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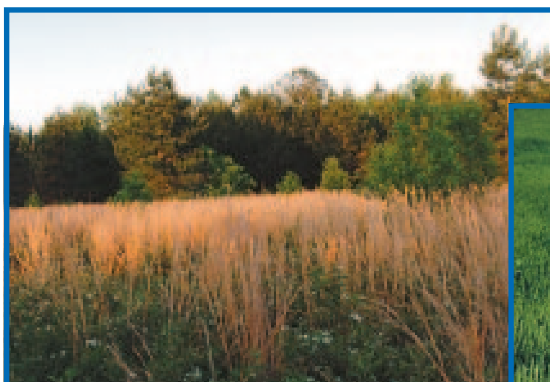
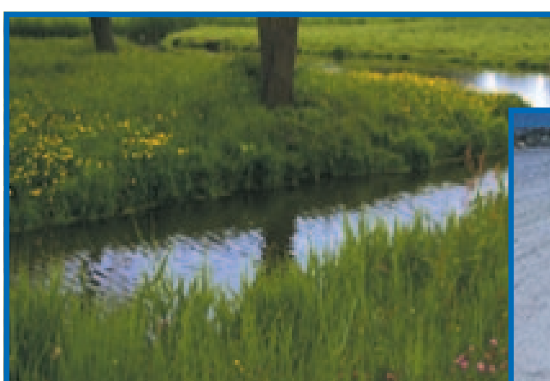
Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Processes





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Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Processes

by
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Critical processes at the ecosystem level influence plant productivity, soil fertility, water quality, atmospheric chemistry, and many other local and global environmental conditions that ultimately affect human welfare. These ecosystem processes are controlled by both the diversity and identity of the plant, animal, and microbial species living within a community. Human modifications to the living community in an ecosystem – as well as to the collective biodiversity of the earth – can therefore alter ecological functions and life support services that are vital to the well-being of human societies. Substantial changes have already occurred, especially local and global losses of biodiversity. The primary cause has been widespread human transformation of once highly diverse natural ecosystems into relatively species-poor managed ecosystems. Recent studies suggest that such reductions in biodiversity can alter both the magnitude and the stability of ecosystem processes, especially when biodiversity is reduced to the low levels typical of many managed systems.

Our review of the available evidence has identified the following certainties concerning biodiversity and ecosystem functioning:

- Human impacts on global biodiversity have been dramatic, resulting in unprecedented losses in global biodiversity at all levels, from genes and species to entire ecosystems;
- Local declines in biodiversity are even more dramatic than global declines, and the beneficial effects of many organisms on local processes are lost long before the species become globally extinct;
- Many ecosystem processes are sensitive to declines in biodiversity;
- Changes in the identity and abundance of species in an ecosystem can be as important as changes in biodiversity in influencing ecosystem processes.

From current research, we have identified the following impacts on ecosystem functioning that often result from loss of biodiversity:

- Plant production may decline as regional and local diversity declines;
- Ecosystem resistance to environmental perturbations, such as drought, may be lessened as biodiversity is reduced;
- Ecosystem processes such as soil nitrogen levels, water use, plant productivity, and pest and disease cycles may become more variable as diversity declines.

Given its importance to human welfare, the maintenance of ecosystem functioning should be included as an integral part of national and international policies designed to conserve local and global biodiversity.

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Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Processes

SUMMARY

INTRODUCTION

One of the most striking features of the earth's biota is its extraordinary diversity, estimated to include about 10 million different species. One of the most conspicuous aspects of contemporary global change is the rapid decline of this diversity in many ecosystems (Figure 1). The decline is not limited to increased rates of species extinction, but includes losses in genetic and functional diversity across population, community, ecosystem, landscape, and global scales (Figure 2). The term "biodiversity" refers collectively to all these aspects of biotic diversity. The wide-ranging decline in biodiversity results largely from habitat modifications and destruction, increased rates of invasions by deliberately or accidentally introduced non-native species, over-exploitation and other human-caused impacts.

On a global scale, even at the lowest estimated current extinction rate, about half of all species could be extinct within 100 years. Such an event would be similar in magnitude to the five mass extinction events in the 3.5 billion year history of life on earth. On local and regional scales, biodiversity declines are already pronounced in many areas, especially where natural ecosystems have been converted to croplands, timber plantations, aquaculture and other managed ecosystems. The diversity of these managed ecosystems is often low, and species composition very different, compared with those of the natural systems they have replaced (Figure 3).

What are the consequences of such declines in biodiversity and how might they affect human welfare? The earth's living organisms contribute to human welfare in a variety of ways. First, humans derive from them goods and products essential to life, including food, medicine, and industrial products, genetic resources for crop breeding, and natural pest control services. Such benefits can be viewed as the market values of biodiversity because they are are readily tied to our economy and often can be assigned a dollar value in the marketplace. Second, biodiversity has nonmarket values that can be expressed in terms such as knowledge, aesthetic, existence and other values. These non-market values of biodiversity are difficult to quantify, but are, for many, sufficient justification for preserving biodiversity independent of market values.

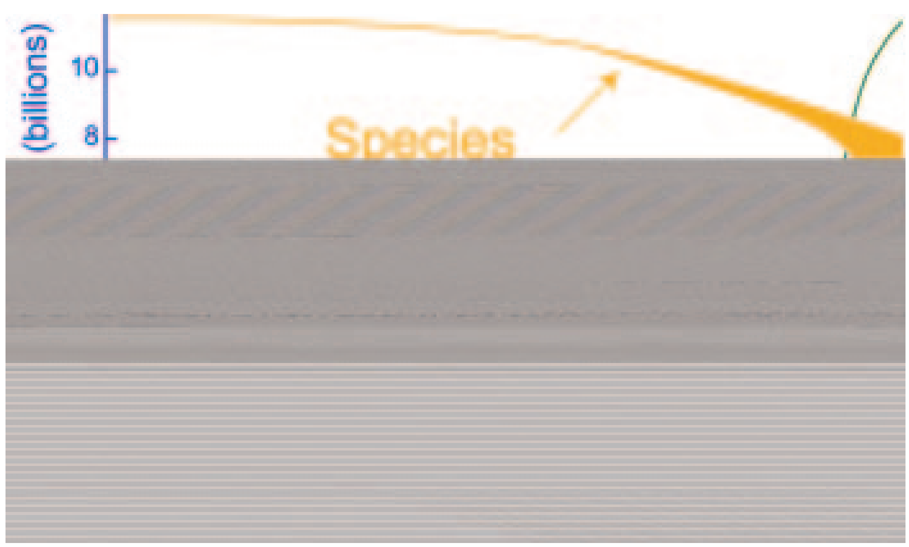


Figure 1 - The predicted decline of biodiversity in association with increases in human populations. Estimates for global biodiversity loss are between 50 and 75% by 2100, but in many transformed habitats, such as crop farms, local declines of similar magnitude have already occurred. (From Soulé 1991 *Science*.)

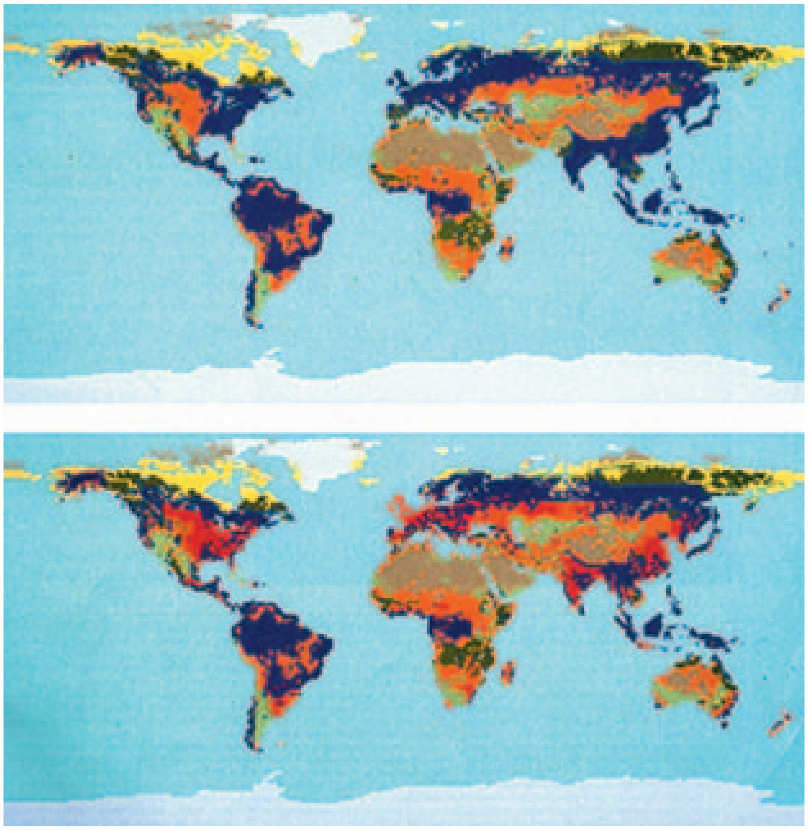


Figure 2 - Biodiversity loss and the earth's changing biomes. The top map shows the earth's major biomes, such as graslands in orange and forests in blue, prior to the introduction of agriculture. The bottom map shows the spread of agronomic and other man-maged ecosystems where red represents a region that is greater than 50% man-aged ecosystems. (After Sisk et al. 1994, BioScience)

A third category of value, ecosystem services, is the focus of this report. The organisms that live, grow, reproduce, and interact within ecosystems help to mediate local and regional flows of energy and materials (Figure 4). Energy flow refers to the capture of light energy by green plant or algal photosynthesis and its dispersal as chemical energy throughout the food web to plant- or algal-feeding animals, predators, and eventually decomposers. The flow of materials involves the recycling of carbon, nitrogen, phosphorus and other elements between living organisms and the air, water, and soil. These biologically mediated energy and materials flows contribute to many ecological or life support services that benefit human welfare such as greenhouse gas regulation, water treatment, erosion control, soil quality control, and plant growth. Ecosystem services can also include cultural benefits, such as religious, aesthetic, recreational, or inspirational values that humans derive from ecosystems.

Determining whether biodiversity per se is important to ecosystem functioning has been difficult, partly because many of the factors such as habitat conversion that reduce local biodiversity also directly affect many ecological processes, masking the more subtle impacts of species loss on functioning. Recent studies, however, have begun to shed considerable light on the issue. These studies have shown that ecosystems are indeed sensitive to changes in the numbers and kinds of species found in their communities. In this report, we provide an overview of ecosystem functioning, review the distinction between taxonomic biodiversity (i.e., species numbers) and functional biodiversity, and evaluate the current status of research concerning ecosystem responses to changes in biodiversity.

ECOSYSTEM FUNCTIONING

Ecosystem functioning reflects the collective life activities of plants, animals, and microbes and the effects these activities — feeding, growing, moving, excreting waste, etc. — have on the physical and chemical conditions of their environment. (Note that "functioning" means "showing activity" and does not imply that organisms perform purposeful roles in ecosystem-level processes.) A functioning ecosystem is one that exhibits biological and chemical activities characteristic for its type. A functioning forest ecosystem, for example, exhibits rates of plant production, carbon storage, and nutrient cycling that are characteristic of most forests. If the forest is converted to an agroecosystem, its functioning changes.

Ecologists abstract the essential features of an ecosystem into two compartments, the biotic and the abiotic. The biotic compartment consists of the community of species, which can be divided functionally into plant producers, the consumers that feed on producers and on each other, and the decomposers (Figure 5). The abiotic compartment consists of organic and inorganic nutrient pools. Energy and materials move between these two compartments, as well as into and out of the system. Ecosystem processes are quantified by measuring rates of these movements (e.g., plant production, decomposition, nutrient leaching or other measures of material production, transport or loss). Ecosystem functioning, in turn, is quantified by measuring the magnitudes and dynamics of ecosystem processes.

Ecosystem functioning results from interactions among and within different levels of the biota, which ecologists describe as a "nested" hierarchy. For example, green plant production on land is the end product of interactions of individual plants nested within populations; interactions among populations nested within a single species; interactions among a variety of species nested within a group of functionally similar species; and so on up to the level of interactions between different types of ecosystems nested within landscapes.

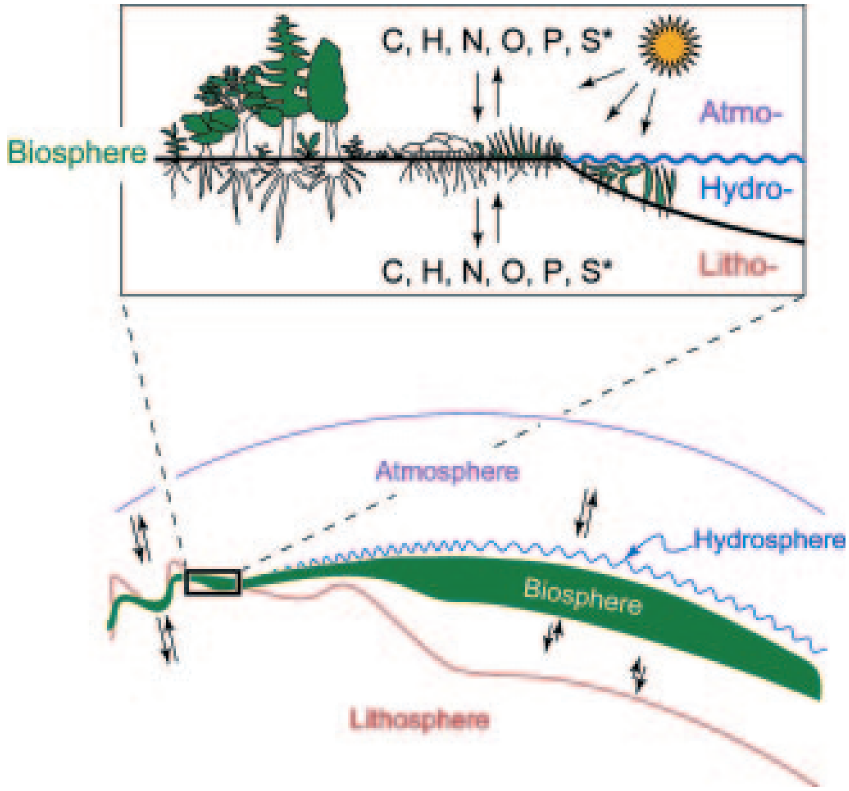
BIODIVERSITY: SPECIES, FUNCTIONAL TYPES, AND COMPOSITION

Although every organism contributes to ecosystem processes, the nature and magnitude of individual contributions vary considerably. Research in biodiversity places much emphasis on the uniqueness of individual species and their singular contributions to ecosystem services. Yet most ecosystem processes are driven by the combined biological activities of many species, and it is often not possible to determine the relative contributions of individual species to ecosystem processes. Species within groups such as grazing mammals, large predators, perennial grasses, or nitrogen-fixing microbes may therefore be functionally similar despite their uniqueness in genes, life history, and other traits.

Groups of species that perform similar roles in an ecosystem process are known as functional types or functional groups. Species may also be divided into functional types based on what they consume or by trophic status (e.g., their place in the food web as producers, decomposers, predators). Within trophic groups, species may be further divided according to life history, climatic or nutrient needs, physiology or other biological traits. Researchers may place a species into several different functional categories depending on the ecosystem process they are studying.

Figure 3 - In the tropics, highly biologically diverse rainforests are replaced by monocultures of bananas.

Figure 4 - The role of earth's biota in biogeochemical processes. Bottom: The major biogeochemical spheres consist of the lithosphere, hydrosphere, and atmosphere, where the biosphere is found. Top: Magnified portion of the biosphere showing its position within the three major biogeochemical spheres. Driven primarily by solar energy, producers, decomposers, and consumers annually move large quantities of materials containing many elements and compounds among the different spheres. The role of the tremendous diversity found within the biosphere is only recently beginning to be understood.



Because species can vary dramatically in their contributions to ecosystem functioning, the specific composition or identity of species in a community is important. The fact that some species matter more than others becomes especially clear in the case of "keystone species" or "ecosystem engineers" or organisms with high "community importance values." These terms differ in usage, but all refer to species whose loss has a disproportionate impact on the community when compared to the loss of other species. For example, a species of nitrogen-fixing tree, *Myrica faya*, introduced to the Hawaiian islands has had large-scale effects on nitrogen cycling, greatly increasing the amount of this essential plant nutrient in soils where the tree invades. The nitrogen-fixing lupine *Lupinus arboreus* also enriches soils and, as a consequence, encourages invasions of weedy grasses. Among animals, moose (*Alces alces*) through their dietary preferences greatly reduce soil nitrogen levels and also influence the succession of trees in the forest. Beavers, too, through their feeding and dam-building not only alter soil fertility and forest succession but increase the diversity of ecosystems in a landscape. Even termites play critical roles in soil fertility and other ecological processes in many arid grasslands.

On the other hand, there are some examples where additions or losses of particular species have had little effect on ecosystem processes.

ECOSYSTEM RESPONSES TO CHANGES IN BIODIVERSITY

Since Darwin, prominent biologists have hypothesized about the relationship between biodiversity and ecosystem functioning. More recently, concerns about increasing loss of biodiversity and questions about resulting degradation of ecosystem services have stimulated unprecedented observational, theoretical, and experimental studies.

Observational Studies

It might seem that observational studies comparing one ecosystem type with another, or comparing similar ecosystems at different locations, could provide ready answers to questions about the impacts of species richness on ecosystem processes. But these studies have invariably proven problematic. For example, an ecosystem such as a tropical forest or a coastal wetland may vary from one site to another not only in species number and composition, but also in physical and chemical conditions such as soil type, slope, rainfall, or nutrient levels. Comparing different ecosystems is likely to yield an unclear result because the response to variations in biodiversity cannot easily be distinguished from responses caused by variations in environmental and other factors. It is possible, though difficult, to control statistically for such potentially confounding factors.

Experimental Studies

Experimental studies, if well-designed, can minimize the confounding factors that plague observational studies. Experiments can provide insights not only into the relationships between biodiversity and ecosystem functioning but also into the possible mechanisms behind the relationships. Studies to date have ranged from large outdoor experiments and trials in large controlled environment facilities to modest-sized pot experiments and tests in small laboratory microcosms (Figure 6). This research has attempted to address two different questions about the link between biodiversity and ecosystem functioning. First, how are levels of ecosystem functioning affected by changes in biodiversity, particularly species richness? Second, how are the dynamics of ecosystem functioning, particularly the resilience and stability of processes, affected by changes in biodiversity? The following two sections review the experimental and theoretical results that shed light on these questions.

Biodiversity and Levels of Ecosystem Functioning

Results from many recent experimental studies conducted in North America and Europe demonstrate that ecosystem productivity increases with species richness. These studies range from large outdoor experiments to controlled laboratory experiments conducted in growth chambers, greenhouses, or small containers. Outdoor experiments such as those conducted in grasslands on nutrient-poor serpentine soils at Stanford, California and on prairie grasslands at Cedar Creek Natural History Area, Minnesota (Figure 7), work with plant communities similar to those found in nature, but researchers vary the number of plant species from one experimental plot to another. This approach is also used in the BIODEPTH experiments (Figure 8), in which seven European countries have established outdoor plots that range in plant diversity from low species numbers to the average numbers typically found at each site. More precise experiments using growth chambers have

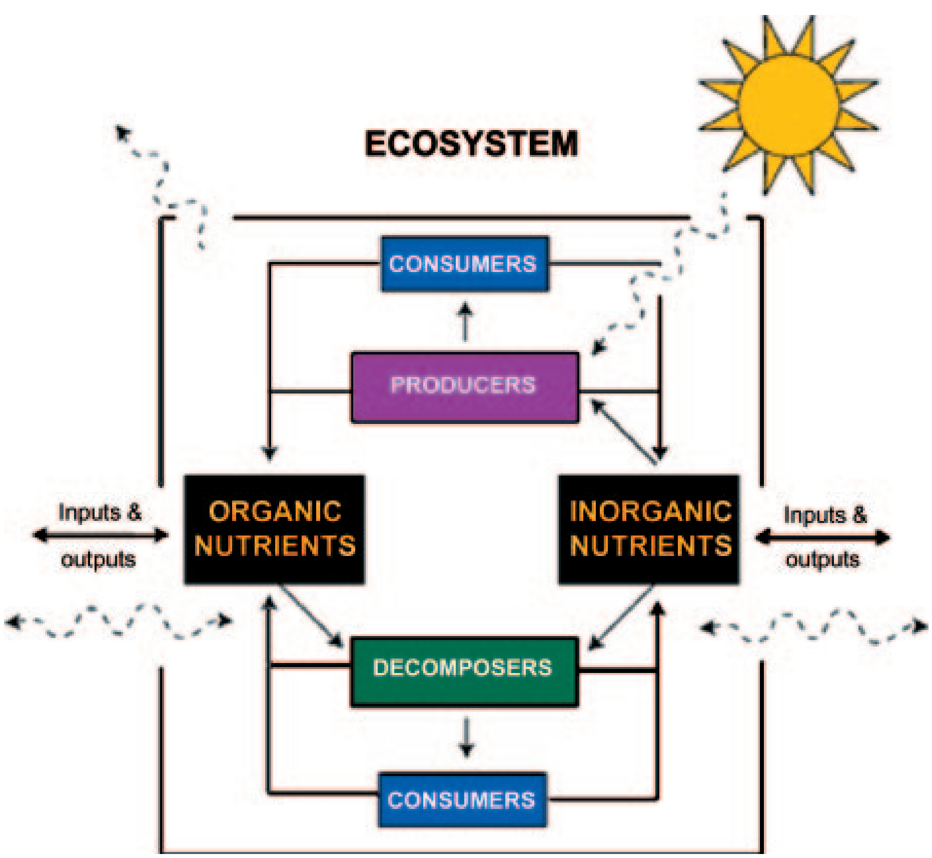


Figure 5 - Basic ecosystem functioning. Producers acquire energy through photosynthesis and take up inorganic nutrients to produce living biomass, forming the food base for consumer species such as herbivores and their predators. Mortality leads to accumulation of organic nutrients which are transformed by decomposers into living biomass, forming the food base for consumers. Decomposers and consumers contribute to formation of inorganic nutrients by mineralization, completing the cycling of nutrients between organic and inorganic forms. Energy flows (wavy, dashed lines) begin with acquisition by producers and end in loss due to the respiration activities of all organisms.

been conducted by researchers at Imperial College of London, Silwood Park, England and Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, France. More recent laboratory experiments in Europe and North America have begun to examine the impact of other components of biodiversity, such as the diversity of soil microorganisms, on plant production and the role of bacteria, predators, and herbivores in freshwater microbial communities.

All of these studies show that ecosystem functioning is decreased as the number of species in a community decreases. Declines in functioning can be particularly acute when the number of species is low, such as in most managed ecosystems including croplands or timber plantations. In addition, recent experimental studies in grasslands indicate that the effects of biodiversity on production can depend on both the number of functional groups present and the identity of the plant species (i.e., on community composition). Other studies have shown that loss of functional groups from a food web, or reductions in the number of species per trophic group (producers, consumers, decomposers) can also cause declines in ecosystem functioning. Finally, another study has shown that some species of plants may be more or less productive or show no response at all to changes in the diversity of their communities, even though total community productivity is, on average, lower at lower diversity.

Studies on plants have been particularly revealing and support results from recent theoretical models which predict that decreasing plant diversity leads to lower plant productivity. These models predict that diversity and composition are approximately equal in importance as determinants of ecosystem functioning. Two possible mechanisms have been identified to explain why levels of ecosystem functioning increase with increasing biodiversity. First is the "sampling effect": When the pool of species available in a region contains individual species that vary in productivity and other contributions to ecosystem functioning, then species-rich ecosystems have a higher probability of containing species with high levels of functioning. Second is the "complementarity effect": This occurs when increasing diversity results in increasing numbers of species that are complementary rather than competitive in their use of resources, exploiting different niches, such as rooting depths, and allowing more effective use of available resources.

Figure 6 - Experimental studies of the relationship between biodiversity and ecosystem functioning. Experiments vary considerably in size and methods. All have shown that loss of biodiversity leads to decreased ecosystem functioning. Clockwise from upper left, a researcher examining growth in potted assemblages of plants, transplanted Mediterranean vegetation in greenhouses, model ecosystems consisting of plants and small invertebrates in a growth chamber, field experiment in Switzerland, microbial microcosms in a growth chamber, and a field experiment in England. (Photos clockwise from top left: S. Naeem, J. Roy, Center for Population Biology, A. Bajpai, A. Hector.)

Figure 7 - An aerial view of experimental grassland plots in Cedar Creek, Minnesota. Two experiments are visible in this photograph. A series of 147 small plots ranging from monocultures to plots containing 24 plant species is visible in the foreground. The largest area in the center is occupied by 342 plots which range from monocultures to 32 species of prairie grassland plant species. These plots were established in 1993.

Biodiversity and Ecosystem Stability, Predictability and Reliability

Few experimental studies of the impact of biodiversity on stability have been attempted, largely because stability is a long term attribute of a system and testing for it requires either long-running experiments or experiments with short-lived organisms. In the one available long-term ecological field study, however, reductions in plant species richness also lowered the resistance of grassland production to drought. Predictably—lower year-to-year fluctuations in community productivity—was also significantly lower at lower diversity. In addition, studies of microbial communities in small experimental chambers have also shown that fluctuations in ecosystem functions such as productivity can be greater when species richness is reduced. Thus, the loss of diversity causes a loss of ecosystem stability (Figure 9).

Several mechanisms could account for these results. One mechanism comes from the ability of competing species to replace or compensate for one another and thus minimize, at higher diversity, the ups and downs in functioning. Another mechanism is the "portfolio effect," a theory which suggests that cumulative properties such as ecosystem functioning show less severe fluctuations in systems with many species, much the way investment portfolios of varied stocks have lower long term variance than portfolios of one or a few kinds of stocks.

Summary

Three points emerge from this growing body of research. First, declining species richness can lead to declines in overall levels of ecosystem functioning. This is especially pronounced at lower levels of diversity. This finding is particularly relevant to current ecological change, since most ecosystems are being transformed into managed systems which typically contain only a few dominant species, whereas the natural ecosystems they replaced typically contained tens to hundreds of species.

Second, at least one species per functional group is essential to ecosystem functioning. Having more than one species per functional group may or may not alter overall levels of ecosystem functioning, but it may nevertheless insure against loss of functioning in times of disturbance if species within functional groups are able to replace or compensate for one another.

Third, the nature of an ecosystem's response to declining biodiversity is dependent on community composition, that is, on which species are lost and which

Photo courtesy of Center for Population Biology, Imperial College of London, UK.

Figure 8 - A biodiversity experiment, performed at eight different European grassland sites ranging from Sweden in the north, to Portugal and Ireland in the west, and to Greece in the south and east, has found that greater plant diversity leads to greater plant community productivity. The results from these studies tend to be similar to earlier studies that suggest that the loss of biodiversity will generally decrease the productivity of plant communities.

remain. Research to date, however, has not identified any clear rules allowing us to predict in advance the impacts of the loss of any particular species on ecosystem processes.

Although these three points have been repeatedly observed in a wide variety of experiments, there is still debate about the mechanisms behind them. Research into the link between biodiversity and ecosystem functioning is a new discipline and much work remains to be done.

FUTURE RESEARCH

Research to date strongly supports the idea that ecosystem functioning is sensitive to changes in local species identities, community composition and diversity. Although current studies are limited in scope, they do demonstrate that plant production, nutrient use, nutrient leaching, soil fertility, and the predictability and stability of ecosystem processes can falter in the face of reductions in biodiversity. Despite this progress, several areas of uncertainty remain to be investigated.

What are the effects of changes in biodiversity at scales other than species or functional groups?

Most studies involving biodiversity and ecosystem functioning have focused only on changes in the number and variety of species and/or functional groups. Yet many important ecological processes occur at the landscape level, and current studies strongly suggest that landscape-level alterations of biodiversity affect ecosystem functioning. There is a need for experimental research that manipulates biodiversity at both larger and smaller (e.g., genetic) scales.

Is current knowledge applicable to all ecosystems?

Studies to date have examined primarily isolated ecosystems. Future experiments across multiple ecosystem types will be needed to test whether findings from lakes or grasslands, for example, can be applied more widely. This approach is already being tested in BIODEPTH, a pan-European biodiversity-ecosystem functioning experiment that may serve as a model of the kind of experiments needed. At eight field sites across

Europe, BIODEPTH researchers have created grass-herb ecosystems with varying levels of biodiversity drawn from local species pools. Results of these studies will expand to the landscape level our understanding of the relationship between biodiversity and such ecosystem processes as production, decomposition and nutrient retention.

How important is diversity at all levels of the food web to ecosystem functioning?

With the exception of some studies conducted inside laboratory growth chambers, most experiments to date have considered only plant species diversity and not variations in the numbers of herbivores, carnivores, parasites, decomposers and other players in the food web. Yet these creatures not only comprise the most numerous portion of the earth's biota but are also significant players in the flow of materials and energy. Experiments that involve multiple levels of the food web are critical to expanding our understanding of the ecological consequences of biodiversity loss.

How will other global changes interact with changing patterns in biodiversity and ecosystem functioning?

Currently, few experiments are explicitly examining interactions among such factors as increased atmospheric carbon dioxide, increased untraviolet-B radiation, increased nitrogen deposition, global warming, habitat fragmentation, and changing patterns of biodiversity. Experiments considering all these factors at once are impractical. Yet one project that examines interactions of three of these factors is currently in progress at Minnesota's Cedar Creek Natural History Area. The experiment, BIOCON, manipulates plant diversity, carbon dioxide, and nitrogen in experimental grassland plots.

What are the economic consequences of ecosystem responses to changing biodiversity?

Currently, economic valuations have focused on market values of either ecosystem services or biodiversity. Future analyses which integrate both biodiversity and ecosystem functioning may provide a better understanding of the potential economic impacts of biodiversity loss.

CONCLUSIONS

Unprecedented changes are taking place in the ecosystems of the world, including species losses through local extinctions, species additions through biological invasions, and wholesale changes in ecosystems that follow transformation of wildlands into managed ecosystems. These changes have a number of important effects on ecosystem processes. Recent evidence demonstrates that both the magnitude and stability of ecosystem functioning are likely to be significantly altered by declines in local diversity, especially when diversity reaches the low levels typical of managed ecosystems. Although a number of uncertainties remain, the importance of ecosystem services to human welfare requires that we adopt the prudent strategy of preserving biodiversity in order to safeguard ecosystem processes vital to society.

Photo courtesy of OAR/NURP.

Figure 9 - Species can be lost from highly diverse systems such as coral reefs due to changes in the inputs of nutrients. An increase in run-off from agricultural and lawn-care nutrients such as nitrogen and phosphorus can result in coral reefs being overgrown by algae.

ACKNOWLEDGMENTS

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SUGGESTIONS FOR FURTHER READING

The references below are representative of the scientific publications and summaries upon which this report is based.

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About the Science Writer

Yvonne Baskin, a science writer, edited the report of the panel of scientists to allow it to more effectively communicate its findings with non-scientists.

About Issues in Ecology

Issues in Ecology is designed to report, in language understandable by non-scientists, the consensus of a panel of scientific experts on issues relevant to the environment. *Issues in Ecology* is supported by a Pew Scholars in Conservation Biology grant to David Tilman and by the Ecological Society of America. All reports undergo peer review and must be approved by the editorial board.

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