Ten Suggestions to Strengthen the Science of Ecology

GARY E. BELOVSKY, DANIEL B. BOTKIN, TODD A. CROWL, KENNETH W. CUMMINS, JERRY F. FRANKLIN, MALCOLM L. HUNTER JR., ANTHONY JOERN, DAVID B. LINDENMAYER, JAMES A. MACMAHON, CHRIS R. MARGULES, AND J. MICHAEL SCOTT

There are few well-documented, general ecological principles that can be applied to pressing environmental issues. When they discuss them at all, ecologists often disagree about the relative importance of different aspects of the science's original and still important issues. It may be that the sum of ecological science is not open to universal statements because of the wide range of organizational, spatial, and temporal phenomena, as well as the sheer number of possible interactions. We believe, however, that the search for general principles has been inadequate to establish the extent to which generalities are possible. We suggest that ecologists may need to reconsider how we view our science. This article lists 10 suggestions for ecology, recognizing the many impediments to finding generalizations in this field, imposed in part by the complexity of the subject and in part by limits to funding for the study of ecology.

Keywords: ecology, ecological theory, environmental policy, scientific method, population dynamics

Ecology is the science that addresses the relationship between living things and their environment (Haeckel 1866). It has also been called the science that accounts for the abundance and distribution of species (Andrewartha and Birch 1954). These simple phrases define a field that encompasses an immense range of organizational, spatial, and temporal scales. Organizationally, ecology deals with the characteristics of individual organisms (e.g., physiological and behavioral ecology) and their evolution (e.g., evolutionary ecology), the dynamics of species populations (e.g., population ecology), and the interactions among populations of different species and their physical–chemical environment (e.g., community, landscape, and ecosystem ecology). Ecology deals with spatial scales ranging from parts of individuals (e.g., leaf physiology) through the entire planet (biosphere dynamics) and with temporal scales of seconds or minutes (e.g., physiology and behavior) through evolutionary time that can reach tens of thousands or even millions of years. Tangentially, ecology also incorporates studies of environments from past times on our planet (paleoecology), studies of our planet's physical characteristics (soil, atmosphere, and geochemistry), and even studies of the potential

Gary E. Belovsky (e-mail: Gary.E.Belovsky.1@nd.edu) is a professor and Gillen Director in the Department of Biological Sciences and director of the Environmental Research Center, University of Notre Dame, Notre Dame, IN 46556. Daniel B. Botkin is a research professor in the Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106. Todd A. Crowl is an associate professor in the Department of Aquatic, Watershed, and Earth Resources, College of Natural Resources, Utah State University, Logan, UT 84322. Kenneth W. Cummins is a senior advisory scientist with the California Cooperative Fishery Research Unit and adjunct professor in the Department of Fisheries Biology, Humboldt State University, Arcata, CA 95521. Jerry F. Franklin is a professor in the Division of Ecosystem Sciences, College of Forest Resources, University of Washington, Seattle, WA 98195. Malcolm L. Hunter Jr. is Libra Professor of Conservation Biology and a professor in the Department of Wildlife Ecology, College of Natural Sciences, Forestry, and Agriculture, University of Maine, Orono, ME 04469. Anthony Joern is a professor in the School of Biological Sciences, University of Nebraska, Lincoln, NE 68588. David B. Lindenmayer is with the Centre for Resource and Environmental Studies, Australian National University, Canberra, Australia. James A. MacMahon is a professor in the Department of Biology, College of Science, Utah State University, Logan, UT 84322. Chris R. Margules is a project leader at the Cooperative Research Centre for Tropical Rainforest Ecology and Management and program leader of the Tropical Landscapes Program at CSIRO (Commonwealth Scientific and Industrial Research Organisation) Sustainable Ecosystems, Tropical Forest Research Centre, Atherton, Queensland, Australia. J. Michael Scott is a professor in the Department of Fish and Wildlife Resources, a research scientist with the US Geological Survey, and the leader of the Idaho Cooperative Fish and Wildlife Unit, University of Idaho, Moscow, ID 83844.

for life beyond our planet. With so many organizational levels, over such a wide range of spatial and temporal scales, a universal understanding of ecological issues has been difficult to achieve, especially in the short time that the science has existed. However, the accelerating impact of human beings and their technologies on every environment on Earth has imparted to the science of ecology an applied imperative that cannot be ignored—to seek sufficient understanding as quickly as possible to predict future ecological conditions (Mayr 1988, 1997).

Beginning as a formal science in the 19th century, ecology grew in popularity with the rise of environmentalism as a political and social movement during the second half of the 20th century and with growing concerns about human impacts on the environment (McIntosh 1985). Before the middle of the 20th century, few knew the word *ecology.* Today, the Ecological Society of America and the British Ecological Society are large organizations with more than 13,000 members, and many government agencies and private consulting companies employ professionals with doctorates and master's degrees in this field. Yet, in spite of ecology's great growth in popularity, we are concerned that ecology is not progressing at a rapid enough pace toward rigorous answers to the science's original issues: understanding the relationships between living things and their environment and the determinants of species abundance and distribution patterns. Consequently, there are few well-documented general ecological principles that can be applied to pressing environmental issues. When they discuss them at all, ecologists often disagree about the relative importance of different aspects of the science's original and still important issues (e.g., competition, energy flow, predation, nutrient cycling) (May and Seger 1986, Cherret 1988, Odum 1992, Thompson et al. 2001).

It may be that the sum of ecological science is not open to universal statements because of the wide range of organizational, spatial, and temporal phenomena, as well as the sheer number of possible interactions. But we believe that the search for general principles has been insufficient to know to what extent generalities are possible. We recognize the impediments imposed by the limited levels of research funding for the study of ecology, but we fear that conceptual impediments have also slowed ecology's progress. Ecologists may need to reconsider some of the ways that we view our science. The spirit of our comments is meant to be self-reflective and is not aimed at particular individuals or subdisciplines; in fact, all of the authors of this article have been subject at times to the listed concerns in our personal research and writings.

Our concerns have been distilled into 10 suggestions for improving ecological theory and practice. The first four of these suggestions deal with the sociology of the science of ecology. The fifth and sixth deal with the ideology that permeates ecological thinking, which may not be supported by observation. The seventh through ninth suggestions deal with the empirical evidence currently available to ecology, and the last deals with the critical application of ecological knowledge to current global environmental problems.

1. Issues come in and out of fashion in ecology, like the latest haute couture, without scientific resolution. Sometimes the emphasis seems to be on novelty itself. This fickleness leads to the same issues resurfacing decades later under a different rubric and a guise of novelty, often without reference to the previous work. Novelty in itself does not make an idea more important. On the contrary, it may be better to solve a long-standing unresolved issue than to address a new question simply because it seems new (Likens 1983).

For example, ecology still has not resolved the basic issue of how populations are limited. Malthus (1798) and Darwin (1859) broached this question; Elton (1927) resurrected it; furiously debated in the 1950s (Andrewartha and Birch 1954, Lack 1954), it resurfaced in the 1980s as the importance of competition (Wiens 1977, Schoener 1983, Strong 1984); and it is once again out of vogue without resolution, no doubt to be resurrected at some future date. Similar patterns in the sociology of ecology can be developed for other ecological fashions: foraging behavior, energy flow and productivity, control of nutrient cycling by consumers, the importance of predation, and so on.

We propose that ecologists identify a set of basic questions and focus on resolving these issues (see May and Seger 1986, Cherret 1988, Odum 1992, Thompson et al. 2001). We acknowledge that it may not be possible to pose universal statements that encompass all ecological scales of organization, space, and time. But we believe that the search for general statements for even a limited set of scales has not been adequately addressed. It would be valuable to identify sets of basic questions that are tractable within limited ranges of organizational, spatial, and temporal scales.

Questions will be removed from this set if they are found to be unimportant, and new questions will emerge, but the periodic appearance and disappearance of what constitutes an important question should not be whimsical. Resurfacing can be constructive as knowledge accumulates and is organized using new ways of framing problems, or when new methodologies allow new kinds of data to be acquired, but this does not happen often enough (and old ideas are often presented as new ones after an inadequate literature search; see below) (Lakatos 1978). When issues come in and out of fashion, concepts are misremembered and redefined. As Ford (2002) points out, a recurring criticism of ecology is that concepts are often not clearly defined or, if they are, the definitions do not hold (Loehle 1988, Peters 1991).

2. There is a lack of appreciation of past literature; this, in part, leads to ecology's fickleness toward central issues. Frequently, ecologists pose seemingly novel ideas without recognizing that the same idea was developed decades earlier in well-known articles by famous ecologists (With 1997). Some classic articles, such as Hutchinson's (1959), have covered a myriad of ideas. Too often current ecologists claim novelty for ideas that in fact have an extensive history. For example, the role of consumers in shaping biogeochemical cycles is not a new topic (Hutchinson and Deevey 1949), but it is now treated as such. Furthermore, ecologists often do not keep abreast of work conducted outside their own country. As an example, Young (1990) reviewed the rediscovery of larval ecology by authors who had refused to read the existing literature.

Ecologists should exhibit greater scholarship by better researching the literature and teaching their graduate students to do the same. Just because an article is more than a decade old does not make it irrelevant or intellectually invalid. There are wonderful intellectual histories of ecological concepts (e.g., Kingsland 1985, McIntosh 1985), a number of compilations of seminal articles in ecology (e.g., Hazen 1970, Dawson and King 1971, Real and Brown 1991, Dodson et al. 1999), and ecological textbooks and review articles that attempt to synthesize ecological knowledge. Too often we observe faculty directing their graduate students to these references with the implication that reading them (and even memorizing dates, authors, and their institutions for preliminary exams) will bring them up to date on the development of ecological thought. These syntheses provide a useful gateway into the literature about a concept, but because histories, compilations of articles, and other syntheses all undergo the subjective filtering of the authors, nothing substitutes for scientists directly tracking the development of the concepts that they are studying in the original works. We know that this is a daunting task, given the proliferation of literature, but it is necessary for good scholarship. Furthermore, although they are improving, computer searches and search methods are still haphazard, especially for older literature. The identification of central questions and themes (see suggestion 1 above) could make this task easier by focusing the use of scientific literature.

3. There is inadequate integration of empirical and theoretical ecology. This weakness has been bemoaned for decades (Watt 1962), but progress seems slow (O'Connor 2000, Ford 2002). Some view ecology as a last bastion of science unencumbered by mathematical formality and do not take advantage of mathematics as a useful tool, while others view ecology as mathematics unimpaired by the bounds of nature and rely too much on untested theoretical predictions. Very simply, mathematics is the purest form of logic and is a useful tool for creating rigorous, testable hypotheses (Hilborn and Mangel 1997). Ecology needs formal theory as a part of a search for unification (Macfadyen 1975) and generalizations. Without theoretical underpinnings, ecologists will, as Watt (1971) wrote, "all be washed out to sea in an immense tide of unrelated information." Theory is essential for both fundamental and applied issues. However, some mathematical elegance may have to be forsaken to produce mechanistic theories built on parameters that are ecologically measurable, so that predictions can be explicitly tested. Ecologists need to understand a theory to be able to design valid tests, because an experiment must meet the assumptions of the theory. For example, the application of a foraging theory that is based on random encounters with food items to a species that does not randomly encounter foods is not a test of that theory.

We encourage ecologists to pay attention to Fretwell's (1972) admonitions on how ecologists should optimally mix theory with empiricism to further their own aspirations and to advance the science. Fretwell, along with O'Connor (2000), stresses the importance of developing rigorous theories and then testing them. Ecologists need to recall what Schoener (1972) cautioned about more than 30 years ago: Ecology has a "constipating accumulation of untested models," and we need to test them. This is very different from the encyclopedic accumulation of facts in the hope that some pattern will emerge with future statistical analysis, as proposed by Peters (1991). Nor is Fretwell's admonition consistent with Shrader-Frechette and McCoy's (1993) claim that ecology will never progress beyond the compilation of case studies that support or refute very general statements about the operation of specific ecosystems.

Ecology, perhaps more than the other natural sciences, often deals with issues of immediate societal concern. It can therefore be difficult to design experiments and make observations that are free of social, cultural, and personal values. We encourage ecologists to acknowledge the role of these values in the conduct of their research (Shrader-Frechette and McCoy 1993). However, we stress that ecologists should strive to minimize the impacts of these values on their results, rather than to encourage them, as some researchers suggest (Shrader-Frechette and McCoy 1993).

4. There is inadequate integration of natural history and experimentation. Some suggest that this is because of the impending death of natural history (Wilcove and Eisner 2000), but this seems to us an unlikely cause of the problem. Natural history qualitatively identifies the patterns that the science of ecology attempts to explain, and through experimentation, ecology attempts to elucidate causal factors (Shurin et al. 2001). Too often natural history becomes encyclopedic enumeration without considering pattern (O'Connor 2000), while too often ecological experiments are designed with no relevance to real-world conditions, so that experimental results may not address patterns that have practical or theoretical importance. For example, experiments can almost always be designed to show that competition or predation is important by introducing sufficiently large numbers of competitors or predators into the experiment. But it is necessary to ask whether the experimental levels of competitors and predators are indicative of abundances found in the field and, therefore, whether they are an important causal factor in the actual operation of a particular ecological system. If the experimental levels needed to produce an effect are greater than those observed in the field, then the pertinent question becomes what prevents the necessary levels from being realized in nature.

Ecological experiments should be designed for realism, to reflect conditions found in the field, and not just to provide statistically significant results. In the context of a realistic experiment, a nonsignificant result becomes meaningful for unraveling an ecological pattern. For example, to address whether or not predation limits a particular prey population, an experiment should compare prey numbers with naturally occurring numbers of the predator and with numbers of prey in the absence of the predator. If a statistically significant difference does not emerge, then predation may not be important, but to conduct an experiment with greater than naturally occurring predator numbers to obtain a statistically significant effect may have little bearing on the question of whether the predator limits the prey in nature (Hairston 1989).

5. There often is an implicit belief that ecological patterns are the result of single causes, but ecology's complex nature may be due to multiple causation (Hilborn and Mangel 1997, Shurin et al. 2001). Attempting to impose an explanation for ecological patterns that is based on the assumption of a single cause can lead to unproductive debates and can further the fickleness of ecological research in relation to central issues. An example of this is the question of whether predation is important in limiting populations and structuring ecological communities. Answers to this type of question are often a trivial affirmative, after which ecologists lose interest in the real issue, which is how the relative impact of one cause changes under different environmental conditions, in the presence of other causal factors, and as a result of previous conditions (i.e., state dependence). Furthermore, it may be naive to assume that causal factors do not change in their action over time and space. This means that experiments should be designed to examine multiple causes over a range of conditions. Ecologists need to realize that there may not be a single, correct explanation to ecological patterns and that similar patterns may arise because of different combinations of causal factors (Dayton 1973, Huston 1994), some of which may not be commonly considered (e.g., indirect effects, diffuse competition, apparent competition).

6. Applications of equilibrial and disequilibrial perspectives are often misguided in explaining ecological patterns. Formerly, ecology was dominated by an acceptance, without proof, that ecological systems achieved equilibria. In recent decades, this idea has been rejected on the basis of the weight of evidence; nonetheless, articles that assume equilibrial conditions, especially theoretical works, continue to appear (consider, for example, the immense body of theory that is based on the logistic model of population growth).

There is sometimes a confused impression in the scientific literature that the failure to achieve equilibrium implies an absence of causality in nature. On the contrary, equilibrial perspectives may elucidate how a causal factor operates, but this does not mean that equilibrial outcomes will be observed in nature. There is also confusion between the failure of a system to achieve equilibrium and the possibility that ecological systems may be attracted to an equilibrium that is never obtained or even closely approached. The essence of a causal factor is that the system is attracted toward the equilibrium that this factor could produce. For example, if a competitive equilibrium is not observed, this does not necessarily mean that competition is unimportant and is not attracting the system to certain states. These characteristics mean that ecologists need more information, because they must understand dynamics and not simply describe states of the system.

Furthermore, given temporal variation in conditions, ecologists need to consider a temporally varying attractor. For example, just one of the reasons that the logistic equation for population growth has been criticized for being an equilibrium theory is that it has a single value for carrying capacity, whereas actual carrying capacity can vary temporally, and the same equation might still apply for specific conditions. There is a need to clarify whether causal ecological processes tend to drive a system toward an equilibrium or steady state, even though external factors—and their variation in time and space—never allow the system to attain that equilibrium or steady state.

A classic assertion in ecology is that life tends to build up structures, while the nonbiological environment tends to tear these structures down. In terms of the second law of thermodynamics, life can be viewed as a local decrease in entropy at the expense of a global increase in entropy, while the physical environment functions locally and globally to increase entropy. This creates a dynamic, not a static, situation. Ecologists need to focus more on the dynamics of ecological systems rather than to emphasize arguments about equilibria and disequilibria that can, by themselves, be both theoretically and empirically empty.

7. There is inadequate replication over time and space in ecological studies. By *replication* we mean repeated studies in different ecosystems and in the same ecosystem over time. This is different from the issue of adequate replication in an experimental design to address problems of statistical power, of type I versus type II error, and of pseudoreplication (Hurlbert 1984, Heffner et al. 1996). No matter how good the design of an individual experiment may be in addressing the causes for an ecological pattern, it may only provide insights into ecological issues for a particular place and time, especially if patterns are multicausal and vary in time and space. Given that there are 1.4 million named species and 20 or more recognized biomes, it is likely that there will be different dynamics in different ecosystems. This does not negate the value of well-designed short-term and local experiments, but ecologists should not adopt as globally applicable the results of one or a few experiments in a single ecosystem type under a very small range of conditions that occur in nature (Harvey and Pagel 1991). The lack of replication over time and space is part of the problem of why ecologists too often fail to adequately test theories (Weiner 1995, Ford 2002). This lack of replication also means that ecologists cannot achieve an adequate understanding of scaling issues, even though these issues have become fashionable (Hewitt et al. 2002).

The need for greater replication is not necessarily the responsibility of individual ecologists; rather, the duty of replicating ecological studies lies with the community of ecologists. Our call for replication differs from Shrader-Frechette and McCoy's (1993) call for numerous case studies that would at best provide weak insights into the operation of specific ecosystems, because we see replication allowing ecologists to construct and test theories that address why particular ecosystems differ in their operation. It might seem that the willingness to accept the results of an experiment in one type of ecological system in a narrow range of conditions as a global result demonstrates that ecologists are searching for universal statements, contrary to our initial assertion (see suggestion 1 above). On the contrary, the lack of a well-defined set of general questions leads ecologists to accept, without adequate reflection, the extent of the meaning of a single experiment.

A corollary to the statement that experiments should be replicated in different environments is that, in general, experiments need to be conducted over the long term so that the results can be observed as the environment varies. Very simply, a greater range of evidence is needed in a multicausal world. The willingness to accept the results from one or a few experiments contributes to ecologists' fickleness toward central issues in the science (see point 1 above). This argument has been made in great detail in a series of recent articles (Hobbie 2003, Kratz et al. 2003, Rastetter et al. 2003, Symstad et al. 2003, Turner et al. 2003). The National Science Foundation's US LTER (Long Term Ecological Research) and ILTER (International Long-Term Ecological Research) programs try to remedy this problem; however, there are too few LTER sites, and there is insufficient coordination among sites in addressing central ecological issues.

We believe that ecology can only progress in answering its critical issues with a comparative approach—conducting the same study in a number of kinds of ecosystems. This would permit ecologists to examine similarities and differences among very different systems to find commonality, where the commonality arises from a well-developed formulation of theories. This differs from comparative approaches that simply catalogue observations without a theoretical framework to place them in context (Peters 1991, Shrader-Frechette and McCoy 1993). We are confident that such an approach would reveal how variable ecological systems can be and yet still function and persist. It would reveal the commonalities and, therefore, the generalizations that may apply to different ecological systems.

8. Data incompatibility and lack of rigor in obtaining data, and especially reliance on qualitative measures of ecological dynamics, often hinder the comparison of existing long-term and multilocation data. How often do ecologists ask whether their data will be comparable with data from previous studies? If measurements are made in common units, they can be compared over time and space, even if the precision of measurements changes (improving, we hope) with new methodology. Instead, ecologists often attempt to find expedient surrogate measures, especially for applied problems. For a surrogate measure to be of value, the surrogate must be highly correlated with the real measure of interest, but this is seldom verified before a surrogate is used in a study. For example, indicator species are frequently invoked to explain what is happening in an ecosystem or to describe and then explain an environmental problem. But a recent review of the use of indicator species suggests that, at least given present knowledge, they provide poor or even misleading explanations (Lindenmayer et al. 2000).

Data compatibility problems particularly apply to the testing of theory: Is the measurement being made with units and at scales of space and time so that data can be compared with what models predict? For example, studies of the photosynthesis of plants as affected by environmental conditions are rarely done for different species under comparable environmental conditions, even though there are many models that make use of such relationships (Botkin 1993). One researcher may use one kind of light source while another uses a different one; one may measure and control humidity while another ignores this variable; soil water concentration may be measured in one study but not in another. It is often remarkable how many studies of an ecological issue can be found in the literature and yet, when the data are combined for comparison, how little has been comparably collected so that valid comparison can be made. In these cases, large quantities of poor data do not substitute for fewer data of high quality. This may sorely restrict the ability to synthesize the currently available data, even though synthesis of existing data, in lieu of collecting more data, is in vogue.

Data inconsistencies and incompatibility contribute to the lack of clarity of concepts, including the inconsistent definition of concepts, and are, in turn, affected by this lack of clarity (Shrader-Frechette and McCoy 1993, O'Connor 2000). A careful and clear description of methods, which is too often lacking in the ecological literature, is a prerequisite for obtaining data compatibility. Ecologists need to ask whether they are making measurements that are appropriate to the issue being addressed and that are comparable to the measurements in other studies related to the issue. This requires better coordination among ecologists, and it would be helpful if ecologists came to some agreement on a list of the major issues, as discussed earlier. The true value of synthesizing data from different studies to meaningfully address important ecological questions may not emerge until new studies provide the necessary high-quality data.

9. Methodology and statistics should not be driving forces in ecology. Questions should be the driving forces, arising from observations, including natural history. Better methods improve ecologists' ability to measure phenomena, and better statistics allow us to better ascertain the meaning of measurements made in complex systems. However, high-powered, novel methods and statistics do not substitute for the quality of primary data, nor do they provide an excuse to avoid careful collection of data. Most important, they do not substitute for a clear definition of fundamental questions and a search for cause and effect (Johnson 1999, O'Connor 2000). For example, geographic information systems, time series analysis, and pooling of data in a meta-analysis typically do not, by themselves, elucidate causal factors. They are tools that help discern patterns, which suggest the direction that research might take to establish cause and effect; that is, they may help to guide the pursuit of a set of general questions that have already been established.

Ecologists should differentiate between the use of, and advances in, research techniques (such as remote sensing, microchemical analytical methods, and new computational and statistical techniques) and fundamental issues in research (such as the search for causality and the quality of evidence addressing an ecological issue), and they should understand the importance of both. Data collection, whether from natural history observations or from experimentation, needs to be designed and analyzed in the context of the specific ecological issue to be addressed. Nothing substitutes for the careful development and testing of concepts; methods and statistics are the tools to aid in this endeavor, not its raison d'être.

10. Ecology as a fundamental science is sometimes seen as distinct from the application of ecology to solve environmental problems. On the one hand, some ecologists do not view the pursuit of solutions to environmental problems as "real" science. On the other hand, some ecologists do not view the pursuit of knowledge as valuable for its own sake, because this activity may not immediately or directly benefit human existence (Shrader-Frechette and McCoy 1993). However, there should be no conflict between ecology as a rigorous science and ecology as a basis for solving environmental problems. On the contrary, a strong science leads to sound management.

For management, ecology must identify the likelihood of a system failure and provide society with choices among alternative actions that will minimize this likelihood. This can be seen as an engineering perspective, and some might believe that the rigorous establishment of scientific principles does not motivate it. On the contrary, however, many advances in science have been driven by the need to solve practical problems (e.g., the search for a more efficient engine led to the development of the science of thermodynamics, which in turn led to the development of the diesel engine). Because of the great complexity of ecological systems, the need to answer a practical question may help focus fundamental scientific inquiry, and practical problems and their solutions can provide a test of ecological theory.

Ecology as science and ecology for environmental decision-making should be equally fostered, and it should be recognized that the two endeavors are equally valuable. There is no reason that an ecologist cannot perform both functions, but an individual's work should receive a different kind of professional evaluation for each one.

In summary, we believe that ecology is too unfocused, that ecology is traveling avenues that are not the most productive, and that ecologists are forgetting the science's antecedents upon which to build. The 10 suggestions in this article are not intended to restrict the freedom of inquiry by ecologists; rather, they are intended to expand the science's horizons by reminding ourselves of the basic attributes of ecology. In thinking about these points, each of us can recall times when we have failed to heed our own admonitions. Furthermore, each of us can find ourselves agreeing on occasion with some of the perspectives that we generally caution against here. All of us are subject to forgetting the points we have set forth here, but we need to try to keep them in mind. There is no way to mandate changes in the science, and most of us would be resentful of such mandates. Therefore, our points reflect questions each of us should ask daily as we conduct our science, in the hope of making more substantive and rapid advances, so that ecology can become more predictive (Kolata 1974, Moffat 1994).

Acknowledgments

We thank Gene Likens and Lee Talbot for helpful comments. As we indicate in the body of this article, we acknowledge our debt to many ecologists, too numerous to list, for their past contributions that formed the basis for this paper.

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