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# CONTRIBUTIONS

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## *Commentary*

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### **Proclaiming a New Ecological Subdiscipline**

#### **Summary**

Assertions by eminent ecologists of the importance of the science of ecology in the coming century depend for their validity on the answers to the following three questions: (1) What legitimate claims can be made for the societal necessity of ecology? (2) What are the objects of ecological research? (3) Is there an independent theory of ecology, as there is a theory of chemistry, physics, or genetics, or is ecology a summary of phenomenological information?

#### **Introduction**

The first loyalty of any scientific discipline must be to truth itself. Over the past several centuries, it has become obvious that neither philosophy nor religion, the classical and ancient purveyors of truth, had the honesty and courage to stick to what they knew as true. They pandered to the powerful, the governmental and fiscal forces that have provided them with funds to support professorships, livings, and endowments. Of course, money and power are valuable partners to searchers for truth, but they also subvert it.

There have been, and are now, exceptional individuals who are im-

mune to this criticism. Nevertheless, I have the impression that the church, synagogue, and academia, as institutions, are no longer seen as unsullied sources of truth.

Scientists are more generally trusted than most intellectuals. But sciences are also subject to skepticism. Only those sciences that are seen to focus on a search for truth survive.

A group of experts may see a need that they feel uniquely capable of meeting, an intellectual quest that they are particularly concerned with following. If this attracts followers, they may have created a new scientific discipline.

Ecology appeared as a science at the beginning of the 20th century, when a group of British botanists and naturalists founded the British Ecological Society to emphasize field studies of plant physiology (Sheail 1988). That was a time when many sciences, belief systems, and technologies began. Many of these (like eugenics, Freudian analysis, steam-operated motor cars, logical positivism, and Soviet Communism) did not last through the century. Ecology as a science survived, although its present foci might have surprised its founders.

Research almost always generates new questions; in some sciences, this is sufficient for a discipline's survival. There is broad agreement on the next big question in some sciences. To answer big questions may require major collaborative projects.

Sensing devices in satellites, oceanographic voyages, and complete deciphering of genetic code all require massive consensus of scientists and remarkably expensive facilities and equipment.

Considering the field of biology as a whole, it has been more difficult to gain consensus about the importance of particular projects. For decades, however, cellular and molecular biology studied basic problems one at a time, almost as if there were a problem of the month or year. I recall when they all seemed to be working on protein structure, later on membranes, then on genetic identification, and so on.

Despite the fact that ecologists have come to use high technology in ways unimaginable a century ago, (e.g., Colwell and Lees 2000), ecology has not focused on single gigantic problems. Different workers work on different organisms and different questions. There is almost a sense that certain investigators or schools own certain locations or certain organisms.

Divisions have appeared within ecology, such as population ecology, landscape ecology, conservation ecology, and more. Some of these are strongly disjunct. Practitioners of biogeochemical ecology and physiological ecology might never meet during their professional lives. Some of the subdivisions of ecology have created separate societies, and specialized ecological journals have proliferated.

Ecology is being divided into workable subspecialties, circumventing the monolithic definition of ecology as “the study of the interaction of organisms and their environment,” which is much too big an area for meaningful research, and also is not an actual question. It is a hopeful intention.

There is no shortage of interesting questions. Any research project generates enough questions to last an investigator’s lifetime. The next century will continue the search for details of the mechanisms of biogeochemistry, will continue to discuss why certain areas have a larger or smaller number of species than other areas, and how different species manage to survive the awkward contingencies of nature.

Obviously, in the next century there will be need for careful field investigations of many kinds. The results of these investigations will have to be effectively used. This requires solutions to problems of data acquisition and storage, and finding ways to use massive data pools in environmental decision making. These are the same kinds of problems ecology has been facing for the past century. But there will also be fundamentally new questions.

Not only must ecology concern itself with what many believe to be crises, such as destruction of habitat, extinction of species, pollution of air and water. It must also deal with crises within the discipline and in the relation between ecology and other sciences. These have received less attention, perhaps because most ecologists are so busy that they don’t see the crises, or are so enthusiastic that they don’t believe the crises are real.

Recent Ecological Society of America proclamations (Carroll et al. 1996, Daily et al. 1997) refer to these questions on an organizational level. They are basically statements of goals.

What are ecology’s chances for the future? Arguably, the optimal strategy for survival of organisms and institutions requires that they change to meet changing conditions (Slobodkin and Rapoport 1974,

Slobodkin 1992). It is not necessarily the case that changes in organizations and institutions are always beneficial for survival. I will examine recent change in ecology from this standpoint.

### The new sub area

Occasionally, new specialties arise from new information or techniques, but sometimes new fields are born by proclamation. New goals for ecology are spelled out in pamphlets, meetings, and resolutions prepared by the Ecological Society of America, the leading professional organization for American ecologists. These proclamations are not scientific critiques of the discipline of ecology itself, nor are they specific research proposals. They are generally concerned with how funding agencies and government bodies can be persuaded to support ecology. For example, a group of senior ecologists recently asserted:

*[Once] good science consisted of . . . (i) doing first-rate research and (ii) publishing it in the technical literature for the benefit of scientific colleagues. . . . [A] third activity must now be added by all scientists: (iii) informing the general public (and, especially, taxpayers) of the relevance and importance of our work. . . . In our view, it is necessary to train students in ecology who will be ready and willing to devote part of their professional lives to stemming the tide of environmental degradation. . . . We believe that such efforts should be rewarded as part of the process by which ecologists are considered for academic posts, granted tenure in universities, elected to membership in learned societies. . . . Ecologists have a responsibility to humanity, one that we are not yet discharging adequately . . . and we pledge ourselves to that task.—Bazzaz et al. 1998 (slight abridgement by L.B.S.)*

This proclamation essentially pledges ecologists to a role of politi-

cal and social activism, and assumes that training as ecologists equips them for this role. It is representative of the emerging specialty of ecological persuasion, which may also be termed social or perhaps societal ecology.

What questions are appropriate for societal ecology? When any group of scientists proclaims its own social importance, there is the danger of losing scientific status and becoming another social activist sect. There are no perfect parallels, but the transformation of Marxism from an academic economic doctrine to a political agency for world revolution may be close to what concerns me.

Three basic questions must be answered as the century of societal ecology begins. If they cannot be answered, the role of expert policy adviser outlined in Bazzaz et al. is an empty boast.

*Basic question number 1.—* What legitimate claims can be made for the societal necessity of ecology? Unlike most academic sciences, the spokesmen of ecology have declared ecology to be the salvation of humanity by offering a set of crusading mottoes. If these ideas were taken seriously, they would result in large investments in ecological research, with the nominal goal of preserving the viability of the planet. For example, a recent Ecological Society of America publication asserts:

*Historically, the nature and value of Earth’s life support systems have largely been ignored until their disruption or loss highlighted their importance. For example, deforestation has belatedly revealed the critical role forests serve in regulating the water cycle—in particular, in mitigating floods, droughts, the erosive forces of wind and rain, and silting of dams and irrigation canals. Today, escalating impacts of human activities on forests, wetlands, and other natural ecosystems imperil the delivery of such services. The primary threats are land use changes that cause*

*losses in biodiversity as well as disruption of carbon, nitrogen, and other biogeochemical cycles; human-caused invasions of exotic species; releases of toxic substances; possible rapid climate change; and depletion of stratospheric ozone.* (Daily et al. 1997)

Based on available scientific evidence, we are certain that ecosystem services are essential to civilization. Ecosystem services operate on such a grand scale and in such intricate and little-explored ways that most of them could not be replaced by technology. Human activities are already impairing the flow of ecosystem services on a large scale.

If current trends continue, humanity will dramatically alter virtually all of Earth's remaining natural ecosystems within a few decades (Daily et al. 1997). Some of the assertions quoted are extremely strong. I believe the world would be a better place if we acted on them as if they were literally true, but are they literally true? On a practical level, metaphor and hyperbole are suspect and literal truth is needed (Slobodkin 1993). For example, it is generally agreed that water and air purification are among the most important of ecological services, but it is possible to argue that the water purification function of a natural ecosystem can be duplicated at reasonable cost, with comparable quality, by an activated sludge sewage plant. Sewage plant design and maintenance is generally done by sanitary engineers with no formal training in ecology. From this, it is possible to conclude that at least some ecological services, essential to civilization, require neither ecologists nor intact ecosystems. Note that this refers only to potability. Other uses of natural aquatic ecosystems must be considered. This generates questions about the assertion that ecosystem services operate on such a grand scale and in such intricate and little-explored ways that most could not be replaced by technology. The definition of ecological services in Ecological Society manifestos (Ehrlich and Daily 1993) is often ambiguous.

The assertion that human activities are impairing the "flow of services" may be true, but is not obvious without careful analysis of what constitutes the "flow of services."

This has been discussed at length by Sagoff (1997). Is there somewhere a list of services that would permit us to judge how they can only be provided by intricate ecosystems, and how intricacy is measured or graded?

The reference in Daily et al. seems to be to the great biogeochemical cycles of elements. It is possible to infer from classical ecological sources that the biogeochemical cycles are predominantly due to the activities of prokaryotes, and would be performed well by a tragically simplified collection of organisms. If this is so, other arguments must be used for the preservation of eukaryotic species diversity.

It is arguable that all aspects of ecology were already altered to some degree by humans centuries ago. Daily et al. seem to be concerned with a pristine natural state that has not existed for millennia. In short, although the assertions in Daily et al. (1997) may, in fact, be valid in some sense, they are stated so strongly that it will be necessary for ecologists in the next 100 years to clarify them, support them, or refute them before claiming that the world is in danger in the sense indicated, or that ecology is in a position to help. If ecology cannot do this within the standards of normal science, the future of support for ecology as a science is endangered by claiming that it can.

*Basic question number 2.*—What are the objects of ecological research? Depending on one's viewpoint, ecologists claim to be studying objects called landscapes, communities, populations, and ecosystems. There are other designations. All of these are in some sense multi-organism aggregations embedded in, and sometimes forming, an inanimate matrix. It has proven difficult to get agreement on which, if any, of these terms designates a fundamental unit for ecological study. Sagoff (1997) has suggested that these terms are

defined in such a way as to be essentially useless in practice.

Some ecological terms, such as "community," "climax," and "natural balance," are actually reifications of empirically empty assertions (Slobodkin 1999). This is not true for all ecological terms. Biogeochemical cycles are real. Also "populations" and even "ecosystems" are empirically meaningful terms if their usage is suitably restricted. Which terms and concepts are needed for dealing with problems, and what are those problems? If societal ecology attempts to protect empty concepts, there is a danger of bringing discredit to the entire field, with associated harmful consequences.

*Basic question number 3.*—Is there an independent theory of ecology, as there is a theory of chemistry, physics, or genetics, or is ecology a summary of phenomenological information?

Should it be true that no discreet theory of ecology exists, it is not necessarily dangerous. Notice that there is no discrete theory of engineering. Might ecology be the art of environmental engineering with special reference to the organisms and chemical and energetic transfers in the environment, and how these are influenced by anthropogenic events? If that should prove to be the case, it would enhance the importance of the proclamation of societal ecology.

The difficulty resides in distinguishing what constitutes a discrete theory. It has recently been argued, on the basis of naive and outmoded reductionism, that all of biology is an epiphenomenon of chemistry and physics (Wilson 1998).

In fact, attempting to use biology for any practical end in a uncontrolled environment, without using entire organisms as objects for theorizing, has not been successful for at least two reasons. One is that any attempt to describe an organism in purely chemical terms, with sufficient completeness to be useful, consumes enormous amounts of information storage and transmission capacity.

A second and ecologically more interesting reason for focusing on organisms, rather than their subcomponents, is that organisms are capable of producing surprises that are not easily predicted on the basis of chemistry and physics alone. These special adaptations are the raw material for ecologists and are often the key to solving ecological problems.

Are these adaptations, their origin and role, what we intend when we say that there exists a theory of ecology? Probably not, since assertions that are called parts of ecological theory are often simple mathematical assertions, which could, in fact, be generated without all but the most elementary biological information about birth, death, and movement. Examples are numerous (Lotka 1956, MacArthur and Wilson 1967, Roughgarden 1983, etc.). In fact, this third basic question is the most difficult to formulate, which leads me to suspect that it will be the most important of the three in the next century.

### The value of the exercise

Scientific questions typically arise from scientific research. On this occasion, I have stepped out of that mode and consider problems on the level of scientific policy. This policy is not that of the usual policy makers, but rather of scientists themselves. Aware of the situation that sciences can be advanced or throttled by nonscientist decision makers, they attempt to modify the policy-making procedure. I suggest that while this may, in fact, be necessary, it is also dangerous and must be carefully done. Regardless of the fiscal or other burdens that we must face, our greatest loyalty must remain with discovery and presentation of truth as we see it.

### Literature cited

Bazzaz, F., G. Ceballos, M. Davis, R. Dirzo, P. R. Ehrlich, T. Eisner, S. Levin, J. H. Lawton, J. Lubchenco, P. A. Matson, H. A. Mooney, P. H. Raven, J. E. Roughgarden,

J. Sarukhan, G. D. Tilman, P. Vitousek, D. H. Wall, E. O. Wilson, and G. M. Woodwell. 1998. Ecological science and the human predicament. *Science* **282**:879.

Carroll, R., C. Augspurger, A. Dobson, J. Franklin, G. Orians, W. Reid, R. Tracy, D. Wilcove, and J. Wilson. 1996. Strengthening the use of science in achieving the goals of the Endangered Species Act: an assessment by the Ecological Society of America. *Ecological Applications* **6**:1–11.

Colwell, R., and D. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* **15**:70–76.

Daily, G. C., S. Alexander, P. Ehrlich, L. Goulder, J. Lubchenco, P. Matson, H. Mooney, S. Postel, S. Schneider, D. Tilman, and G. Woodwell. 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. Ecological Society of America, Washington, D.C., USA.

Ehrlich, P., and G. Daily. 1993. Science and the management of natural resources. *Ecological Applications* **3**:558–560.

Lotka, A. 1956. *Elements of physical biology*. Dover, New York, New York, USA.

MacArthur, R., and E. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.

Roughgarden, J. 1983. Competition and theory in community ecology. *American Naturalist* **122**:583–601.

Sagoff, M. 1997. Can we put a price on Nature's services? Report from the Institute for Philosophy and Public Policy **17**:7–12.

Sheail, J. 1988. *Seventy-five years in Ecology*. British Ecological Society, Oxford, UK.

Slobodkin, L. 1992. *Simplicity and complexity in games of the intellect*. Harvard University Press, Cambridge, Massachusetts, USA.

Slobodkin, L. 1993. Scientific goals require literal empirical assumptions. *Ecological Applications* **3**:571–573.

Slobodkin, L. 1999. The good the bad and the reified. In A. Travis, editor. *History of pollution and environmental management*. Jerusalem, Israel.

Slobodkin, L., and A. Rapoport. 1974. An optimal strategy of evolution. *Quarterly Review of Biology* **49**:181–200.

Wilson, E. O. 1998. *Consilience: the unity of knowledge*. Alfred A. Knopf, New York, New York, USA.

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## Eight Ways to be a Colonizer; Two Ways to be an Invader: A Proposed Nomenclature Scheme for Invasion Ecology

In 1981, Deborah Rabinowitz wrote an article entitled “Seven forms of rarity,” in which she presented a simple classification scheme of species rarity based on three dichotomous criteria—species range (large or small); habitat specificity (wide or narrow); and local population size (large or small). The paper, still regularly cited in textbooks and research articles, has become a minor classic, and Rabinowitz clearly succeeded in accomplishing her stated goal, which was to “contribute some clarity” to the investigation of rarity and encourage “new perspectives for people engaged in more practical concerns.”

We believe that the investigation of biological invasions could benefit from a similar contribution of clarity and new perspectives. Recent evaluations of the field of invasion ecology (Williamson 1996, 1999,

Lonsdale 1999) have concluded that little progress has been made in the more than 40 years since Charles S. Elton (1958) initiated the modern discipline of invasion ecology with his book, *The Ecology of Invasions by Animals and Plants*. We believe that inconsistent and imprecise use of invasion terminology is one factor that is contributing to the ongoing difficulties of the field. Thus, in a clear, unabashed imitation of Rabinowitz' efforts, we propose a similar classification scheme for invasion nomenclature in an attempt to provide some clarity to the field of invasion ecology and to promote new perspectives.

Depending on the author, a species in the invasion literature might be referred to as *alien* (Crawley et al. 1996), *exotic* (Green 1997), *invasive* (Daehler 1998), *nonindigenous* (Pimentel et al. 2000), *imported* (Williamson and Fitter 1996), *weedy* (Fox 1990), *introduced* (Lonsdale 1994), *non-native* (Davis et al. 2000), *immigrant* (Bazzaz 1986), *colonizer* (Williamson 1996), *native* (Meyer and Florence 1996), *naturalized* (Hussey et al. 1992), *endemic* (Williamson 1996), or *indigenous* (Sauer 1988). In many cases, these terms are not defined, or if they are defined, they are not always defined consistently. Until a commonly accepted vocabulary is adopted by invasion ecologists, we think the field will continue to have difficulty developing reliable generalizations, partly due to misunderstandings and misinterpretations among investigators.

Because species invading a new region and successional species moving into a habitat following a disturbance are both colonizing new sites, the development of a nomenclature scheme based on types of colonizers might clarify communication within the field of invasion ecology. Just as important, we believe such a scheme may help bring to an end the notion that invasions and invading species are unique ecological phenomena, thereby requiring unique explanations.

We acknowledge that not all colonization events are alike. For example, some colonizations occur over

a short distance, some over a very long distance; some colonizers are new to the region, some are not; some colonizers have a negligible effect on the new environment, whereas some have very large impact. We think it would be useful to distinguish among different types of colonizers while recognizing the fundamentally similar ecological processes that govern all colonization episodes. To this end, we propose a simple classification scheme for colonization terminology modeled after Rabinowitz's (1981) classification of rarity forms.

The organizing criteria for this classification scheme are based on strictly ecological and geographical concepts. The scheme is organized around three distinctive aspects of the colonizer: dispersal distance (short or long), uniqueness (novel or common to the region colonized), and impact in the new environment (small or great). According to this scheme, there are 2<sup>3</sup> combinations of categories, or "eight ways to be a colonizer" (Fig. 1). The three different criteria will be described in more detail.

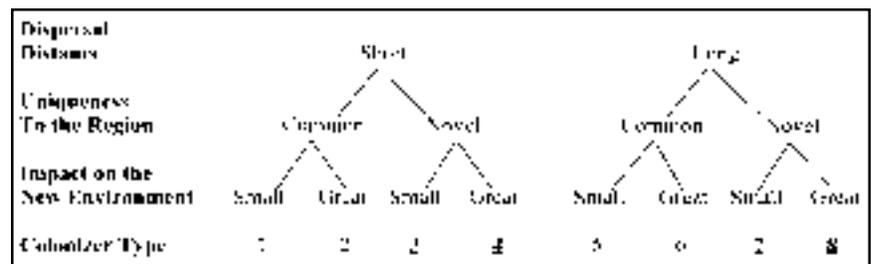
### Dispersal distance

Whether a dispersal distance is declared to be short or long will largely depend on the system and particular colonizer under scrutiny. Clearly, this category is scale dependent. Nonetheless, short-distance dispersal is considered to be primarily between adjacent, or nearly adjacent, environments. This could be

considered *diffusion dispersal*. On the other hand, long-distance dispersal can be viewed as movement typically between widely distant environments, usually separated by a barrier of some sort, a process that could be termed *saltation dispersal* or *punctuated dispersal*. We expect that diffusion dispersal would likely be a much more common event than the latter, which probably occurs only rarely, unless facilitated by humans. Note that an initial colonization episode precipitated by punctuated dispersal may often be followed by subsequent diffusion dispersal originating from within the newly colonized environment. For example, zebra mussels, *Dreissena polymorpha*, were introduced into North America via a saltation dispersal event (Benson and Boydston 1995). Subsequent spread of this species in North America has been due to both diffusion dispersal (via natural dispersal within and among connected water systems) and saltation dispersal, e.g., mussels transported between water systems on the bottoms of boats (Griffiths et al. 1991).

### Origin of colonizer

"Common" or "novel" refers to whether the colonizer is already a resident in the region or a newcomer to the region and therefore expanding its range. This category is also necessarily scale dependent, in space and time. The actual boundaries of "the region" will be largely defined in the context of the system and spe-



**Fig. 1.** The eight colonizer types shown as the result of the proposed classification scheme. According to this scheme, Types 1, 2, 5, and 6 can be considered *successional colonizers*; Types 3 and 7 can be considered *novel, noninvasive colonizers*; and Types 4 and 8 can be considered *novel, invasive colonizers*. It is recommended that the word *invader* be used only for colonizer Types 4 and 8.

cies under consideration. In most instances, an expansion of a species' range would involve an extension of the range's latitude, longitude, or altitude. However, range expansion could also include the establishment of the species in a new type of environment, without an extension of the range's latitude, longitude, or altitude. In this special case, it would be appropriate to term the colonizer a "novel" species, even though the species was already present in the region. Whether a species is common or novel to a region is also a function of temporal scale. For example, the old-field plant species of central and eastern North America are largely European in origin. Yet, today, they are some of the most widespread and successful plant species on the continent. Like it or not, these species are here and they are not going back. Continuing to refer to them at this point as alien invaders, or exotics, or even novel plant species, is beginning to make little ecological sense. (As the Romans said, *tandem aliquando invasores fiunt vernaculi* "in time invaders become the natives"). In any case, it will be up to the ecologist to define "novel" and "common" in the context of the system under investigation.

### Presence or impact on the new environment

The term "invader" is often used indiscriminately to refer to all alien (novel) species in an environment. Yet, the term "invader" has distinctive connotations. Common synonyms for "invader" are "attacker," "aggressor," "raider," and "assailant." Clearly, an invader is not just any newcomer, but one that has a large impact on the new environment. This impact could involve community, ecosystem, and/or economic effects. Thus, in our classification scheme, newcomers that have a large impact in the new environment are distinguished from newcomers that have a small impact.

As shown in Fig. 1, the classification scheme yields eight different types of colonizers.

*Type 1.*—These are short-distance (diffusion) colonizers, common to the region (no range expansion), with a negligible impact in the new environment. Examples of such species are the many minor species that colonize, or recolonize, a habitat following a disturbance.

*Type 2.*—These are short-distance (diffusion) colonizers, common to the region (no range expansion), with a large impact in the new environment. Exemplary species would be any dominant species colonizing, or recolonizing, a habitat following a disturbance, e.g., quaking aspen, *Populus tremuloides*, dominating a postfire habitat, or pocket gophers, *Geomys* spp., that move into an adjacent field once it has been cleared of trees. Any species (common to the region) that plays a keystone role in the new community or ecosystem, e.g., as a predator, herbivore, pollinator, landscape engineer, pathogen, or nitrogen fixer, would be a Type 2 colonizer.

*Type 3.*—These are short-distance (diffusion) colonizers, novel to the region (range expansion), with a negligible impact in the new environment. Minor species incrementally expanding their ranges, e.g., due to climate or other environmental changes, represent this type of colonizer. Examples are numerous, e.g., the many species of European butterflies that are believed to be gradually expanding their ranges northward in response to the past century's warming trend (Parmesan 1999).

*Type 4.*—These are short-distance (diffusion) colonizers, novel to the region (range expansion), with a large impact on the new environment. Such colonizers would include dominant or keystone species incrementally expanding their range. In most cases, dispersal by these species is occurring without significant human assistance. Examples are the spread of House Sparrows, *Passer domesticus*, throughout the United States in the 19th and 20th centuries, and the current spread in the United States of buckthorn, *Rhamnus cathartica*.

*Type 5.*—These are long-distance (saltation) colonizers, common to the region (no range expansion), with a negligible impact in the new environment. This is probably a relatively uncommon type of colonization. One way in which it could occur is during the recolonization of an area that recently experienced a very large disturbance, e.g., the recolonization of the ecosystems on and surrounding Mount St. Helens following its eruption (Turner et al. 1997). In this case, colonizers of species common to the region often had to disperse from great distances (Dale 1991). Another way in which this type of colonization could occur is following the creation of an entirely new habitat in a region, e.g., the creation of a lake or reservoir as part of the construction of a hydroelectric project. Unless other aquatic systems were immediately adjacent to the reservoir, colonists would have to disperse from a long distance. In any case, once established, Type 5 colonizers would have a small impact in the new environment.

*Type 6.*—These are long-distance (saltation) colonizers, common to the region (no range expansion), with a large impact on the new environment. These colonization events could occur in the same scenarios described for Type 5 colonizers, with the difference that these would be dominant or keystone species. An example is fireweed, *Epilobium angustifolium*, a forb that became very abundant in many areas of Yellowstone National Park shortly after the 1988 fire (Turner et al. 1997).

*Type 7.*—These are long-distance (saltation) colonizers, novel to the region (range expansion), with a negligible impact on the new environment. This group of colonizers probably represents the largest group of novel species that have colonized environments from a great distance. Despite the impression given by headlines (in both the popular and scientific press), many, if not most, novel species have little impact in their new environment (Williamson 1999).

For example, *Epilobium brunnescens* (native to New Zealand) and *Veronica filiformis* (native to the Caucasus) are both extremely common plants in England, but neither is having any discernible impact on their environments. Given the common connotations of the term “invader,” referring to such species as “invaders” makes little ecological sense and can be misleading.

*Type 8.*—These are long-distance (saltation) colonizers, novel to the region (range expansion), with a large impact on the new environment. This group of colonizers has received the most attention, both in the popular press and the scientific community, since Elton (1958) brought invasion ecology to the public’s attention. These are the quintessential invaders, arriving from great distances (often, if not usually, due to human facilitation), and rapidly spreading throughout the new environment, often via both diffusion and saltation dispersal, usually with ecological and economic consequences deemed undesirable by humans. Examples are numerous and well known, e.g., the brown tree snake, *Boiga irregularis*, and purple loosestrife, *Lythrum salicaria*.

An examination of the eight colonizer types reveals that they fall into three main categories. Four of the eight types (1, 2, 5, and 6) are principally colonizers during succession, e.g., colonizing or recolonizing habitats following a disturbance. These are colonization episodes in habitats within the established range of the species. These four types can be referred to as *successional colonizers*. Types 3 and 7 differ from the successional colonizers in that their colonization episodes involve range expansion. However, since these novel colonizers have only a minor impact on the new environment, it does not make sense to call them invaders, under the normal, rather perjorative understanding of the word. Thus, they can be considered *novel, noninvasive colonizers*. Types 4 and 8 are novel and have a large impact, usually undesirable, on the new environment.

These colonizers are the *novel, invasive colonizers*, the true invaders.

We are not advocating that ecologists cease using the words “invasion” or “invader.” We believe that these terms can be very useful *as long as their usage is restricted to colonizer Types 4 and 8, and as long as invasion is viewed as just a specific case of the more general process of colonization*. However, ecologists should think carefully before using words such as “alien” and “exotic.” With synonyms such as “strange,” “outlandish,” “barbarian,” and “hostile,” usage of these words may serve to perpetuate the recalcitrant conviction that invasions by novel species are governed by different ecological processes than colonizations of habitats by resident species.

The view that invaders and species invasions are unique ecological phenomena requiring unique explanation has been challenged in the past by Johnstone (1986), Huston (1994), and Thompson et al. (1995). However, their calls to bring invasion ecology back into the fold of the rest of ecology have largely been ignored. The recent proposal of a theory of invasibility based on findings and theory from succession ecology (Davis et al. 2000) is evidence that the field of invasion ecology can benefit greatly from existing ecological data and theory obtained and developed outside the field of invasion ecology.

In summary, our eight-celled classification scheme for colonization/invasion nomenclature is intended to promote more consistent use of terminology within the field of invasion ecology, and also to emphasize that species invasions are not ecologically unique events. Thus, it is our hope that the proposed nomenclature scheme will bring some needed clarity to the vocabulary of invasion ecology, while at the same time suggesting some new and productive ways of thinking about species invasions that will accelerate the process of making invasion ecology a quantitative, analytic, and predictive science (Parker and Reichard 1998).

## Literature cited

- Bazzaz, F. A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. Pages 96–110 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.
- Benson, A. J., and C. P. Boydston. 1995. Invasion of the zebra mussel into the United States. Pages 445–446 in E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of US plants, animals and ecosystems. National Biological Service, Department of the Interior, Washington, D.C., USA.
- Crawley, M. J., P. H. Harvey, and A. Purvis. 1996. Comparative ecology of the native and alien floras of the British Isles. Philosophical Transactions of the Royal Society of London **B351**:1251–1259.
- Daehler, C. 1998. The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. Biological Conservation **84**:167–180.
- Dale, V. H. 1991. The debris avalanche at Mount St. Helens: vegetation establishment in the ten years since the eruption. National Geographic Research and Exploration **7**:328–341.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**, *in press*.
- Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.
- Fox, M. D. 1990. Mediterranean weeds: exchanges of invasive plants between the five Mediterranean regions of the world. Pages 179–200 in F. Di Castri, A. J. Hansen, and M. Debussche, editors. Biological invasions in Europe and the Mediterranean basin. Kluwer Academic, Dordrecht, The Netherlands.

- Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *Journal of Animal Ecology* **66**: 25–35.
- Griffiths, D. W., D. W. Schloesser, J. H. Leach, and W. P. Koalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes Region. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 1381–1388.
- Hussey, B. M. J., D. Anderson, and S. Loney. 1992. A checklist of plants found growing in a native or naturalized state on Culeenup Island, Yunderup, Western Australia. *West Australian Naturalist* **19**:35–43.
- Huston, M. A. 1994. Biological diversity. Cambridge University Press, Cambridge, UK.
- Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. *Biological Review* **61**:369–394.
- Lonsdale, W. M. 1994. Inviting trouble: introduced pasture species in Northern Australia. *Australian Journal of Ecology* **19**: 345–354.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522–1536.
- Meyer, J. Y., and J. Florence. 1996. Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomaceae). *Journal of Biogeography* **23**: 775–781.
- Parker, I. M., and S. H. Reichard. 1998. Critical issues in invasion biology for conservation science. In P. L. Fiedler and P. M. Kareiva, editors. *Conservation biology for the coming decade*. Second edition. Chapman and Hall, London, UK.
- Parmesan, C. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**:479–583.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of non-indigenous species in the United States. *BioScience* **50**:53–65.
- Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–218 in H. Synge, editor. *The biological aspects of rare plant conservation*. Wiley, New York, New York, USA.
- Sauer, J. D. 1988. Plant migration: the dynamics of geographic patterning in seed plant species. University of California Press, Berkeley, California, USA.
- Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: more of the same? *Ecography* **18**:390–402.
- Turner, M. G., V. H. Dale, and E. H. Everham III. 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. *BioScience* **47**: 758–768.
- Williamson, M. 1996. Biological invasions. Chapman and Hall, London, UK.
- Williamson, M. 1999. Invasions. *Ecography* **22**:5–12.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. *Ecology* **77**:1661–1666.

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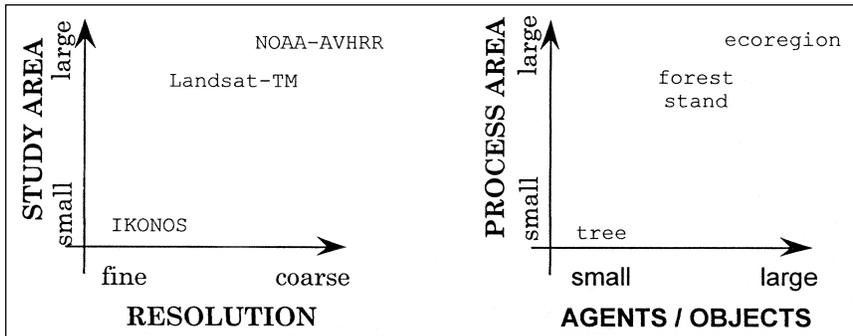
## On the Limits and Extensions of the Definition of Scale

Ecologists' increased interest in issues of scale and scaling is clearly illustrated by the terminological confusion targeted by a recent *ESA Bulletin* contribution (Jenerette and Wu 2000). The prime stimulus for us to respond here to the definition(s) of scale is that their suggestion for "recognizing . . . multiple meanings" is partially misleading, as a rigorous scientific attempt to clarify

the reasons for and the possible solutions to the confusion. The potential for misinterpretation is always high when the same word means many things, particularly when those things are directly contradictory, as in cartographic scale, ecological scale, and geographic scale.

We strongly believe that the complementarity of two sizes, that of the observations and that of the study area, cannot be well expressed by one term, such as scale. It is important to note that, in this context, we strictly discriminate the size of observations (such as the sampling unit) from the size of the ecologically

meaningful entities (e.g., a bird, a tree, or other agents), as well as the size of the study area, from the size of the area over which those ecological entities exhibit relevant spatial characteristics. The former elements of these two pairs characterize the data; the latter ones characterize processes about which we would like to make inferences. Therefore, we suggest that operative terms must be used for: (1) the characterization of the size and shape of the observation, (2) the size and shape of the study area, (3) the characterization of agents, and (4) the process area (Fig. 1). The first pair (1 and 2)



**Fig. 1.** Relationships between observational and ecological characteristics related to “scale.” Assuming that the size of the study area is 10 x 10 km, it would be imaged by 100 000 x 1000 m (e.g., NOAA-AVHRR) pixels, approximately 10,000 30 x 30 m (e.g., Landsat TM) pixels, and approximately 100,000,000 1 x 1 m (e.g., IKONOS) pixels. The corresponding process-area and agents/objects that we would want to observe are trees, forest stands, and ecoregions/landscapes. Clearly, there should be a reasonably good match between these two sets of parameters. For example, deer habitat should not be mapped at 1000-m resolution, nor should biomes be monitored at 1-m resolution, because the discrepancy between the observation resolution and the ecological entities and processes comes at a very high price in terms of uncertainty.

provide the technical characteristics; the second pair (3 and 4) provide the context. Finally, the conceptual linkages between the pairs should be clearly and critically evaluated. Hence, instead of one expression of spatial property (such as scale), at least four separate characteristics should be reported in every study, as well as a discussion about their relationships, in order to avoid contradictory conclusions due to incompatible observations and/or context.

It is possible that geographers are as much responsible for the confusion (e.g., Tobler [1988], which practically equates cartographic scale and operational resolution) as in some other related disciplines that have generated their own terminology, such as remote sensing (Strahler et al. 1986), geostatistics (Olea 1990), and landscape ecology (Forman 1995).

The classical cartographic approach to scaling is usually discussed under *generalization*. Work on this topic (i.e., McMaster 1989) contradicts the assertion that “once a map is entered into a GIS, alterations of cartographic scale are trivial” (Jenerette and Wu 2000). Although the precision of data representation in GIS is limited only by

computer memory, the accuracy reduction caused by errors associated with data transformations (such as resampling, for example) and their propagation makes this a worrisome statement (Heuvelink and Goodchild 1998). Rapid advances of geographical information systems exposed the shortcomings of the tradition of Sinton (see Chrisman 1989), which views data models in a strictly three-dimensional Cartesian scheme along the axes of space, time, and attributes. A conceptual model and its data representation cannot be well described as one point in this framework.

Although GIS software is one of the core modern black boxes of spatial data processing, remote sensing is one of the major data sources for landscape environmental studies. For remotely sensed data, resolution is the standard scale-related term, a function of both the spatial area and the value of an observation. Its dependence on value has been largely left by the wayside; current practice is to refer to a nominal resolution as the area represented by a pixel. The relationship of the pixel observation to the size of “meaningful entities” was emphasized by Strahler et al. (1986) in their taxonomy of H-resolu-

tion (cases in which pixel observations represent smaller areas than the size of meaningful entities) and L-resolution (cases in which pixel observations are made over larger areas than the size of meaningful entities). Recently, entire volumes have been devoted to the impact of modern remote sensing technologies on scaling studies (Goodchild and Quattrochi 1997, van Gardingen et al. 1997), demonstrating the diversity of concepts related to scale, but falling short of defining an integrated terminology. In the absence of this integrated terminology, clear specifications of spatial aspects of phenomena, their model representation and observations, are needed. This information can be considered metadata or metainformation (Beard, *in press*), which is helpful for reducing uncertainty in the use of spatial data.

In geostatistics, a tool increasingly used by ecologists, scale-related terminology (support, lag, range, regularization) is clear (Olea 1990). However, these geostatistical terms refer only to the observations and the statistical assumptions of geostatistical (stochastic) models, not to the spatial characteristics of processes or phenomena being studied. Geostatistics, therefore, provides useful terms for only two of the four spatial scale characteristics previously listed.

A detailed survey of the concepts and vocabulary of scale in landscape ecology (Withers and Meentemeyer 1999) recently summarized the issues by research foci. Although their study attempted to harmonize the duality of “grain size and extent” with “minimum sampling unit and (broad vs. fine) scale,” the dominant usage in the landscape ecological literature is to define scale by grain *and* extent (Turner et al. 1989, Gustafson 1998, Jenerette and Wu 2000). We propose that grain (size) and extent, and their reference to either observation or context, should be used as separate scale characteristics.

The potential problems related to the inequality of *what we measure* and *what we infer about*, enhanced by computerized data representation, gets exposure in some ecological dis-

cussions explicitly referring to scaling landscape characteristics (Levin 1992, Li and Reynolds 1995). However, the everyday practice of ecological studies seems to ignore it almost completely. For example, a recent survey of more than 200 productivity–richness research papers (Wade et al. 1999) found that close to 50% of them gave no precise report on one or more of the spatial characteristics listed above.

We agree that science, and therefore its terminology, is dynamic (Jenerette and Wu 2000). We also believe that clear terminology and clear definitions are necessary requirements for scientific progress. The single numerical descriptor known as cartographic scale (the ratio of map distance over real distance) expresses only part of the information that ecologists and other scientists dealing with spatial data need to communicate. We would like to encourage ecologists to include all relevant technical, contextual, and conceptual pieces of information, and journal editors to demand it, in scientific publications.

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## Literature cited

Beard, K. *In press*. Roles of meta-information in uncertainty management. *In* C. Hunsaker, M. F. Goodchild, T. J. Case, and M. Friedl, editors. *Spatial uncertainty*

in ecology. Springer-Verlag, New York, New York, USA.

Chrisman, N. 1998. *Exploring geographic information systems*. J. Wiley & Sons, New York, New York, USA.

Forman, R. T. T. 1995. *Land mosaics. The ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.

Goodchild, M. F., and D. Quattrochi, editors. 1997. *Scale in remote sensing and GIS*. Lewis, Boca Raton, Florida, USA.

Gustafson, E. 1998. Quantifying landscape spatial pattern: What is the state of the art? *Ecosystems* **1**: 143–156.

Heuvelink, G. B. M., and M. F. Goodchild, editors. 1998. *Error propagation in environmental modelling with GIS*. Taylor & Francis, London, UK.

Jenerette, G. D., and J. Wu. 2000. On the definitions of scale. *ESA Bulletin* **81**:104–105.

Levin, S. 1992. Concepts of scale at the local level. Pages 7–20 *in* J. R. Ehleringer and C. B. Field, editors. *Scaling physiological processes: leaf to globe*. Academic Press, New York, New York, USA.

Li, H., and J. F. Reynolds. 1995. On definition and quantification of heterogeneity. *Oikos* **73**:280–284.

McMaster, R., editor. 1989. Numerical generalization in cartography. *Cartographica* **26**, Special Issue.

Strahler, A. H., C. E. Woodcock, and J. A. Smith. 1986. On the nature of models in remote sensing. *Remote Sensing of Environment* **20**: 131–138.

Tobler, W. 1988. Resolution, accuracy and all that. *In* H. Mounsey and R. Tomlinson, editors. *Building databases for global science*. Taylor & Francis, London, UK.

Turner, M. G., V. H. Dale, and R. H. Gardner. 1989. Predicting across scales: theory development and testing. *Landscape Ecology* **3**: 245–252.

van Gardingen, P. R., G. M. Foody, and P. J. Curran, editors. 1997. *Scaling-up: from cell to landscape*. Society for Experimental Biology Seminar Series 63. Cam-

bridge University Press, Cambridge, UK.

Wade, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* **30**: 257–300.

Withers, M. A., and V. Meentemeyer. 1999. Concepts of scale in landscape ecology. *In* J. M. Klopatek and R. H. Gardner, editors. *Landscape ecological analysis: issues and applications*. Springer-Verlag, New York, New York, USA.

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## Where the Ocean Meets the Sky . . .

. . . you get air deposition. Technically, air deposition happens when the sky—or the pollution in it—comes down to the ocean (or continent), but Rod Stewart had the right idea. Air and water do meet, and not only in poetry and old Irish song lyrics. Air pollution is often a significant source of water quality problems. Furthermore, ecologists have a

role in making it possible for air and water resource agencies to solve them.

Although atmospheric deposition might not appear, at first glance, to be an ecological issue, its effects most surely are. Those effects include eutrophication and its associated problems, and contamination of fish, shellfish, birds, and mammals with toxic compounds. Ecologists understand how these things affect ecosystems better than do any other scientists. In addition, ecologists, with their experience integrating other disciplines and working at the intersections with biologists, chemists, botanists, behavioral biologists, geologists, geographers, and many others, are well positioned to expand their horizons once again to embrace the work of atmospheric chemists and modelers. The study of and solutions to atmospheric deposition require this type of synthesis among both researchers and policy makers.

In my job, I do not try to teach ecologists about atmospheric deposition; most already know about it. Instead, I try to make it a research priority. Further, I try to present research needs to policy makers in an accurate, pertinent, and timely fashion. The debate over the extent to which scientists—and ecologists—should be active in crafting policy continues, but from my vantage point, the following points have merit. First, those who use taxpayers' money to conduct research owe the taxpayers whatever wisdom they have gained, however slight. Second, those who believe that science should be one of the legs supporting policy decisions need to take responsibility for their share of the two-way process and communicate with managers and policy makers. As someone with a graduate degree in science who works at the intersection of science and policy, I have a desperate need to communicate well and often with ecologists.

The Ecological Society of America, as an organization, has been involved in the atmospheric deposition debate for several years, and many members have been involved much longer. In 1997, ESA held a workshop on atmospheric deposition of nitro-

gen to the coastal waters; in 1999 ESA held one workshop on ecological effects of nitrogen deposition in forests and another on nitrogen deposition in the Mississippi River watershed. In 2000, ESA held a workshop on atmospheric deposition to the Pacific coast. The goal of these workshops has been to bring together experts in the field to share their knowledge with one another and with the coastal and ecosystem managers who need to use it. Full workshop reports are available on ESA's web page, with some findings summarized here.

No report from a group including scientists would be complete without the call for more research to answer all of the remaining questions. These workshop reports are no exception. Many of the reports call for similar research actions, including:

- accurate estimates of the amount of atmospherically deposited nitrogen and toxic pollutants entering coastal and sensitive (high-altitude) ecosystems;
- accurate analyses of the sources of these pollutants;
- models or modeling systems that can trace emissions from the source through the atmosphere, through the process of deposition, and through the watershed and terrestrial and/or aquatic ecosystems to an ecological result.

There are also calls to collect more information in order to make accurate assessments:

- inventories that include the kinds of pollutants emitted from all sources;
- explanations of chemical, physical, meteorological, and ecological relationships that will allow us to build accurate models.

Every workshop also highlighted the need for specific management actions, including:

- year-round reductions in nitrogen emissions;
- inclusion of water quality benefits in analyses of the costs and benefits of air regulations;

- incorporation of atmospheric deposition into nonpoint source (run-off) management and total maximum daily load programs.

There were also recommendations unique to particular workshops. The first workshop, held in Rhode Island in 1997 and entitled "Atmospheric Nitrogen Deposition to Coastal Watersheds," was convened with the policy implications of the research very much in mind. At the time, the process of atmospheric deposition was not included in any air regulations covering nitrogen at a federal level other than the Acid Rain program. The participants clearly saw the need to change that. Just a few years later, it is clear that they succeeded—and that there is still a long way to go. The 1997 Ozone and Particulate Matter NAAQS (National Ambient Air Quality Standards), which include some water quality benefits from reducing nitrogen emissions in the cost : benefit analysis, are still held up in litigation. A similar analysis of water quality benefits was only conservatively included in the next major nitrogen control regulation, the 1998 NO<sub>x</sub> SIP Call. The NO<sub>x</sub> SIP Call, which places seasonal limits (instead of the year-round limits that workshop participants recommended) on nitrogen oxide emissions from 22 Eastern states, was also held up in court, and additional legal action has won only about half of the originally proposed NO<sub>x</sub> reductions. All of this maneuvering indicates, at least to me, that the participants in the Rhode Island meeting were right to worry about how much science would get incorporated into policy. I think they are also right to do what they can to make sure the research is used to the full extent possible in policy development.

In the hypoxic zone workshop, held in New Orleans in 1999 and entitled "Where Air and Water Meet: Atmospheric Deposition and the Gulf of Mexico Hypoxic Zone," participants focused on the science. In particular, they emphasized the need to accurately quantify how much indi-

rect deposition (deposition that falls on the watershed) reaches the Gulf of Mexico. This nitrogen is suspected to be a significant percentage of the runoff, especially in agricultural areas. Not everyone agrees with this theory, however. The conventional wisdom states that most atmospherically deposited nitrogen stays in the soil or is taken up by biomass. It also states that when nitrogen fertilizer is applied in excessive amounts (which happens regularly as a sort of “cheap insurance” in agricultural areas), a significant percentage of that nitrogen runs off. Does it make sense to assume that a soil with excessive nitrogen from fertilizer, which loses nitrogen in runoff every time it rains, stores most of the nitrogen deposited from the atmosphere? If not, estimates of the indirect deposition contribution to the Gulf are probably underestimated. If much of the runoff is from atmospheric deposition, the management strategy would be more effective if it controlled both air emissions and runoff, instead of simply runoff.

The Pacific Coast workshop, “Where Air and Water Meet: Atmospheric Deposition to the Pacific Coast,” was held in Los Angeles in 2000. Of all the ESA air deposition workshops, only this one focused on deposition of toxic pollutants rather than nitrogen. Meeting participants highlighted the need to document a situation on the Pacific Coast, where atmospheric deposition is a significant contributor to coastal water quality problems. It is relatively well known that atmospheric deposition is significant in ecosystems at high elevations in the Rockies and Sierras, but much less is known about coastal ecosystems. Initial work has been done on coastal ecosystems and is beginning to pick up steam, but there is, as yet, no strong evidence of ecological impacts in coastal ecosystems. Given the strong interest by many West Coast organizations, and the knowledge that deposition has ecological impacts at high elevations, this kind of research needs to be initiated.

One ESA workshop took a step beyond looking at atmospheric depo-

sition and focused on the ecological impacts of acid deposition to terrestrial and freshwater ecosystems. This workshop, entitled “Acid Deposition: the Ecological Response,” was held in Washington, D.C. in 1999. Although there is substantial evidence of ecological impacts—lake acidification, poor health for certain tree species, leaching of cations from soils, mobilization of toxic compounds (or toxic amounts of compounds) in soils and lakes and streams—the research on ecological response and recovery is still inconclusive and frequently site specific. In response to that concern, participants emphasized the need for a commitment to long-term monitoring of changes in deposition rates and the ecosystem responses to those changes. In particular, the first signs of recovery are now appearing in some ecosystems that have been severely impacted by acidic deposition, and workshop participants believe that it is critical to monitor and assess those ecological changes.

In the realm of atmospheric deposition, management and research are often two yoked horses moving at unequal speeds. In some cases, the management capability is not keeping up with the scientific knowledge; in others, managers need answers that scientists cannot provide. For example, the science of dry deposition measurement has not changed significantly in almost 30 years. I have one colleague who has been in this field longer than he cares to discuss—since before I could read, I frequently point out—who says the technology has not changed since his graduate school days. The management needs, on the other hand, have changed dramatically. Water resource managers in coastal southern California now want to know how much atmospheric deposition (which in low-altitude southern California is predominantly dry deposition) is contributing to their water resource problems. Without better measurement technologies, scientists can barely give them an answer, let alone compare the answers between watersheds. On the flip side, scientists have known for years that deposition of

ammonia, regardless of how imprecisely we can measure it, can cause the same water quality problems that any other source of nitrogen can. National policy, however, has yet to include ammonia under any air quality regulations.

There are many more pieces to the atmospheric deposition puzzle. In a number of coastal watersheds, atmospheric deposition is responsible for anywhere from 10% to 40% of the nitrogen, and sometimes up to 80–90% of some toxic compounds entering estuaries. These aquatic habitats are home, at least during some life stage, to most of the plants and animals we rely on for commercial use and recreational enjoyment. The land surrounding these same aquatic habitats is home to fully half of the population in the United States. That population has been growing quickly over the last two decades, and is projected to grow even faster over the next two. Reducing atmospherically deposited nitrogen is critical if coastal populations are to grow without destroying the beauty they first came to enjoy. The same is true of toxic pollutants that cause fish and shellfish advisories. Coastal watersheds will continue to serve their functions in the ecosystem and be desirable places for people to live only if there is strong ecological science to support smart environmental policy. Ecologists, both terrestrial and aquatic, have a role in making sure that happens. If they do not participate, one of the largest collections of ecosystem management decisions will take place without the voices of those who know the most about ecosystems and who can do the most to help the rest of us understand them.

For information on what is happening in the national atmospheric deposition arena, contact EPA’s Atmospheric Deposition group in the Office of Water at (202) 260-2729, or the Office of Air at (202) 564-2667 or (919) 541-5447.

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## Biodiversity and Ecosystem Function: an Issue in Ecology

Much of the primary ecological research is published diffusely throughout a range of specialist scientific journals. With the increasing body of primary literature, there is a growing need for publications that synthesize the main points of this literature, particularly those that may have important implications for science policy, into a form accessible to a broader audience of nonspecialists, including policy makers. The "Issues in Ecology" series produced by the ESA is clearly intended to fulfill such a role.

The first three articles in the "Issues" series did just this. They each synthesized, in a balanced and fair manner, the major points emerging from an ever-burgeoning literature on the topics that they covered. We believe, however, that this does not hold for the fourth member of this series, *Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Systems*. We feel that this publication is biased, adequately considers only one of the two major schools of thought on the whole diversity–function issue, selectively ignores a large subset of the published literature, and states opinions as facts. While the authors are obviously entitled to their points of view and are welcome to submit them for publication in peer-reviewed journals, in this case, we see the work of a few people being presented as the position of a society with over 7300 members.

The "Issues" series is not only published by the ESA, but also is "supported by the Ecological Society of America," an "Official Publication of the Ecological Society of America," sold by the ESA's Public Affairs office, bears the ESA logo, and can be downloaded from the ESA web site. Indeed, the cover letter from ESA's Washington, D.C. office that accompanied the first "Issues" paper states that, "This pub-

lication is one way that ESA seeks to inform the public about ecological topics and promote the responsible application of ecological principles to the solution of environmental problems." Readers of the "Issues" articles would therefore reasonably arrive at the conclusion that the articles represent ESA's official position on the topics being covered. ESA's apparent endorsement of only one of two major schools of thought on a major topic of international scientific debate is an action that, to our knowledge, is unprecedented by any major scientific society worldwide, and we believe that by publishing this document ESA has set a dangerous precedent. We outline here why we believe the "Issues" paper to be biased, and consider the implications of ESA's apparent endorsement of it.

### Two schools of thought

There are clearly two major schools of thought with regard to the diversity–function issue, or the so-called "Diversity Debate." One, which draws its inspiration from classical population biology and is experimentally focused, is of the view that there are clear, causative relationships between diversity and ecosystem functioning, particularly above ground (e.g., Naeem et al. 1994, 1995, Tilman 1996, 1999, Tilman et al. 1996, Naeem and Li 1997). Both the Chair and the Editor of this "Issues" paper are key proponents of this point of view. The other school, to which we subscribe, is that ecosystem properties are not necessarily driven by species diversity per se, but rather that the main drivers of ecosystem properties are the key functional attributes or traits of the dominant species present and the composition of functional types (e.g., Grime 1987, 1997, 1998, Wardle et al. 1997a, Berendse 1998, Mikola and Setälä 1998, Hooper and Vitousek 1998, Laakso and Setälä 1999). The evidence presented by the first of these schools of thought, which consists of experimental data purporting to show cause–effect relationships

between diversity and function, has been criticized (e.g., by Huston 1997, Wardle 1999) on the basis that other factors that co-vary with diversity in these studies confound their results. Evidence presented by the second school of thought has been criticized (e.g., by Tilman et al. 1997b, Naeem 1999), on the basis of its partial reliance on data from observational studies. A balanced "Issues" document would have given significant coverage to both points of view.

### Stating of opinions as facts

We are concerned that the authors of the "Issues" paper have presented a number of controversial experimental studies, for which conflicting interpretations have been published, as undisputed evidence for their point of view that diversity and ecosystem function are causally related. It is not our intention here to argue in detail the relative merits of our point of view relative to that of the authors of the "Issues" paper; this is being done widely in peer-reviewed scientific journals and belongs better there. Rather, we will summarize the alternative interpretations that exist with regard to the evidence used to support indefensible statements in the text such as "Results from many recent experimental studies conducted in North America and Europe demonstrate that ecosystem productivity increases with species richness," "All of these studies show that ecosystem functioning is decreased as the numbers of species decreases," and "All [experiments depicted in Fig. 6] have shown that loss of biodiversity leads to decreased ecosystem functioning." The alternative interpretations of these experiments are as follows:

1) *The ECOTRON study* (Naeem et al. 1994). The fact that this paper represents the first published attempt to experimentally investigate the diversity–function issue across a wide diversity range remains undisputed. Although this study claims to demonstrate positive effects of diversity on aboveground properties,

several critiques of it have been published (e.g., André et al. 1994, Garnier et al. 1997, Huston 1997, Hodgson et al. 1998). In our view, the fatal flaw of this work is that highly productive plant species were only included in the highest diversity treatment, making detection of a relationship between diversity and productivity inevitable (Huston 1997).

2) *The Cedar Creek diversity experiments* (Tilman et al., 1996, 1997a). Although these studies claim to show positive effects of diversity on various ecosystem properties, any apparent diversity effects can be explained entirely in terms of “sampling effect” or “selection probability effect,” in which diversity–productivity relationships occur simply through the most diverse treatments having a greater probability of containing the most productive species in the entire species pool (Aarssen 1997, Huston 1997). While Tilman (1997, 1999) maintains that this effect is a legitimate mechanism by which diversity effects express themselves, and this is stated as undisputed fact in the “Issues” paper, we believe that this effect actually represents an artifact in such experiments, because it requires us to make the unrealistic assumption that biological communities are randomly assembled with regard to the ecosystem property being investigated (Wardle 1999). The currently unpublished Cedar Creek BIOCON experiment profiled in the “Issues” paper is conceptually based on the same design.

3) *The Cedar Creek fertilization experiment* (Tilman 1996). This is presumably the study used to support the claim in the “Issues” paper that “in the one available long term field study, however, reductions in plant species richness also lowered the resistance of grassland production to drought.” In fact, the nitrogen fertilization gradient that induced the diversity gradient that Tilman considered also selected for different plant functional types, with known differential responses to drought, at the opposite ends of the diversity gradi-

ent (Givnish 1994, Huston 1997). Further, the effects of fertilization are likely to induce phenotypic responses in the flora that will reduce its resistance to drought. While this experiment clearly represents a valuable study on how fertility affects plant communities, all diversity–stability interpretations that have been derived from those data are, we believe, entirely invalid.

4) *The serpentine grassland experiment* (Hooper and Vitousek 1997, 1998). We believe that this is an important study clearly pointing to the importance of composition of plant functional types in driving ecosystem function. Its use in the “Issues” paper, in the context of productivity increasing with species richness, is not only incorrect (they actually worked with functional groups), but it also contradicts key interpretations made by the original investigators.

5) *The microbial microcosm experiment* (Naeem and Li 1997). This experiment found that replicates of those microcosms that were set up with a greater diversity were more similar in terms of ecosystem function at the time of harvest than were replicates of those that had fewer species. The authors used this observation to conclude that systems with higher diversity had greater “reliability.” However, community composition at the time the experiment was set up was also more similar for replicates of the higher than the lower diversity treatments (as a consequence of “sampling effect”). This makes the outcome that they observed inevitable, and we believe that this invalidates the results of their study (Wardle 1998).

6) *The BIODEPTH experiment* (Hector et al. 1999). Although this very recently published work clearly represents a major international research effort, there are major conclusions drawn from the published data with which we do not agree, particularly their conclusion that the same log-linear relationship could be used to relate productivity to biodiversity

for all eight sites that they considered. Further, it is unclear as to how effectively their design can separate the importance of “sampling effect” (which we do not accept as a diversity mechanism) from resource complementarity. We look forward to lively and constructive discussion in future literature on this work.

### Selective citation of literature

A common tactic among advocacy groups is to selectively present a subset of the available evidence, i.e., that which agrees with their position, and to dismiss the evidence that does not. This is frequently seen, for example, when two opposing factions selectively present evidence and research that supports their viewpoint with regard to some controversial environmental issue. However, we do not believe that this is acceptable behavior from scientists, who are widely expected to be able to provide impartial, objective advice based on the best scientific evidence available. Indeed, even the ESA’s own *Code of Ethics* is specific about discouraging the dissemination of “erroneous, biased, unwarranted or exaggerated statements involving ecology.” We do not believe that ESA’s support of this “Issues” paper is consistent with such a code.

The impression that one would gain from reading this “Issues” paper is that all major studies on the diversity–function issue show that diversity benefits ecosystem properties. This is not so. There are numerous studies that have investigated the diversity–function issue, and that use approaches differing from those criticized above, in which the primary conclusion is that species or functional group diversity does not operate as a causative agent influencing ecosystem function (see the discussion in Wardle 1999). These studies have all been ignored, except for the Hooper and Vitousek study, which has been misused.

Little attention has been given to the vast agronomic literature relevant to the diversity–function issue (see Trenbath 1974, Vandermeer 1989,

Garnier et al. 1997). In their quest to enhance agronomic yields, crop and forage scientists have extensively studied diversity–productivity relationships at low ends of the diversity spectrum (where the largest diversity responses may be expected), but their main conclusions, which are inconsistent with the position taken in the “Issues” paper, have been largely ignored. Further, in listing issues for future research or several areas of uncertainty that “remain to be investigated,” the authors ignore already published studies in these areas and instead refer only to the BIODEPTH and currently unpublished BIOCON studies.

The selective use of literature to support a particular point of view (and the ignoring of literature presenting data and opinions that contradict that point of view) is an unacceptable practice for any publication that is likely to be seen as a position document of an independent scientific society. The obvious counter-response to our view is that those studies and points of view not cited are somehow less worthy of citation or have had less impact in the field. However, the ignored literature includes publications in leading journals such as *Science*, *Nature*, and several major ecological journals, and some of these publications are among those being most heavily cited in this topic at present.

### Observational studies

The two schools of thought on the diversity issue differ markedly in their views on the relevance of observational data sets to the diversity–function issue. There is little evidence from unmanipulated systems for the existence of a causal relationship between function and diversity (Grime 1997, Wardle et al. 1997a), and observational data sets provide little support for the point of view profiled in the “Issues” paper. Only one of these two viewpoints on this issue (i.e., that expressed by Tilman et al. 1997b, Naem 1999) is seriously acknowledged in the “Issues” paper, i.e., that there are “confound-

ing issues that plague observational studies.” Our position is that if diversity is an important determinant of ecosystem function in nature, then there should be detectable patterns in natural ecosystems in which we would see evidence for such a relationship, because diversity effects should be able to explain a subset of variation that could not be explained by factors other than diversity. Such evidence is at best very scarce, and indeed diversity and biomass or productivity are frequently negatively correlated in nature (e.g., Al Mufti et al. 1977, Huston 1980, Wheeler and Giller 1982). The impression given by the “Issues” paper is that experimental approaches are somehow superior to observational approaches. However, as has been stated elsewhere (Wardle et al. 1997b), experimental studies are “only a means to an end (the end being to better understand what happens in real ecosystems) rather than an end in themselves.” If a body of experimental ecological studies is showing evidence for a phenomenon that is not known to operate widely in nature, then we believe it is the experimental studies that need to be queried. In our view, experimental studies have their greatest relevance when they are used to better understand observed pattern and process in nature.

### Decomposer studies

The “Issues” paper has a strong aboveground focus and is clearly dominated by examples in which aboveground diversity and primary productivity have been monitored. Given that there are no soil biologists among the authors, this is perhaps not surprising, and indeed this issue often emerges whenever groups of ecologists who work in other systems present apparent consensus views on matters relevant to policy. For example, see the response by a group of soil ecologists (Klopatek et al. 1992) to the Sustainable Biosphere Initiative. Given that in most terrestrial ecosystems the majority of the resident species occur below ground, and that decomposition is on a par

with productivity in terms of global importance, omission of this topic from the “Issues” paper makes it incomplete. The belowground biotic component of ecosystems, and the issue of whether soil biodiversity drives ecosystem function, is of considerable interest to policy makers because decomposition and nutrient mineralization often greatly influence productivity of crops and forests, and therefore help to determine the long-term well-being of both natural and managed ecosystems. A growing number of publications in leading ecological journals report experiments that have manipulated functional and species diversity of decomposer biota, as well as plant litter, none of which claims evidence for causative effects of diversity on the ecosystem processes measured. None of this work has been mentioned.

### Implications

We believe that ESA’s endorsement of this “Issues” paper may have negative consequences for both the credibility of ESA and the broader issues of biodiversity conservation, for two reasons. The first is that, while it is presented as a document representing a consensus view of leading scientists in this field, it is clearly not. A large body of literature representing a major school of thought on this topic has been simply ignored. Indeed, at least three co-authors of the “Issues” article have themselves either authored or co-authored other publications that take a noticeably different position on the diversity–function issue to that taken in the “Issues” article.

The second reason is, however, far more important. The policy community is not uninformed, and given the high profile of both sides of the diversity debate, many who read the “Issues” paper will already know that another major point of view exists. The concern is often expressed that fundamental differences between the two schools of thought with regard to the “diversity debate” may undermine attempts aimed at conserving

diversity. We agree with this concern. The authors of the "Issues" paper have had a golden opportunity handed to them to prepare a document that could have a real impact throughout the policy sector, and could reduce the risks that the "diversity debate" may pose for conservation attempts. What they could have done was to present both points of view of the debate in a fair manner, together with a balanced array of examples, and then focus on the areas of agreement. They could have pointed out, for example, that it is still extremely important to conserve species because of the ecosystem services that they provide, irrespective of whether or not experiments demonstrate causation between species richness and function. However, they have lost this opportunity and have instead produced what amounts to little more than a propaganda document for their point of view and an advertisement for the research programs of some of the authors. (Eighteen of the 25 cited references, including all 10 that present primary research results, are authored or co-authored by the authors of this document.) We do not believe that the battle for conservation of species has been well served by this tactic.

We believe that the position taken by the authors creates a dangerous situation for biodiversity conservation. By setting up their interpretations of experimental studies alongside remarks such as ". . . the maintenance of ecosystem functioning should be included as an integral part of national and international policies designed to conserve local and global biodiversity," and ". . . we adopt the prudent strategy of preserving biodiversity in order to safeguard ecosystem processes vital to society," they leave the reader to conclude that those experimental studies claiming to show causative effects of diversity on function provide the strongest reason for why we should conserve diversity. We believe that this line of reasoning is harmful to conservation of biodiversity, because if this house of cards is weakened or collapses (e.g., by the emergence of

published data sets that support other conclusions, reassessments of experiments claiming diversity effects that reveal errors of interpretation), then their argument for conserving biodiversity is also damaged. Our concern is that unjustifiable actions are being made to protect this single rationale for biodiversity conservation, and that scientific objectivity is being compromised as a result. In the long run, the biggest loser is likely to be the conservation of the very biodiversity that the authors are presumably attempting to assist. We also emphasize that we are not disputing the possibility of immediate or long-term (*sensu* Grime 1998) benefits of biodiversity to ecosystems, but are also of the view that the experimental evidence obtained to date to support the claim that biodiversity directly benefits ecosystem properties can be subjected to other interpretations.

We are curious to know how this document came to be published with ESA endorsement. Because of its selective presentation of material, we believe that serious questions must be asked within the hierarchy of ESA about the development and publication of this document. We believe that the publication of a document such as this has the potential to damage the reputation of ESA as a leading impartial professional body of ecologists aimed at fostering ecological research without favoring any particular scientific or political agenda.

#### Literature cited

Aarssen, L. W. 1997. High productivity in grassland ecosystems: affected by species diversity or productive species? *Oikos* **80**:183–184.

Al Mufti, M. M., C. L. Sydes, S. B. Furness, J. P. Grime, and S. R. Band. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* **65**:759–791.

André, M., F. Bréchinac, and P. Thibault. 1994. Biodiversity in model ecosystems. *Nature* **371**:565.

Berendse, F. 1998. Effects of dominant plant species on soils during succession in nutrient poor ecosystems. *Biogeochemistry* **42**:73–88.

Garnier, E., M. L. Navas, M. P. Austin, J. M. Lilley, and R. M. Gifford. 1997. A problem for biodiversity–productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures. *Acta Oecologica* **18**:657–670.

Givnish, T. J. 1994. Does diversity beget stability? *Nature* **371**:113–114.

Grime, J. P. 1987. Dominant and subordinate components of plant communities—implications for succession, stability and diversity. Pages 413–428 in A. Gray, P. Edwards, and M. Crawley, editors. *Colonization, succession and stability*. Blackwell Scientific, Oxford, UK.

Grime, J. P. 1997. Biodiversity and ecosystem function: the debate deepens. *Science* **277**:1260–1261.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**:902–910.

Hector, A., B. Schmid, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Dannell, J. Joshi, A. Jumpponen, C. Körner, P. W. Leadley, M. Loreau, A. Minns, C. P. H. Mulder, G. O'Donovan, S. J. Otway, J. S. Pereira, A. Prinz, D. J. Read, M. Scherer-Lorenzen, E.-D. Schulze, A.-S. D. Siamantziouras, E. N. M. Spehn, A. C. Terry, A. Y. Troumbis, F. I. Woodward, S. Yachi, and J. H. Lawton. 1999. Plant diversity and productivity in European grasslands. *Science* **286**:1123–1127.

Hodgson, J. G., K. Thompson, P. J. Wilson, and A. Bogaard. 1998. Does biodiversity determine ecosystem function? The Ecotron experiment revisited. *Functional Ecology* **12**:843–848.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant compo-

- sition and diversity on ecosystem processes. *Science* **277**:1302–1305.
- Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**: 121–149.
- Huston, M. A. 1980. Soil nutrients and species richness in Costa Rican forests. *Journal of Biogeography* **7**:147–157.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449–460.
- Klopatek, C. C., E. G. O'Neill, D. W. Freckman, C. S. Blesdoe, D. C. Coleman, E. R. Ingham, D. Parkinson, and J. M. Klopatek. 1992. The sustainable biosphere initiative: a commentary from the U. S. Soil Ecology Society. *ESA Bulletin* **73**:223–228.
- Laakso, J., and H. Setälä. 1999. Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos* **87**:57–64.
- Mikola, J., and H. Setälä. 1998. Relating species diversity to ecosystem functioning: mechanistic backgrounds and an experimental approach with a decomposer food web. *Oikos* **83**:180–194.
- Naeem, S. 1999. Power behind Nature's throne. *Nature* **401**:653–654.
- Naeem, S., K. Håkansson, J. H. Lawton, M. J. Crawley, and L. J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. *Oikos* **76**:259–264.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* **390**:507–509.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–737.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:97–106.
- Tilman, D. 1997. Distinguishing between the effects of species diversity and species composition. *Oikos* **80**:185.
- Tilman, D. 1999. Ecological consequences of biodiversity: a search for general principles. *Ecology* **80**:1455–1474.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997a. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300–1302.
- Tilman, D., S. Naeem, J. Knops, P. Reich, E. Siemann, D. Wedin, M. Ritchie, and J. Lawton. 1997b. Biodiversity and ecosystem properties. *Science* **278**:1866–1867.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**:718–720.
- Trenbath, B. R. 1974. Biomass productivity of mixtures. *Advances in Agronomy* **26**:177–210.
- Vandermeer, J. H. 1989. *The ecology of intercropping*. Cambridge University Press, New York, New York, USA.
- Wardle, D. A. 1998. A more reliable design for biodiversity study? *Nature* **394**:30.
- Wardle, D. A. 1999. Is "sampling effect" a problem for experiments investigating biodiversity–ecosystem function relationships? *Oikos* **87**:403–407.
- Wardle, D. A., O. Zackrisson, G. Hörnberg, and C. Gallet. 1997a. The influence of island area on ecosystem properties. *Science* **277**:1296–1299.
- Wardle, D. A., O. Zackrisson, G. Hörnberg, and C. Gallet. 1997b. Biodiversity and ecosystem properties. *Science* **278**:1867–1869.
- Wheeler, B. D., and K. E. Giller. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above-ground plant material. *Journal of Ecology* **70**:179–200.

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## What *Issues in Ecology* Is, and Isn't

*Issues in Ecology* is designed to communicate, to nonscientists, accurate and unbiased summaries of the current status of scientific knowledge on environmental issues. *Issues in Ecology* was motivated by the belief that it is the obligation of scientists and scientific societies to communicate relevant findings with the public and public officials in an open, honest, unbiased manner. Each report represents a consensus reached by a panel of scientists who have skills relevant to the topic being addressed. Like papers submitted to *Ecology*, all reports considered by *Issues in Ecology* undergo extensive review, which is discussed below. Such review is appropriate and necessary because the process of synthesizing an area of inquiry and of reaching consensus is difficult. Indeed, it is the nature of good synthetic science to highlight major points rather than to list every alternative theory and viewpoint. Although such syntheses will unavoidably lead to controversy within the discipline, it is the reasoned synthesis of current knowledge that is of interest and importance to society as a whole.

Given the comments of Wardle et al. (2000) in this issue of the *ESA Bulletin*, it is important to point out what *Issues in Ecology* reports are not: they are not ESA position papers. Contrary to the assertions of Wardle et al., an *Issue in Ecology* report is no more a statement of ESA's position on a topic than is the Wardle et al. letter, or any other paper appearing in *Ecology*, *Ecological Applications*, *Ecological Monographs*, or the *ESA Bulletin*. Each *Issues in Ecology* is a free-standing, reviewed publication that contains the opinions of its authors, opinions that have withstood formal and unusually thorough review.

*Issues in Ecology* differs from the usual scientific journal in several important ways. These differences

were designed to allow *Issues in Ecology* to better meet its objectives. Reports are not spontaneously submitted by their authors. Rather, topics for reports arise via suggestions from ESA members and from members of the *Issues in Ecology* Editorial Board. If the Editorial Board decides that a proposed topic is worthy of review, it nominates potential members for a panel of scientists, including its chair. The chair also nominates and helps recruit members, all of whom must be approved by the Editorial Board. The goal of this process is to assemble a panel of experts that seems likely to be able to reach a reasoned and unbiased synthesis.

Once a panel has reached a consensus and submitted its report, the report is sent to all eight members of the Editorial Board for formal review (but not to any members who are co-authors of the report). Depending on the topic and the skills of the Editorial Board, the report may also be sent to two or three additional reviewers. Each reviewer is asked if the report should be rejected, accepted, or re-reviewed pending major revisions, and to provide an extensive written review. This part of the review process differs from that of *Ecology* and other journals only in the larger number of reviews obtained.

For those reports that are accepted (and not all have been accepted), the next step is the condensation and translation of the report from the usual language of science into standard newspaper-like English. This is essential if the report is to be accessible to nonscientists. This is done with the assistance of a science writer, whose work is also subject to review by both the authors (especially the panel chair) and the Editorial Board. When this translation is completed, ESA staff in the Washington, D.C. office work with the chair of the panel to choose appropriate illustrations and to fit the report into the format of *Issues in Ecology*. All of these procedures are overseen

by the editor-in-chief. In addition, the scientific (nonpublic) versions of the accepted reports may be published in *Ecological Applications* if the authors and reviewers judge them to be sufficiently novel and important. See, for instance, Vitousek et al. (1997; *Ecological Applications* 7:737-750).

Skepticism is an important part of the scientific process, as is synthesis. However, skepticism about the process of preparation of *Issues in Ecology* harms its credibility, and might discourage some scientists from contributing more broadly to society. We believe that the procedures already in place have assured that all *Issues in Ecology* reports published to date have been accurate and unbiased summaries of the current status of scientific knowledge on environmental issues. The comments of Naeem (2000) reinforce this view with respect to the biodiversity report. However, the Editorial Board of *Issues in Ecology* wants to dispel any possibility of even a perception of inaccuracy or bias. To help achieve this, the Editorial Board has decided always to seek at least two formal reviews on each report by outside experts thought to be "neutral" on the topic, to assure that the final public version of each report is distributed to and approved by all authors (not just the panel chair), and to engage an ad hoc acting editor-in-chief for any report co-authored by the editor-in-chief. Society is investing an increasing share of its resources in ecological research. *Issues in Ecology* is one means whereby scientists who are the recipients of this public support can provide society with the knowledge it seeks.

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## Reply to Wardle et al.

*Issues in Ecology*, Number 4, on biodiversity and ecosystem functioning, provides a brief overview of basic principles concerning biotic influences on ecosystem processes and a conservative summary of current evidence that directly addresses the role of biodiversity in these processes. The report is a distillation of a longer document that more fully detailed the views of the panel members (Shahid Naeem [chair], T. Chapin, Robert Costanza, Paul Ehrlich, Frank B. Golley, David Hooper, J. H. Lawton, Robert O'Neill, Harold Mooney, O. Sala, Amy Symstad, and David Tilman). This longer document was condensed to produce a report that was deemed by the editors and science writers to be accessible to a broad, nonscientific audience, including high school students, while remaining true to its content. In this issue of the *ESA Bulletin*, Wardle et al. express concern that their opinion did not receive a strong enough voice, and therefore call into question the validity of the document, the process of its production, and motivation of its authors. I regret their dissatisfaction, but am frankly puzzled by all three aspects of their response.

Although the production process could have benefited from more extensive input in its final stages, especially if time and resources had permitted, the main message and the bulk of the report's content would not have been altered. The report is both accurate and fairly represents the diversity of opinion surrounding the issues. This *Issues in Ecology* brochure will serve the public by providing an introduction to this topic and motivating deeper appreciation of the potential roles of the earth's extraordinary, but rapidly declining, biodiversity.

This *Issues in Ecology* volume reflects the viewpoints of the panel and contains much information, of which Wardle et al. disagree only with a portion. There are three parts to the report: (1) its overview of fundamentals, (2) its summary of evi-

dence, and (3) its suggestion for future research to address uncertainties. Wardle et al. are concerned primarily with the second part, expressing consternation that their interpretation of the experiments of others were not discussed. Here, I suggest that their dichotomization of the issues is misplaced and masks the true balance found within the report and the discipline. I will also show that a wide breadth of opinions is reflected in the report's cautionary tone and throughout the body of the report. In total, the concerns of Wardle et al. are unwarranted.

### "Debate" in new disciplines

The hallmark of a new and active science is a dynamic exchange of ideas and information among scientists. This exchange is frequently mistaken as evidence that a particular discipline lacks useful scientific insight. For example, exchange of ideas among evolutionary biologists over constantly emerging new ideas is frequently misinterpreted as a lack of evidence for evolution (Futyuma 1983), when nothing could be more solidly documented in biology than evolution itself.

Study of the ecosystem consequences of biodiversity decline is a relatively new focus in ecological research, so, not surprisingly, there is an active exchange of ideas. The recent explosion of research in biodiversity can be traced to a conference in 1992 (Schulze and Mooney 1993), although its intellectual roots can be traced to Darwin and possibly further (McNaughton 1993). Experimental research on the relationship between biodiversity and ecosystem functioning is less than a decade old, and publications of experimental results appeared only in 1994 (Naeem et al. 1994, Tilman and Downing 1994). Wardle et al. are concerned primarily with recent exchanges among authors (André et al. 1994, Givnish 1994, Aarssen 1997, Garnier et al. 1997, Grime 1997, Huston 1997, Wardle et al. 1997b, Hodgson et al. 1998, Wardle 1998, Naeem 1999, Wardle 1999). Although known

to Wardle et al., their response did not reference replies to these opinions and other related issues (Naeem et al. 1995, Allison et al. 1996, Tilman 1997, Tilman et al. 1997b,c, 1998, Doak et al. 1998, Hector 1998, Lawton et al. 1998, Loreau 1998, Naeem and Li 1998, Allison 1999). There is an ongoing, active exchange of opinions and ideas that is typical of an emerging discipline.

Wardle et al. feel that this exchange is not reflected in the *Issues in Ecology* brochure on biodiversity–ecosystem functioning (henceforth, the BD–EF *Issues*). The majority of articles Wardle et al. refer to (André et al. 1994, Givnish 1994, Aarssen 1997, Grime 1997, Wardle et al. 1997b, Wardle 1998, 1999, Naeem 1999) are commentaries. Most of these are short (1–4 pages) opinion pieces that express concerns over interpretations of findings. Some of these reports are longer reevaluations of the experiments themselves (Garnier et al. 1997, Huston 1997, Hodgson et al. 1998), and these papers have stimulated new approaches to analyzing, modeling, and conducting empirical research. Similar commentaries (Naeem et al. 1995, Tilman 1997, Tilman et al. 1997c, Naeem and Li 1998) and longer studies (Allison et al. 1996, Tilman et al. 1997b, 1998, Doak et al. 1998, Hector 1998, Lawton et al. 1998, Loreau 1998, Allison 1999) have addressed these and other issues. *Issues in Ecology* does not document such technical exchanges concerning experimental design, statistical issues, and theory, although its coverage of topics balances ideas and evidence according to their relative weights. For the part that focused on evidence, the report summarized important, well-replicated findings. Wherever necessary, however, coverage was cautious, generally reflecting the variation in opinions expressed in published exchanges.

### Is our report biased?

The biggest question raised by Wardle et al. is this: Does our report truly reflect majority opinion, or is it slanted? Certainly we feel that the

report is balanced and objective. Indeed, if anything, the report possibly understates the magnitude of biodiversity's role in ecosystem functioning. Two studies support this conclusion. Schlöpfer and colleagues (Schlöpfer and Schmid 1999, Schlöpfer et al. 1999) have written literature reviews on this issue, and their conclusions agree with that of the *BD-EF Issues*. Over 56 different hypotheses stemming from seven core biodiversity hypotheses were identified in their review, 20 of which have been addressed scientifically (Schlöpfer and Schmid 1999). In spite of this overwhelming richness of ideas, their conclusion was, "While some of the studies found negligible effects of biodiversity, effects that are beneficial to humans were found in a wide range of ecosystem contexts, even at the limited time scale of ecological experiments." In a survey of expert opinion concerning the discipline (Schlöpfer et al. 1999), the majority opinion was that ". . . (1) ecosystem process rates are strongly correlated with biological diversity, and (2) these same processes are (although to a varying extent) important for the delivery of humanly defined 'ecosystem services' by natural systems." Thus, an independent recent scientific literature review and results of a recent survey and summary of expert opinions both lead to conclusions that are congruent with, but stronger, than our *Issues in Ecology* report.

### One school of thought, not two

The "diversity debate," as Wardle et al. have chosen to call it, is not described correctly. Wardle et al. describe a debate in which one party subscribes to a "population biology" perspective, while another subscribes to an "ecosystem property" perspective, suggesting that such perspectives are mutually exclusive. This description is incorrect. The panel members represent, in much the same way Wardle et al. do, a group of scientists who combine population and ecosystem perspectives in their own research and writings. The "de-

bate" Wardle et al. refers to more accurately reflects issues concerning the disentanglement of the functional and taxonomic components of biodiversity. Some studies (Naeem and Li 1997, Tilman et al. 1997a, Symstad et al. 1998, Naeem et al. 1999) have simultaneously manipulated both functional and taxonomic diversity, and have argued that variation in functional diversity or functional identity of species can be a dominant factor in ecosystem functioning. Studies that have manipulated only functional groups (Hooper and Vitousek 1997, 1998, Hooper 1998) suggest that the strongest biotic influences of ecosystem functioning concern functional properties of species. Many studies have shown an asymptotic relationship between species richness and ecosystem functioning, but not all (Schlöpfer and Schmid 1999). All of these points are raised in the report (see below). Functional and taxonomic diversity are, however, inextricably linked. As one randomly increases species, invariably functional group representation will increase.

The importance of functional diversity is not a new idea, and has been examined and discussed by many researchers (Raunkier 1934, Root 1967, Körner 1993, Smith et al. 1993, Chapin et al. 1996, Mooney et al. 1996, Hooper and Vitousek 1997, Smith et al. 1997, Hooper and Vitousek 1998), and has important bearing on many issues in ecology, not just biodiversity and ecosystem functioning (Barbault et al. 1991, Walker 1992, Lawton and Brown 1993, Cowling et al. 1994, Andren et al. 1995, Beare et al. 1995, Walker 1995, Gitay et al. 1996, Jaksic et al. 1996, Ehrlich and Walker 1998, Mikola and Setälä 1998, Naeem 1998). The studies by Grime, Wardle, Berendse, Mikola, Hooper, Setälä, and their colleagues cited by Wardle et al. also make important contributions to this literature. These studies, however, are often not related to the issues surrounding the ecosystem consequences of declining biodiversity, nor are they in conflict with the report. As defined by the report,

biodiversity refers to the "genetic and functional diversity across population, community, ecosystem, landscape, and global scales." The majority of studies have shown that change in biodiversity, whether it be functional or taxonomically defined, can affect ecosystem functioning, and the report summary claims no more than this.

Creating dichotomies, although a useful heuristic device, generally misrepresents scientific exchange. Labels such as "population" vs. "ecosystem" or "functional diversity" vs. "species diversity" reflect endpoints of a continuum, not discrete schools of thought. There is only one school of thought, and that is that composition and nature of the earth's biota, or biodiversity, contributes to ecosystem functioning.

### Correlational studies and other evidence

Evidence by which fundamental principles in ecology are derived consists of a blend of theory, simulation, experiment, and observation. The trade-offs, known as internal vs. external validity (Manly 1992), prevent either pure theory or pure observation from providing reliable insights into the mechanisms that govern and permit us to predict community and ecosystem properties (Naeem, *in press*). These issues are well known, and several volumes review and discuss them (Hairston 1989, Peters 1991, Manly 1992, Scheiner and Gurevitch 1993, Hilborn and Mangel 1997, Underwood 1997, Resetarits and Bernardo 1998). The need for experiments in ecology is well known, and panel members, as well as Wardle et al., have contributed to theory, simulation, experimental, and observational studies.

In the section entitled, "Observational studies," we explicitly acknowledged that correlations between biodiversity and ecosystem functioning can show a variety of relationships. We state, however, that it is difficult to control statistically for confounding effects; therefore we turn our attention to experimental results

for further insight. Interestingly, a figure presenting results from six studies, three observational and three experimental, was included in the original document, but the science writers, editors, and peer reviewers all strongly advocated removal of this figure. We regret Wardle et al.'s dissatisfaction with the collective decision of many individuals not to discuss the classic arguments concerning the relative merits of descriptive vs. experimental, but perhaps they may appreciate that this small brochure simply cannot accommodate extensive coverage of such a complex issue.

Curiously, Wardle et al. claim that decomposers were inadequately covered. Both the panel members and Wardle et al. have examined decomposers and the rates of decomposition in experimental studies and recognize the importance of these organisms and associated ecosystem functions. Fig. 5, for example, shows decomposers to be as important as producers, and the lead text (page 4) clearly indicates that plant production, decomposition, and other processes are the primary functions of interest. Furthermore, in "Future Research," the brochure expressly lists decomposers along with consumers as important areas for further development to address uncertainties.

A few recent studies (Van der Heijden et al. 1998, Naeem et al. 2000) have suggested that decomposer diversity, or perhaps more importantly, detritivore identity and composition (Mikola and Setälä 1998), are quite important to ecosystem studies. Studies of rates of decomposition in which biodiversity was manipulated have reported negative (Naeem et al. 1994) or weak trends (Knops et al., *submitted*, Hector et al., *in press*). One study manipulated diversity of plant litter and found little evidence for effects of plant litter diversity on decomposition processes (Wardle et al. 1997a), which is largely in agreement with other findings. In comparison to plant studies, however, this research, although well known to the panel members, is not as well developed.

Agro-ecological studies were not discussed in the report because their findings are mixed and the diversity of manipulated plants is seldom more than two or three species, although many studies show greater production with greater diversity (Swift and Anderson 1993). Of larger concern is that agricultural research is biased toward looking for overyielding and conducts its research on heavily managed soils, all of which makes the interpretation of this literature difficult. Finally, although the agricultural literature is well known to the panel, the report was clearly concerned with the loss of diversity from unmanaged ecosystems. The cover and Figs. 2 and 3, for example, clearly show that the report considers agro-ecosystems as the lower boundary for diversity. Thus, agricultural research is not readily adaptable to the needs for this report.

Wardle et al.'s sense that decomposers or agro-ecological research were not treated sufficiently is a matter of opinion, but we suggest that inspection of the report will reveal otherwise and should allay their concern. The report defines a strong and important role for decomposers and calls for further work in this important area. The report considers agro-ecosystems and associated literature to be quite distinct from biodiversity research.

### **Conclusions and a look to the future**

The production of a report such as the *Issues in Ecology* report on biodiversity and ecosystem functioning is most likely unfamiliar to many researchers. Scientists are more familiar with agency, inter-agency, or governmental panel reports reflecting symposia, many iterations of report writing, and the production of longer volumes or reviews that contain executive summaries. *Issues in Ecology* is clearly quite different. An *Issues in Ecology* report does not permit lengthy discussions of technical issues or extensive coverage of exchanges among scientists, even though these

are central to the scientific process. Contrary to Wardle et al.'s opinion, this report is very much in line with others in the series (Daily et al. 1997, Vitousek et al. 1997, Carpenter et al. 1998).

Expert opinion is provided by many scientific panels when urgency dictates the need for a summary of current evidence and a clear statement of majority opinion. As in most reports of this nature, the full richness of individual opinions is seldom found in such documents. Reports for the Intergovernmental Panel on Climate Change, for example, are frequently controversial. The Sustainable Biosphere Initiative (Lubchenco et al. 1991), though the product of an extensive process by the ESA, was also controversial, as Wardle et al. note.

Finally, we must note that our report reflects the concerns that Wardle et al. raise. Not only does the report explicitly address observational studies, decomposers, and the issues surrounding functional vs. taxonomic diversity; the tone of the report also reflects the need for caution, given differences in opinions on some issues. First, each bulleted point concerning current research uses the word "may" to acknowledge that the verdict is still out on many issues. Second, the fourth bulleted point states, "the identity and abundance of species in an ecosystem can be as important as changes in biodiversity in influencing ecosystem processes." Third, in the *Summary*, the report states, "although these three points have been repeatedly observed . . . there is still debate about the mechanisms behind them." Fourth, the *Conclusions* state, "although a number of uncertainties remain, the importance of ecosystem services to human welfare requires that we adopt a prudent strategy of preserving biodiversity in order to safeguard ecosystem processes vital to society." Finally, five uncertainties are discussed (pages 9–10) that reflect issues raised by Wardle et al. and others.

I hope that the comments in this paper clear up the "curiosity" expressed by Wardle et al. about the

production of such a document. Certainly it should inform others who engage in such a process that providing accessible summaries of contemporary issues in the ecological sciences is difficult. The accumulation of additional experimental data and the development of effective theory will provide us with the tools necessary to better explain and predict the ecosystem consequences of declining biodiversity. The panel members, Wardle et al., and many others will continue to work toward a clearer understanding of this potential role of biodiversity, and hopefully a rich and lively exchange will continue.

### Literature cited

- Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* **80**: 183–184.
- Allison, G. W. 1999. The implications of experimental design for biodiversity manipulations. *American Naturalist* **153**:26–45.
- Allison, G. W., B. A. Menge, J. Lubchenco, and S. A. Navarrete. 1996. Functional roles of biodiversity. Pages 371–392 in H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulze, editors. *Functional roles of biodiversity: a global perspective*. John Wiley and Sons, New York, New York, USA.
- André, M., F. Bréchnignac, and P. Thibault. 1994. Biodiversity in model ecosystems. *Nature* **371**:565.
- Andren, O., J. Bengtsson, and M. Clarholm. 1995. Biodiversity and species redundancy among litter decomposers. Pages 141–151 in H. P. Collins, G. P. Robertson, and M. J. Klug, editors. *The significance and regulation of soil biodiversity*. Kluwer Academic, Amsterdam, The Netherlands.
- Barbault, R., R. K. Colwell, B. Dias, D. L. Hawksworth, M. Huston, P. Laserre, D. Stone, and T. Younès. 1991. Conceptual framework and research issues for species diversity at the community level. Pages 37–71 in O. T. Solbrig, editor. *From genes to ecosystems: a research agenda for biodiversity*. IUBS, Paris, France.
- Beare, M. H., D. C. Coleman, D. A. Crossley, P. F. Hendrix, and E. P. Odum. 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant and Soil* **170**:5–122.
- Carpenter, S., N. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. Smith. 1998. Nonpoint pollution of surface water with phosphorous and nitrogen. *Issues in Ecology*.
- Chapin, F. S., III, H. L. Reynolds, C. M. D'Antonio, and V. M. Eckhart. 1996. The functional role of species in terrestrial ecosystems. Pages 403–428 in B. Walker and W. Steffan, editors. *Global change and terrestrial ecosystems*. Cambridge University Press, Cambridge, U.K.
- Cowling, R. M., P. J. Mustart, H. Laurie, and M. B. Richards. 1994. Species diversity; functional diversity and functional redundancy in fynbos communities. *South African Journal of Science* **90**:333–337.
- Daily, G. C., S. Alexander, P. R. Ehrlich, L. Gouler, J. Lubchenco, P. A. Matson, H. A. Mooney, S. Postel, S. H. Schneider, D. Tilman, and G. M. Woodwell. 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. *Issues in Ecology*.
- Doak, D. F., D. Bigger, E. Harding-Smith, M. A. Marvier, R. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability–diversity relationships in community ecology. *American Naturalist* **151**:264–276.
- Ehrlich, P., and B. Walker. 1998. Rivets and redundancy. *BioScience* **48**:387.
- Futyuma, D. J. 1983. *Science on trial: the case for evolution*. Pantheon Books, New York, New York, USA.
- Garnier, E., M.-L. Navas, M. P. Austin, J. M. Lilley, and R. M. Gifford. 1997. A problem for biodiversity–productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures? *Acta Oecologica* **18**:657–670.
- Gitay, H., J. B. Wilson, and W. G. Lee. 1996. Species redundancy: a redundant concept? *Journal of Ecology* **84**:121–124.
- Givnish, T. J. 1994. Does biodiversity beget stability? *Nature* **371**: 113–114.
- Grime, J. P. 1997. Biodiversity and ecosystem function: the debate deepens. *Science* **277**:1260–1261.
- Hairston, N. G. S. 1989. *Ecological experiments*. Cambridge University Press, Cambridge, UK.
- Hector, A. 1998. The effects of diversity on productivity: detecting the role of species complementarity. *Oikos* **82**:597–599.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective*. Princeton University Press, Princeton, New Jersey, USA.
- Hodgson, J. G., K. Thompson, A. Bogaard, and P. J. Wilson. 1998. Does biodiversity determine ecosystem function? The Ecotron experiment reconsidered. *Functional Ecology* **12**:843–848.
- Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* **79**: 704–719.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302–1305.
- Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**: 121–149.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449–460.
- Jaksic, F. M., P. Feinsinger, and J. E. Jimenez. 1996. Ecological redundancy and long-term dynamics of vertebrate predators in semi-arid Chile. *Conservation Biology* **10**:252–262.
- Körner, C. 1993. Scaling from species to vegetation: the usefulness of functional groups. Pages 117–

- 132 in E.-D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem functioning. Springer-Verlag, Berlin, Germany.
- Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems. Pages 255–270 in E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.
- Lawton, J. H., S. Naeem, L. J. Thompson, A. Hector, and M. J. Crawley. 1998. Biodiversity and ecosystem functioning: getting the Ecotron experiment in its correct context. *Functional Ecology* **12**:843–856.
- Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. *Oikos* **82**: 600–602.
- Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Risser. 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* **72**:371–412.
- Manly, B. F. J. 1992. The design and analysis of research studies. Cambridge University Press, Cambridge, UK.
- McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystems. Pages 361–384 in E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.
- Mikola, J., and H. Setälä. 1998. Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. *Oikos* **83**.
- Mooney, H. A., J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulze, editors. 1996. Functional roles of biodiversity: a global perspective. John Wiley and Sons, New York, New York, USA.
- Naeem, S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* **12**:39–45.
- Naeem, S. 1999. Power behind Nature's throne. *Nature* **401**:653–654.
- Naeem, S. *In press*. Experimental validity and ecological scale as tools for evaluating research programs. In R. H. and V. K. Gardner, editors. Scaling relationships in experimental ecology.
- Naeem, S., D. Byers, S. F. Tjossem, C. Bristow, and S. Li. 1999. Plant neighborhood diversity and production. *Ecoscience*, *in press*.
- Naeem, S., D. Hahn, and G. Schuurman. 2000. Producer–decomposer co-dependency modulates biodiversity effects. *Nature*, *in press*.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* **390**:507–509.
- Naeem, S., and S. Li. 1998. A more reliable design for biodiversity study?—Reply. *Nature* **394**:30–31.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–737.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1995. Biodiversity loss in model ecosystems. Reply. *Nature* **375**:561.
- Peters, R. H. 1991. A critique for ecology. Cambridge University Press, Cambridge, UK.
- Raunkier, C. 1934. The life form of plants and statistical plant geography. Oxford University Press, Oxford, UK.
- Resetarits, W. J., Jr., and J. Bernardo. 1998. Experimental ecology: issues and perspectives. Oxford University Press, New York, New York, USA.
- Root, R. B. 1967. The niche exploitation pattern of the Blue-Gray Gnatcatcher. *Ecological Monographs* **37**:317–350.
- Scheiner, S. M., and J. Gurevitch, editors. 1993. Design and analysis of ecological experiments. Chapman and Hall, London, UK.
- Schläpfer, F., and B. Schmid. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecological Applications* **9**:893–912.
- Schläpfer, F., B. Schmid, and I. Seidl. 1999. Expert estimates about effects of biodiversity on ecosystem processes and services. *Oikos* **84**:386.
- Schulze, E. D., and H. A. Mooney, editors. 1993. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.
- Smith, T. M., H. H. Shugart, and F. I. Woodward, editors. 1997. Plant functional types. Cambridge University Press, Cambridge, UK.
- Smith, T. M., H. H. Shugart, F. I. Woodward, and P. J. Burton. 1993. Plant functional types. Pages 272–292 in A. M. Solomon and H. H. Shugart, editors. Vegetation dynamics and global change. Chapman and Hall, New York, New York, USA.
- Swift, M. J., and J. M. Anderson. 1993. Biodiversity and ecosystem function in agricultural systems. Pages 15–41 in E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.
- Symstad, A. J., D. Tilman, J. Wilson, and J. Knops. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* **81**:389–397.
- Tilman, D. 1997. Distinguishing the effects of species diversity and species composition. *Oikos* **80**: 185.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* **367**:363–365.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Sieman. 1997a. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300–1302.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence? *American Naturalist* **151**:277–282.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997b. Plant diversity

- and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences* **94**:1857–1861.
- Tilman, D., S. Naeem, J. Knops, P. Reich, E. Siemann, D. Wedin, M. Ritchie, and J. Lawton. 1997c. Biodiversity and ecosystem properties. *Science* **278**:1866–1867.
- Underwood, A. J. 1997. *Experiments in ecology*. Cambridge University Press, Cambridge, UK.
- Van der Heijden, M. G. A., J. N. Klironomas, M. Ursic, P. Moutogolia, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**:69–72.
- Vitousek, P. M., J. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: causes and consequences. Pages 1–15 in *Issues in Ecology*. Ecological Society of America, Washington, D. C.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* **9**:747–752.
- Walker, B. H. 1992. Biological diversity and ecological redundancy. *Conservation Biology* **6**:18–23.
- Wardle, D. A. 1998. A more reliable design for biodiversity study? *Nature* **394**:30.
- Wardle, D. A. 1999. Is “sampling effect” a problem for experiments investigating biodiversity–ecosystem function relationships? *Oikos* **87**:403–407.
- Wardle, D. A., K. I. Bonner, and K. S. Nicholson. 1997a. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* **79**:247–258.
- Wardle, D. A., O. Zackrisson, G. Hornberg, and C. Gallet. 1997b. Biodiversity and ecosystem properties. *Science* **278**:1867–1869.

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## To Bonferroni or Not to Bonferroni: When and How Are the Questions

Statistical tables (e.g., ANOVA, regression, correlation coefficients, and chi-square values) are commonly reported in *Ecology* and similar journals. Rice (1989) pointed out that tests for the statistical significance of individual components of such tables are often biased, so that too many of these components are considered “significant” (i.e., the null hypothesis is rejected when it is actually true, or a Type I error). As an example, he noted that in a hypothetical table of 10 correlation coefficients, there is a 40% probability of observing at least one significant ( $P < 0.05$ ) individual correlation by chance alone. Rice detailed a sequential Bonferroni correction procedure (originally developed by Holm 1979) to control this problem while simultaneously maintaining adequate power to correctly reject one or more false component null hypotheses within a given statistical table.

However, Rice (1989) noted that, as pointed out by Miller (1981), there is no clear criterion for deciding exactly what constitutes a family of statistical tests, nor is it clear when a simultaneous-inference test such as the sequential Bonferroni correction is required. He argued that such choices depend upon the desired group-wide Type I error rate, and suggested that simultaneous inference be employed whenever:

1) a group of two or more tests is scanned, and the  $P$  values of component tests are used to determine where significant differences occur (i.e., a posteriori testing), or

2) two or more tests (that cannot be pooled) address a common null hypothesis, and rejection of the null hypothesis is possible when only some of the tests are found to be individually significant.

Our goals in this note are to (1) assess the extent to which the use of Bonferroni corrections has increased following Rice’s (1989) widely cited paper; (2) examine the level of agreement on when and how to employ Bonferroni corrections; and (3) offer some recommendations for dealing

with multiple tests of significance. We will focus on the more conceptual/philosophical side of these issues, and will not attempt to evaluate the various methodologies available for performing Bonferroni significance corrections. (For an examination of these more technical aspects, see discussion and references in Holm 1979, Miller 1981, Simes 1986, Hotchberg 1988, Wright 1992, and Scheiner and Gurevitch 1993.)

To assess the extent to which Rice’s (1989) paper affected the subsequent use of Bonferroni corrections, we used the JSTOR database to perform full-text searches for the word “Bonferroni” in all *Ecology* papers published between 1920 and 1999. We then manually examined each flagged paper to determine if and how Bonferroni corrections were performed. Since there were no papers containing the word “Bonferroni” prior to 1982, we divided the remaining years into two time periods to examine the change in usage of Bonferroni corrections before and after Rice’s (1989) sequential Bonferroni correction procedure. Between 1982 and 1989, we found a mean of 2% of

all papers per year used some type of Bonferroni correction, and 9% per year between 1990 and 1999 (Table 1). Although there clearly was an increase in the use of these corrections after 1989, many authors still appeared to avoid using Bonferroni corrections for statistical procedures that arguably met Rice's (1989) criteria. For example, even though after 1989 there was an almost threefold increase in the percentage of papers using Bonferroni corrections on correlation and regression statistics (Table 1), we estimated (based on a complete manual search of one randomly selected issue from each *Ecology* volume published in the 1990s) that over 80% of the papers reporting these statistics during this time period still did not present any Bonferroni corrections or adjusted *P* values.

Based on this literature survey, we inferred three general philosophies on when to employ Bonferroni corrections: (1) never (by far the most common), (2) when the same data are analyzed repeatedly, and (3) when the same hypothesis is analyzed repeatedly (least common). However, in many instances it was difficult for us to follow the underlying logic determining if, when, and how Bonferroni corrections should be performed, as many authors did not explicitly state their procedures and/or were inconsistent in their usage. For example, some correlation or multiple comparison statistics re-

ceived Bonferroni corrections, when other seemingly similar analyses in the same paper did not. Nevertheless, we found that in both the 1980s and 1990s, ANOVA was by far the most commonly used statistic receiving Bonferroni corrections (Table 1), with most authors using Bonferroni procedures to correct for multiple means comparisons, and almost no authors correcting for examining several related ANOVAs that arguably tested a common null hypothesis.

To assess the extent to which there is agreement on when and how to use Bonferroni corrections, in January 1996, we sent a brief multiple-choice anonymous questionnaire to the editors of *American Naturalist*, *Ecology*, and *Evolution* (over 90 editors in total). Of the 33 respondents, 51% answered that, in their editorial experience, whether and how to use Bonferroni adjustments was often or sometimes an important issue. (The remaining 49% stated that this issue was seldom/never important or not relevant to their area of expertise; these respondents were instructed to skip the remainder of the survey.) Only 1 of the 18 editors who completed the full survey claimed always to be comfortable with his/her ability to evaluate an author's use of Bonferroni adjustments. We also found little consensus on whether and when some type of Bonferroni adjustment should be employed. For example, there was only one (out of

five) hypothetical statistical scenarios in which two-thirds or more of the editors agreed on whether or not they would expect some type of Bonferroni adjustment. In addition, when presented with an example of Rice's (1989) hypothetical example of 10 correlation coefficients, 18% of respondents felt there was no need for a Bonferroni correction.

Our intent is not to fault editors, nor to present the one true and correct approach to applying the Bonferroni correction. On the contrary, we wish to point out that the decision on when and how to use this procedure often is neither simple nor cut and dried. This difficulty may be illustrated by using an example from our own research. We were interested in testing the null hypothesis of no genetic differences between two groups of plants, using chi-square tests on data from 10 electrophoretic loci. One might decide not to use any Bonferroni correction, since each locus is considered independent, and only one analysis per locus is being performed. However, one could also argue that, in this case, the same null hypothesis is being tested 10 times, and thus a sequential correction beginning with 0.05/10 should be employed. We believe that both of these viewpoints are defensible, and thus investigators with different interests might legitimately come to different conclusions about which statistical approach is appropriate.

**Table 1.** Results of our full-text JSTOR database survey of all *Ecology* papers published between 1920 and 1999 for the use of Bonferroni corrections. The percentage of papers using Bonferroni corrections on the different test statistics does not sum to 100 because some papers used Bonferroni procedures on more than one kind of analysis.

| Total no. papers published | No. papers with Bonferroni corrections | Mean % papers per year with Bonferroni corrections | Type of statistic using Bonferroni correction |                            |                          |               |        |       |
|----------------------------|--|--|---|----------------------------|--------------------------|---------------|--------|-------|
|                            |  |  | ANOVA   | Mann-Whitney <i>U</i> test | Correlation & regression | <i>t</i> test | MANOVA | Other |
| From 1982 to 1989          |  |  |   |                            |                          |               |        |       |
| 1636                       | 36                                     | 2.2  | 67  | 14                         | 6                        | 6             | 8      | 6     |
| From 1990 to 1999          |  |  |   |                            |                          |               |        |       |
| 2289                       | 206                                    | 9.0  | 52  | 1                          | 16                       | 10            | 6      | 21    |

We also found it difficult to objectively decide at what point the “same data” or “same hypothesis” is being analyzed repeatedly. For instance, in the above example, we performed one set of analyses on allele frequencies, and another set to test for differences in heterozygosity. (Both of these analyses employed the same core electrophoretic data, albeit in different forms.) Should the correction be applied “table-wide” or “manuscript-wide”? Clearly, such increases in the scale of Bonferroni corrections can quickly degenerate into the absurd. For example, should authors who repeatedly test the same data and/or hypothesis over the course of their professional career delay publishing until they are dead or at least retired, so that their total lifetime number of statistical tests of the same data/hypotheses can be tabulated and a single grand sequential Bonferroni correction be performed?

Although overzealous use of Bonferroni corrections needlessly increases Type II error rates (i.e., accepting the null hypothesis when it is actually false), failing to use these corrections when needed inflates Type I error rates. Both errors are important, and slavish attention to one or the other will compromise the integrity of many statistical procedures. Unfortunately, the line between overzealousness and laxity is, in most cases, neither clear nor generally agreed upon. Determining what constitutes an appropriate grouping of statistical tests requires careful consideration of the way the statistics relate to the data and hypotheses of interest, and there are many situations in which reasonable and well-intentioned researchers may disagree about how to make these groupings and apply appropriate corrections.

We have three recommendations for dealing with multiple tests of significance. First, authors, editors, reviewers, and readers should recognize that in many situations the decision about whether and how to apply Bonferroni corrections may be highly subjective. Authors should therefore

be as explicit as possible about the assumptions they make and the logic behind these decisions, and editors, reviewers, and readers should evaluate the author’s logic with an open mind. Second, when the situation may reasonably suggest the necessity of Bonferroni correction to some readers, authors should consider including a statement about if and how their conclusions would have been altered if they had used an alternative statistical approach. Finally, authors, referees, and readers should strive to avoid blind adherence to particular *P* values (Yoccoz 1991, Scheiner 1993); effect sizes, biological significance, and common sense ultimately may be the most important criteria for interpreting the results of all statistical tests.

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### Literature cited

Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* **6**:65–70.

Hotchberg, Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* **75**:800–802.

Miller, R. G., Jr. 1981. *Simultaneous statistical inference*. McGraw-Hill, New York, New York, USA.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**: 223–225.

Scheiner, S. M. 1993. Introduction: theories, hypotheses, and statistics. Pages 1–13 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman & Hall, New York, New York, USA.

Scheiner, S. M., and J. Gurevitch, editors. 1993. *Design and analysis of ecological experiments*. Chapman & Hall, New York, New York, USA.

Simes, R. J. 1986. An improved Bonferroni procedure for multiple tests of significance. *Biometrika* **73**:751–754.

Wright, S. P. 1992. Adjusted *p*-values for simultaneous inference. *Biometrics* **48**:1005–1013.

Yoccoz, N. G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *ESA Bulletin* **72**:106–111.

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## Comments on a Report of the Union of Concerned Scientists and The Ecological Society of America: “Confronting Climate Change in California—Ecological Impacts on the Golden State”

*(The senior author of “Confronting Climate Change” has been contacted. If the authors wish to respond, their statement will be published in the earliest possible issue of the ESA Bulletin.)*

In general, we find this report (Field et al. 1999) very interesting and stimulating. We hope that after reading this document many California inhabitants, including politicians

and decision makers, will realize that climatic changes are no fiction and may affect California ecosystems and their well being. We would like to offer some overlooked information from our area of expertise that could strengthen a few sections of the report.

On page 38, the last paragraph of a chapter "Future distribution of California ecosystems," we read:

*In the southern Sierra Nevada, serious ozone injury has been documented in Jeffrey and ponderosa pine, affecting their susceptibility to bark beetles. The impacts of ozone and bark beetles depend strongly on the water balance of the tree and are thus closely tied to climate (Cahill et al. 1996). In southern California, damage from ozone and nitrogen oxides may interact with changing climate and fire patterns to cause expansion of exotic grasslands at the expense of shrublands in Riverside and San Diego counties (Minnich and Dezzani 1998).*

These statements overlook a larger body of knowledge on air pollution impacts on California ecosystems. Serious ozone injury to yellow pines (Jeffrey and ponderosa) and increased susceptibility to bark beetles have been observed and described for the San Bernardino Mountain mixed-conifer forest zone. The person who discovered this phenomenon more than 30 years ago is Dr. Paul Miller of the Pacific Southwest Research Station, U.S. Forest Service, Riverside, California. Although this phenomenon is also observed in Sierra Nevada forests (as seen during the 1980s, when air pollution and drought were predisposing pines and firs to bark beetle attacks), it has not been described in the peer-reviewed literature. Conversely, there are several publications describing air pollution effects on mixed conifer forests of the San Bernardino Mountains. (The most recent ones, summarizing many years of original research are: Miller 1992, Arbaugh et al. 1998, Miller and Arbaugh 2000.)

Although ambient concentrations of ozone produce injury to a variety of native plants in the mixed-conifer forests of the San Bernardino Mountains (Temple 1998), no injury to plants from ambient levels of nitrogen oxides has been recorded (see a review by Bytnerowicz et al. 1998a). There is, however, a potential for toxic effects of nitric acid vapor (a secondary pollutant formed in photochemical smog) on plants (see Bytnerowicz et al. 1998b). In regard to the effects of N deposition on expansion of grasslands in southern California, Dr. Edith Allen and her group at the University of California at Riverside were the first ones to show this phenomenon in California coastal sage communities (Allen et al. 1997, Padgett and Allen 1999, Padgett et al. 1999). We believe that she should be credited for these findings. Dr. Rich Minnich, a well-recognized authority on fire effects and vegetation type conversion (and the co-author of some of Dr. E. Allen's articles) did not have a leading role in studies on the effects of nitrogen deposition on plant communities.

Another area of concern is in the "Forestry" chapter (page 46, the third paragraph). We read:

*In some parts of the world, the human-generated rain of nitrogen pollution could at least partially alleviate soil nutrient shortages (Holland et al. 1997). Nitrogen deposition could be important in California, although current rates of deposition are too low to play a dominant role in nutrient budgets.*

This statement overlooks the findings of our group, published in several peer-reviewed articles (Riggin et al. 1985, Bytnerowicz and Fenn 1996, Fenn and Poth 1998, 1999, Fenn et al. 1998, Grulke et al. 1998). We have shown that N deposition in chaparral and mixed-conifer zones of the San Bernardino and San Gabriel Mountains could approach 30–35 kg · ha<sup>-1</sup> · yr<sup>-1</sup>, values well above the critical load levels (which, in the southern California mixed-conifer stands growing on granite soils, are about 12–15

kg N · ha<sup>-1</sup> · yr<sup>-1</sup>). Significant changes such as reduced fine root biomass, changes in species composition, contamination of stream and ground water with nitrate, and increased susceptibility to other stresses (especially drought) and modified responses to ozone have been found at the levels of deposition exceeding the critical load levels. Although the Sierra Nevada forests still do not experience the levels of N deposition seen in the southern California mountains, deposition on the western slopes of the Sierra Nevada may reach about 10 kg N · ha<sup>-1</sup> · yr<sup>-1</sup> (Chorover et al. 1994). This is much higher than the values of <1 kg N · ha<sup>-1</sup> · yr<sup>-1</sup> found on the eastern slopes of the Sierra Nevada (Bytnerowicz and Fenn 1996, Bytnerowicz et al. 2000). Such levels of N deposition have a potential for increasing growth of plants and may also affect the composition of forest flora. With rapidly increasing air pollution in the Central Valley, it is also plausible that critical load values of N on the western slopes of the Sierra Nevada may be reached in the near future.

We hope that the authors of this report will take our remarks into consideration and that appropriate action will be taken to clarify the foundation for conclusions reached.

## Literature cited

- Allen, E. B., P. E. Padgett, A. Bytnerowicz, and R. A. Minnich. 1998. Nitrogen deposition effects on coastal sage vegetation of southern California. Pages 131–139 in A. Bytnerowicz, M. J. Arbaugh, and S. Schilling, technical coordinators. Proceedings of the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystems, Riverside, California. U.S. Forest Service General Technical Report **PSW-GTR-166** <<http://www.rfl.psw.fs.fed.us/pubs/psw-gtr-164/fulltext/allen/allen.html#anchor1473574>>
- Arbaugh, M. J., D. L. Peterson, and P. R. Miller. 1998. Air pollution effects on growth of ponderosa pine, Jeffrey pine, and bigcone

- Douglas-fir. Pages 179–207 in P. R. Miller and J. R. McBride, editors. Oxidant air pollution impacts in the montane forests of Southern California. *Ecological Studies* **134**.
- Bytnerowicz, A., J. J. Carroll, B. K. Takemoto, P. R. Miller, M. E. Fenn, and R. C. Musselman. 2000. Distribution and transport of air pollutants to vulnerable California ecosystems. Pages 93–118 in K. M. Scow, G. E. Fogg, D. E. Hinton, and M. L. Johnson, editors. Integrated assessment of ecosystem health. Lewis, Boca Raton, Florida, USA.
- Bytnerowicz, A., T. Dueck, and S. Godzik. 1998. Nitrogen oxides, nitric acid vapor, and ammonia. Pages 5-1 through 5-17 in R. Flagler, editor. Recognition of air pollution injury to vegetation—a pictorial atlas. Air and Waste Management Association, Pittsburgh, Pennsylvania, USA.
- Bytnerowicz, A., and M. Fenn. 1996. Nitrogen deposition in California forests: a review. *Environmental Pollution* **92**:127–146.
- Bytnerowicz, A., P. Padgett, K. Percy, M. Krywult, G. Riechers, and J. Hom. 1998. Direct effects of nitric acid on forest trees. Pages 270–287 in P. R. Miller and J. R. McBride, editors. Oxidant air pollution impacts in the montane forests of Southern California. *Ecological Studies* **134**.
- Cahill, T. A., J. J. Carroll, and T. E. Gill. 1996. Air quality. Pages 1227–1262 in F. W. Davis, editor. Assessment and scientific basis for management options. Volume II. Sierra Nevada Ecosystem Project: Final Report to Congress. Report 36, University of California Center for Water and Wildland Resources, Davis, California, USA.
- Choreover, J., P. M. Vitousek, D. A. Everson, A. M. Esperanza, and D. Turner. 1994. Solution chemistry of mixed-conifer forests before and after fire. *Biogeochemistry* **26**:115–144.
- Fenn, M. E., and M. A. Poth. 1998. Nitrogen deposition and cycling in Mediterranean forests: the new paradigm of nitrogen excess. Pages 288–314 in P. R. Miller and J. R. McBride, editors. Oxidant air pollution impacts in the montane forests of Southern California. *Ecological Studies* **134**.
- Fenn, M. E., and M. A. Poth. 1999. Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California. *Journal of Environmental Quality* **28**:822–836.
- Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Baron, B. T. Bormann, D. W. Johnson, A. D. Lemley, S. G. McNulty, D. F. Ryan, and R. Stottlemeyer. 1998. Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. *Ecological Applications* **8**:706–733.
- Field, C. B., G. C. Daily, F. W. Davis, S. Gaines, P. A. Matson, J. Melack, and N. J. Miller. 1999. Confronting climate change in California: ecological impacts on the Golden State. Union of Concerned Scientists, Cambridge, Massachusetts, USA, and Ecological Society of America, Washington, D.C., USA.
- Grulke, N. E., C. P. Anderson, M. E. Fenn, and P. R. Miller. 1998. Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California. *Environmental Pollution* **103**:63–73.
- Holland, E. A., et al. 1997. Examination of spatial variation in atmospheric deposition and its impacts on the terrestrial ecosystems. *Journal of Geophysical Research* **106**:849–866.
- Miller, P. R. 1992. Mixed conifer forests of the San Bernardino Mountains, California. Pages 461–492 in R. K. Olson, D. Binkley, and M. Bohm, editors. The response of Western forests to air pollution. *Ecological Studies* **97**.
- Miller, P. R., and M. J. Arbaugh. 2000. Ozone impacts on Californian forests. Pages 147 in J. L. Innes and J. Oleksyn, editors. Forest dynamics in heavily polluted regions. IUFRO Research Series 1. CABI Publishing in association with The International Union of Forest Research Organizations (IUFRO), Wallingford, UK.
- Minnich, R. A., and R. J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds* **29**:266–391.
- Padgett, P. E., and E. B. Allen. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecology* **144**:93–101.
- Padgett, P. E., E. B. Allen, A. Bytnerowicz, and R. A. Minnich. 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. *Atmospheric Environment* **33**:769–781.
- Riggan, P. J., R. N. Lockwood, and E. N. Lopez. 1985. Deposition and processing of airborne nitrogen pollution in Mediterranean-type ecosystems of southern California. *Environmental Science and Technology* **19**:781–189.
- Stylinski, C. D., and E. B. Allen. 1999. Lack of native species recovery: exotic disturbance in southern California shrublands. *Journal of Applied Ecology* **36**:544–554.
- Temple, P. J. 1998. Effects of ozone on understory vegetation in the mixed conifer forest. Pages 208–234 in P. R. Miller and J. R. McBride, editors. Oxidant air pollution impacts in the montane forests of Southern California. *Ecological Studies* **134**.

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