should attempt to be both theoreticians and empiricists. Modellers should learn as much as possible about the natural history of the systems they are trying to model, and empiricists should learn as much as possible about any models that may be relevant to their research. Perhaps only when the tension between these two aspects of ecological research is brought into single heads will this tension be most productive. There is probably a trade-off, but I am suggesting we might make more progress if more of us were both competent empiricists and theoreticians, rather than being excellent in one area and disinterested (or incompetent) in the other.

Because ecology as a science is weak, researchers tend to get distracted into other fields of study. For example, how many statistically oriented ecologists become focused on statistical techniques, to the point of being statisticians disguised as ecologists? Others become taxonomists, or mathematical modellers. Ecology seems to be a science with many branches but without a centre. Often the quality of work in the branches is evaluated more in terms of some other field (e.g. mathematics, statistics, physiology) than in terms of its contribution to ecology. Ecology as a subject seems to be 'cannibalized': it is a source of interesting questions for other fields, but questions that often do not advance ecology itself. Because it is difficult to make progress in ecology, we are perhaps attracted to other activities in which we feel we can make progress. We must fight these centrifugal forces and remain focused on our goal. The guiding principle should be what works *in ecology.* In a sense, the message in this essay is simply that we should remain focused on our subject, and not get distracted into other subjects or activities. For ecology is among the most important of sciences, and, even more compelling to some of us, it is the most fascinating.

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