
17 What We Have Learned about the Ecosystem Functioning of Biodiversity

H.A. MOONEY, J. HALL CUSHMAN, ERNESTO MEDINA,
OSVALDO E. SALA AND E.-D. SCHULZE

17.1 BACKGROUND

Here we summarize the contents of this book as well as the results of the overall SCOPE Ecosystem Functioning of Biodiversity Program and the Global Biodiversity Assessment (GBA) (UNEP 1995). This book gives in-depth syntheses of the ecosystem functioning of biodiversity for a number of the worlds' major biomes. A number of biomes (tropical, Orians *et al.* 1996; savannas, Solbrig *et al.* 1996; Mediterranean, Davis and Richardson 1995; arctic and alpine, Chapin and Körner 1995; those found on islands, Vitousek *et al.* 1995) are covered in even greater detail in the specific volumes cited above. The GBA, in contrast, treats these same ecosystems, plus a few others, in a highly condensed form that facilitates cross-biome comparisons.

We start this chapter with the summary statements of the overall program that are taken directly from the GBA Sections 5 and 6. Documentation for these conclusions are contained in the GBA volume. These summaries noted that understanding the role of elements of biodiversity in the functioning of ecosystems is a relatively new research endeavor that addresses the structural and functional properties of ecosystems, and the degree of sensitivity of these properties to changes in the underlying diversity. Understanding the functional role of biodiversity has crucial implications for the management of the Earth System. Valuable scientific principles and guidelines for making ecosystem management decisions are beginning to emerge in spite of the field's youth and the relatively small number of experimental studies from which it draws. These emerging principles are embodied in a series of statements that deal with the importance of diversity at different levels of integration.

Functional Roles of Biodiversity: A Global Perspective

Edited by H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala and E.-D. Schulze

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17.2 GENERAL PROGRAM CONCLUSIONS

1. The loss of genetic variability within a population of a species of a given area can reduce its flexibility to adjust to environmental change and narrow the options for adjustments to climate change, for example, as well as for rehabilitating specific habitats.
2. The addition or deletion of a species can have profound effects on the capacity of an ecosystem to provide services. We are beginning to develop the potential to predict which species these will be. They are those with unique traits within an ecosystem for fixing nitrogen, capturing water, emitting trace gases, causing disturbance and so forth. We can predict the consequences of their removal or addition *a priori*. Although the success of an alien species in a new habitat may be difficult to forecast, its impact on ecosystem functioning upon establishment can be predicted based on whether the new species utilizes or produces a unique resource.

Certain species, without readily recognized traits, when deleted can have profound effects on ecosystem functioning. These are so-called "keystone" species and at present, due to our lack of a general theory, their potential effects on removal can only be assessed by direct experimentation.

3. Recent studies are confirming the proposition that the capacity of ecosystems to resist changing environmental conditions, as well as to rebound from unusual climatic or biotic events, is related positively to species numbers.
4. The simplification of ecosystems in order to produce greater yield of individual products comes at the cost of the loss of ecosystem stability and of such free services as controlled nutrient delivery and pest control, which thus needs to be subsidized by the use of fertilizers and pesticides.
5. Certain ecosystems, such as those found in arid regions and on islands, appear particularly vulnerable to human disruptions and hence alteration of their functioning. These sensitive systems all have low representation of key functional types (organisms that share a common role).
6. Fragmentation and disturbance of ecosystems and landscapes have profound effects on the services provided, since they result in shifting the balance of the kinds of species present—from large, long-lived species to small, short-lived ones. These shifts result in the reduction of the capacity of these systems to store nutrients, sequester carbon and provide pest protection, among other things. Ecosystems, and the services they provide, must be considered in a total landscape context, and in some cases even on an intercontinental basis.
7. We have been more successful in simplifying than in reconstructing ecosystems. Our lack of success in ecosystem restoration suggests the need for great caution in reducing biodiversity through management

practices because of the potential loss of goods and services over the long run. As society exerts ever greater control and management of the ecosystems of the world, great care must be taken to ensure their sustainability, which is in large part due to the buffering capacity provided by biotic complexity.

17.3 LESSONS FROM SPECIFIC BIOMES

Information from specific biomes, as well as comparisons among them, give us insights into diversity/functional relationships. Below we note observations from particular ecosystems, taken from this volume, that particularly illustrate specific biodiversity issues. The order of the systems discussed here differs from that of the text since here they are organized by specific lessons learned.

17.3.1 Mediterranean ecosystems

On disturbance/diversity/functioning It has been well documented that disturbance, at a moderate level, can promote diversity. In the Mediterranean basin, human-induced landscape variation – fields, pastures, scrublands and forests – leads to high diversity at all levels as well as to multiple services to humankind. Even complex manipulation of ecosystems, such as in the “dehesa” agro-ecosystem in southern Spain, has provided a diversity of organisms and services and has been sustainable, at least until recently. Contrast this with the recent dramatic massive conversion of the native vegetation of western Australia to wheat fields, resulting in large alterations of ecosystem functioning, particularly related to water balance. This conversion has resulted in salinization of soils and losses of many services, including nutrient supply, and pest and erosion control. There are now efforts to repair the damage by reintroducing perennial systems. In the Mediterranean case, in a sense, there has been adaptive management practices through the centuries – with any management experiment being small-scale because of the lack of the mechanical means to do otherwise, as well as the complex land tenure system which also led to small-scale, and patchy, alterations. In western Australia the recent development of this region was rapid and extensive, aided by fully mechanized conversion of vast areas. By the time the problems were recognized, extensive damage had already been done.

The lesson is that even in a world that is increasingly impacted by human activities, we can manage landscapes to produce sustainable ecosystems that provide ample services, but there is a considerable challenge in doing so. The examples are there: we need to learn from them.

17.3.2 The open ocean

Managing in the dark We lack details on the ecological structure and function of the open-ocean ecosystem, and for good reasons. This system is vast and difficult to study. We are only now learning of the rich diversity of the benthic system. In general, we have very little understanding of the interactions of the components of the open oceans. This lack of knowledge has put us all at peril, as evidenced by the sudden and dramatic decline of the oceans fisheries. The drivers of this demise are no doubt complex, but most certainly includes the overfishing made possible by "industrial" harvesting. There is little understanding of the ecosystem consequences of the demise of specific fisheries, since research has generally been more commodity-based (a particular fish) rather than system-based. It could be that total ocean productivity has not declined, but that there has only been a shift in the abundances of various species. We do not know. It is stated in this volume that there may not be as much functional equivalency in the oceans as there is on the land, and thus the possibilities for functional replacement are low, for functions other than production. This is an important proposition that needs further study. We are already seeing a great interest in a new approach to fisheries management. It is quite clear that this new approach will, for the first time, be imbedded in an ecosystem paradigm, where functions and services are considered, and where humans are considered an increasingly dominant element in this ecosystem.

17.3.3 Tropical forests

The time dimension Tropical forests illustrate the importance of the time dimension in considering the roles of species in ecosystem functioning. Through selective harvesting of plants and animals we have performed many "experiments" to test the role of various species and functional groups in the functioning of total ecosystems. However, interpreting the results of these experiments may take a long time, since many organisms live for centuries and many ecosystem processes have very long time constants, e.g. soil formation. Tropical forests provide a good example of this. As pointed out in the tropical forest chapter, only 50 tree generations have elapsed since the last glacial retreat, when temperatures were considerably cooler. In much more recent time there has been a massive, and selective, harvesting of the large mammals of the tropical forests by humans. Because of the long life-span of the dominant trees, we may not readily see the dramatic and long-term impact of the shifting balance of herbivores and carnivores in this system on plant reproductive biology, and hence the structure and function of the forest.

17.3.4 Mangroves

The link between the land and the sea Mangrove systems illustrate many dimensions of the diversity–function relationship. At the landscape level these systems represent a crucial link between the land and the sea. On the one hand, they protect the land from erosion induced by storms, and on the other they provide the foundation, in terms of nurseries, for many fisheries that lie off the coast. The amount of destruction of mangrove forests is staggering in many parts of the world, and represents severe losses of the multiple services that these systems provide. The mangrove systems provide a particularly good test system for refining our knowledge of the relationship of ecosystem functioning and biodiversity. Along the east coasts of Australia, for example, mangrove forests exist with over 30 dominant species. Going eastward, along the islands of the South Pacific, mangrove plant diversity declines progressively until only one species is found in Samoa. This striking gradient is apparently driven by dispersal distance from the mainland. The climate does not vary much along this tropical longitudinal gradient. We do not yet know how system functioning responds to this loss of diversity, or if the diversity of other components of the ecosystem scale in the same manner as the dominant plants. These systems provide abundant material for examining the role that particular keystone organisms play in regulating decomposition. In many regions, crabs apparently play a central role in the initial shredding of litter, whereas in other regions gastropods play this role.

17.3.5 Agroecosystems

On simplification and substitution Agroecosystems provide a particularly good example of how we have substituted the services provided by natural ecosystems for those provided by organisms of particular interest to humankind. It would seem, on the face of it, that comparisons of the diversity–function relationship would be easy between natural and managed ecosystems. However, in agroecosystems, no matter how simple or intensive, the services lost, such as nutrient and water regulation, are compensated for by human-provided substitutions, often at a considerable energy cost.

The data available suggest that, for a given function such as productivity or organic matter accumulation, it does not take many species to provide full services. However, the few analyses available are generally unidimensional in nature and do not consider all functions and their interactions in a system context at a given time, much less through time. Clearly, there is ample opportunity to explore more fully the role of genetic, species and landscape diversity in ecosystem functioning in agroecosystems versus natural systems.

One message that emerges clearly is that in agroecosystems, landscape diversity is an essential component of sustainability.

17.3.6 Island ecosystems

On simplicity due to dispersal Islands, of course, do not represent a special ecosystem type since virtually all of the world's major ecosystems can be found on islands in one place or another. What is special about them is that they generally represent a special case of any ecosystem, in that they are simpler than their continental counterparts. This generally means that they have fewer representatives of a given functional group, or may even have whole groups missing. It is thus not surprising that islands are of particular value in studying the role of species in ecosystem functioning. Most of our knowledge on these issues come not from observing deletions, or species extinctions, but from documenting the effects of additions brought about by successful invasions. Most of the spectacular cases of deletions, such as flightless birds, have preceded the era of scientific inquiry. On the other hand, there are a number of well-studied examples of the ecosystem consequences of relatively recent species additions which have shown the dramatic effects that can result, particularly if the addition represents a new functional type. It is clear that islands will most certainly be utilized as the testing ground for emerging hypotheses on the role of diversity and function.

17.3.7 Cold and dry ecosystems

On simplicity due to limiting water Arid ecosystems share with islands the characteristic that they have few representatives of any functional group. In this case, however, climatic severity rather than dispersability is the filter on diversity. The results are apparently the same, however. Some of the most dramatic examples of the consequences of species removals and additions come from these arid systems, where resulting major shifts in functioning have been documented with the alteration of species composition. Also, the fact that the structural dominance of desert ecosystems is dependent on only a few species makes any loss result in cascading effects on the whole system. The removal of a single arboreal species, or a shift from grasses to a single tree being dominant, totally alters the structure and function of the entire ecosystem.

On simplicity due to cold temperature As in deserts, arctic and alpine systems have both structural and taxonomic simplicity. Because of evolutionary constraints, entire functional groups are missing from the extremes of cold-dominated ecosystems. Humans have also been responsible for deletion of many of the large grazers. The arctic, because of the ease of

performing certain types of ecosystem manipulation, has been an important testing ground for the diversity-function issue.

17.3.8 Lakes and rivers

Responses to massive impacts Fresh water bodies, and the organisms that inhabit them, have been impacted more by humans than virtually any other system on Earth. In a direct sense humans compete, and win, against organisms for limiting fresh water. Rivers are massively dammed or diverted, and lakes are extensively utilized for recreation. The biotic composition of water bodies has been greatly impacted by these activities, as well as others which include deliberate biotic introductions and the effects of pollutants, including acid deposition.

Lakes in particular provide excellent examples for examining the consequences of changes in biotic composition on ecosystem functioning. They are relatively clearly circumscribed systems, and limnologists, by training, generally have a more holistic view of their systems than terrestrial ecologists. Many important insights about ecosystem functioning and population dynamics have come from lake studies.

Chapter 12 in this volume illustrates these issues and system advantages. The enormous and complex impact of a single species addition, such as the cases of the opossum shrimp and the Nile perch, has been well documented. These effects have been mainly through food web alterations, or trophic cascades. At the same time, lake systems have been shown to undergo dramatic shifts in species structure under stress conditions, and yet certain ecosystem processes, such as primary productivity, have shown little change at first because of species compensations.

Because of the ease of experimentally manipulating lake systems, they offer particularly powerful models for deriving general rules of where species additions or deletions will, or will not, have a major impact on ecosystem processes. Unfortunately, we already have thousands of uncontrolled experiments in progress on biotic additions and deletions to lake and river systems, the consequences of which are poorly monitored. We should certainly make the effort to remedy this as soon as possible.

17.3.9 Coastal ecosystems

Keystones and compensations It was in an intertidal system that the presence of a keystone species was first experimentally demonstrated. Since then, many other examples of keystones have been illustrated, and extensions of the concept have been made. One important finding is that the role of a species may vary along with its distribution; it may play a strong keystone role in one place but not in another, since the complex of associate

species changes in widely distributed species. Also, in intertidal systems it has been shown how humans themselves play a keystone role.

Where keystones are lacking, species compensations are evident, with function being maintained after species removals by replacement of the activity by the remaining species.

17.3.10 Coral reefs

Complexity Coral reefs represent a remarkable collection of organisms, many of which have co-evolved commensal relationships. Thus it is no surprise that dramatic instances of major ecosystem rearrangements have been noted by either the deletion or increase of one species or another. These systems also provide strong support for the notion of the cascading influence of the loss of a single guild, such as algal grazers, on the health of entire coral systems, and in turn on the loss of such ecosystem services as coastal protection and attributes of interest to tourists. Since these systems are bathed in water and colonized by larvae, the distances between reef systems and the currents between them are crucial. The importance of virtually all dimensions of biodiversity, from genes to seascapes, is readily demonstrated in coral ecosystems.

17.3.11 Boreal forests

Low diversity and low redundancy Boreal systems illustrate many aspects of diversity-function relationships. Low species richness translates into low representation in any functional type. Thus, the impact of the removal of any single species can be great. No doubt the characteristic boom and bust cycles of many animal grazers in these systems is related to system simplicity, and thus intrinsic instability. There are many examples of large influences by single species, not only on local systems but on whole landscapes, as in the case of beaver. Also remarkable because of system simplicity is the dramatic ecosystem impact of a single trait within the small functional group of tree species, depending on whether they are evergreen or deciduous. It is the boreal forests, along with the deserts and tundra, which provide the best evidence for the importance of functional group diversity in maintaining ecosystem stability.

17.3.12 Temperate and tropical grasslands

Where experiments are most tractable Temperate grasslands have provided most of the available experimental evidence on the relationship between species diversity and ecosystem functioning. The relatively short life-span of grasses or their small size may partially explain the concentration of manipu-

lative experiments in this biome. Results of these experiments, in conjunction with new conceptual models, suggest ways of predicting the effects of different species on ecosystem functioning. A common feature of most ecosystems is that a few species account for a large fraction of a given ecosystem process (e.g. primary production), but account for a small fraction of system diversity. Removal of grass species has a different impact on ecosystem functioning depending on the abundance of the removed species in the original ecosystem. Removal of subdominant species is generally compensated by the remaining species, but removal of the dominant species does not result in full compensation, at least in the short time-span of most experiments.

Grasslands have also provided experimental evidence for the relationship between species diversity and ecosystem stability. Long-term monitoring of a large set of grassland plots with differing diversities, in conjunction with the impact of a severe drought, provided the evidence to show the importance of species diversity on ecosystem resistance and resilience. The most diverse plots showed the least reduction in productivity during the drought, and were the plots which recovered their full capacity the fastest.

It was in the savannas of Africa that the first good evidence was gathered showing the importance of species richness to ecosystem resilience. The large numbers of species within a single functional type, grasses, provides enormous buffering against environmental perturbation. It is also in savannas that a clear differentiation in the ecosystem role can be seen among certain functional types, such as in the deep-rooted but sparse trees and the continuous cover of shallow-rooted herbs.

17.3.13 Temperate forests

Diversity and function over evolutionary time The temperate forests of the world are remarkable in that each continent has not only different species dominating them, as would be expected, but also a large difference in the numbers of dominants they have, which is related to the glacial history of these continents. The temperate forests of China have the greatest number of dominants, followed by the northeastern United States and then western Europe. The slim evidence we have now would indicate comparable flux rates of water and nutrients, as well as other functional similarities. Thus, in evolutionary time, comparable growth forms will utilize all of the available resources. The SCOPE project, however, focused on the impacts of humans on diversity – and the results of these perturbations – a very different issue from evolutionary niche partitioning. Results from other biomes predict that the responses to, and recovery from, species losses would potentially be greatest in the less-rich forests of Europe. We are now seeing in Europe a very substantive shift in species composition due to the effects of nitrogen

