BIOLOGICAL DIVERSITY, ECOSYSTEMS, AND THE HUMAN SCALE

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Abstract. This paper considers the significance of biological diversity in relation to large-scale processes in complex and dynamic ecological–economic systems. It focuses on functional diversity, and its relation to production and maintenance of ecological services that underpin human societies. Within functional groups of organisms two important categories of species are identified: keystone process species and those essential for ecosystem resilience. The latter group represents "natural insurance capital." In addition to basic research on the interplay among biological diversity, functional performance, and resilience in complex self-organizing systems, we suggest that a functional approach has two main implications for a strategy for biodiversity conservation: (1) Biodiversity conservation to assure the resilience of ecosystems is required for all systems, no matter how heavily impacted they are. It should not be limited to protected areas. (2) The social, cultural, and economic driving forces in society that cause biodiversity loss need to be addressed directly. Specifically, (a) differences between the value of biological diversity to the private individual and its fundamental value to society as a whole need to be removed; (b) social and economic policies that encourage biodiversity loss should be reformed, especially where there is a risk of irreversible damage to ecosystems and diversity; and (c) institutions that are adaptive and work in synergy with ecosystem processes and functions are critical and should be created at all levels.

Key words: biodiversity; biological diversity; conservation of; critical ecosystem processes; disturbance, capacity to buffer; ecological services, maintenance of; ecosystem function and resilience; functional diversity; market externalities; multiple equilibria; nature reserves; transboundary effects.

INTRODUCTION

It is generally accepted that the significance of biodiversity includes much more than the mix of species. Wilson (1992:393) defines it to include "... the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live." This is also the position taken by the Convention on Biological Diversity of the United Nations Conference on Environment and Development in Rio de Janeiro 1992, signed by more than 150 nations (UNEP 1992).

Despite this, much research and policy on biodiversity conservation assumes that what matters is the number of genetically distinct organisms. There has been a tendency for biologists to estimate extinction rates, stress the importance of the abundance of taxa, and discuss the potential for preservation of genetic information (Olney et al. 1993, Prendergast et al. 1993, Smith et al. 1993). This approach has led to a conservation strategy dominated by the establishment of protected reserves in the mega-diversity regions of the world.

We strongly support the ethical argument for conserving the uniqueness and diversity of life. However, we question whether the focus on genotypic diversity and megadiversity hot-spots is the most appropriate way to conceptualize, analyze, or respond to biodiversity loss. Nor is it clear to us that it actually satisfies the ethical goal. We are suggesting an approach that complements the conventional approach, but which has a different focus. We will discuss biological diversity in large-scale ecological processes, and the intensifying human driving forces behind its loss. Specifically, we will analyze biodiversity loss in terms of its impact on the ability of interdependent ecological–economic systems to maintain functionality under a range of environmental conditions. Human demographic, social, cultural, and economic trends are not seen as external to...
ecosystems, but as parts of the biogeochemical and hydrological flows of the ecosphere. That is, we take an ecological–economics approach.

Whether we like it or not the growing human impact on the planet is a fact. "Keeping humans out of nature" through a protected-area strategy may buy time, but it does not address the factors in society driving the loss of biodiversity. This paper stresses the importance of creating incentives for people and economies to act more in harmony than in conflict with essential processes that control the dynamics and structure of ecosystems, and of which biological diversity is a crucial part. Incentives need to be created to conserve biodiversity not just in protected areas but everywhere.

The approach requires that the functional relationship between the diversity of organisms and the set of ecological services on which humanity depends is addressed (Ehrlich and Mooney 1983, Perrings et al. 1992, 1995a). In addition to the fact that they house the genetic library, organisms help to sustain a flow of ecological services that are prerequisites for economic activities. These include photosynthesis, provision of food and other renewable resources, soil generation and preservation, pollination of crops, recycling of nutrients, filtering of pollutants and waste assimilation, flood control, climate moderation, operation of the hydrological cycle, and maintenance of the gaseous composition of the atmosphere. These functions sustain and protect human activities, and so human well being (Folke 1991, de Groot 1992, Ehrlich and Ehrlich 1992).

In economic terms, ecosystems are fundamental "factors of production"—factors that are becoming increasingly scarce as a consequence of the rapid human population growth, and human behavior towards the natural capital base (Barbier et al. 1994, Jansson et al. 1994).

Increasing globalization of human activities and large-scale movements of people mean that humankind is in an era of novel co-evolution of ecological and socio-economic systems at regional and even planetary scales (Holling 1994). Ensuring the capacity of ecosystems to continue to generate ecological services on which the well being of human societies depends is a major challenge. Developing a feasible and useful strategy for biodiversity conservation is a central component of this challenge.

FUNCTIONAL DIVERSITY IN LARGE-SCALE ECOSYSTEMS

The critical aspect of the diversity of organisms and their environments in this context is functional diversity (Schulze and Mooney 1993). We know that for any ecosystem function to be sustained, a minimum composition of organisms is required to develop the relations between primary producers, consumers, and decomposers that mediate the flow of energy, the cycling of elements, and spatial and temporal patterns of vegetation. We also know that this composition varies with the environmental conditions in which the system operates. What is currently missing is detailed knowledge of the critical thresholds of diversity associated with different environmental conditions at different temporal and spatial scales. It is not clear, for example, how specific sets of genes, genotypes, species, populations, and communities influence ecosystem functions over the existing range of environmental conditions, or what the critical levels of diversity in communities and ecosystems and the factors that control them are (Solbrig 1991, Schulze and Mooney 1993). Nor is it clear how things would change with a change in environmental conditions. To a large extent this is a consequence of the fact that organisms and their environments are connected by a complex web of interrelations and feedbacks that are non-linear, and contain lags and discontinuities, thresholds, and limits (Kay 1991, Costanza et al. 1993).

Recent small-scale, multi-species experiments indicate that species deletion under given environmental conditions may lead to loss of function (Naeem et al. 1994, Tilman and Downing 1994). Such experiments have been undertaken in 1–4 m² plots or enclosures and contain species that live their life at those scales. It is not self-evident that results from small assemblages of species on small scales are valid for large-scale ecosystems.

Empirical findings from large-scale ecosystem studies of lakes, forests, marine and savanna ecosystems indicate that there are differences in the link between species and functional diversity and the generation of ecosystem services. Studies of natural, managed, and disturbed or impacted ecosystems have shown that individual species population dynamics are more sensitive to stress than are ecosystem processes (Schindler 1990, Vitousek 1990). This implies that an ecosystem under stress may be expected to keep more of its functional performance than its species composition (Holling et al. 1995). This functional robustness is based on evidence that a relatively few processes, having distinct frequencies in space and time, structure ecosystems and set the rhythm of ecosystem dynamics (Holling 1992), a pattern that seems to be particularly true for terrestrial ecosystems (Holling et al. 1995). A limited number of organisms and groups of organisms seem to drive or control the critical processes necessary for ecosystem functioning, while the remaining organisms exist in the niches formed by these keystone process species. Such organisms modify, maintain, and create habitats. Jones et al. (1994) refer to them as "ecosystem engineers." We prefer the term "keystone process species," to avoid confusion with the field in applied ecology called "ecological engineering" (e.g., Mitsch and Jorgensen 1989). Nor is the set of such species necessarily constant over time, since it depends on environmental conditions (Lawton and Brown 1993, Holling et al. 1995).

As ecosystems are complex self-organizing systems, they are characterized by multiple locally stable equilibria or persistent states, each of which may corre-
spond to a distinct set of environmental conditions, and may be controlled by distinct sets of keystone process species (Schneider and Kay 1994, Perrings et al. 1995a). But keystone process species alone will not guarantee the continuation of the ecosystem in question. It is in this context that the concept of ecosystem resilience becomes crucial in biodiversity conservation. “Resilience,” as the term is conventionally used in ecology, refers to resistance to disturbance and speed of return to a stable equilibrium state (Pimm 1984)—what might be termed “efficiency of function.” Following the work of Holling (1973), we use resilience to capture the existence of function in systems that, at any given moment, will be away from any one of a number of locally stable equilibrium states. Resilience in this sense is a measure of the perturbation that can be absorbed before an ecosystem in the attractor domain of one equilibrium state is dislodged into that of another equilibrium state. It is the capacity of the system to buffer disturbance. As an example of multiple equilibrial states, forest land cleared for agriculture in Amazonia, once abandoned, tends to develop into grassland or savanna and may not revert to the original forest. Different sorts of interacting physical and biological processes and organisms control ecosystem functioning in each of the equilibrium states. Such phenomena have been documented in savanna ecosystems, and are also observed in boreal forests, fisheries, and agriculture (Regier and Baskerville 1986, Westoby et al. 1989, Trenbath et al. 1990, Gunderson et al. 1995).

The significance of functional diversity involving the controlling species in such cases may be illustrated by the semi-arid grasslands of eastern and southern Africa. There are (at least) two equilibrium states in these ecosystems, one dominated by grasses, and one by shrubs. The grassland state is controlled by two groups of grasses, each of which has different functions. One group contains species that are tolerant to grazing and drought, with the capacity to hold soil and water because of deep roots. The second group is more productive in terms of plant biomass than the first group, which makes it attractive to grazers, but is less drought tolerant. The species of the second group have a competitive advantage over the first group during periods when grazing is less intensive, and when rainfall is higher. The reverse occurs during transient but intense grazing pulses of migrating herbivores like zebras or antelopes. In this way, a diversity of both types of grass species is maintained in a manner that assures that the ecological functions underpinning ecosystem productivity are preserved, over a range of climatic conditions.

When fixed management rules are applied, such as the stocking of ranched cattle at a moderate but “sustained” level, the functional diversity of the system is gradually lost. This is due to a shift from the natural intense pulses of grazing to more modest but persistent grazing pressure. Continuous moderate grazing shifts the competitive advantage to the productive group of grass species, at the expense of the drought-resistant grasses. As a consequence, it slowly reduces diversity to one type of function, with the consequence that the system loses its capacity to function under a wide range of climatic conditions. That is, the resilience contracts. An episode of drought that previously could be absorbed can flip the ecosystem into a state that is dominated and controlled by woody shrubs of low value for cattle ranching (Perrings and Walker 1995).

This sort of behavior is also observed in other managed systems (Ludwig et al. 1993, Gunderson et al. 1995). Many ecosystems evolve through management to become more spatially uniform, less functionally diverse, and more sensitive to disturbances that otherwise could have been absorbed. They lose resilience.

**Biological Diversity as Insurance**

The problem to be addressed in developing a strategy for biodiversity conservation is that current institutions in society, including markets, do not respond to environmental feedbacks (Berkes and Folke 1994). That is, many of the most important environmental effects of human behavior are not recognized in the set of market prices. They are external to the market. The implication of this is that individual users of biological resources will not take the true cost of their actions into account. The problem is frequently exacerbated by governmental policies that, by subsidizing users of biological resources, deepen the wedge between the private and social cost of their behavior. Indeed, the failure of markets and the inability of government policies to correct the failure of markets can be seen as the prime driving force behind the loss of biodiversity.

The problem is also exacerbated by the fact that ecosystems themselves often “fail to signal” the long-term consequences of loss of resilience, continuing to function in the short term even as resilience declines. That is, large-scale ecosystems continue to function even when the composition and number of organisms is reduced. It seems like ecosystems frequently signal loss of resilience only at the point at which external shocks, previously absorbed by a diversity of organisms with overlapping influences, now flip those systems into some other regime of behavior, as in the grassland case above (Holling et al. 1996).

An important ecological objective of a biodiversity conservation strategy to avoid such flips is the protection of those organisms that establish and maintain the niches formed by keystone process species. These species provide a buffer to rare and extreme events. The vulnerability of key structuring processes is a function of the number of organisms that can take over and run such processes when the system is perturbed (Holling et al. 1995). Such organisms are essential for ecosystem resilience. Their loss implies a reduction in ecosystem plasticity and capacity for self-organization and evo-
ution, which, in turn, threatens the capacity of the system to produce valuable ecological services that are needed for human existence. These organisms can therefore be viewed as "natural insurance capital" for securing the generation of ecological services, both at present and in the future (Barbier et al. 1994).

The insurance function of biodiversity certainly includes its role in the genetic evolution of microbial, plant, animal, and human life. But it also includes the capacity of the ecosystems in which those reservoirs are contained to function under current and future environmental conditions. When loss of biodiversity reduces ecosystem resilience, it threatens the functions of that system, and hence the foundation for economic activity and human welfare (Perrings et al. 1995a). In most cases, however, the reduction in the "insurance value" of biodiversity is not signalled in the incentive structures of human society, including the price mechanism. Nor is it within the reach of the policies of any one government.

The problem may be illustrated by the link between migratory insectivorous bird populations and changes in insect outbreaks in boreal regions of Canada. A set of insectivorous birds is one of the controlling factors of the forest renewal patterns produced by budworm population cycles. Their existence contributes to the resilience of the boreal forest. Simulations based on long-term studies of budworm–forest systems dynamics indicate that the total bird population would have to be reduced by \( \approx 75\% \) before the system would flip to a different pattern of behavior (Holling 1988). A large proportion of the bird species spend the winter in Central America and parts of South America. Radar images of flights of migratory birds across the Gulf of Mexico over a roughly 20-yr period have revealed that the frequency of trans–Gulf flights has declined by almost 50% (Gauthreaux 1992), approaching the range of uncertainty in the simulation estimate above. Hence, in addition to regional forest fragmentation and its negative effects on nesting success of migratory birds (Robinson et al. 1995), Canadian boreal forests and the economic activities dependent upon their functioning seem to be threatened by increasing land-use pressures in neo-tropical countries and along the migration paths of insectivorous birds (Holling 1994).

Similarly, the widespread cutting of mangrove eco-
systems in Southeast Asia and South America for shrimp farming causes the loss of resilience of these coastal ecosystems to provide spawning and nursery grounds for fish and shellfish. In this case the degradation takes place in the coastal area of one country, but can cause reduced or lost yields of adult fish harvested in feeding grounds that belong to other countries. In neither case is it possible for the government of the country that is most affected to address the problem directly (Barbier et al. 1994).

Biodiversity loss through ecosystem modification is a new form of international environmental impact, a new type of "transboundary pollution." Many of the ecosystem modifications and the environmental effects that they cause, which today are regarded as of only local or national concern, are in fact of regional and ultimately global concern. The web of connections linking one ecosystem with the next is intensifying across all scales in both space and time. Local human influences on air, land, and oceans slowly accumulate to trigger sudden abrupt changes when thresholds are reached, directly affecting the generation of ecological services and the vitality of human societies elsewhere. Local environmental problems may have their cause half a world away, as illustrated by the above examples. Everyone is now in everyone else’s backyard.

**IMPLICATIONS FOR BIODIVERSITY CONSERVATION**

What implications does this have for a strategy of biodiversity conservation? In addition to basic research to increase our understanding of the interplay among biological diversity, functional performance, and resilience in complex and nested self-organizing systems, we suggest that there are two main implications.

First, preserving biodiversity through nature reserves and other protected areas is an important short-term step, which we endorse, but it is not sufficient to solve the problem of biodiversity loss. Nature reserves are embedded in their larger environments. Most reserves cannot alone deal with ecological attributes that cover larger scales, such as those discussed in this article. For example, wading birds in the Everglades National Park depend on areas more than 10 times the size of the park. Conservation efforts should be planned at the scale of the regional landscape. Small reserves will lose their distinctive species if they are surrounded by a hostile landscape (Askins 1995). A hostile landscape is, generally, the result of increasing and intensifying human activities. Human influences at scales from the local ecosystem to the planet as a whole are becoming so extensive and pervasive that conditions that justified locating a protected area in one place originally may disappear over decades and move elsewhere. A biodiversity-conservation strategy that only focuses on preserving as much of the genetic library as possible in a few small areas may not be effective even in its own terms.

Second, we have argued for a strategy that aims at conserving the capacity of ecosystems to continue to deliver life-support and other ecological services to humanity under a wide range of environmental conditions. The role of biological diversity in the functioning of ecosystem performance is not limited to protected areas. Hence the conservation of biodiversity should be addressed everywhere. From this perspective, the heavily debated concept of "sustainability" might be interpreted as the maintenance of a level of biological diversity that will guarantee the resilience of ecosystems that sustain human societies. The goal
of a conservation strategy should be to protect not all biodiversity in some areas, but biodiversity thresholds in all areas. Conserving essential self-organizing processes and the resilient patterns that they produce is the foundation for preservation of the biodiversity heritage (Holling et al. 1996). This approach has several implications.

1) To do this, it is necessary to identify the major social and economic forces that are currently driving the loss of functional diversity and to create incentives to redirect those forces. This includes both the proximate and the underlying forces (Perrings et al. 1992). The proximate forces refer to the direct reduction of biodiversity because of over-exploitation of species, land-use changes, and landscape fragmentation. The underlying forces include inappropriate government policies, the structure of property rights, pressure of human population growth and poverty, patterns of consumption and production, and the values of society. It is the underlying forces that need to be addressed in a strategy for biodiversity conservation (Barbier et al. 1994, Perrings et al. 1995b).

2) Following (1), it is necessary to create economic incentives that reduce the differences between the value of biological diversity to the private individual and its value to society as a whole. That is, it is necessary to internalize the external costs of biodiversity loss (in the language of economists). Internalizing only a few of the external costs of biodiversity loss is often enough to motivate the conservation of biodiversity.

3) A precondition for this is the development of effective institutions for biodiversity conservation. Institutions are the humanly devised constraints that shape human interaction. They structure incentives in human exchange, whether political, social, or economic, and shape the way societies evolve through time (North 1990). Institutions provide the framework for human actions, but to be effective they have to be adaptive (Gunderson et al. 1995). Being adaptive means, among other things, being able to respond to environmental feedbacks before those effects challenge the resilience of the entire resource base and the economic activities that depend on it. That is, it is necessary to frame the level of economic activity in a way that minimizes the risk of irreversible damage to the systems on which human activity depends (Perrings and Opschoor 1994). While many recent institutional innovations tend to do just the opposite, there are success stories from both traditional and contemporary societies from which we can learn (Feeny et al. 1990, Ostrom 1990, Berkes et al. 1995).

4) Rather than focusing attention on areas with the highest count of genetically distinct organisms, we should be stimulating the development of institutions, policies, and patterns of human consumption and production that work in synergy with ecosystem functions and processes. We should be reversing the trend towards large-scale and intensive monoculture. These simplified ecosystems are characterized by very low levels of diversity and even lower levels of resilience. They need to be redirected to mimic functional ecosystems (Jordan et al. 1987, Mitsch and Jörgensen 1989, Soulé and Piper 1992). In this way biodiversity may be conserved and even enhanced, while ecosystem resilience and the insurance value of biological resources may be increased. Nature reserves in both terrestrial and aquatic environments become important in this context, as a source of immigrant organisms for redevelopment and restoration of degraded areas.

Conclusion

Biodiversity loss includes not just the extinction of species, but any change in the mix of species and ecosystems that results from human activity and compromises the structuring processes upon which human well being and survival depend (Perrings et al. 1992, 1995a, b). This approach to biodiversity conservation supports a strategy that reorients biodiversity research and policy away from genetic information and the preservation of species for tourism and recreation in nature reserves, and towards conservation for the protection of ecosystem function and resilience. This complementary view of biodiversity implies that the benefits derived from its conservation are much wider and more fundamental than previously conceived both in science and in policy. It illuminates the fact that people depend on biological diversity for their well being and survival. The emphasis in research and conservation work should not be as closely tied, as it currently is, to protected areas in the mega-diversity zones. Biodiversity loss is a matter of consequence in any ecosystem in which resilience is threatened by the deletion of populations, irrespective of the species head-count in such systems. Moreover, the most powerful instrument for biodiversity conservation is not the park fence in isolation, but policies and reforms that make conservation a matter of private as well as social interest.

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