Biodiversity and Ecological Redundancy

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Abstract: This paper addresses the problem of how to choose to best satisfy the conservation goals for a particular region in the face of inadequate resources. Biodiversity is taken to be the integration of biological variability across all scales, from the genetic, through species and ecosystems, to landscapes. Conserving biodiversity is a daunting task, and the paper asserts that focusing on species is not the best approach. The best way to minimize species loss is to maintain the integrity of ecosystem function. The important questions therefore concern the kinds of biodiversity that are significant to ecosystem functioning. To best focus our efforts we need to establish how much (or how little) redundancy there is in the biological composition of ecosystems. An approach is suggested, based on the use of functional groups of organisms defined according to ecosystem processes. Functional groups with little or no redundancy warrant priority conservation effort. Complementary species-based approaches for maximizing the inclusion of biodiversity within a set of conservation areas are compared to the functional-group approach.

Preface

This paper presents a functional approach to analyzing biological diversity, in the belief that this approach provides a more effective means of minimizing the decline in biodiversity brought about by human disturbance. Its take-home message is this: If scientists are to contribute usefully to the inevitable increase in management and political decisions relating to biodiversity, they need to address the issue of functional diversity and ecological redundancy in community composition. To do this requires development of a functional approach to describing biological composition, rather than sole reliance on the conventional taxonomic approach. Adherence to a policy that places equal emphasis on every species is ecologically unsound and tactically unachievable.

Introduction

The developing concern about human impact on the globe has focused attention on the issue of biodiversity and pushed it into prominence on many agendas. It is reflected in a number of new developments, such as the...
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IUCN international convention on biodiversity and the most recent programs adopted by the Scientific Committee on Problems of the Environment and the International Union of Biological Sciences, to name just a few. It will be a major agenda item for the 1992 United Nations Conference on Environment and Development.

Unfortunately, the rhetoric surrounding the debate is often confusing and superficial and could divert policies and activities into directions where desired goals won't be achieved. There are various interpretations of what is meant by "biodiversity," and its constant use and misuse in the media has induced a negative reaction to the term in some sections of the scientific community, leading to its rejection as a serious scientific topic. The popularization of declining biodiversity has unfortunately put it in the category of a "flavor-of-the-month" issue when in fact it is a serious and difficult problem that deserves long-term scientific consideration.

Decline in biodiversity includes all those changes that have to do with reducing or simplifying biological heterogeneity, from individuals to regions. Included are such phenomena as phenotypic plasticity; genetic variability within a population (allowing for a wide range of genotypic responses to environmental conditions); ecotypic variation (genetic variability between populations within a species); species richness (the number of species in a community); species (alpha) diversity (involving both the number of species and the relative numbers of individuals per species); functional diversity (the relative abundances of functionally different kinds of organisms); gradient (beta) diversity, which extends to diversity resulting from speciation of ecological equivalents (gamma or delta diversity—see Cowling et al. 1989); community diversity (the number, sizes, and spatial distribution of communities, sometimes referred to as patchiness); and even the diversity of the scales of patchiness (landscape diversity). Taken together, "ecological complexity" is a better term for all these aspects of biological heterogeneity.

A decline in any of these represents simplification and therefore loss of "biodiversity." The question we need to answer is "So what?"

I divide the reasons for maintaining biodiversity into two categories: ecological and "others." Noreen (1988) puts these "other" concerns into three categories of values—commodity, amenity, and moral. I exclude here the moral or ethical arguments, not because they are unimportant, but because they are nonscientific. There are gray areas in all such distinctions, and arguments in favor of conserving pandas or koalas generally involve a mixture of moral concerns and scientific awareness of genetic uniqueness and rarity (to which I will return later). I am referring here to the genuinely moral arguments—which nevertheless are usually associated with "charismatic megavertebrates" rather than fungi or nematodes. The ethical implications of species loss is an important topic, but for a different essay. The amenity issues are generally rather vague, except for specific examples where values are attached to particular species. The commodity issues mostly seem to relate to future possible benefits from as-yet-unknown specific pharmacological properties, etc. Such issues can be grouped under the heading of option foreclosure; and while no one would argue against it, it is difficult to attach levels of probability and potential benefits in the absence of appropriate information.

The major reasons advanced for concerns about biodiversity are ecological. Each of the various aspects of ecological complexity described above, has been implicated in a greater or lesser degree in the ways in which ecosystems and communities function and (in particular) persist. Initially, there was uncrirical acceptance of an assumed positive relationship between species richness and "stability," but this was brought into question by May (1972) and others, and the focus switched to the kinds of diversity. Based on both theoretical and empirical evidence it seems that it is diversity at the community level (patchiness), if anything, that is important in long-term stability. Nevertheless, it is species richness that is most commonly invoked in concerns about biodiversity, and the approach to the problem usually involves devising means (including political and legal) to prevent decline in biodiversity. In itself this is perfectly reasonable. From a conservation viewpoint efforts to prevent the loss of any species are laudable. However, the survival of particular target (favored) species can usually be assured by correct habitat management, control of exploitation, or both. This is not to say that correct habitat management is simple, and it should not be dismissed in a facile way. Its most difficult aspect is probably dealing with habitat or landscape fragmentation and its consequent denial of access to refugia at critical times (which reflects the importance of changes in landscape diversity). Resolving the overall problem of decline in biodiversity requires more than focusing on particular cases of species conservation. It requires understanding the relations between biodiversity and ecosystem function and applying this understanding.

Biodiversity and Ecosystem Function

Given that the objective is to minimize reduction in biodiversity (including the loss of species), the important questions in this debate concern the kinds of biodiversity that are most significant to the ways ecosystems function, because this is how to best focus our conservation efforts. Which kinds, and what amounts, of biological simplification lead most readily to significant or irreversible changes in the inherent structure and function of an ecosystem (i.e., to an unsustainable decline in its resilience)? Put another way, which aspects
of diversity, and which kinds of species are most important to ecosystem function?

Ecologically, all species are not created equal. At one extreme, some are determinants, or "drivers," of the ecosystem of which they form a part. At the other extreme are those that are "passengers." Removing the former causes a cascade effect, but loss of the passengers leads to little change in the rest of the ecosystem. Apparent passengers, at one time scale, may of course turn out to be infrequent determinants, and this distinction needs to be treated carefully. It raises the major legitimate argument against classifying species in terms of their contribution to ecosystem function. Nevertheless, attempting to deal with each species individually becomes impossible—consider, for example, just the number of invertebrate species in a heath of tropical rain forest. Provided we deliberately and iteratively reexamine the guild composition, the advantages of a functional approach argue in its favor. This does not mean that we should ignore what we know about particular "keystone" or otherwise important species, but rather that we should include this knowledge in a more systematic and thorough analysis of ecosystem function.

Putting the problem another way, we need to ask how much, or rather, how little, redundancy there is in the biological composition of ecosystems. This question is at the heart of ecological science—the relations between structure and function of ecological communities—and as such should excite anyone who is interested in ecology.

Without knowing anything about ecological redundancy, how can we value a decline in biological diversity?

Contrast, for example, an ecosystem where a single, wide-ranging ant predator is prominent, with the situation involving the southeastern Australian jack-jumper ants (nominally Myrmecia pilosula), which were thought until recently to constitute such a species. "M. pilosula" is now known to include at least five sibling southeastern taxonomic species. They differ dramatically in chromosome numbers, but only slightly in morphology (Imai et al. 1988). Their collective distribution in suitable habitats runs from the Blue Mountains to Tasmania and parts of southern South Australia, and several species are very widespread. In some places only one species is found, but in others up to three may be sympatrically associated. None occupy the whole area, but the three most common species together cover virtually the full geographical range of the group (R. W. Taylor, personal communication). There are no apparent ecological distinctions between these entities, so that, although they are reproductively distinct gene pools, and clearly "good" species, they constitute in effect a single functional ecological unit. Although it is of great scientific interest to understand the nature and evolutionary history of their diversity, few would dispute that according all of these species the same priority (and therefore conservation effort and expenditure) as the single-species predator might be misdirected, under some circumstances.

Regrettable as it might be, it is most likely that global biodiversity concerns will ultimately reduce to a cost-benefit analysis. Without a knowledge of redundancy, or more broadly, the relationships between levels of biodiversity and ecosystem function, we cannot estimate either the costs or the benefits.

One adverse but absurd response to this assertion is that acknowledging that the loss of some species may not be as ecologically critical as the loss of some others is tantamount to advocating their removal. Critics invoke Erlich and Erlich's (1981) fable about rivet poppers on an aeroplane. What I am suggesting is that the best way to succeed in our efforts to reduce the decline in biodiversity is to focus initial attention on the aspects of biodiversity that are critical for maintaining the resilience of the ecosystems concerned. Resilience in this context is taken to be the capacity of the ecosystem to maintain its characteristic patterns and rates of processes (such as primary productivity, allocation of photosynthesis, surface hydrology, energy exchange, nutrient cycling, herbivory, etc.) in response to the variability inherent in its climatic regime. By maintaining the integrity of ecosystem function we minimize the chances of losing the many species we have not yet described and those of whose very existence we are as yet unaware.

If we consider the case of a decline in numbers of individuals within a species, the analogous issue is population viability analysis. What are the required conditions, and what is the critical number of interacting individuals, to maintain a population? Or, in a more general sense, what is the relationship between density and population viability, and what determines it? The problem involves both longer-term (e.g., genetic variability loss) and more immediate processes (effects of extreme events, density-dependent effects of competition, minimum breeding levels, dispersal and reinvasion rates, and so forth). At the multispecies level, the same issues remain a concern, but perhaps more important are the issues relating to species interactions and the ecosystem processes described above.

A Suggested Approach

How do we address the problem?

As implied earlier, a necessary step in analyzing the functional relationships between biological diversity and persistence in an ecosystem is to get away from a purely species-centered view of biodiversity, and to
consider it instead in terms of functionally different kinds of organisms. The appropriate basis for defining the species functional types (guilds) is the way the biota regulates ecosystem processes. Defining them in this way focuses attention on the processes that maintain ecosystem and community function, and on how changes in the relative or absolute abundances of the functional groups concerned, and in their patterns of distribution, will influence these processes.

Step one, therefore, is an iterative procedure involving analyses of ecosystem function (identifying the rate-limiting or otherwise relatively important processes in the system of concern) coupled to the development of appropriate corresponding functional classifications of the biota, through guild analyses of one sort or another. The objective should be to try to further subdivide the species in a guild on the basis of nontrivial functional attributes (nontrivial in the sense that they are related to limiting or dominant ecosystem processes for that ecosystem). If this cannot be done and there are still several different species in the group, then on the basis of current knowledge, there is some ecological redundancy within the guild concerned. An obvious problem in this regard is the time scale on which function is considered. The separate significance of a particular species may only become apparent under particular environmental conditions, and such time-dependent, episodic features of guild analysis constitute a difficulty that must be considered from the perspective of long-term ecosystem function.

Step two is to determine the number of species within each guild. Those represented by only a few or even a single species are clearly unable to withstand any loss of species and constitute an obvious, immediate conservation focus.

Step three is to further examine the interactions among the species in each guild. Complete functional redundancy only occurs if, following the removal of one species, there is density compensation among the remaining species. A complicating factor is that the different species in a guild, while all performing the same function, may respond differently to different environmental conditions. With the complete set of species, net guild abundance (or function) may remain relatively constant under a fluctuating environment. Loss of some species may well lead to an increase in abundance of others (i.e., density compensation occurs), but because the diversity of response to environmental conditions has been reduced, net guild abundance may then fluctuate more in response to environmental fluctuations. Once again, in the absence of adequate information, we need to adopt a successive approximation approach based on what we do know.

The final step is to consider the relative importance of the functional groups (the analogue to the question about species importance). The logical progression in ecological studies, from structure to function and then to the relations between them, indicates that the approach to this step is to examine how a change in abundance of a functional group directly affects ecosystem and community processes, and how such a change influences the net effect of the biota (through changes in the timing and overall rates of predation, dispersal, herbivory, decomposition, nutrient retention and uptake, biomass accumulation, etc.). In other words, all the issues involved in ecological stability analysis are considered, but using functional groups instead of taxonomic species. Achieving this step involves developing conceptual and analytical models using a combination of existing knowledge (see step one above) and a range of experiments specifically designed to examine these relations. It is a fruitful area for experimental ecologists and will most likely involve reciprocal experiments in which, on the one hand, functional groups are removed from an ecosystem and the effects on function are measured, and on the other, function is altered (changes in nutrient cycling, hydrological regime, etc.) and changes in functional group abundance or performance are measured. Functional groups considered (on the basis of present knowledge) to be the major drivers of the system warrant initial attention in this approach.

Complementary Species-based Approaches

Given the complexities of defining and establishing functional groups, particularly the extent of lumping or splitting, there is a danger that (as one reviewer of an early draft put it) we may replace one taxonomic approach with another, more confusing one. However, as indicated earlier, I do not advocate a complete switch. Too often in the development of ecology there has been a swing from one extreme to another (the “association” vs. the “continuum,” equilibrium vs. disequilibrium, etc.) with the eventual realization that both approaches were valid and that the extent to which each was important depended on the nature of the system. No doubt, in the ensuing debate on how to maintain biodiversity, the use of both species and functional groups will turn out to be appropriate, at different scales.

One species-based approach, which perhaps best complements the functional approach, is concerned with weighting species (or other taxa) according to their taxonomic distinctness, and in this way identifying priority choices for conserving biodiversity. The approach has so far been most comprehensively dealt with by Vane-Wright and colleagues (Vane-Wright et al. 1991) and is encapsulated in May’s (1990) account of the problem. The approach involves deriving some measure of taxonomic distinctness based on the topology of a hierarchical taxonomic classification. Using these weightings, Vane-Wright and colleagues have shown
how the priority order for the minimum set of reserve areas needed to conserve biodiversity in a particular taxonomic group differs markedly from the set derived by giving all species equal weight. May (1990) has indicated that the method used to derive the weightings needs further work, and Faith (in press) has developed a measure of phylogenetic diversity that resolves some of the difficulties. The significance of the measure in the context of this paper is that the value of a species is based on its contribution to overall feature diversity. Functional groups are also characterized by their different features, so that similar measures of feature diversity may be useful in placing relative importance values (functional as opposed to phylogenetic importance) on different functional groups.

The main difference between the functional group approach I have suggested and the taxonomic-distinctness approach of Vane-Wright et al. has to do with the scale of concern. Taxonomic distinctness is a valuable tool for helping to choose among many different areas to ensure that maximum biodiversity is included (for example, in a reserve network). The functional group approach focuses attention on which species are of major concern in managing, or identifying appropriate boundaries for, a particular area or region to minimize the loss of biodiversity. The two are therefore complementary in devising an overall conservation strategy.

Conclusion

In future political and economic tradeoffs that will decide how much nations are prepared to pay to maintain biodiversity (in terms of foregone production or direct restoration costs), ethical and commodity arguments will certainly play a role, but the weight of evidence will most likely come from the ecological side. The worrisome cost of decline in biodiversity, particularly to politicians who may be held accountable, is the threat of a collapse in the “stability” of ecosystems (whatever that means). This threat, however, will become progressively less an issue as the passage of time reveals scientists’ inability to demonstrate it.

There will always be highly motivated conservation organizations that collectively take on the plight of some hundreds or even thousands of visible, identified species, but this is an immeasurably small part of the problem. If these species act as “umbrella” species, and enhancing them unwittingly helps the plight of others, then the efforts of such organizations are positively magnified. Such claims, however, are statements of faith and there is generally no effort to consider whether the actions taken to promote the welfare of elephants or lemurs, for example, are having a positive or negative effect on the welfare of loosely connected species, such as butterflies or soil-surface lichens. Identifying these focal species in the context of a functional analysis will permit an evaluation of their umbrella role and will also highlight appropriate (and inappropriate) conservation activities.

Five categories of species have been, and are, used to justify special conservation effort (Noss 1990). In summary they can be labeled as ecological indicator, key-stone, umbrella, flagship (charismatic), and vulnerable species. If a strategy to enhance one or more such species turns out to have an overall negative effect on the viability of many other species in the ecosystem, then the arguments in favor of such a strategy obviously need to be questioned. Although many reserves were originally established around focal species and some are still intentionally managed to conserve just those species, conservation organizations are responsible for managing an area generally avoid such a stance, and their actions constitute a genuine effort to enhance the welfare of all species. They are, unfortunately, confronted with the problem of not knowing enough about all these species to be confident of achieving their objective. Changing the focus from particular species to functional groups, and coupling this with an analysis of ecological redundancy, particularly in those functional groups that are on the “driver” side of the continuum, is a good start to improving the situation.

In terms of an overall approach to conserving biodiversity we need to resolve two issues: (1) how to choose the optimal set of bits of a region or of the world to maximize the biodiversity they include, and (2) how to manage any area or region to ensure the long-term persistence of all its biota (including species we don’t yet know exist). The functional group approach addresses the latter issue.

What I have suggested here clearly raises more problems than it solves. But this is largely due to its stage of development. Thus far, the idea of functional groups has been restricted to very general or global classifications. Functional aspects of biodiversity have been discussed in general terms (e.g., Noss 1990), but the notion of functional groups has yet to be applied in a detailed way to particular ecosystems. Given the disappointing progress in achieving programs using individual species approaches to biodiversity, the analysis of ecological redundancy deserves serious attention.

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Literature Cited


