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“Biodiversity: Interfacing Populations and Ecosystems”

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Biodiversity: Interfacing Populations and Ecosystems

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Introduction

We are in the midst of a global environmental crisis, of a magnitude unknown since humans first populated the planet. Species and genetic diversity are being lost at record paces, although we still do not have the tools to do more than provide crude estimates of the magnitude of the tragedy. Indeed, we barely understand what it is that we are losing.

The argument for preserving biodiversity can be made on a wide variety of grounds. Most straightforward is the aesthetic argument: "Biological diversity should be conserved as a matter of principle, because all species deserve respect regardless of their use to humanity" (IUCN/UNEP/WWF 1991). What we see in nature is the result of a long evolutionary process, and extinction is forever. We are keepers of a rich biological heritage, and bound not to destroy it.

The aesthetic mandate for preservation is the purest, but an equally compelling case rests on the utilitarian aspects of biodiversity. Such a rationale necessarily assumes some system of valuation, based to large extent on an anthropocentric perspective. It leads inevitably to a view that some components of biodiversity are more important than others and that some species are more important than others. The aesthetic argument does not draw such distinctions.

The idea that humans might make decisions regarding which species to preserve and which to sacrifice is an arrogance that does not sit well on our shoulders. Indeed, the logic taken to its extreme has influenced the current debate on the remaining stocks of smallpox virus, the destruction of which would be the first case of humans deliberately causing the extinction of a species. To preserve a virus in the name of biodiversity is, for most people, not a logical imperative; but that the argument even is advanced is evidence of how strongly the basic preservation ethic appeals to people's sensitivities. The World Charter for Nature, adopted by the United Nations General Assembly in 1982, states that "Every form of life is unique, warranting respect regardless of its worth to man, and, to accord other organisms such recognition, man must be guided by a moral code of action." The basic principle (Noss and Cooperrider 1994) is that the most fundamental argument for the preservation of biodiversity is "appreciation of wild creatures

and wild places for themselves."

The utilitarian argument rests on the services, direct and indirect, that are provided to humans by biodiversity. "Species...are all components of our life support system. Biological diversity also provides us with economic benefits and adds greatly to the quality of our lives" (IUCN/UNEP/WWF 1991). For example, one-fourth of all prescription drugs contain active ingredients originally derived from wild plants (Noss and Cooperrider 1994; WRI/IUCN/UNEP 1992). The World Wildlife Fund (1991) estimated that only 2% of the quarter-million described species of vascular plants have been screened for potentially useful chemical compounds. How many cures for human diseases lie undiscovered in nature's treasures, and how many will never be identified before they are destroyed? Loss of genetic diversity by the destruction of natural habitats is, in the words of E.O. Wilson, "the folly our descendants are least likely to forgive us."

Even more basically, we exploit living resources for food and fiber. Wild species contribute an estimated 4.5% to the gross domestic product of the United States (Prescott-Allen and Prescott-Allen 1986), and fisheries provided 100 million tons of food worldwide in 1988 (FAO 1988). Our overexploitation of some stocks, especially of marine fisheries, is cause for immediate concern. Many of the most desired fish species, such as salmon, Atlantic bluefin tuna (Safina 1993), and cod and haddock (Hammer et al. 1993; NOAA 1992) have experienced huge declines. The implications are manifold: reduced availability and higher costs, increased energy inputs to extract the declining resources, and serious socio-economic effects (Regier and Baskerville 1986; Barbier et al. 1994).

That we exploit biodiversity directly for a variety of resources and products is clear, and well understood. More subtle and less appreciated, but of equal importance, are the ecosystem services nature provides to humans, services that rely on biodiversity. Forests and other natural systems mediate climate, and more generally regulate the flows of essential as well as undesirable materials. Benthic communities sequester toxic substances, preventing them from reaching humans; submerged aquatic vegetation performs similar functions in mediating the flow of materials and stabilizing habitat. Coral reefs and algal communities buffer coastlines against the ravages of ocean dynamics. Biological diversity will have a great deal to do with how natural and managed ecosystems respond to global change, although we are only beginning to understand the magnitude of the influence.

Measuring Biodiversity

The measurement of biodiversity may seem simple in concept; it is, however, very complicated in practice. The most straightforward approach, and the most easily communicated, relies simply on species counts (e.g., May 1992). No statistic is more compelling in discussion of the topic than to recount the accelerating loss of species. At least 71 species of vertebrates and more than three times as many species of full plants have gone extinct in the United States and Canada during the

past 500 years (Nature Conservancy 1992; Russell and Morse 1992; Noss and Cooperrider 1994). Total extinction rates for all species are estimated to be in the tens to hundreds of thousands of species per year in the tropics alone (Wilson 1988; Diamond 1990). According to Wilson (1985), these extinction rates are about 400 times those recorded through recent geological time and are accelerating. Worldwide, of course, the figures are much higher (Barbier et al. 1994). For purposes of communicating the magnitude of the problem, there is no better and clearer method than simply to list the lost species. And although we cannot know exactly how many species we can afford to lose, it is clear that our tolerance for lost species diversity is limited:

Ecosystems, like well-made airplanes, tend to have redundant subsystems and other "design" features that permit them to continue functioning after absorbing a certain amount of abuse. A dozen rivets, or a dozen species, might never be missed. On the other hand, a thirteenth rivet popped from a wing flap, or the extinction of a key species involved in the cycling of nitrogen, could lead to a serious accident. (Ehrlich and Ehrlich 1981)

There are, however, several limitations to an approach that relies on species counts. Only a small fraction of species have been identified, and this fraction varies dramatically from one taxon to another. We are, at best, in the position of estimating species numbers from catch and effort data. Furthermore, the definition of a species has always been problematic and is virtually meaningless for bacteria and other organisms that reproduce clonally and may exchange much genetic information horizontally across clones. For these, a "species" is simply a level of taxonomic aggregation, largely arbitrary. And even for sexual organisms for which the diploid species may be defined fairly unequivocally, it must be recognized that species differ substantially in terms of how much genetic diversity they embody.

Wilson (1992) has written,

Although the species is generally considered to be the "fundamental unit" for scientific analysis of biodiversity, it is important to recognize that biological diversity is about the variety of living organisms *at all levels*—from genetic variants belonging to the same species, through arrays of species, families and genera, and through population, community, habitat and even ecosystem levels. Biological diversity is, therefore, the "diversity of life" itself.

For plant communities, an ecologist would measure both the within- and among-community components of diversity (Whittaker 1975) and recognize each as contributing to diversity. Similarly, in the measurement of biodiversity, one must recognize the diversity within species as well as the diversity in terms of number of species, or do away with the notion of species entirely in favor of "continuum" measures of the genetic and functional diversity of communities. Such continuum measures are more robust and probably more nearly represent the functional complexity of the system and its ability to respond to perturbations.

Barbier et al. (1994) wrote "Although species extinction is an important manifestation and indicator of biodiversity loss, it is not the crux of the problem... Although species extinction is the most fundamental and irreversible

manifestation of biodiversity loss, the more profound implication is for ecological functioning and resilience." Indeed, one view (Steneck and Dethier 1994; Hay 1994) is that details about species composition represent noise, obscuring our perception about what communities really are. The validity of this interpretation, of course, is a matter of scale: Much of the detail about species composition will be irrelevant in terms of influences on ecosystem properties (Levin 1992).

One of the advantages of a continuum description is that it allows easily for weighting of diversity components according to their importance. But importance to what? How to weight a unit depends on its contribution to some performance criterion. That requires both a decision as to what is important and a scientific determination of the relationship between the unit and overall system properties. I return to this in later sections, without purporting to give a complete answer. Nor would I attempt to make such arguments to Aldo Leopold, who in 1953 wrote "The last word in ignorance is the man who says of an animal or plant: 'What good is it?' ... To keep every cog and wheel is the first precaution of intelligent tinkering."

Another and equally difficult problem in the measurement of biodiversity is the problem of spatial scale (Levin 1995). The ecosystem is not well defined as a spatial unit, and the measurement of diversity is very much conditioned by the scale of investigation (e.g., MacArthur and Wilson 1967; Levin 1992). Numerous studies (e.g., Williamson 1988; Hubbell and Foster 1986) have characterized the relationship between the area surveyed and the number of species counted; the shape of the species-area curve is a fundamental aspect of the description of diversity, capturing much more than simply the total number of species in the community (even if the boundaries of the community were known). Whatever controls the shape of this curve controls biodiversity, but we are only beginning to understand the relative importance of factors such as fragmentation, isolation, migration, and mutation (e.g., May 1986; Tilman et al. 1994; Durrett and Levin 1996; Hubbell 1997). An extremely promising approach to such matters is the use of individual-based models to help bridge the gap between our understanding of how individuals respond to varying conditions and the patterns observed on broad spatial scales.

The Importance of Species in Ecosystems

The role of species in ecosystems can be addressed only with regard to how one characterizes the ecosystem and its features. No single perspective is the unique, right one for valuation of ecosystem services, and one simply must recognize the bias that an individual perspective imposes on the assessment of the role of biodiversity. Beyond the spatial ambiguity already raised is the dichotomy between the perspectives of a population or community biologist, for whom biotic structure and organization are central, and an ecosystem scientist, for whom flows and exchanges assume precedence.

The strongest functional argument for directing attention to individual species is provided by the notion of keystone species, as introduced by Paine (1966). In his classic experiments in the marine intertidal, removal of a single starfish species, a top predator, resulted in qualitative changes in food web structure, and in other ecosystem properties. In the rocky intertidal system studied by Paine, the predator controlled the subdivision of essential resources among competing species, largely through local exclusion of a dominant competitor. Work by Estes and Palmisano (1974) showed that similar dramatic changes were associated with the removal of the sea otter from nearshore ecosystems on the U.S. West Coast. The absence of the sea otter led to increases in urchin abundance, resultant decline in offshore kelp beds, and the shifting of the local fisheries from finfish to shellfish. Like the starfish, the otter was a keystone predator whose removal led to qualitative shifts in ecosystem properties and determined "the integrity of the community and its unaltered persistence through time, that is, stability" (Paine 1969).

The starfish- and otter-dominated ecosystems are powerful and convincing models for how particular ecological communities are organized and led to more general studies of the role of disturbance in maintaining community structure (Levin and Paine 1974; Paine and Levin 1981). But how general are these examples? How broadly can the notion of a keystone species (or "critical species"; Paine 1994) be extended, beyond the top predators in these examples? The challenge has been one of the most attractive ones for community theorists ever since Paine's classic and seminal paper.

Castilla and Paine (1987) reviewed the keystone concept as it applies to the marine intertidal, and show a wide application of the notion for those systems. More generally, Bond (1994) summarized a quarter-century of research on keystone species—predators, competitors, mutualists, pathogens, among others—demonstrating a diversity of situations in which individual species play critical roles, at least in determining community structure. As regards ecosystem properties, however, the case is less compelling for the role of particular species. One of the most likely candidates for examination would seem to be nitrogen fixers, such as the leguminous shrub *Myrica faya*, which invaded Hawaiian lava fields (Vitousek and Walker 1989). *Myrica* was able to invade in large part because it is a nitrogen fixer (through a mutualism with an endosymbiont), and thus it might be expected that its introduction would have had major effects at least on nitrogen cycling. Alterations in local nitrogen dynamics, however, do not seem to have had any major effect on other species abundances; direct competition by *Myrica* was a much more important factor (Mueller-Dombois and Whitteaker 1990). Biodiversity clearly is important in mediating ecosystem properties, but it is difficult to cite examples where individual species are documented to have made a difference.

Where keystone species exist and can be identified, they provide a handle on understanding community structure. More generally, however, the notion of the keystone species must be broadened. Functional groups, in which individual species may be to some extent functionally interchangeable, control critical system properties. The argument for the maintenance of biological diversity is

equally strong in either case. Where keystone species exist, their protection obviously is vital to the maintenance of system integrity. But even when functional groups play the same role, the reduction of diversity within those groups reduces redundancy and the ability of the functional group to withstand stress.

The notion of a functional group is a very attractive one. From the point of view of systems theory, it is to be expected that large ensembles of interacting components will self-organize into clusters that interact more strongly among themselves than with other such clusters, and that the within-group dynamics will occur on much shorter scales than dynamics among groups (Simon and Ando 1961; Iwasa et al. 1987, 1989). Such hierarchical organization is characteristic of ecosystems (O'Neill et al. 1986; Paine 1980, 1994; Holling 1992). Soil microorganisms clearly form a keystone or critical group, in the sense of Paine's definition. But there is a great deal of functional redundancy within groups (Hay 1994; Lawton and Brown 1994; Steneck and Dethier 1994); indeed, the great majority of soil microorganisms cannot be identified to species. An important exception to the general view that large groups of species perform similar functions, and can substitute for one another, might be provided by the genus *Rhizobium*, which is of major importance in nitrogen fixation, along with bacteria of the family Azobacteraceae; these form a functional group. There is functional redundancy within this group, but *Rhizobium* plays a vital and nonsubstitutable role. Perhaps only our ignorance of microbial taxonomy limits the list of such examples, but it remains that the notion of functional groups is a valuable and appropriate concept for the understanding of the control of many critical ecosystem processes. Meyer (1994), in an excellent review of functional groups of microorganisms, categorizes microorganisms according to function, and concludes that "it is likely that we would not realize the extinction of a specific microbial species in nature unless a complete functional group was affected."

Schulze (1982) developed a functional group approach to vegetation, building on properties such as life form and phytosociological association. Solbrig (1994), in his approach to functional groups for plants, relies on the interplay between evolution and plant adaptive strategies as an organizing principle. In many other cases, functional groupings may make much more sense than taxonomic ones for understanding community organization, even if that implies a clustering that divides species; for example, in marine ecosystems, one might lump juveniles of diverse benthic-feeding fish into one cluster and adults into another.

A fundamental point made by Solbrig, and which is broadly applicable to the notion of functional groupings in any ecosystem, is that even when the roles of species within groupings cannot be distinguished, diversity and redundancy within groupings are critical features of the system's ability to respond to change and disturbance. Thus is provided one of the most compelling arguments for the maintenance of biodiversity: in the short term, elimination of redundancy within groups may result in no noticeable change in system dynamics. Over time, however, systems with reduced within-group diversity will be less able to respond to change and more likely to exhibit collapse. This is not to say that ecosystems have evolved these traits as adaptive strategies, but rather that diversity and associated

stability are emergent properties of these self-organizing systems and of the evolution of the component species.

Steneck and Dethier (1994) have provided one of the most compelling studies to date of the utility of the notion of functional groups. Drawing from experiments and experiences in subtidal algal communities in Maine, Washington state, and the Caribbean, they developed a view of the organization of such communities which argues that functional groupings of taxonomically distinct species share morphological attributes, and that convergent biogeographic patterns in ecosystem organization may be discerned clearly when the approach of functional groupings is taken. Environments are characterized by productivity and herbivore pressure, and these prove sufficient for the prediction of algal community composition. Moreover, communities viewed in terms of functional groupings prove much more stable and predictable than when viewed in terms of species composition. The regularity seen in these communities is reminiscent of the regularity seen in the organization of trophic webs (Pimm 1982; Sugihara 1984; Cohen et al. 1990) when attention is on the macroscopic properties of those webs rather than on the identities of individual species.

Biodiversity and Ecosystem Function

Although it may be difficult to demonstrate the importance of individual species to ecosystem properties, biodiversity more generally conceived certainly is critical to ecosystem properties such as net primary productivity. The points made in the last section direct attention to a problem of fundamental importance: How much detail, in terms of the species composition or even the genetic composition of a community, is necessary and sufficient to understand and maintain the dynamics as observed at the ecosystem level? The answer depends on the scale of interest (Levin 1992). Short-term dynamics are more likely to be governed by gross properties of community structure, while longer term dynamics, involving the response of systems to disturbance and feedbacks, will involve much more of the detail of community structure.

One of the challenges facing scientists today is an understanding of the responses of ecosystems to global change and the associated feedbacks to climate systems. General circulation models, tools to predict changes in climate, have reached very sophisticated stages of development but do not in themselves incorporate biological detail. In coupling such models to the dynamics of regional vegetation, simplifying assumptions must be made (Melillo et al. 1993; Potter et al. 1993; Schimel et al. 1994). The usual approach is to ignore spatial and compositional detail, representing the vegetation in grid cells hundreds of kilometers on a side by a homogeneous superspecies or "big leaf," parameterized by averaging the properties of extant species or, worse, by assuming that the vegetation evolutionarily will achieve a cooperative optimum performance in some physiological function.

A cooperative optimum is a poor approximation to reality because, by ignoring competition within a group, one overestimates the collective performance of the

group; the competitive equilibrium may be far below what a coalition would produce in terms of physiological performance. Communities do not evolve as superorganisms, but rather represent in their properties the evolution of their components. On the other hand, while assumption of an evolutionary optimum will overstate performance, the static approach based on current composition may understate at least the short-term response. The biotic heterogeneity within a group will lead naturally to selection and consequent shifts in system properties, usually resulting in an increase in short-term mean performance; nonlinearities would be expected to modify this on longer time scales. Indeed, by introducing diversity within the vegetational functional group and allowing for shifts and feedbacks from natural selection, Bolker et al. (1995) found that the classical static assumption led to a significant underestimation of the response of the biota in terms of increase in basal area, on time scales of 50–100 years.

How much biodiversity is important, in theory as well as in practice? There is no simple answer. On the very shortest time scales, average properties of systems will dominate, and biotic detail is probably irrelevant. But as the example just given demonstrates, short may mean very short: 50–100 years is not a long time in the lifetimes of forests, or in the horizons of interest to humans. On the slightly longer scales, biotic diversity and consequent feedbacks may fundamentally alter the responses of systems to stress. The elaboration of the functional group approach is central to the problem of scaling from the species to the ecosystem (Koerner 1994), but no formula for relevant detail is possible without reference to the problems and scales of interest. For net primary productivity, as is likely to be the case for any system property, biodiversity matters only up to a point; above a certain level, increasing biodiversity is likely to make little difference (Baskin 1994).

Understanding what is appropriate biotic detail requires understanding the relationship between the structure and function of ecosystems. The health of an ecosystem is measured in terms of both its biotic composition and the flow of elements among its compartments. Yet an understanding of the interconnections among these is woefully lacking. Among all studies that have been carried out to examine the effects of diversity on ecosystem properties, even the best nonagricultural examples are equivocal in their conclusions (Vitousek and Hooper 1994). Despite this paucity of information, there is hope for substantial progress in the next decade. "The background knowledge and techniques are now in place to begin a rigorous examination of the effects of species diversity on ecosystem biogeochemistry" (Vitousek and Hooper 1994). The problem clearly is one of fundamental importance in our evaluation of the role of biodiversity.

Conclusion

Where do we go from here? Much information, both from the empirical and from the theoretical literature, suggests strong links between biological diversity and the structure and function of ecosystems. In some systems, particular "critical" or

"keystone" species can be clearly identified as linchpins whose removal can lead to cascading effects in system properties. In other systems, the notion of the keystone species must be replaced by that of the critical functional group, but many of the lessons are the same. When species are at issue, genetic diversity within them governs their capability for resilience in the face of perturbations; when functional groups are involved, resilience comes from diversity within those groups. Efforts to measure diversity solely in terms of numbers of species, therefore, while a logical place to start, miss much essential detail.

On the other hand, although we know that diversity is important, we cannot quantify how important...yet. As Schulze and Mooney (1994) argued, "There is evidence that biotic diversity at levels ranging from genetic diversity among populations to landscape diversity is critical to the maintenance of natural and agricultural ecosystems. We still know little, however, about the critical thresholds of diversity and the conditions or time scales over which diversity is particularly important. Given the rapid declines in biodiversity, research programs must be planned promptly in a manner that allows results to be effectively incorporated into policies if we are to maintain the biodiversity of the globe."

How should diversity be measured, and how do system attributes respond to changes in diversity? We are at the threshold of being able to provide answers to these questions, through combined empirical and theoretical studies; Lawton (Chapter 12, this volume) reports on some of the most exciting recent progress in this direction. We are not yet at a point, however, where definitive statements can be made. The population-ecosystem interface has been one of the most challenging areas for conceptual development ever since the notion of the ecosystem was introduced by Tansley (1935), but sociological and other barriers have limited progress. The times are changing, as Vitousek and Hooper (1994) pointed out, and we are now equipped and of a mind to develop the essential theoretical linkages. In part, this must come from a proper theory of ecosystem development and evolution, in which system properties are seen to emerge from the self-organizing development of ecosystems and landscapes (Holling 1992), within the context of the evolution of individual species (Levin et al. 1990; Holt 1994).

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