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Conservation implications of the link between biodiversity and ecosystem functioning

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Abstract The relationship between biodiversity and individual ecosystem processes is often asymptotic, saturating at relatively low levels, with some species contributing more strongly than others. This has cast doubt on arguments for conservation based on maintenance of the functioning of ecosystems. However, we argue that the link between biodiversity and ecosystem functioning is an important additional argument for conservation for several reasons. (1) Although species differ in importance to ecosystem processes, we do not believe that this argues for preservation of just a few species for two reasons: first, it is nearly impossible to identify all species important to the numerous systems and processes on which humans depend; second, the important species themselves may depend on an unknown number of other species in their communities. (2) Arguments for conservation based on ecosystem functioning are complementary to other utilitarian, ethical and aesthetic justifications. No single reason will convince all people or protect all species, however the combination produces a strong case for conservation of biodiversity. (3) Even if the relationship between biodiversity and ecosystem functioning is asymptotic at local spatial scales and in the short term, effects of biodiversity loss are likely to be important at larger temporal and spatial scales. (4) Initial arguments for the importance of biodiversity for ecosystem functioning were largely based on a precautionary approach (points 1–3). However, we are now moving to a scientific position based on accumulating experimental evidence. The future challenge is the integration of this scientific research with policy.

Keywords Diversity · Species richness · Ecosystem processes · Precautionary principle · Conservation ecology

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Introduction

A recent review in *Oecologia* (Schwartz et al. 2000) asked first whether ecosystem functioning is positively correlated with biodiversity, and second whether functioning saturates at low levels of diversity relative to those used in experiments or observed in nature. Of the studies reviewed, 95% supported a positive relationship, but most showed an apparent asymptote in levels of ecosystem processes beginning at half, or less, of the maximum levels of diversity. Recent results from the BIODEPTH project (Hector et al. 1999), of which most of the authors here are participants, are broadly in line with these conclusions. We found a linear relationship between productivity and diversity in experimental grassland communities when plant species richness was put on a log scale that predicts an initially weak but accelerating loss of productivity with loss of species. The paper by Schwartz and colleagues is one of the first to comprehensively address the issue of how we as ecologists should interpret experiments of this type in terms of their implications for conservation, and is particularly important given that opinions differ so widely in this contentious area. Schwartz and colleagues concluded that there is little evidence for strong dependence of ecosystem functioning on the full complement of diversity within sites and that “conservationists must temper enthusiasm for the claim that species richness supports ecosystem functioning lest our arguments, along with supporting data, force us to adopt the position that we could make a list of ten integral species for a given ecosystem and dispense with the remaining diversity". We all need to decide how strongly considerations of ecosystem functioning support the conservation of biodiversity both in our professional capacities as ecologists and from a personal level. The paper by Schwartz and colleagues stimulated us to put together some additional points we have encountered in trying to interpret our own research on the linkage between biodiversity and ecosystem functioning, particularly with respect to implications for conservation. We briefly draw attention to several relevant points currently in press elsewhere (Lawler et al. 2001) while concentrating on several relevant issues we believe have not been discussed in the ecological literature so far.

Could ecosystem functioning be maintained with fewer, but carefully selected species?

The idea that short-term experiments could allow us to select the species essential for ecosystem functioning and discard the rest, relies on two assumptions. First, that we can correctly identify the subset of species on which functioning is dependent (Chapin et al. 2000; Purvis and Hector 2000) and second, as Schwartz and colleagues point out, that this same subset of species will continue to maintain full ecosystem functioning in the longer-term despite environmental fluctuation. While the widespread success of the functional group classifications in ecology, including many recent biodiversity experiments (Hooper and Vitousek 1997; Tilman et al. 1997a; Hector et al. 1999) suggests we can identify many of the species traits important for ecosystem functioning, it does not mean that we can identify which species within a group are more or less important, particularly in the long-term. In addition, we do not have the ability to predict what effect each species has on the full range of biogeochemical processes in all, if any, ecosystems. Moreover, while the results of many biodiversity experiments are encouraging for a future basis for prediction of ecosystem functioning, some results appear to contradict a priori expectations and predictions (Hector et al. 2001). For example, in some plant biodiversity experiments (Hooper and Vitousek 1997; Hector et al. 1999) communities are not dominated by the species that are most productive when grown alone as some models predict. The relationship between species and processes also seems sure to vary in the longer term, potentially strengthening the importance of biodiversity for ecosystem functioning, since more species are likely to be involved than over the short-term (Field 1995; Doak et al. 1998; Tilman et al. 1998; Yachi and Loreau 1999; McCann 2000). This suggests that selecting subsets of species to accomplish ecosystem functioning over the long term is not possible, let alone desirable.

This uncertainty over the effects of species on ecosystem functioning means that we are good at explaining relationships in hindsight but poor at setting up detailed a priori predictions. Several similar general frameworks of alternative possible relationships between biodiversity and ecosystem functioning have been developed (e.g. Vitousek and Hooper 1993; Lawton 1994; Naeem 1998; Schläpfer et al. 1999), together with more detailed relationships based on theory (Tilman et al. 1997b; Loreau 1998, 2000), but when it comes to generating graphs of processes versus diversity these schemes are currently qualitative rather than quantitative. Interpretation of actual biodiversity experiments may be less contentious if we could generate a set of alternative hypothetical relationships on diversity-function graphs with scaled axes (if not absolute then at least relative) and agree how biologically important the alternative relationships would be deemed if observed. However, statements about the importance of results are likely to remain controversial since they are inevitably subjective to a large degree – a 20% reduction in an ecosystem process may seem biologically significant to one ecologist or policy maker but trivial to another. This problem is not limited to the study of the relationship between biodiversity and ecosystem functioning of course but is widespread in ecology and science in general.

In practical terms, what does a positive relationship between increasing biodiversity and ecosystem functioning mean? Current relationships predict the general outcome of random changes in species numbers and define an envelope of points that reflects variability around this mean response due to compositional effects. Of course, in most cases changes in diversity are unlikely to be random, the selection of crops in multi-species agro-ecosystems for example (Vandermeer et al. 1998). Nevertheless, the random scenario provides a general expectation in the absence of more detailed predictions. However, current studies show that some species are much more important to ecosystem functioning than others (Power et al. 1996) which suggests that species loss could take the system through a variety of downward trajectories within the response envelope, depending on the order of species loss. The general point, often raised in ecology, is that the variance can be as important as the mean.

If we concentrate on a single scenario of species loss, when the effects of different species on functioning are very unequal, we are likely to see an unpredictable idiosyncratic pattern (however, in well-replicated experiments idiosyncratic patterns would average out to produce some mean trend with high variance). Idiosyncratic patterns (Lawton 1994) do not mean that the loss of species is unimportant. On the contrary, the effects of species loss are likely to be large and unpredictable. Only if species are very similar and/or highly redundant in their effects on processes is functioning likely to be little affected by changes in diversity. Current experiments have also tended to focus on a single or small number of ecosystem processes. However, there is no reason to believe that different processes will respond in similar ways to a given series of species omissions. We expect species richness to be more important when ecosystem stability is dependent on the functioning of a wide range of different processes that are influenced by different sets of species.

What constitutes a strong argument for the conservation of biodiversity?

The framework of Schwartz and colleagues implies that strong arguments for conservation require relationships where all species are contributing significantly. Since some species affect ecosystem processes more than others, they suggest that the argument for conservation based on linkages between biodiversity and ecosystem functioning cannot be "strong". The maintenance of ecosystem functioning is only one argument among many for the conservation of biodiversity. There are many alternative schemes for categorising arguments for conservation (e.g. Krutilla 1967; Edwards and Abivardi 1998; Kellert 1996; Kunin and Lawton 1996; Seidl and Gowdy 1999; Lawler et al. 2001). These comprise a mixture of utilitarian and intrinsic value arguments including:

1. Direct benefits (e.g. fish, game, timber) and option values – biodiversity provides a reservoir of ecosystem goods and resources (e.g. genetic) for humans, many of which are probably currently unknown (discovery of new medical drugs or pathogen resistant strains of crop plants are good examples).
2. Ethical arguments – to cause or allow species to go extinct is wrong based on moral, cultural or religious grounds.
3. Aesthetic arguments – we should conserve biodiversity because we enjoy its existence just as we enjoy our cultural and artistic heritage of music, painting, football games and so on.

If we apply the same criterion used by Schwartz and colleagues to assess the strength of these additional reasons for conservation we could argue that none of the potential motivations are "strong". Most of the justifications for conservation do not involve an important role for all species. Despite widespread acknowledgement of the need to conserve biodiversity by the United Nations Environment Programme Convention on Biological Diversity (1992), the ethical argument is limited by the fact that this position is not held by everyone. Likewise, all species are unlikely to provide as-yet-unidentified resources to humankind. The aesthetic arguments are limited because people may find only a minority of species aesthetically appealing and actually dislike many others. Recognising the importance of a variety of species in supporting ecosystem functioning provides a utilitarian reason for preserving diverse ecosystems that include numerous functionally important species in addition to attractive species and those likely to yield marketable products. This argument also translates into an ethical reason for preserving as much biodiversity as possible for posterity, when currently 'unimportant' species may fill new roles in ecosystem functioning in a changing environment. Ethical, aesthetic and utilitarian arguments all have validity, motivating different groups of people to support conservation, therefore none should be discarded.

Some of the objection in principle to the use of biodiversity-functioning linkages as a justification for conservation appears to come from the view that different arguments for conservation are competing alternatives (Wardle et al. 2000a). However, we see no reason why alternative arguments, including those relating to ecosystem functioning, cannot be complementary (this is not to say that different conservation arguments will not conflict in some practical situations). As positive relationships between biodiversity and ecosystem functioning appear to be relatively common, surely they add to the general argument for conservation even when they are not "strong" linear relationships to which all species contribute equally (Lawler et al. 2001)?

Unpredictability in time, space and across multiple trophic levels

The loss of biodiversity is not an ephemeral or localised problem (Sala et al. 2000). The history of expanding human activity has seen a prolonged and widespread reduction in biodiversity from many, if not most of Earth's ecosystems. Substantial losses also seem set to continue for the foreseeable future and may even intensify (Myers et al. 2000; Sala et al. 2000). Therefore, given the global and ongoing nature of biodiversity reduction, effects could be judged as important even when the relationship between biodiversity and ecosystem functioning is asymptotic. A 20% decrease in productivity (or of another ecosystem process) may be small compared to variation at larger scales but could nevertheless be important locally. Furthermore, if small local effects are truly widespread they could be seen as important at the global scale. Moreover, even if ecosystem processes are sustained at half, or less, of the maximum levels of diversity at the small scale of experimental studies (Naeem et al. 1994; Hooper and Vitousek 1997; Hector et al. 1999; Tilman 1999b), a larger regional and global species pool may be required to maintain local diversity (Schmid et al. 2001). Tilman (1999a) used his Minnesota prairie study system and standard species-area relationships, to calculate the number of species needed in a square kilometre to obtain a local species richness of 16 plants per square metre – it is about an order of magnitude greater at 127–270 species. Chesson et al. (2001) and Yachi and Loreau (1999) use models to demonstrate an analogous effect of temporal scale (Lawler et al. 2001).

Our current estimates of the effects of species loss rely on experiments limited not only in spatial and temporal scale but also in trophic breadth. Most recent experiments largely examine only single aspects of diversity such as numbers of species or functional groups at a limited number of trophic levels (but see for example Wardle et al. 2000b). However, changes in diversity at one trophic level may generate important feedback at others. For example, a recent manipulation of the diversity of plants and mycorrhizas found a stronger effect of the loss of plant species in the absence of mycorrhizas than when they were present (Klironomos et al. 2000). Thus the presence of one group could buffer the effects of the loss of species within another. We also know little yet of the effects of ecosystem engineers and keystone species on ecosystem processes, both of which could be easily overlooked if diversity manipulations are limited in scope.

The element of unpredictability of longer-term and larger-scale biodiversity losses, particularly given predictions of global change, argues against conserving only a few 'integral' species and discarding the rest. The idea of redundancy as a desirable property of systems, so prevalent in engineering, does not seem to have been widely appreciated in ecology and conservation (Naeem 1998) with the exception of the recognition of its potential value in agroecology (e.g. Vandermeer et al. 1998; Trenbath 1999). Most studies to date hold species richness constant or are relatively short-term and, therefore, may not fully capture community dynamics. In naturally occurring communities, species loss is likely to alter the probability of further species loss. Thus, a single species deletion may not have immediate consequences for ecosystem functioning, but loss of dependent species may affect functioning in the longer term. Such effects are particularly likely if the species lost has strong trophic (keystone species) or other interactions (e.g. ecosystem engineering) with other members of the community (Vitousek 1990; Chapin et al. 2000).

The recognition that loss of biodiversity can have negative impacts on ecosystem functioning, combined with uncertainty over the current and future roles of most species in many ecosystem processes, argues for a precautionary approach in conservation. Because the precautionary approach inevitably involves a lack of knowledge, it sometimes carries little weight in the face of hard economics. However, we now know that changing biodiversity usually affects ecosystem processes; 95% of cases in the Schwartz et al. review showed such effects (see also Schläpfer et al. 1999; Schmid et al. 2001). Thus we are moving beyond a precautionary position based on a lack of knowledge to arguments based on evidence of impacts. Although the debate over the exact implications of recent research for ecosystem functioning looks set to continue (Kaiser 2000; Wardle et al. 2000b), there is evidence from a recent assessment of expert opinion (Schläpfer et al. 1999) for progress beyond a purely precautionary approach. In addition, a review of recent ecological work on the functional and societal consequences of changing biodiversity led a wide range of ecologists to call for more intensive social, scientific, political and economic efforts to be put into conservation to preserve options for future solutions to global environmental problems (Chapin et al. 2000). We argue for a shift in the burden of proof (Dayton 1998) when assessing the consequences of biodiversity loss that eliminates the implicit assumption that there will be no impact on ecosystem functioning.

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